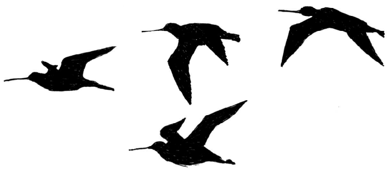
Consequences of winter habitat use in a migratory shorebird



Consequences of winter habitat use in a migratory shorebird

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Abstract

In this thesis I explore the importance of using different habitat types in winter for a migratory shorebird, the Icelandic Black-tailed godwit *Limosa limosa islandica*. Godwits use a mixture of estuarine and freshwater wetland habitats across all major wintering regions. The Irish wintering population of black-tailed godwits makes up *c*, 20% of the flyway population, and these birds use coastal mudflats and adjacent grassland habitats throughout the winter. In addition, very large numbers congregate on inland wetland 'callows' in late winter and spring. The Icelandic godwit population is currently increasing, however, numbers of godwits wintering in Ireland have not increased as rapidly as elsewhere in the winter range over the last 40 years. Using detailed behavioural studies, I show that grasslands in Ireland provide essential resources for godwits, as prey consumption rates on the mudflats are insufficient to meet energetic requirements. Despite their importance, grasslands receive virtually no protection. Surveys of field selection by godwits throughout southern Ireland indicate that small, enclosed fields are avoided but that godwits use large, open fields in both urban and rural dominated areas. Levels of urbanisation also have little impact on the use of resources on mudflats or grasslands by godwits. Candidate fields for inclusion within protected areas would therefore ideally be large, open fields situated throughout urban and rural areas. Finally, I explore the evidence for increasing use of grassland habitats by godwits wintering in the east of England, where rates of population increase have been particularly high and annual survival has been estimated to be lower than other winter regions. Count information and records of individually marked godwits indicate a rapid shift in habitat use since the 1990s, with inland grasslands now being used by large numbers of godwits. These sites are also being used progressively earlier in the winter, which may indicate that estuarine prey resources are also limited in the east of England. Thus, while there is evidence that estuarine habitats are preferred by godwits in winter, grasslands are also essential for maintaining a large proportion of the Icelandic black-tailed godwit population, and improving protection of these habitats should thus be a priority.

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Introduction

Introduction

Many species can occupy a range of different habitat types, both spatially and temporally. Species may vary in their use of different habitat types across their range or, in mobile species, individuals may occupy different types of habitats at different points in time. As habitats can differ in the availability or quality of critical resources such as food-supplies, shelter or suitable breeding sites, habitat occupancy can potentially influence individual fitness (Orians and Wittenberger 1991, Rosenzweig 1991, Sutherland 1996, Newton 1998, Munday 2001). For example, the abundance and quality of food supplies have been shown to influence density and breeding success in many species, including red grouse *Lagopus l. scoticus* (Moss 1969), pigeon guillemot chicks *Cepphus columba* (Litzow *et al.* 2002) and ground squirrels *Spermophilus townsendii* (Van Horne *et al.* 1997). Similarly, the availability of nesting sites can influence breeding densities (e.g. Brawn and Balda 1988, Lõhmus and Remm 2005, Mand *et al.* 2009), and breeding site quality can influence productivity (Tye 1992, Holmes *et al.* 1996, Nagy and Holmes 2005). Habitat quality can also be influenced by the costs incurred in occupying a habitat, such as variation in predation risk or the energetic costs associated with different climatic conditions. For example, the costs of thermoregulation have been shown to differ among habitats for a variety of taxa, from large-bodied mammals such as moose *Alces alces* (Belovsky 1981), to small-bodied wading birds such as red knot *Calidris canutus* (Wiersma and Piersma 1994). Variation in the costs of occupying different habitats can result in behavioural trade-offs that may influence individual fitness. For example, in order to minimise predation risk, adult redshank *Tringa totanus* have been shown to preferentially forage on habitats in which prey intake rates are lower than in the habitats with higher predation risk (Cresswell 1994). Thus, understanding the implications of different patterns of habitat use in a population may require consideration of multiple determinants of habitat quality.

When individual fitness varies among different habitat types, local population changes can potentially be driven via changes in environmental conditions that influence habitat availability and/or quality (Sutherland 1996, Sibly and Hone 2002). However, the extent to which a population responds to changing environmental conditions can depend on species-specific density-dependent processes (Goss-Custard *et al.* 1995, Sutherland 1998, Pettifor *et al.* 2000), and there is a wealth of theoretical research describing the influence of population density on changing patterns of spatial and temporal use of habitats of varying quality (e.g. Fretwell and Lucas 1970, Sutherland 1983, McNamara and Houston 1990, Sutherland 1996, McPeek *et al.* 2001, Cressman *et al.* 2004). At low population densities, individuals are expected to predominantly occupy the better quality patches and, as the population increases, poorer quality patches are increasingly used. When fitness varies in relation to habitat quality, the proportion of the population occupying good or poor quality habitat can influence rates of population change. Disproportionate expansion into poor quality habitats during periods of population increase, resulting in a decrease in *per capita* fitness, has been termed ‘the buffer effect’ (Brown 1969, Sutherland 1996, Gill *et al.* 2001, Gunnarsson *et al.* 2005b). This pattern of population expansion into poorer quality habitats has been shown in a number of species (Mearns and Newton 1988, Moser 1988, Halama and Dueser 1994, Suter 1995, Lõhmus 2001). However, the fitness implications of progressive occupation of poorer quality sites have only been demonstrated in a few studies. For example, in two increasing raptor populations (Spanish Imperial Eagles *Aquila adalberti* and Ospreys *Pandion haliaetus*), declines in *per capita* fecundity have been recorded due to an increasing proportion of the expanding population occupying poorer quality sites (Ferrer and Donazar 1996). In the case of the Spanish Imperial Eagle, these declines in *per capita* fitness have been suggested as a possible reason why the population is no longer expanding (Ferrer and Donazar 1996).

A large proportion of the world’s bird species are migratory (Newton 2008), and the ranges of many migratory populations cover large geographical distances. Identifying the impact of habitat quality on individual fitness in migratory species is complicated by the fact that individuals may be influenced by conditions experienced in more than one part of the world. It has been long acknowledged that the control of migratory populations can be influenced by factors that operate on individuals at both ends of the migratory range (Alerstam and Högstedt 1982, Sutherland 1996, Marra 1998, Newton 2004, Sorensen *et al.* 2009). These 'carry-over' effects operating in a migratory population mean that observed changes in numbers or fitness in one location may be due to changes experienced at the other end of the migratory range. In addition, the fitness consequences of individuals occupying poorer quality habitats in one season can potentially be exacerbated by carry-over effects. For example, individuals in poor condition may have to delay departure for the breeding grounds in order to gain the resources needed to make the journey, resulting in late arrival which may influence mate and territory acquisition, and subsequent breeding success. Such links have been shown at the level of the individual and the level of the population (Lundberg *et al.* 1981, Kokko 1999, Gill *et al.* 2001, Norris *et al.* 2004, Gunnarsson *et al.* 2005b). In addition, if habitat quality varies in both the breeding and non-breeding seasons, then the consequences of buffer effects will be influenced by whether individuals tend to occupy similar or different quality habitats in both seasons, a pattern which has been termed 'seasonal matching' (Gunnarsson *et al.* 2005a). If similar quality habitat is occupied in both seasons then expansion into poorer quality habitats may result in reduced *per capita* survival *and* fecundity. Seasonal matching could therefore inflate fitness inequalities between parts of the population occupying good or poor quality habitats in summer and winter (Gunnarsson *et al.* 2005a).

Effective conservation policies need to consider habitat quality in the design of protected areas. For example, current international policies for the protection of migratory bird species typically use the measure of a percentage of a flyway population being recorded on a site as the primary criterion for inclusion in a protected area network (e.g. (Delany and Scott 2002). However, high quality sites supporting individuals with high survival and reproductive success may or may not reach these limits but they can be of equal or greater importance to the population. Understanding the extent of variation in habitat quality across the range of a species and the relative importance of different habitats necessary to maintain the population could therefore potentially improve the effectiveness of protected area design. Given the current widespread declines in many migratory species (IWSG 2003, Boere *et al.* 2006, Sanderson *et al.* 2006), identifying and improving conservation strategies for these species is an issue of increasing urgency. Shorebirds are typically long-lived, migratory species, many of which spend a large part of the non-breeding season on specialised intertidal habitats; discrete patches of habitat in an otherwise unsuitable landscape (Piersma and Baker 2000). However many shorebird species actually use a range of habitats throughout the non-breeding season, including freshwater wetlands and agricultural habitats including arable crops, pasture and rice fields, in combination with intertidal sandflats and mudflats (Goss-Custard 1969, Colwell and Dodd 1999, Masero and Perez-Hurtado 2001, Smart and Gill 2003, Evans Ogden *et al.* 2005, Lourenco and Piersma 2009). Understanding the relative importance of this wide range of habitats in supporting shorebird populations is important, especially as the primary commercial purpose of agricultural means that they are rarely included within protected areas.

The Icelandic black-tailed godwit *Limosa limosa islandica* is an example of a generalist shorebird that is known to use estuarine mudflats and freshwater grasslands as foraging habitats on the wintering grounds (Gill *et al.* 2002). Icelandic black-tailed godwits breed almost exclusively in Iceland and winter predominantly on the west coast of Europe. Studies of this population over the last decade suggest that the type of habitat used in winter plays a key role in driving carry-over effects. Stable isotope analysis of feathers taken from godwits on the breeding grounds that were grown during late winter has indicated habitat type used in late winter is linked in some way to habitat quality occupied and breeding success. Godwits that use saline habitats (primarily estuarine mudflats and saltpans) more extensively in late winter occupy higher quality breeding sites and have higher breeding success (Gunnarsson *et al.* 2005a) than individuals that use freshwater habitats (grasslands and wetlands). However, the mechanisms determining why individuals from freshwater winter habitats tend to breed in poorer quality areas is not known.

This Icelandic black-tailed godwit population has undergone a sustained increase in numbers over the last century, resulting in changes in distribution, habitat use and abundance across the migratory range (Gill et al. 2001, 2007 Gunnarsson et al 2005b). The most rapid rates of population increase have been apparent on estuaries on the east coast of England since the 1970s (Rehfisch *et al.* 2003, Austin *et al.* 2008), and Gill et al. (2001) showed that godwits on these sites have lower rates of prey consumption, lower annual survival and later arrival on the breeding grounds than individuals that winter on traditionally occupied sites on which population sizes have remained stable in recent decades. This expansion into poorer quality winter locations in which individual fitness is lower than in traditionally occupied sites is indicative of a buffer effect (Brown 1969, Gill et al. 2001). A buffer effect has also been apparent in the breeding grounds through the period of population increase, as godwits have expanded into parts of Iceland in which poorer quality habitats, on which breeding success is lower, are proportionately more abundant than in traditionally occupied sites (Gunnarsson et al. 2005b). Stable isotope analyses of feathers of birds around Iceland have also indicated that birds in recently occupied breeding sites tend to be those that use freshwater habitats in winter. Thus the role of saline and freshwater habitats in carry-over effects in godwits may also have implications for the rates of population expansion, and may ultimately play a key role in regulating population growth (Gunnarsson *et al.* 2005b).

Ireland is the closest wintering location for many waterbirds that migrate from breeding grounds in Iceland and Greenland each year. Consequently Ireland supports a large proportion of the flyway populations of a number of waterbird species including whooper swan *Cygnus cygnus* (61%), brent goose *Branta bernicula hrota* (100% of Nearctic race) and ringed plover *Charadrius hiaticula* (20%) (Crowe *et al.* 2008). There is a long history of Icelandic black-tailed godwits wintering in Ireland (Prater 1975), and current population estimates indicate that Ireland supports *c.* 20% of the flyway population (Gunnarsson *et al.* 2005c, Crowe *et al.* 2008). Ireland's location on the flyway, its relatively mild climate and importantly the abundance and diversity of foraging areas for waterbirds is likely to influence its importance as a wintering location for these species. In comparison to the UK and other wintering locations for black-tailed godwits, Ireland still has extensive areas of pastoral grassland, and godwits are known to use both mudflats and grasslands quite extensively in Ireland (Hutchinson 1979, Hutchinson and O'Halloran 1994, Crowe 2005). Ireland is therefore an ideal location in which to investigate the importance of freshwater and saline habitats for black-tailed godwits in the non-breeding season.

In this thesis, I use extensive field data in combination with historical survey information and population-wide marking and tracking of individual godwits to explore patterns of habitat use by godwits, and the implications for the godwit population and for the design of protected areas for this species. The population of Icelandic godwits has expanded rapidly over the last century but patterns of population increase have varied among different winter locations. In **Chapter 1,** I use historical survey information to explore the population trends and distribution of Icelandic black-tailed godwits wintering in Ireland over the last 40 years. These analyses indicate that godwit numbers in Ireland have changed far less rapidly than numbers in some other winter locations, although there are indications of increasing use of some estuaries, particularly in eastern Ireland. I also examine patterns of seasonal use of coastal and inland sites across Ireland, which highlights the extensive availability of mudflat and grassland resources on coastal sites throughout Ireland, and the particular importance of inland grasslands in late winter and early spring. Potential reasons for the population trends in Ireland are explored in this chapter.

In **Chapter 2,** I explore the relative quality of mudflat and grassland habitats for godwits in Ireland using behavioural and distributional data collected during three seasons of fieldwork on the south coast of Ireland. These data are used to compare the costs and benefits of foraging on mudflat and grassland habitats and to attempt to determine the relative importance of each in supporting the wintering population. These analyses indicate that foraging on grasslands in the coastal zone entails costs of increased disturbance and vigilance rates. However, grassland foraging also appears to be essential for these godwits, as the resources available on the mudflats do not appear to be sufficient to support the godwit population throughout the winter.

Given the importance of grasslands for godwits in Ireland, **Chapter 3** explores the factors that influence the selection of grassland foraging sites by godwit flocks. In south Ireland, there is still an abundance of grassland fields around most estuaries. However, while most of the intertidal areas are designated as protected areas, very few of the grasslands are included within these protected areas. The main purpose of these analyses was therefore to identify the key features of the grassland fields that are selected by godwits in order to provide guidance for which areas should be prioritised for potential protection from development.

High rates of urbanisation in Ireland over the last two decades have resulted in extensive loss of coastal grasslands, and some estuarine areas are now quite highly urbanised. Observation of high levels of development around study sites for this thesis led to me to explore the influence of urbanisation on godwit use of resources on mudflat and grasslands (**Chapter 4).** Across nine estuarine complexes in south Ireland, levels of urbanisation vary extensively but this does not appear to influence the foraging or vigilance behaviour of godwits across these sites. These findings suggest that protecting grasslands is likely to be equally important in urbanised and rural areas.

Grasslands are an important habitat for godwits across other winter regions, but particularly in the east of England where high rates of population increase have been apparent in recent decades. Godwits in the east of England used to be largely restricted to estuarine habitats but use of inland wetlands has been increasingly reported since the mid-1990s. In **Chapter 5,** I explore how the extent and timing of use of these inland sites has changed in recent years, and considers what part grasslands have played in the continued increase of the godwit population wintering in this region. As the five data chapters have been written as manuscripts for publication, there is some repetition of methodological details in some chapters.

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Chapter 1

Population trends, distribution and habitat use of Icelandic black-tailed godwits in Ireland

Abstract:

1. The Icelandic population of black-tailed godwits, *Limosa limosa islandica*, has undergone a sustained increase in population size and distribution over the last century. The non-breeding range of Icelandic godwits extends from Britain and Ireland in the north to Iberia in the south, and monitoring in these areas over the last three decades has indicated that numbers on some sites have remained stable while numbers on other sites have increased sharply, offering opportunities to identify drivers of population growth and regulation by comparing patterns of population change across wintering locations.
2. Ireland is estimated to support *c*. 20% of the flyway population of Icelandic black-tailed godwits in winter. Coastal mudflats and wetlands throughout Ireland are used by godwits throughout the winter but it is not known whether the overall population increase has influenced the spatial, seasonal or habitat distribution of godwits in Ireland.
3. Waterbird numbers in Ireland have been monitored through three major initiatives since the 1970s. Counts of black-tailed godwits from these surveys are used here to explore the evidence for changes in numbers of Icelandic black-tailed godwits wintering in Ireland over the last 40 years, changes in the spatial or seasonal distribution of wintering godwits across Ireland, and to identify potential explanations for population changes across these wintering locations.
4. Across the sixteen major coastal and three major inland sites in Ireland there has been little change in total numbers of godwits over the last 40 years; between 4000 and 5000 have regularly been recorded on these sites. However, numbers on some more recently used estuaries, particularly on the east coast, have increased, while numbers on south coast and inland sites have remained quite stable.

5. Northern and southern sites appear to be used more in autumn while east coast sites are used more in winter and spring, indicating that there may be some seasonal shift in distribution. This is unlikely to be driven by habitat availability as mudflats and grasslands are available at all the major sites included in these surveys. The use of inland sites also tends to be greater in late winter and spring.
6. Since the 1970s, the numbers of godwits wintering on these sites in Ireland have not shown the rapid increases that have been recorded in other parts of the non-breeding range. As Irish wintering godwits breed all over Iceland, these differences are unlikely to have arisen because Irish wintering godwits comprise a distinct part of the breeding population. An alternative explanation could be that the environmental conditions within Ireland are not sufficient to support a rapid population increase.

Introduction

Expanding populations provide an opportunity to explore the drivers of population change and habitat selection that can be important in regulating or facilitating population growth. The manner in which habitats of varying quality are predicted to be used by an expanding population has been described as the ‘buffer effect’ (Brown 1969); at low population densities only high quality habitats are occupied and, as the population expands, the increase in numbers is greatest on poor quality habitats that initially supported low densities. If there are fitness consequences of occupying poor quality habitats, population expansion into poorer quality habitats can potentially be a mechanism for population regulation (Sutherland 1996). However, as buffer effects assume that differences in habitat quality are maintained over time, changes in distribution of an expanding population could also result from changes in the availability or quality of sites and habitats. Changes in the relative use of habitats of varying quality may therefore be either a cause or a consequence of population expansion.

In migratory species, identification of drivers of population change is complicated by the fact that environmental changes and density-dependent processes can operate at either or both ends of the migratory range, and processes may interact between breeding and wintering sites (Sutherland 1996, Newton 2004). Interactions between seasonal processes in migratory birds have been described as carry-over effects, where conditions experienced in one season impact on fitness in subsequent seasons (Ebbinge and Spaans 1995, Marra 1998, Webster *et al.* 2002, Sorensen *et al.* 2009). For example, conditions experienced on the wintering grounds can impact on individual survival probabilities but can also influence body condition for migration and subsequent breeding (Madsen 1995, Bearhop *et al.* 2004, Reed *et al.* 2004). Variation in rates of local population change across the range of a migratory species could therefore result from changes in conditions in either or both of the breeding and non-breeding locations.

The Icelandic population of the black-tailed godwit has shown a sustained increase in numbers over the last century from *c.* 5000 around 1900 to recent estimates of *c.* 50,000-75,000 individuals (Gill *et al.* 2007). This expansion has been evident both in Iceland, as new breeding grounds have been colonised (Gunnarsson *et al.* 2005b), and on the wintering grounds in the UK (Gill *et al.* 2001). The causes of this population increase have not been fully identified but possible drivers that have been proposed include changes on the breeding grounds such as climate amelioration and/or changes in habitat structure increasing the area available for breeding godwits, or climatic and habitat changes in the non-breeding range improving survival and/or body condition for migration and subsequent breeding (Gill *et al.* 2007).

The number of godwits wintering in the UK has increased from a few thousands to around 25,000 over the last 40 years (Prater 1975, Austin *et al.* 2008). During the period of population increase, traditionally occupied sites on the south coast of England have maintained stable numbers of wintering godwits, while there have been rapid increases in numbers of godwits on recently occupied sites on the east coast of England since the late 1970s (Gill *et al.* 2001). On the traditionally occupied sites, godwits have been shown to have higher prey intake rates, higher annual survival and earlier arrival dates on the breeding grounds than godwit populations wintering on recently occupied east coast estuaries. Thus this pattern of expansion into poorer quality habitat has been described as a buffer effect (Gill *et al.* 2001). There is also evidence that a buffer effect is operating in the breeding season, as godwits are expanding into areas in which poorer quality breeding habitats are proportionately more abundant (Gunnarsson et al. 2005b), and individuals tend to use similar quality habitats in both seasons; a type of carry-over effect that has been termed *seasonal matching* (Gunnarsson et al. 2005a). Tracking of colour-marked individuals has shown that individuals from traditionally occupied winter sites tend to also breed in traditionally occupied areas where good quality breeding habitat is more abundant, and individuals in recently occupied winter sites tend to also breed in recently occupied areas of Iceland, where poorer quality breeding habitat is more abundant (Gunnarsson et al. 2005a).

Icelandic godwits winter predominantly in the UK, Ireland, France and Iberia. Throughout the winter range, godwits forage primarily on estuarine mudflats and freshwater wetlands, and the extent of use of these saline and freshwater habitats has been implicated as a factor influencing the presence of seasonal matching in this population (Gunnarsson et al. 2005a). Stable isotope analysis of feathers taken from godwits on the breeding grounds that were grown during late winter has shown that birds that spend the late winter feeding predominantly on saline habitats tend to breed in good quality breeding sites, while birds that primarily use freshwater habitats in late winter tend to breed in poorer quality sites. This indicates that the use of estuarine and freshwater habitats in winter is likely to be a key component of winter habitat quality and a driver of subsequent carry-over effects (Gunnarsson *et al.* 2005a).

Ireland, with its relatively mild, wet climate and diversity of wetland habitats and agricultural land supports internationally important numbers of many species of wintering waterbirds, including *c.* 20% of the flyway population of Icelandic black-tailed godwits (Crowe 2005, Gill *et al.* 2007). Black-tailed godwits are thought to use freshwater habitats quite extensively in Ireland (Hutchinson and O'Halloran 1994, Crowe 2005), which could have implications for relative habitat quality and resulting patterns of population change. Counts of black-tailed godwits from surveys in Ireland from 1970 to 2006 are used here to explore the evidence for any changes in 1. numbers of Icelandic black-tailed godwits wintering in Ireland over the last 40 years, 2. the spatial distribution of wintering godwits, 3. the seasonal variation in numbers across Ireland and 4. to identify potential explanations for population changes across these wintering locations.

Methods

Sources of data

In the Republic of Ireland and Northern Ireland, counts of godwits during the non-breeding season are available for sixteen major coastal sites (Table 1A) and three inland wetlands (Table 2). Three major surveys of waterbirds have taken place since 1970 (Fig. 1): the Wetlands Enquiry (1970/71 to 1975/76) (Hutchinson 1979), the Irish Wildfowl Conservancy (1985/86 to 1986/87) (Sheppard 1993) and the Irish Wetland Bird Survey (I-WeBS) (1994/95 to present) (Crowe 2005). The I-WeBS data also include an additional seven coastal sites on which godwits have been recorded in the last two decades (Table 1B) (Crowe 2005). In Northern Ireland, two major sites were surveyed between 1969/70 to 2006/07, as part of the BTO/RSPB Birds of Estuaries Enquiry (BoEE) which subsequently became the Wetland Bird Survey (WeBS) (Table 1A, Fig. 1); only counts from the same years for which counts were also conducted in the Republic were incorporated in these analyses.

All of the surveys involved monthly coordinated high-tide counts between September and March inclusive. Counts are carried out by skilled amateur ornithologists and members of staff from partner organisations (BirdWatch Ireland (BWI), British Trust for Ornithology (BTO), Joint Nature Conservation Committee (JNCC), National Parks and Wildlife Service (NPWS), Royal Society for the Protection of Birds (RSPB), Wildfowl and Wetlands trust (WWT)).

Long-term variation in numbers of black-tailed godwits in Ireland

The total number of godwits on the 19 major sites (16 coastal and 3 inland, Fig. 1) in winter was calculated by summing the maximum count recorded across all sites in any winter month (November, December or January) of each year. These peak winter counts were then summed and an average annual peak total was calculated for the years surveyed within each decade. Sites included in this analysis had a minimum coverage of one month (out of the possible three in each winter) and were counted in two or more winters during the Wetlands Enquiry (1970s), IWeBS (1990s and 2000s) and WeBS (1970s, 80s and 90s), but since only two winters were counted in the 1980s (Irish Wildfowl Conservancy), a single count was accepted from that period.

Changes in the distribution of black-tailed godwits in Ireland

In order to investigate whether the distribution of black-tailed godwits within Ireland has changed over the last 40 years, the number of godwits recorded on the 16 major estuaries each winter were collated within each coastal county (County Louth and County Dublin were combined for this analysis) (Table 1A, Fig. 1). Each coastal county contained one to five estuaries, and the peak number of godwits in each county was calculated as the sum of the maximum winter count (in either November, December or January) from each of these estuaries, and these annual peak counts were averaged within three time periods (1970/71 - 1975/76, 1984/86 - 1986/87 and 1994/95 to 2006/07). Coverage for most sites is concentrated on winter months so peak winter counts were used for all sites except for the Shannon and Fergus Estuary, where peak counts in any month from November to March inclusive were used as the aerial surveys which are conducted on this site particularly when large flocks are likely to be present, (usually in spring months). For the three inland sites (Table 2, Fig. 1), the timing of use by godwits is highly variable depending on water levels, so the annual peak count was taken from any month, September to March inclusive, and averaged for the same years as specified above.

Seasonal variation in numbers and distribution of black-tailed godwits in Ireland

Seasonal variation in the use of sites across Ireland was explored on the 23 coastal sites counted between 1994/95-2006/07 (Table 1A & B). Peak seasonal counts (autumn = September - October, winter = November - January, spring = February - March) from each county (1 - 7 estuaries per county) were summed across each county as described above. The seasonal county peak was then averaged over four time periods (1994/95 - 1996/97, 1997/98 - 2000/01, 2001/02 - 2003/04 and 2004/05 - 2006/07). Count coverage was only sufficient in all seasons to include one inland site (the Little Brosna Callows) in this analysis. For all coastal sites, the availability of each habitat type (mudflats and grasslands) was summarised from site descriptions of count areas in Crowe (2005) (Table 1).

Breeding distribution of Irish-wintering black-tailed godwits

Since 1995, Icelandic black-tailed godwits have been individually colour-marked at sites throughout the migratory range (Gill *et al.* 2001, Gunnarsson *et al.* 2004, Gill *et al.* 2007). A network of volunteer observers across the range regularly report sightings of these birds, which has allowed the winter and breeding locations of several hundreds of individuals to be identified (Gunnarsson *et al.* 2005a). In order to explore whether Irish-wintering godwits breed within a specific part of the wintering range, and hence whether any changes in population size within Ireland may be a consequence of processes operating outside of Ireland, the known breeding locations of all Irish-wintering godwits were mapped.

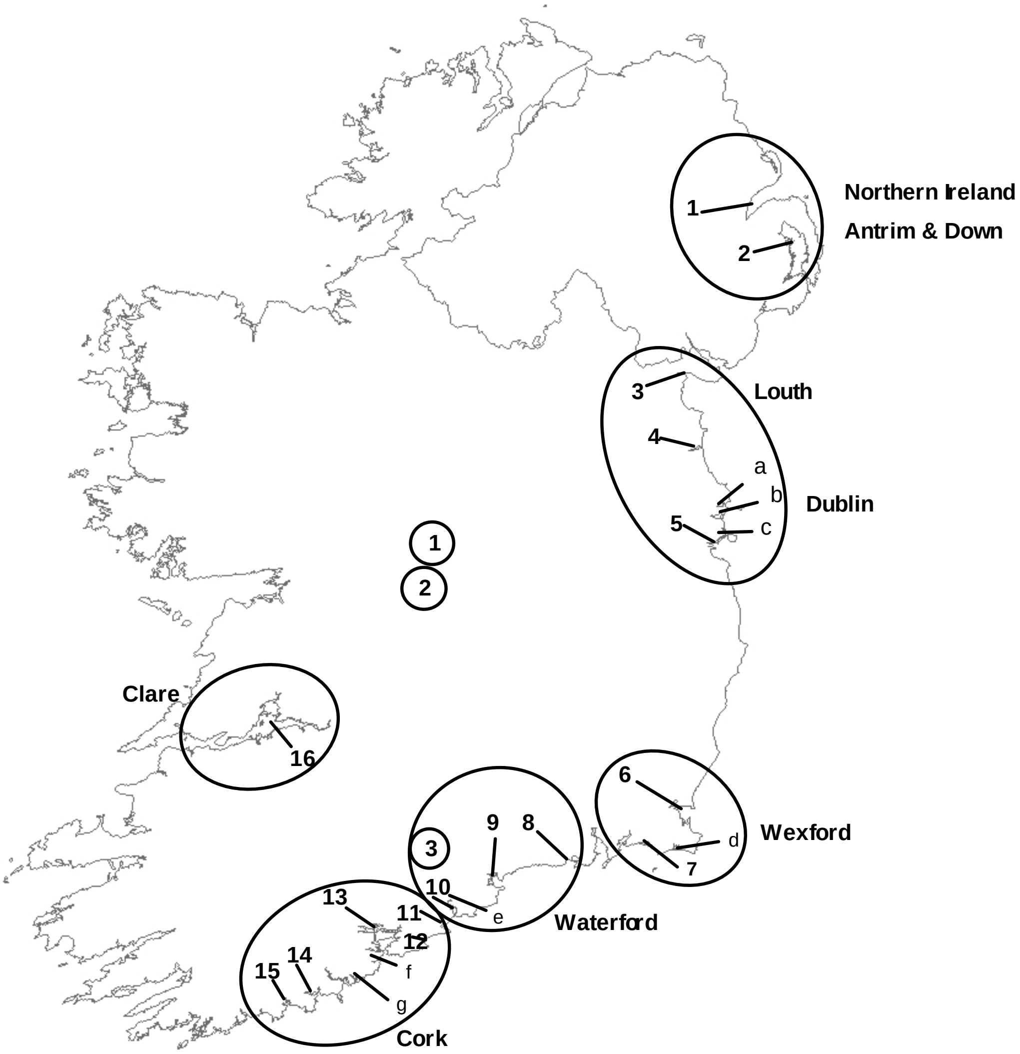

Figure 1. Locations of the major coastal (1 - 16) and inland (1 - 3 circled) sites counted during all waterbird surveys between 1970 and 2006. For the seven coastal counties (indicated with ovals, Counties Louth and Dublin combined), additional counts are available from seven additional sites (a - g) for 1994-2006. See Tables 1 and 2 for site details.

Table 1. Mean (± se) winter (Nov-Jan, except *Nov-Mar) peak counts of black-tailed godwits for **A.** 16 coastal sites included in each survey and **B.** seven additional sites surveyed in the 1990s and 2000s. The number of winters included in the calculation of mean is given in parentheses. The available habitats within each site are listed (m = mudflats, g = grasslands, l = lagoon), as is the inclusion of fields within the surveys and whether those fields are used by waders (summarised from descriptions of IWeBS areas in Crowe 2005).

Map ID	**County**	**Site**	**Mean peak winter counts (± se) (number of winters)**				**Habitat**		**Fields counted**	**Fields used**
A.			**70s**	**80s**	**90s**	**00s**				
1	Down	Strangford	92 ± 15 (5)	159± 74 (2)	161 ± 70 (6)	169 ± 49 (7)	m	g	Y	Y
2	Antrim	Belfast	-	33 ± 2 (2)	254 ± 25 (6)	370 ± 22 (7)	m	g	Y	Y
3	Louth	Dundalk	239 ± 128 (4)	258 ± 243 (2)	403 ± 146 (6)	1340 ± 181 (7)	m	g	N	Y
4	Louth	Boyne	286 ± 71 (5)	482 ± 82 (2)	192 ± 50 (5)	60 ± 26 (3)	m	g	N	Y
5	Dublin	Dublin Bay	31 ± 12 (6)	150 ± 92 (2)	217 ± 55 (5)	529 ± 114 (7)	m	g	Y	N
6	Wexford	Wexford Slobs	1341 ± 271 (6)	235 ± 75 (2)	462 ± 95 (6)	1255 ± 252 (6)	m	g	Y	Y
7	Wexford	Cull & Killag	276 ± 98 (6)	103 ± 39 (2)	268 ± 120 (4)	239 ± 63 (5)	m	g	Y	Y
8	Waterford	Tramore	148 ± 37 (3)	120 (1)	283 ± 25 (5)	173 ± 55 (4)	m	g	Y	Y
9	Waterford	Dungarvan	889 ± 158 (6)	745 ± 278 (2)	447 ± 136 (6)	576 ± 235 (5)	m	g	N	Y
10	Waterford	Youghal	24 ± 14 (3)	429 ± 160 (2)	307 ± 102 (6)	503 ± 107 (6)	m	g	N	Y
11	Cork	Ballymacoda	693 ± 181 (6)	386 ± 111 (2)	640 ± 207 (6)	884 ± 152 (7)	m	g	Y	Y
12	Cork	Ballycotton	54 ± 14 (5)	29 ± 6 (2)	60 ± 31 (6)	104 ± 33 (6)	l	g	Y	Y
13	Cork	Cork Harbour	835 ± 364 (6)	681 ± 261 (2)	456 ± 91 (6)	608 ± 86 (7)	m	g	Y	Y
14	Cork	Courtmacsherry	15 ± 78 (2)	150 (1)	288 ± 44 (5)	434 ± 68 (7)	m	g	N	N
15	Cork	Clonakilty	588 ± 364 (6)	460 (10	643 ± 172 (5)	183 ± 121 (2)	m	g	N	Y
16	Clare	Shannon and Fergus*	3389 ± 1134 (5)	2769 ± 2601 (2)	876 ± 290 (6)	84 ± 15 (6)	m	g	Y	Y
B.										
a	Dublin	Rogerstown	-	-	85 ± 38 (5)	198 ± 35 (7)	m	g	Y	Y
b	Dublin	Malahide	-	-	326 ± 112 (6)	203 ± 58 (7)	m	g	Y	Y
c	Dublin	Seagrange	-	-	361 ± 100 (5)	382 ± 79 (7)		g	Y	Y
d	Wexford	Tacumshin	-	-	414 ± 340 (5)	69 ± 34 (3)	l	g	Y	Y
e	Waterford	Blackwater R.	-	-	79 ± 43 (6)	74 ± 25 (6)	m	g	Y	N
f	Cork	Ringabella	-	-	18 ± 8 (3)	197 ± 37 (7)	m	g	N	N
g	Cork	Oysterhaven	-	-	77 ± 28 (4)	121 ± 21 (7)	m	g	Y	N

Table 2. Mean (± se) annual peak counts of black-tailed godwits on three inland grassland sites (locally known as Callows) included in surveys carried out in each decade (1970s to 2000s). The number of years included in the calculation of mean is given in parentheses, and the location of each site (numbered circles, 1-3) is indicated in Figure 1.

Map ID	**County**	**Site**	**Mean annual peak counts (± se) (number of winters)**			
			70s	**80s**	**90s**	**00s**
1	Offaly/Roscommon	Shannon Callows	613 ± 163 (3)	600 (1)	615 ± 166 (4)	256 ± 91 (5)
2	Offaly/Tipperary	Little Brosna	1875 ± 653 (6)	2375± 25 (2)	2920 ± 362 (4)	2551 ± 388 (7)
3	Waterford	Blackwater Callows	1292 ± 782 (3)	938 ± 97 (2)	318 ± 173 (6)	735 ± 168 (5)

Statistical analyses

Multivariate analyses of variance were used to explore changes in the numbers of black-tailed godwits from surveys carried out between 1970 to 2006. The spatial distribution of wintering godwits across Ireland (for 6 coastal counties and 3 inland sites) was analysed using an ANOVA with peak count from winter months (Nov-Jan) as the dependent variable and time period as a fixed factor. The seasonal variation in counts (across 7 coastal counties and 1 inland site) was analysed using a multivariate general linear model (GLM using a normal error distribution) with peak count from each season summed across the county as the dependent variable and season and time period as fixed factors and a season x time period (S x T) interaction term. All analyses carried out in SPSS (v16.0).

Results

Changes in the number of godwits recorded wintering on major coastal and inland sites in Ireland

The total numbers of godwits recorded on 16 major coastal and 3 inland sites surveyed in each decade (1970 - 2006) have remained relatively stable since the 1970s (Fig. 2). There is some evidence of a slight increase in numbers using coastal sites, however this is not significant; in the 1970s and 1980s, these coastal sites typically supported between 4000 and 5000 godwits in winter but by the 2000s the total number recorded on these sites exceeded 6500 in four out of seven years, peaking at nearly 9000 in 2004/05. The inland callows have supported a large number of godwits since surveys began in 1970; the mean total annual peak supported on the three inland sites exceeds 3000 in every decade (Fig. 2).

Distribution of godwits across major coastal and inland sites

Population trends have not been stable in all sites; since the 1970s there has been a significant increase in the number of godwits recorded in the north and east: counties

Down and Antrim in Northern Ireland, and Louth and Dublin in the Republic (Fig. 3). In the 1970s and 1980s, between 600 and 1000 birds in total were recorded using five estuaries in the north and east (Strangford Lough, Belfast Lough, Boyne Estuary, Dundalk Bay and Dublin Bay), and by the early 2000s these estuaries held nearly 2500 birds each winter (Table 1A). County Wexford has two major sites that were counted in each decade (Wexford Slobs and the Cull and Killag), at which *c.* 1500 godwits were regularly recorded in the 1970s (Fig. 3c) however, during the 1980s and 1990s, numbers did not exceed 500 (Table 1A). In recent years, godwits have been recorded in similar numbers to the 1970s; more than 1500 godwits were recorded there in four out of the seven winters surveyed in the 2000s.

In contrast, the eight estuaries in southern counties have had relatively stable numbers of godwits in winter over the last forty years (Table 1A). Peak numbers of godwits recorded wintering in County Waterford and County Cork have been around 1000 and 2000, respectively (Fig. 3). Dungarvan, Ballymacoda and Cork Harbour have regularly supported a large proportion of the godwits in these two counties (Table 1A), although Cork Harbour and Dungarvan have seen a slight decrease from around 900 birds each in the 1970s to between 500 - 600 in the 2000s. Two other estuaries have shown an increase in numbers over the same period; Courtmacsherry in west Cork and the Blackwater Estuary at Youghal in County Waterford have both increased from fewer than 50 birds in the 1970s to around 500 in the 2000s, indicating that there may be some shifts in site use within these counties over the last 40 years. The Shannon and Fergus estuaries on the west coast appear to have undergone quite severe declines in numbers since the 1970s (Fig. 3). However, counts on this site are complicated by the huge area of mudflats (over 50,000 ha) and the complexity of habitats formed by the two river systems they encompass. In order to maximise coverage, aerial counts are conducted at least once a season in late winter or spring.

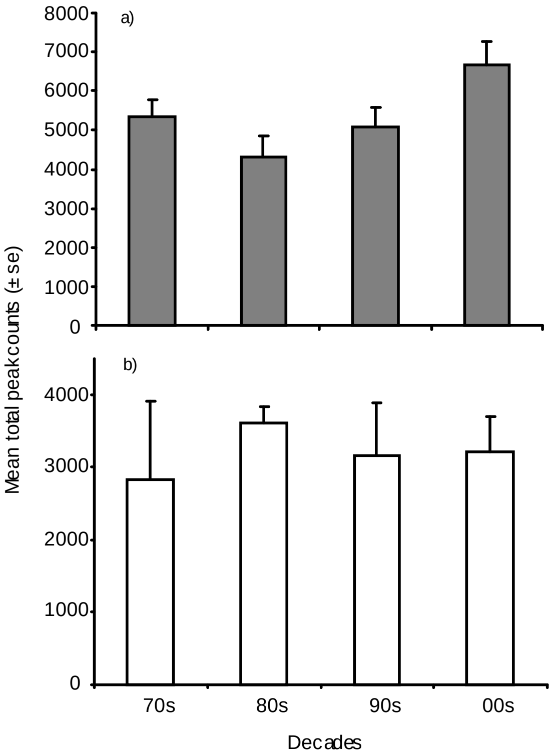

Figure 2. Mean (± se) peak numbers of godwits counted on a) 16 coastal sites in winter (November - January) and b) three inland grassland callows (September - March) in surveys carried out in each decade (1970s - 2006s).

Numbers using the inland callows have not varied greatly over time; the three inland sites (Fig. 3) hold a significant proportion of the peak number of godwits recorded across all sites in Ireland (Crowe 2005), and around two thirds of birds recorded inland (Fig. 2b) occur on a single inland site, the Little Brosna Callows (Table 2). The Little Brosna Callows and the adjacent Shannon Callows are huge wetland areas (1155 ha and 5841 ha respectively) located about 70 km inland of the Shannon and Fergus estuaries. Peak counts were recorded on both sites simultaneously in a number of months and the whole area has been shown to hold over 5000 godwits. In the south, the Blackwater Callows, just 25 km inland from Cork Harbour, Ballymacoda and Dungarvan, has had up to a thousand birds recorded in most winters since the 1970s, the peak count of 3500 in February 1974 has not been exceeded in these surveys but, in recent years, flocks of over 2000 godwits have been recorded in 2006 and 2007 (Chapter 3).

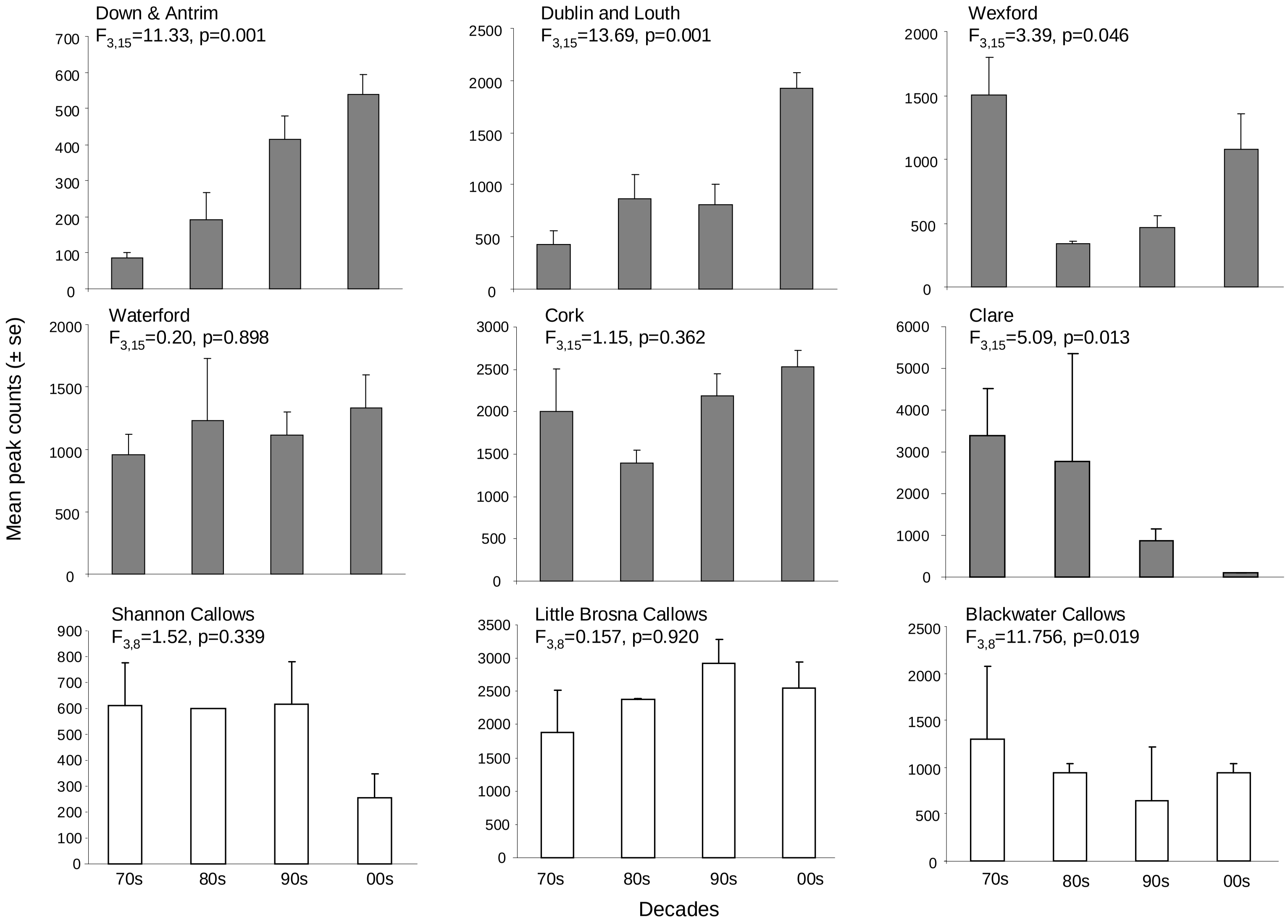

Figure 3. Mean (± se) peak counts of godwits across six coastal (filled bars) counties in winter and on three inland (open bars) sites annually in each decade. The number of estuaries included in each coastal county is given in parentheses.

Seasonal distribution of black-tailed godwits in recent years

Seasonal counts across all 23 coastal sites surveyed since the 1990s indicate that the seasonal pattern of site use by godwits varies spatially and has changed on some sites in the last 15 years (Fig. 4, Table 3). Coastal sites throughout Ireland are used in all seasons, but godwits typically only occur on inland grasslands through winter and spring months (Little Brosna; Rig 4). Sites in Northern Ireland and County Cork are used most extensively in autumn (Fig. 4); in County Cork *c.* 3000 godwits have been present in Cork Harbour and Ballymacoda in September and October in the 2000s. There is a suggestion that there is a shift in distribution through the non-breeding season as numbers of godwits are typically higher in winter and spring than autumn. In the last decade there has been a change with use of sites in the east of the country increasing significantly in spring, notably in Northern Ireland, County Louth and Dublin areas (Fig 4, Table 3). The varied seasonal use of sites in Waterford contrasts with the pattern in neighbouring County Cork. The significant season x time period interaction in County Waterford is due to fluctuations in the timing of peak counts alternating between autumn and winter. Whereas peak counts in County Cork have always occurred in autumn and show some signs of increasing, the number recorded in winter and spring has remained relatively stable. Sites in County Cork also play an important role during spring migration large congregations have been recorded on a single roost in Cork Harbour in late spring in recent years March/April 2006 - 2009 mean ± se peak count = 2013 ± 83 (Jim Wilson, *pers comm.*).

Habitats available on coastal sites in Ireland

All 23 coastal sites included in these surveys have mudflat or lagoon areas and grassland habitat available to godwits (Table 1). On all but seven sites the grassland fields are included in the I-WeBS count area (since the 1990s), and waders (including godwits) are stated to use these fields on all but six of these sites (Crowe 2005). Godwits use one site in Dublin that has only grassland; Seagrange Park, a recreational park area which floods in winter and is less than 1 km from the mudflats at Dublin Bay (Crowe 2005). The inclusion of these grassland habitats in wetland count sectors indicates that the

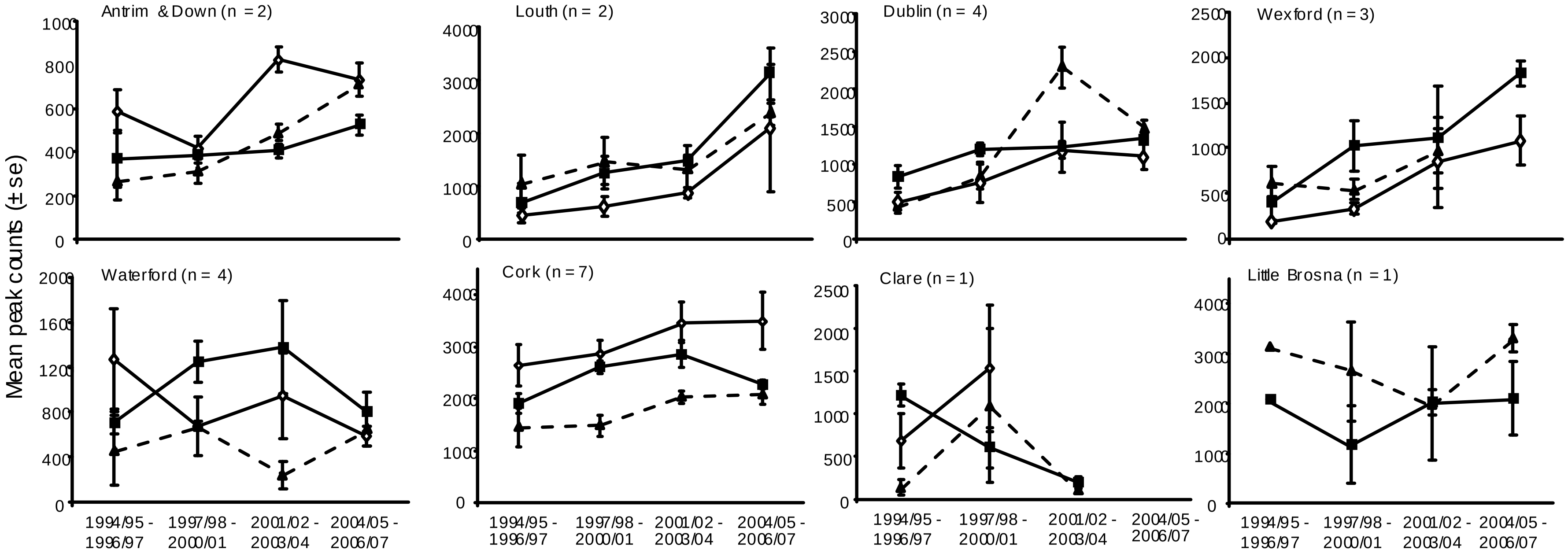

Figure 4. Changes in the mean (± se) peak counts of black-tailed godwits in seven coastal counties (number of estuaries within each county indicated in parentheses) and one inland (h) site in autumn (open diamonds), winter (filled squares) and spring (filled triangles and dotted line) over four time periods.

combination of grassland and mudflat habitats on coastal sites is recognised to be important and extensively used by wintering shorebirds.

Table 3. Results of GLMs of changes in the seasonal (S) peak counts of black-tailed godwits in seven coastal counties in autumn, winter and spring. Distribution was analysed over four time periods (T); 1994/95 - 1996/97, 1997/98 - 2000/01, 2001/02 - 2003/04 and 2004/05 - 2006/07, and the changes in seasonal distribution over these time periods is examined using an interaction term (S x T).

County	Season (S) (df = 2,9)		Time period (T) (df = 3,9)		S x T (df = 2,9)	
	F	p	F	p	F	p
Down & Antrim	8.55	0.008	3.92	0.048	8.02	0.010
Louth	0.54	0.601	9.58	0.004	2.83	0.112
Dublin	4.49	0.044	12.79	0.001	0.14	0.874
Wexford	3.25	0.086	8.09	0.006	3.74	0.066
Waterford	3.56	0.072	0.17	0.913	7.56	0.012
Cork	13.37	0.002	2.94	0.091	0.22	0.803
Clare	0.44	0.656	0.67	0.593	1.47	0.280

Variation in breeding distribution of Irish-wintering black-tailed godwits

The breeding locations of 44 godwits that winter in Ireland have been identified since colour-marking studies began in 1995; ten of these winter on east and north-east sites and 34 winter on south coast sites. The breeding locations of these birds are distributed across all six main breeding regions in Iceland (Fig. 5). Thus birds that winter in Ireland breed throughout Iceland, making it very unlikely that Irish-wintering birds constitute a distinct part of the breeding population.

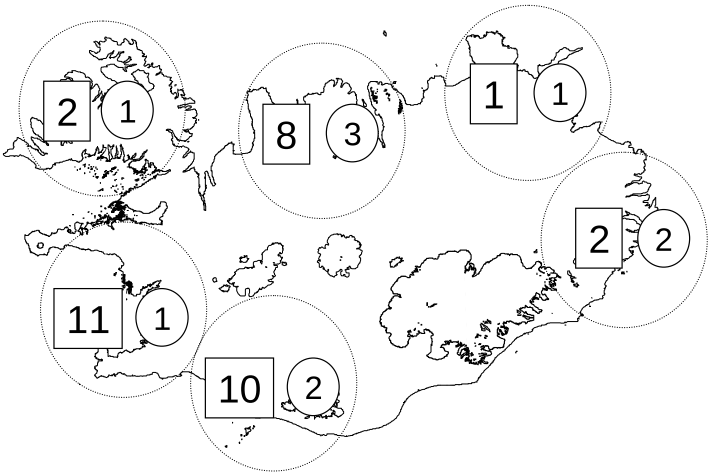

Figure 5. The breeding locations throughout Iceland of individually-marked godwits from winter locations in the south (squares) and east (circles) of Ireland.

Discussion

The total numbers of black-tailed godwits using the major coastal and inland sites across Ireland during the non-breeding season have remained relatively stable over the last 40 years. The average annual totals each decade since the 1970s across 16 major coastal sites have been around 5000-6000 individuals. However, totals calculated for recent years including counts conducted on an additional seven sites indicate that between *c.* 8000 and 10,000 godwits were supported on 23 coastal sites in the 1990s and 2000s, respectively. This additional site coverage during the I-WeBS survey since 1994 indicates that the Irish wintering godwit population has expanded into sites that were not used extensively in the 1970s and 1980s, as godwits were rarely recorded on these sites prior to the 1990s.

Inland grassland sites have also been used by a large proportion of the godwit population in Ireland since the 1970s, and total annual numbers exceeding 3000 birds have been regularly recorded inland over the last 30 years. While all estuarine sites have grassland pasture in close proximity, and these fields are often used by foraging godwits, shifts inland to flooded callows are apparent with peaks occurring inland typically in January and February. It is likely that use of the inland callows could be considerably higher than the recorded counts due to movement of birds between sites. The Little Brosna and Shannon Callows are in close proximity to each other and the Blackwater Callows are only 25 km from major south coast sites such as Youghal, Ballymacoda and Cork Harbour. This could be exacerbated in spring when pre-migratory movements could result in high turn-over of individuals moving north.

The godwit population trends on individual coastal sites vary, providing further evidence that there may be some population expansion into previously unused sites. Sites that held high numbers of godwits when the surveys began, mainly on the south coast in County Cork and County Waterford, have maintained similar numbers in each decade. In contrast, sites in Northern Ireland and on the east coast of Ireland that only held a few hundred godwits in the 1970s have shown a sustained increase in numbers. This pattern may be indicative of a buffer effect operating, with expansion of the population into poorer quality sites, as has been shown elsewhere in the godwit winter range (Gill et al. 2001).

In the 1970s, the black-tailed godwit was much more numerous in Ireland than it was in Britain (Prater 1975). The UK wintering population was estimated to be 3735 by Prater (1975), at which time the estimated wintering population of Ireland was 8,000-10,000. The survey information reported here indicates that (on the major sites for which data are available), Ireland still supported numbers around this magnitude in the 2000s, in comparison to the UK winter maximum which only fell below 30,000 in one year between 2002/03 and 2006/07 (Austin *et al.* 2008).

Potential reasons for this difference in population trends between the two neighbouring countries could include the Irish wintering population comprising a distinct breeding population in Iceland. Godwit breeding success in Iceland varies in relation to the habitat type, and this varies between traditionally and newly occupied sites across the country; high quality marsh habitat is more widely available in the traditionally occupied southern lowlands and more recent expansion has been into areas where the poorer quality, dwarf birch bog has been more common (Gunnarsson *et al.* 2005b). However, Irish-wintering godwits have been found on breeding grounds throughout Iceland, so it is highly unlikely that the population trends in Ireland are a consequence of changes in breeding distribution or the types of habitat being occupied in Iceland.

Habitat quality for godwits across European wintering locations appears to be related to the extent to which saline and freshwater habitats are used (Gill et al. 2001, Gunnarsson 2005a). In Ireland, the extent of freshwater habitat use could indicate that mudflat prey resources in Ireland are limited and that this is restricting further population growth in these wintering locations. Freshwater grassland habitats are regularly used on the coast and a large proportion of the winter population uses the inland grassland sites during late winter and spring. This is also true for a number of other shorebirds species wintering in Ireland (e.g. curlew *Numenius arquata*, oystercatcher *Haematopus ostralegus*, redshank *Tringa totanus* and lapwing *Vanellus vanellus* (Quinn and Kirby 1993, Crowe 2005)), suggesting that mudflat resources may potentially be limited for a range of shorebirds in Ireland. There may be benefits of using grassland sites, particularly the huge wetland habitats of the callows, which are unique habitats to Ireland. The huge congregations of birds on these sites might provide benefits of being in a large flock, such as reducing time lost to vigilance whilst foraging and ultimately reduced risk from predation (Pulliam 1973, Caraco 1979, Glück 1986, Cresswell 1994) Other authors have suggested that being in a large flock may also have benefits for finding high quality feeding areas (Clark and Mangel 1986, Valone and Templeton 2002). Effective flock size is further elevated when godwits feed in mixed species flocks with large numbers of other species present, which they frequently do on these inland sites. The callows may therefore provide an essential habitat which, along with the coastal grasslands, may be the mechanism by which Ireland supports such large numbers of waterbirds over winter despite possible constraints in resource availability on coastal mudflats. Identifying the relative quality of mudflat and grasslands as foraging locations, and assessing whether resources on any of these habitats are limited, will thus be key to understanding whether patterns of godwit population change are indicative of buffer effects in Ireland, and whether Ireland can continue to support an increasing godwit population.

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Chapter 2

Shorebird use of a habitat matrix during winter: relative profitability of intertidal and terrestrial habitats

Abstract

1. Although most migratory shorebirds are restricted to coastal areas in winter, many species use a combination of intertidal and terrestrial habitats. The relative importance and patterns of use of these habitats will depend upon the extent to which they vary in availability and quality, both locally and throughout the winter range. Understanding variation in habitat quality and availability can be key to identifying priorities for habitat conservation and protection.
2. During the non-breeding season, Icelandic black-tailed godwits (*Limosa limosa islandica*) use both estuarine mudflats and freshwater grassland habitats to varying extents throughout the range. Grassland use is particularly apparent in Ireland, where many estuaries are surrounded by pastoral farmland. Godwit flocks use both habitats throughout the winter months, providing an opportunity to explore the relative profitability of each habitat.
3. Across eight coastal mudflat and grassland complexes and one inland flooded river valley, large-scale surveys and detailed foraging behaviour studies were carried out during the winters of 2006-2008. These data are used to quantify the pattern of use of intertidal and terrestrial habitats by godwits throughout the winter, and to explore variation in the relative profitability of each habitat, the consequences of habitat choice for godwit foraging success and the implications for the relative importance of each habitat for godwits.
4. Use of grasslands did not vary with the tidal cycle, but a seasonal pattern was evident with greater use of both coastal and inland grasslands in the middle of winter. Despite higher perceived predation risk on coastal grasslands resulting in three times more disturbance flights per hour than on mudflats, godwit flocks spend about half their time foraging on grassland sites in the coastal zone

throughout the winter. However, estimates of daily food consumption on each habitat indicate that mudflat foraging alone is insufficient to meet the energetic requirements of godwits, and that the availability of grasslands as foraging habitats is essential to support the godwit population in Ireland throughout the whole winter.

5. The freshwater grasslands used in Ireland by shorebirds are primarily managed as grazing pasture and, in contrast with the adjacent mudflats, have little or no legal protection. As Ireland supports *c*. 20-30% of the entire Icelandic black-tailed godwit population in winter, and use of grasslands by godwits is common throughout the country, protecting these grasslands may be critical for maintaining the internationally important godwit population.

Introduction

Variation in habitat quality and the extent to which animals can exploit different habitats can be a key driver of individual fitness (Pulliam and Danielson 1991, Sutherland 1996, Newton 1998), both in terms of survival and breeding success in subsequent seasons. In migratory species, the cross-seasonal effects of occupying habitats of varying quality during the non-breeding season are particularly complex to identify, but a growing body of literature is highlighting the importance of carry-over effects over large spatial scales (Bryant and Jones 1995, Szep 1995, Gill *et al.* 2001, Newton 2004). Conditions in wintering areas have been linked to annual fluctuations in numbers of several migratory bird species breeding in Europe; for example numbers of Sedge warblers, *Acrocephalus schoenobaenus*, on northern breeding grounds have varied in relation to rainfall (and hence food supplies) in west African wintering quarters (Peach 2008) and more direct links between winter conditions and subsequent breeding success have been described in Dark-bellied Brent Geese (*Branta bernicula bernicula*), in which females that returned to the wintering grounds successfully with young had, on average, been heavier on spring departure from the staging grounds (Ebbinge and Spaans 1995).

Migratory animals encounter varied and heterogeneous environments throughout their annual cycle and have to exploit different habitat types that may vary in quality and availability, both spatially and temporally. The impact of winter habitat quality will vary among individuals or groups that occupy different areas or exploit different resources. For example, habitat-specific stable isotope signatures in American Redstarts (*Setophaga ruticilla*) wintering in Jamaica have been used to show that individuals occupying low quality scrub habitat in winter departed later and in poorer physical condition for the breeding grounds than conspecifics wintering in higher quality forest habitat (Marra 1998). Early departure for the breeding grounds is likely to be advantageous in gaining good quality territories and raising more young (Kokko 1999). Similarly, Icelandic black-tailed godwits (*Limosa limosa islandica*) show strong seasonal matching between either good quality summer and winter habitats or poor quality habitats in both seasons (Gunnarsson *et al.* 2005a).

It is clear from these studies that population trends could vary depending on the condition of habitats throughout the migratory cycle. In order to identify habitats of conservation importance for maintaining populations it is therefore important to understand the variation in habitat quality and the relative importance of different habitats. For migratory shorebirds in the non-breeding season, habitat quality is generally related to variation in foraging opportunities in a tidally constrained environment, for example habitats may differ in the abundance, quality or accessibility of prey (Goss-Custard 1980, Gillings 2007, Grandeiro 2007). In addition, issues such as predation risk (Yasue *et al.* 2003), human disturbance (Stillman and Goss-Custard 2002) and site availability (Masero and Perez-Hurtado 2001, Lourenco and Piersma 2009) can also influence relative habitat quality. Thus shorebirds face a choice of foraging locations and individuals may have to trade-off factors including the quality of foraging opportunities and the distance between foraging and roost sites (Rogers *et al.* 2006). The perceived risk of predation and the subsequent levels of vigilance activity can also influence habitat choice (Lima and Dill 1990, Repasky 1996, Yasue *et al.* 2003). Vigilance activity is assumed to occur at the expense of food intake (Pulliam 1973), thus individuals may adapt foraging behaviour on habitats that differ in predation risk, for example individuals can increase the duration or frequency of scans for predators in high risk locations (Brown *et al.* 1988, Cresswell 2008). Quantifying the variation in foraging opportunities and costs associated with the use of different habitats can therefore provide insights into the relative profitability and costs incurred by foraging in each habitat.

When habitats vary in quality and availability, the order of use can indicate an animal's preference for one habitat over another; in many cases less preferred habitats may only be used when resources in the preferred habitat have been depleted. For example, brent geese (*Branta bernicla*) have been shown to shift from foraging on intertidal algal beds and saltmarshes to grasslands and agricultural crops in response to depletion of the saltmarsh vegetation (Vickery *et al.* 1995), and poor intertidal food supplies have been shown to result in turnstone (*Arenaria interpres*) increasing their use of alternative food sources such as of wheat grain (Smart and Gill 2003). Preference can also be indicated if an additional habitat is only used when the preferred habitat is unavailable. For example, redshank (*Tringa totanus*) use supratidal salinas in Spain as a supplementary foraging habitat at high tide when mudflats are unavailable (Masero *et al.* 2000). Factors affecting habitat choices may vary through the season or with the condition of the animal (Beale and Monaghan 2004) and, for species occupying the intertidal zone, habitat choice may be restricted by the tidal cycle. Therefore in complex, heterogeneous and temporally variable landscapes, studies may need to go beyond order of use of habitats and consider how distribution of animals may be influenced by the combination of habitat options (e.g. (Lourenco and Piersma 2009)). Gaining an understanding of the relative importance of different habitats can inform prioritisation of habitat conservation efforts; this requires studies that fully explore the range of habitats used by a population. When habitats of varying quality are used this will be especially important to understand in order to protect the combination of habitat resources necessary to maintain populations (Masero and Perez-Hurtado 2001).

The Icelandic black-tailed godwit is a migratory shorebird that breeds almost entirely in Iceland and winters in the coastal regions of western Europe. During the non-breeding season, godwits aggregate in flocks to forage primarily in soft coastal mudflats, but freshwater grasslands are also used across the range (Hutchinson and O'Halloran 1994, Gill *et al.* 2001, Gill *et al.* 2002). These freshwater habitats range from coastal grasslands and pasture to inland wetlands. In Ireland, several seasonally flooded river valleys (known locally as “callows”), are also used by godwits when surface flood water is present (Crowe 2005).

In this study we explore patterns of habitat use by black-tailed godwits and the relative profitability of freshwater and estuarine habitats, in order to quantify 1. seasonal patterns of use of intertidal mudflats and grasslands by godwits throughout the winter, 2. variation in the relative profitability of intertidal and terrestrial habitats, 3. the costs associated with foraging on different habitats and 4. the implications for the relative importance of each of the habitat types throughout the non-breeding season.

Methods

Study area

Black-tailed godwit use of estuarine and freshwater habitats was explored on the south coast of Ireland (County Cork and County Waterford), from October to March in the winters of 2006/07 and 2007/08. The habitat types were studied in two major zones; the coastal zone included eight estuarine complexes along *c*. 100 km of coast and the inland zone comprised one flooded river valley complex (Fig. 1). Coastal complexes encompassed extensive mudflat areas (mean ± SE = 110 ± 24 ha, range = 25 to 224 ha, n = 25) and surrounding freshwater grazing pastures sites (blocks of fields that can be viewed from one location, mean ± SE = 15 ± 2 ha, range = 3 to 28 ha, n = 18). The study area includes four areas of international and one of national importance for wintering black-tailed godwits (Crowe 2005).

Godwit habitat use throughout the winter range

Since 1995, a programme of marking and tracking black-tailed godwits has maintained. *c*. 1 – 2% of the population individually colour-marked (Gunnarsson *et al.* 2005b) and, with the help of a large network of volunteer observers, the winter locations and habitats used by *c*. 50% of these birds have been identified (Gunnarsson *et al.* 2004). For each of the seven major wintering areas throughout the range, the proportion of sightings of individually marked birds on either saline habitats (mudflats and saltpans) or freshwater habitats (grasslands, river valleys and rice fields) in autumn (October and November), winter (January and February) and spring (March and April) between 1995 and 2006 was used to explore seasonal and geographic variation in winter habitat use.

In Ireland, study sites were selected from within eight coastal zone complexes (Fig. 1), each of which encompass the mudflats of an estuary and the grassland fields surrounding them. Within each complex, between 2 and 5 separate mudflat sites and 2 and 4 grassland sites that were used by godwits were included in the study. Each grassland site comprised a block of 1 - 8 separate fields that could all be viewed from one location. Between October and March, each complex was visited four times in each season: autumn (Oct/Nov), winter (Dec/Jan) and spring (Feb/Mar). The number of godwits foraging on each mudflat and grassland site was recorded on arrival, and all flocks were checked for colour-ringed birds. Within each complex, godwits typically foraged in one discrete flock on one habitat at any one time and movement between habitats tended to involve the whole flock moving over the course of a few minutes. Within each site, flocks were observed for 20 - 130 minutes, and scan sampling every 20 minutes was used to record the behaviour of each individual (foraging, roosting or loafing/preening) within the flock (Table 1, only flocks with a minimum of 20 individuals were included in these analyses). The mean percentage of the flock foraging during each observation period was estimated to be the proportion of time that the flock spent foraging (Altmann 1974), thus the proportion of time a flock spent foraging on any particular habitat each day could be calculated from the percentage of observation time spent on that habitat and the percentage of time spent foraging within that time period. Time of day was recorded and the time relative to high tide was then determined using published tide tables (http://www.ukho.gov.uk). Tidal states were categorised as high tide (two hours either side of published high tide time), falling tide (2 – 4 hours after high tide), low tide (2 hours either side of published low tide time) and rising tide (2 – 4 hours after low tide) (Table 1).

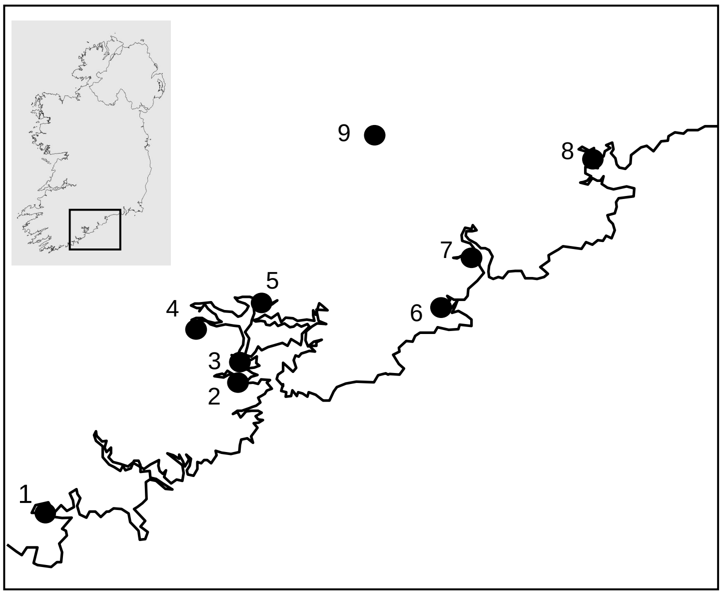

Figure 1. Map of Ireland detailing the study area on the south coast (County Cork and County Waterford) and the locations of the nine study sites: 1. Timoleague/Courtmacsherry 2. Owenabue 3. Loughbeg 4. Douglas 5. Cork Harbour North 6. Ballymacoda 7. Youghal 8. Dungarvan 9. Blackwater Callows.

The inland zone grassland complex known locally as the Blackwater Callows (site 9 on Fig. 1) is an 83 ha river valley located *c.* 23 km inland and comprised of three distinct sites (mean ± SE area = 28 ± 7 ha). Each site was visited once each month but visit frequency was increased after periods of rainfall of greater than three days (which typically results in flooding of the grasslands from the adjacent river) to a minimum of once every two weeks. When godwits were present, all three sites were visited weekly until the flock left the valley. The movements, activity and foraging behaviour of all flocks on these sites were recorded as described above. On every visit, the percentage of each site covered by surface water was estimated visually.

Invertebrate sampling

Variation in prey density across grassland sites was explored by sampling invertebrate abundance and biomass on nine fields (one inland field and eight across seven coastal complexes). On each field, 20 randomly distributed 8 cm diameter cylindrical soil cores were collected in November/December 2007 and again in March/April 2008. In addition, between December 2006 and January 2007, the effect of variation in local rainfall on prey availability on grasslands was investigated on five fields (three fields sampled twice each, one field four times and one field once, a minimum of one month between repeating a sample on the same field) by sampling invertebrate abundance using the same 8 cm diameter cylindrical soil cores at 20 evenly spaced points along a diagonal transect across each field. Cumulative rainfall in the preceding three days was recorded for each field with funnel rain gauges (diameter 12.6 cm) placed at the edge of each field. All sample cores were bagged, labelled, sealed and hand sorted within 10 days of collection. All potential godwit prey items (Hutchinson and O'Halloran 1994) were measured (unstretched wet length for earthworms, maximum body length for Diptera larvae). Earthworms were the most common potential prey encountered during these surveys; a reference collection was preserved in 70% ethanol for subsequent biomass estimations.

Godwit foraging behaviour

Foraging godwit flocks consisting of a minimum of 20 birds (flock size range: coastal complexes = 25 - 435; inland complex = 158 - 2000) were observed for between 10 and 121 minutes (depending on the length of time for which flocks stayed within a site). The mean number of disturbance flights per hour was calculated for each observation period (disturbance flights were defined as occasions when > 80% of the flock simultaneously took flight). Focal sampling was used to record the foraging behaviour of individual godwits within flocks (Table 1). Instantaneous prey intake rates of randomly located individuals were measured by recording the time taken to make ten paces, during which the number of successful and unsuccessful pecks was also counted. In addition, the time each individual spent being vigilant (head and bill above the level of the body) or in aggressive interactions was also recorded, and subtracted from the total observation time in order to calculate prey intake over the time spent actively foraging. A minimum of 25 individual intake rates (range = 28 - 80) were recorded for each flock and averaged to give a mean intake rate per foraging flock. These data allow direct calculation of peck rate (pecks per second of foraging time) as a measure of foraging effort, and step rate (steps per second of foraging time) as a measure of effort expended in foraging. All variables recorded during these surveys are detailed in Table 1. The prey type (bivalve or polychaete (on mudflats) or earthworm (on grassland) was recorded and the size of each prey item was estimated in the field as small, medium, large, or very large (Table 2).

Biomass calculations

Samples of bivalves were collected in Cork Harbour in February 2008, and earthworms in 10 fields across all coastal complexes from December 2007 - March 2008. The ash-free dry mass (AFDM) of each individual was measured using the protocol described by Crisp (1971). No polychaetes were encountered during the sampling periods and so values for polychaete AFDM were taken from J.A. Gill (unpublished data from England). The number of each prey size consumed by each focal bird was multiplied by the ash-free dry mass (g) of that prey size category (Table 2), summed and averaged across all focal individuals to give a mean biomass intake rate (mgAFDM.sec^{-1}) for each flock.

Table 1. Definitions and units of all variables recorded during the surveys of black-tailed godwit habitat use and foraging behaviour.

Variables	**Unit**	**Description**
Godwit use of habitat complexes		
Peak count	no. individuals	Maximum number of godwits on each complex each month
Site occupancy	% sites	Average percentage of individual sites within a complex used by godwit flocks monthly and tidally
Godwit foraging behaviour		
Foraging activity	% flock	Percentage of time spent foraging
Intake rate	mg.sec^{-1} AFDM	Average biomass intake rate of flock on each habitat in each season
Prey size consumed	%	Percentage of each prey size and type consumed on each habitat in each season
Prey consumption rate	prey items. sec^{-1}	Average number of prey items consumed by an individual per second of foraging time on each habitat
Peck rate	probe.sec^{-1}	Average number of pecks made by an individual per second of foraging time on each habitat
Step rate	step.sec^{-1}	Average number of steps made by an individual per second of foraging time on each habitat
Costs associated with use of each habitat		
Vigilance frequency	%	Average percentage of foraging observations in which birds were vigilant at least once
Disturbance levels	Flights.hour^{-1}	Average number of disturbance flights during a flock foraging bout on each habitat
Distance to safe roost	m	Distance from foraging location to nearest roosting location (shallow pool or tide edge)
Categorical variables		
Zone		Coast (mudflat and coastal grassland considered together) and Inland
Complex		Coastal complexes numbered 1-8 and inland complex number 9
Site		Discrete habitat areas surveyed within each complex
Habitat type		Mudflat, coastal grassland, inland grassland
Month		October – March inclusive in both years
Season		Autumn (Oct-Nov), Winter (Dec-Jan), Spring (Feb-Mar)
Year		Year 1 = 2006/07, Year 2 = 2007/08
Tide		H = high & L = low tide (two hours either side of published high or low tide times respectively) and R = rising & F = falling (defined as 2 hours before or after high or low tide time respectively). Adjusted for local site variation.

Table 2. Body lengths and ash-free dry mass of each prey type and size class. Length-weight regression equations and sources are also shown.

Prey type	Size class	Length (mm) (class midpoint)	AFDM (mg)	Source
Bivalves:	Small	5	0.0008	Log (AFDM) = 2.68 x Log (length) - 4.75 (individuals sampled: n = 69, length range= 8.9 - 59.6 mm)
Scrobicularia plana	Medium	10	0.0034	
	Large	15	0.0154	
	Very large	20	0.0380	
Polychaetes	Small	15	0.0034	Log(AFDM) = 1.87 x Log (length) - 4.72 (from J.A. Gill, unpublished data from England).
Nereis diversicolor	Medium	30	0.0111	
	Large	60	0.0407	
	Very large	80	0.0870	
Earthworms spp.	Small	10	0.0093	Log(AFDM) = 2.334 x Log (length) - 5.70. individuals sampled (n = 45, range = 15.4-103.0 mm). Foraging observations indicated that smaller worms were primarily broken sections of larger worms (i.e. large fragment diameters), thus AFDM of small, medium and large categories were estimated as fractions of a 100 mm worm (a typical very large worm).
	Medium	30	0.0280	
	Large	55	0.0514	
	Very large	85	0.0636	

Calculations of daily consumption rates

The mean intake rate (AFDMmg.sec^{-1}) of godwit flocks foraging on mudflats in each season was used to estimate the maximum potential daily energetic consumption if birds foraged continuously on mudflats for the average period for which the mudflats are exposed by the tide (12 hours.day^{-1}). Published estimates suggest that black-tailed godwits require a minimum of 173.3 kJ/Day to meet basal metabolic rate (BMR) requirements (Kersten and Piersma 1987). The energetic content of the estuarine prey in this study (bivalves and polychaetes) was estimated as 21.67 kJ.g^{-1} AFDM, which is the mean of the following reported values: *Nereis diversicolor* 21.8 kJ.g^{-1} AFDM (Zwarts and Wanink 1993); cold water marine benthic invertebrates; 22.9 kJ.g^{-1} AFDM (Wacasey 1987) and 20.5 kJ.g^{-1} AFDM (Dauvin and Joncourt 1989).

Statistical analyses

Variability in godwit use of zones, complexes and sites (Table 1) was modelled using mean monthly peak flock size as the dependent variable in general linear models (GLMs). Each GLM used appropriate normal error distributions. Zone, habitat, complex, month (or season) and tide were included as fixed factors and year as a random factor, with habitat x month, zone x month, and tide x season interactions to explore any seasonal variation in use of habitats or locations and in the effect of tidal variation on godwit distribution. Differences in foraging behaviour on mudflats and grasslands were explored in GLMs with each component of foraging behaviour (Table 1) as dependent variables, mudflat was compared to all grasslands (coastal fields and inland combined), and habitat (mudflat or grassland) and month (or season) were included as fixed factors with year as a random factor. Vigilance behaviour, disturbance rates and roost distances on each of the three habitat types were modelled in GLMs with zone, habitat and complex as fixed factors and month (or season) and year as random factors. A paired t-test was used to assess seasonal variation in earthworm densities across grassland fields in seven complexes (including one inland site) on each field, and the relationship between earthworm density and cumulative rainfall in the previous three days was analysed using linear regression.

Results

Habitat use across the non-breeding range

In the south of the winter range (France and Iberia), godwits make occasional use of rice fields and river valleys but they are mainly restricted to intertidal mudflats and adjacent saltpans, as over 80% of all sightings of colour ringed birds were on saline habitats in all seasons (Fig. 2). The use of freshwater grassland is quite common in England, but the majority of grassland sightings are typically from when flocks make large-scale movements to a small number of seasonally flooded inland wetland sites, as there are few remaining coastal grasslands. In contrast, in Ireland the estuarine areas are typically surrounded by freshwater grazing pastures which are used by godwit flocks throughout the winter (Fig. 2).

Seasonal and spatial variation in godwit habitat use in Ireland

Throughout the non-breeding season in both years of the study (2006-07 and 2007-08), the number of godwits using the eight coastal zone complexes each month totalled *c.* 1000 birds (Fig. 3a). The monthly peak flock sizes on each complex in the coastal zone varied from 50 to 500 but there was no significant difference in peak flock size between years ($F_{1,23} = 1.64$, $p = 0.214$) or months ($F_{5,23} = 0.41$, $p = 0.999$). Observations of colour-ringed individuals across Ireland indicate that godwits are highly site-faithful to coastal complexes; of the 104 individuals that have been seen more than once, 50% have only been recorded on one estuary complex, and a further 30% have been seen on sites less than 20 km apart. Within the coastal complexes, godwit flocks used mudflat and grassland habitats in all months (Fig. 3b) and were frequently observed moving from one habitat to another during the 20 - 120 minute observation periods.

In contrast to the continuous presence of godwit flocks on coastal complexes, occupancy of the inland grassland site varied strongly in relation to the level of standing water present; godwits were only observed inland when the amount of standing water exceeded 15% of the total site area (Fig 3a). Consequently, there were significant effects of month and a zone x month interaction on the total number of birds present on each zone throughout the winter (Table 3a).

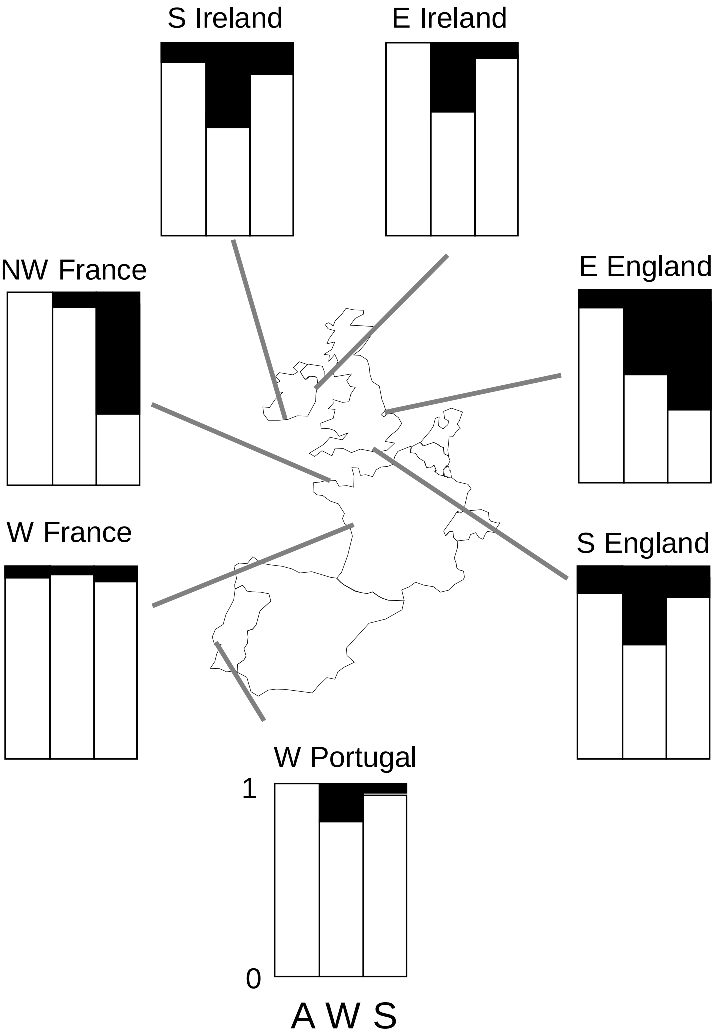

Figure 2. Schematic diagram of the proportion of colour-ring sightings of individual black-tailed godwits on saline (white bars) and freshwater (black bars) habitats in seven of the major godwit wintering sites in each season (A: Autumn (Oct-Nov), W: winter (Dec-Jan) and S: spring (Feb-Mar)).

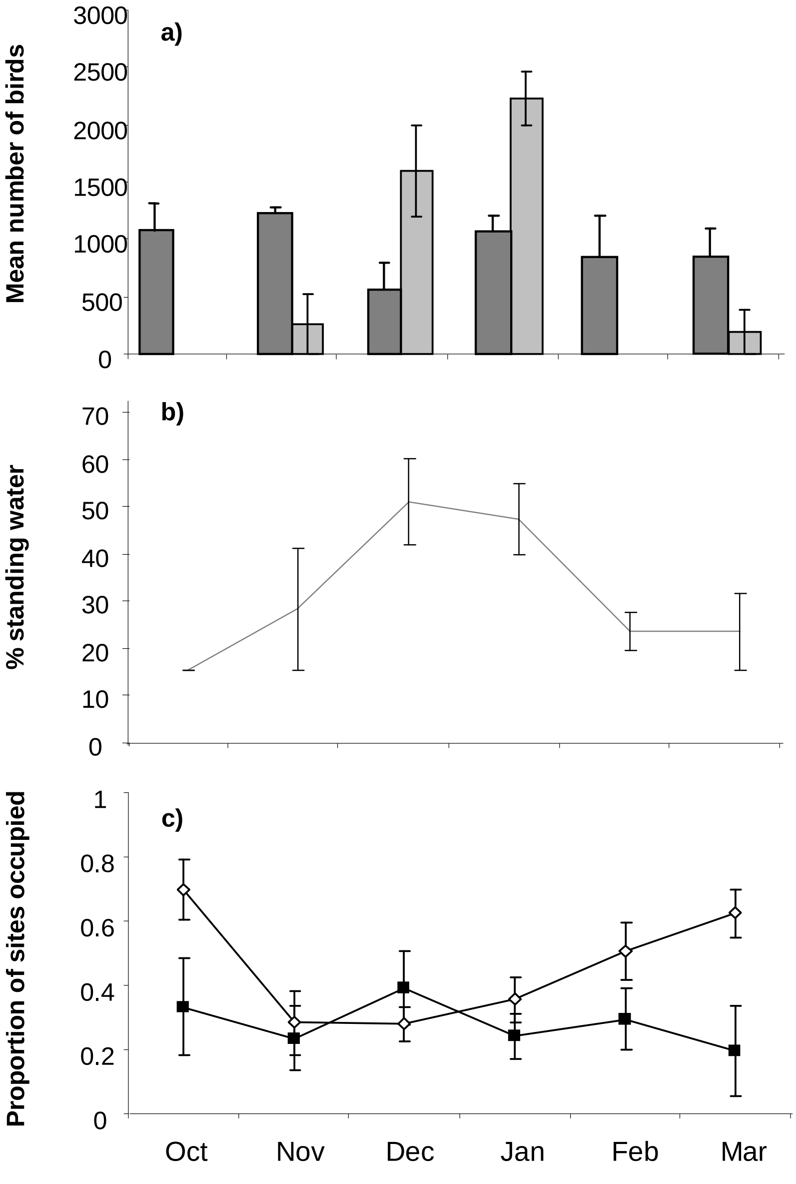

Figure 3. Variation in habitat use by black-tailed godwits in S Ireland throughout the non-breeding season of 2006-07 & 2007-08. a) mean (± SE) total number of birds recorded in each month on the eight coastal complexes (dark bars) and three inland sites (light bars). b) variation in the mean (± SE) percent of standing water on the inland sites. c) mean (± SE) proportion of mudflat (open diamonds) and coastal grassland (filled squares) sites occupied by godwit flocks within coastal complexes.

The decrease in the total number of birds on the coastal zone in December is a consequence of the congregation of godwits inland. Of 18 individually colour-ringed individuals seen at the inland sites, 14 were also recorded on the eight nearby coastal complexes in the same year, thus the majority of birds on the inland sites are likely to have come from these local coastal complexes. Although the number of godwits on coastal complexes declines during the period when godwit congregate on the inland sites (Fig. 3a & Table 3a), the proportion of occupied sites in the coastal complexes varies little throughout the season (Site occupancy model: month x site interaction; $F_{14,51}$ = 0.74, p = 0.723) or on each habitat type (Site occupancy model: Habitat x month interaction; $F_{5,51}$ = 2.15, p = 0.074, Fig. 3b), indicating that the move inland is not restricted to godwits abandoning a subset of complexes or habitats. The proportion of mudflat sites occupied throughout the season is significantly greater than grassland sites (Fig. 3b, Table 3a). Godwit flocks did not show any tendency to use grassland habitats as solely supplementary foraging sites when mudflats were unavailable at high tide, as use of grasslands occurred at all states of tide (Site occupancy model: tide x habitat interaction; $F_{3,117}$ = 0.571, p = 0.635, Fig. 4). Occupancy of mudflats was always higher than grasslands except in winter at high and falling tide.

Table 3. Results of GLMs of a) seasonal variation in godwit use of zones (coast or inland) and habitat complexes, b) zone, season and habitat (mudflat or grassland) variation in godwit foraging behaviour and c) the costs associated with use of different habitat types. Only statistically significant results are reported. See Table 1 for definitions.

a) Godwit use of habitat complexes		df	F	p
Zone peak count:	month	5,59	21.58	0.001
	coast/inland x month	6,59	19.74	0.001
Site occupancy:	habitat	1,113	14.53	0.001
b) Godwit foraging behaviour				
% time spent foraging	habitat	2,132	12.32	0.001
No. prey consumed per second	habitat	1,33	30.56	0.001
Peck rate (no. pecks per second)	habitat	1,33	6.12	0.019
	season	2,33	13.87	0.001
Step rate (no. steps per second)	habitat	1,33	19.63	0.001
c) Cost associated with each habitat				
Vigilance levels	habitat	2,35	10.00	0.001
Disturbance levels	habitat	2,190	7.86	0.001
Distance to safe roost site	habitat	2,54	3.97	0.025

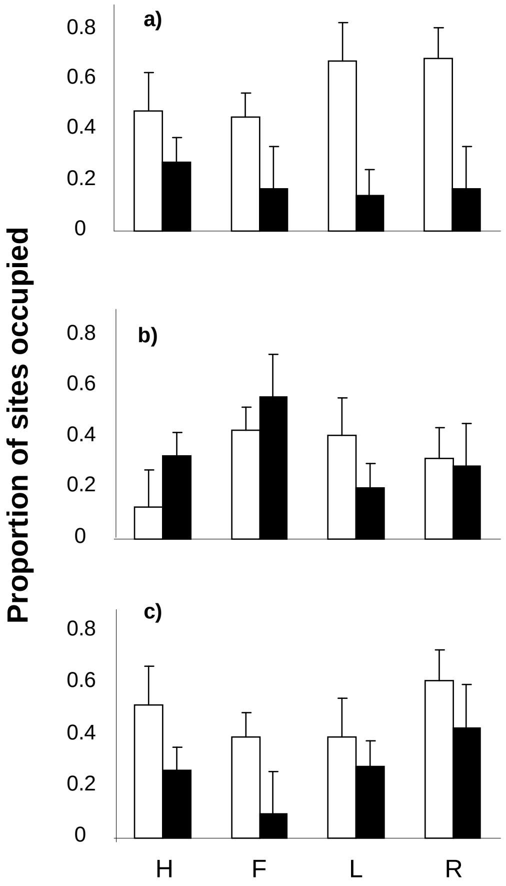

Figure 4. Variation in the mean (± SE) proportion of mudflat (open bars) and grassland (filled bars) sites occupied by black-tailed godwits on coastal complexes in S Ireland through the tidal cycle (H=high, F=falling, L=low, R=rising) in a) autumn (Oct/Nov), b) winter (Dec/Jan) and c) spring (Feb/Mar).

Earthworms made up the majority (c. 77%) of potential godwit prey items found in soil cores across all 8 fields surveyed. All other invertebrates were considered to be smaller than the minimum sizes typically consumed by godwits; Enchytraeidae (22.4%) and earthworm cocoons (6.7%) or were too rare to be of significance in the diet (Diptera larvae = 0.5%). There were no significant differences in mean earthworm density (ind.m^{-2}) across the eight fields sampled early (281 ± se = 41) and late (266 ± se = 20) in the season (paired t-test; t = 0.34, df = 7, p = 0.74) in 2007/08. There was no significant effect of localised rainfall on earthworm abundance ($R^2 = 0.015$, $F_{1,9} = 0.13$, $p = 0.724$) in 2006/07 (Fig 5).

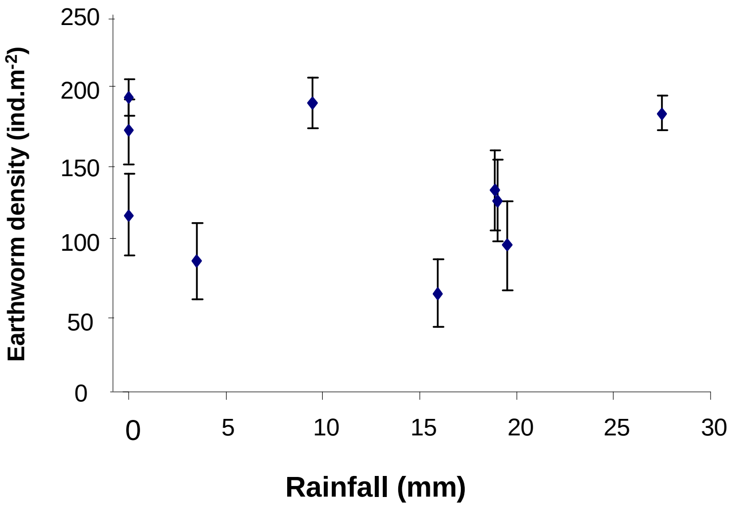

Figure 5. Variation in the mean (± SE) earthworm density on four grassland fields in relation to localised cumulative rainfall for three days prior to sampling Dec - Jan 2006/07.

Levels of foraging activity in godwit flocks varied markedly between mudflats and grasslands (Table 3b). On coastal grasslands, the percentage of time spent foraging by godwits was 80 - 90%, in comparison to 50 - 70% of time spent foraging on mudflats throughout the winter (Fig. 6). On inland grasslands, levels of foraging activity were similar to those of flocks on mudflats, with 50 - 70% of time spent foraging during the months in which inland sites were used (Fig. 6).

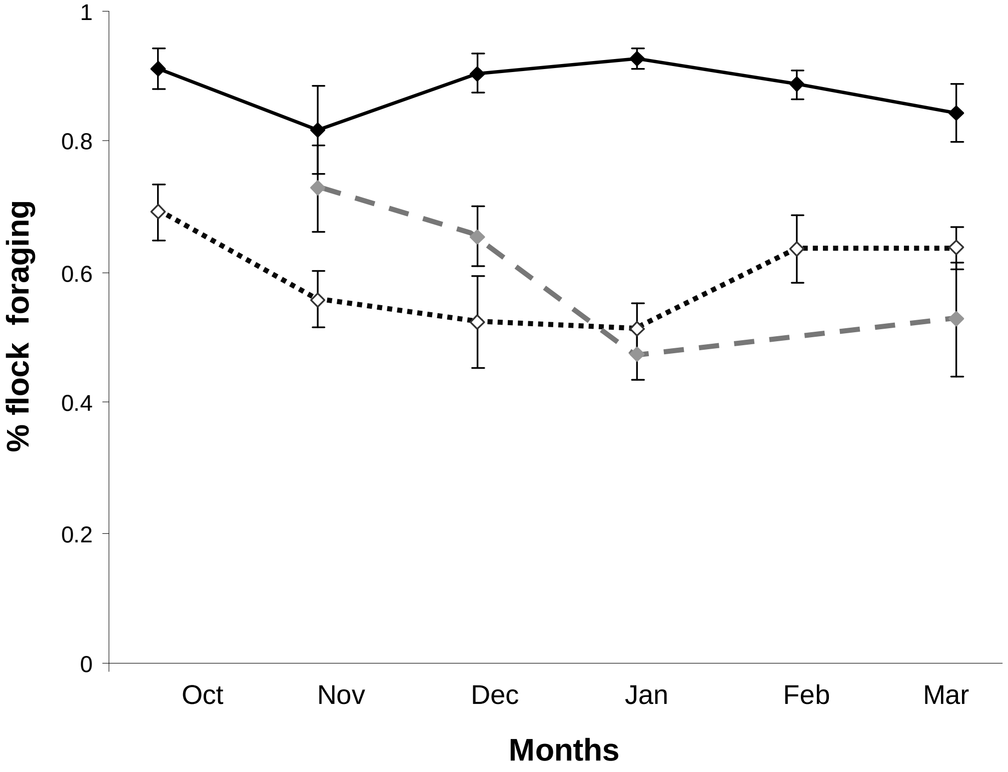

Figure 6. Variation in the mean (± SE) percent of individuals within godwit flocks observed foraging on mudflats (open diamonds, dotted line), coastal grasslands (filled diamonds, solid line) and inland grasslands (filled diamonds, dashed line) during each month of the winters of 2006-07 and 2007-08.

Although instantaneous prey intake rates of godwits on coastal grasslands were consistently slightly higher than those on mudflat or inland grasslands, there was no significant difference between the three habitats (Fig. 7, habitat: $F_{2,37} = 1.65$, $p = 0.206$). Although the highest prey intake rates on mudflats occur in the autumn, there is no evidence for seasonal declines in intake rate on any habitat (season x habitat: $F_{2,37} = 0.30$, $p = 0.744$).

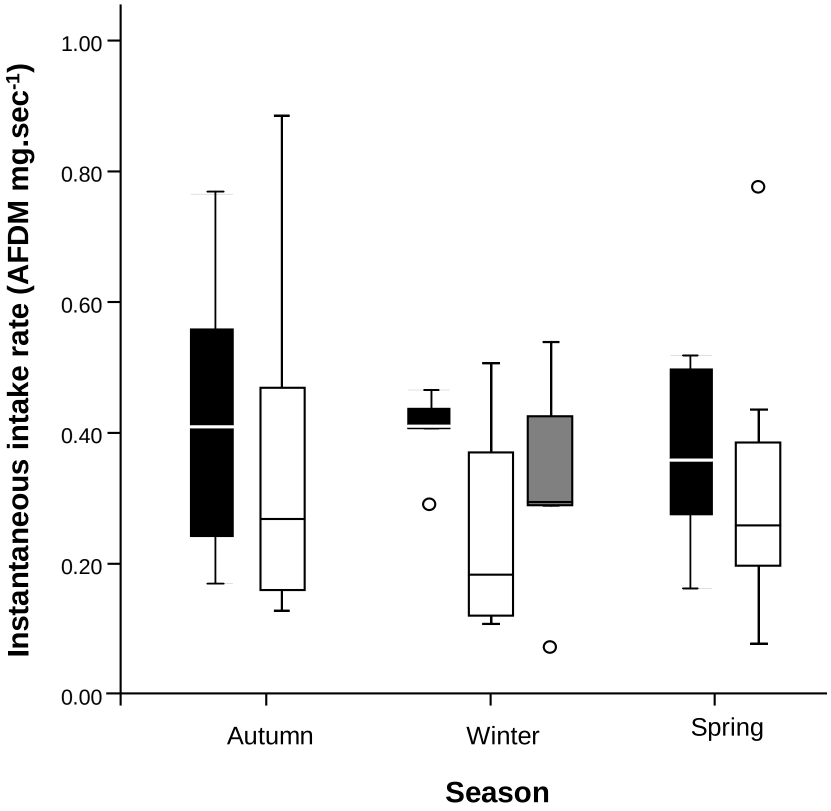

Figure 7. Seasonal variation in the prey intake rates of godwits foraging on coastal grasslands (black), mudflats (white) and inland grasslands (grey). Boxes represent the inter-quartile range and the line bisecting each box is the median value, error bars indicate the data values that are within 1.5 times the inter-quartile range and values exceeding this range are represented by open dots.

These intake rates could be masking depletion of prey in the environment if the proportion of the diet comprising prey of different sizes were changing over the winter. However, diet composition varied little between seasons, with very few large prey items consumed on any habitat, and medium and large prey items combined (> 10 mm length) only just exceeding 5% of the prey consumed on mudflats (Fig. 8). On coastal and inland grasslands, more than 95% of prey were small (≤ than 10 mm in length) throughout the winter (Fig. 8).

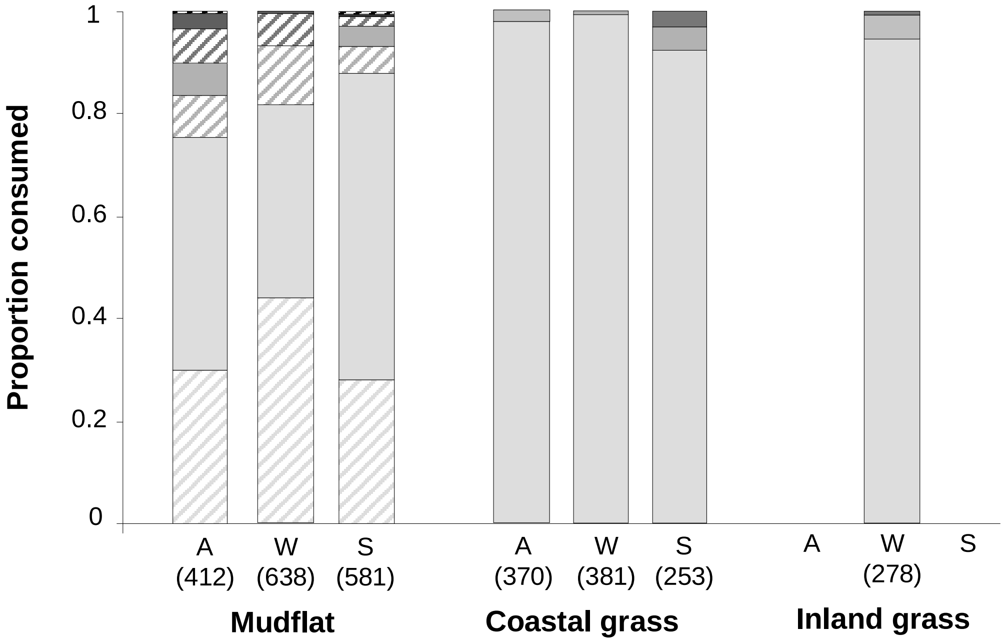

Figure 8. Seasonal variation in the proportion of prey types and sizes consumed by black-tailed godwits on different habitats. Hatched bars = bivalves on mudflats, filled bars = polychaetes on mudflats and earthworms on grassland, and colour represents size classes (pale grey = small, mid grey = medium, dark grey = large) in A: autumn (Oct/Nov), W: winter (Dec/Jan) and S: spring (Feb/Mar)). Numbers of individual observations are given in brackets under each column.

As the components of godwit foraging behaviour (intake rates, peck rates and step rates) varied little (GLMs, $p > 0.05$ in all cases) between inland and coastal grasslands, these were combined in order to compare foraging behaviour on grasslands and mudflats. The number of prey items consumed per second was significantly higher on mudflats than grasslands in all three seasons (Fig. 9a, Table 3) but both peck and step rates were higher on grasslands than mudflats in each season (Fig. 9b, c, Table 3b). Peck rates increase by more than 50% on both habitats over the course of the season but there is no such seasonal variation in intake rates. Step rates are lower on mudflat than grassland and increase from 1 to c. 1.5step.sec^{-1} on mudflat between autumn and spring (Fig. 9) although this increase is not statistically significant.

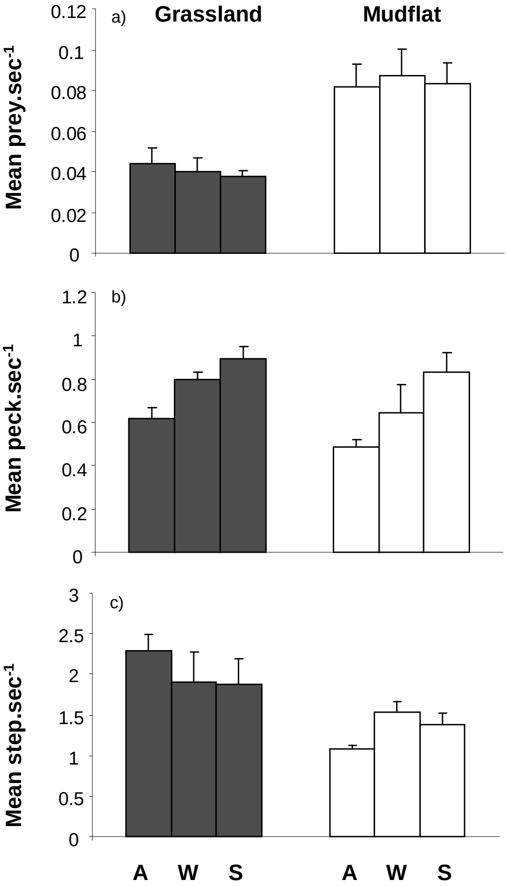

Figure 9. Seasonal variation (A=Autumn, W=Winter and S=Spring) in mean (± SE) a) prey consumed per second, b) peck rate and c) step rate of black-tailed godwits foraging on coastal grasslands (filled bars) and mudflats (open bars).

Costs associated with use of different habitats

During observations of individual foraging bouts, the frequency of vigilance events was *c*. 2 - 3 times higher on grassland than on mudflats (Fig. 10a, Table 3c). Godwits foraging on coastal grasslands took flight in response to disturbance events approximately once every 15 minutes, whereas godwits foraging on mudflats and inland grassland were disturbed less than half as frequently (Fig. 10b). The great majority (grass: 96%, n = 144; mudflat: 98%, n = 59) of disturbance flights had no identified cause; raptor attacks were observed on fewer than 3% of disturbance flights on grassland and never on mudflats, human disturbance was identified as the cause of *c*. 1% of disturbance flights on all habitats. Disturbance events frequently caused godwit flocks to return to a roosting location, which is typically the nearest area of shallow water (either the tide edge or a shallow pool). The distance to the nearest roosting site was *c*. 3 times greater for flocks foraging on grasslands (Fig. 10c) than on mudflats or inland grasslands, where godwits rarely foraged further than 100 m from the waters edge.

Implications of habitat profitability

Published estimates of the basal metabolic rate of black-tailed godwits suggest they require a minimum of 173.3 kJ/day (Kersten *et al.* 1998). Based on average instantaneous intake rates recorded in this study and energy content values from the literature, estimations of maximum potential energy consumption were made for mudflats. Continuous foraging on the mudflats at the rates reported in Fig. 7 for 12 hours per day would provide only *c*. 20 kJ/day in excess of BMR. As tidal constraints mean the mudflats are not exposed for 12 hours on all days, and as digestive constraints mean that continuous foraging is rarely possible in shorebirds (Van Gils *et al.* 2005), the combination of mudflat and grassland habitats appears to be essential for the Irish wintering population of black-tailed godwits to meet their energetic requirements throughout the winter.

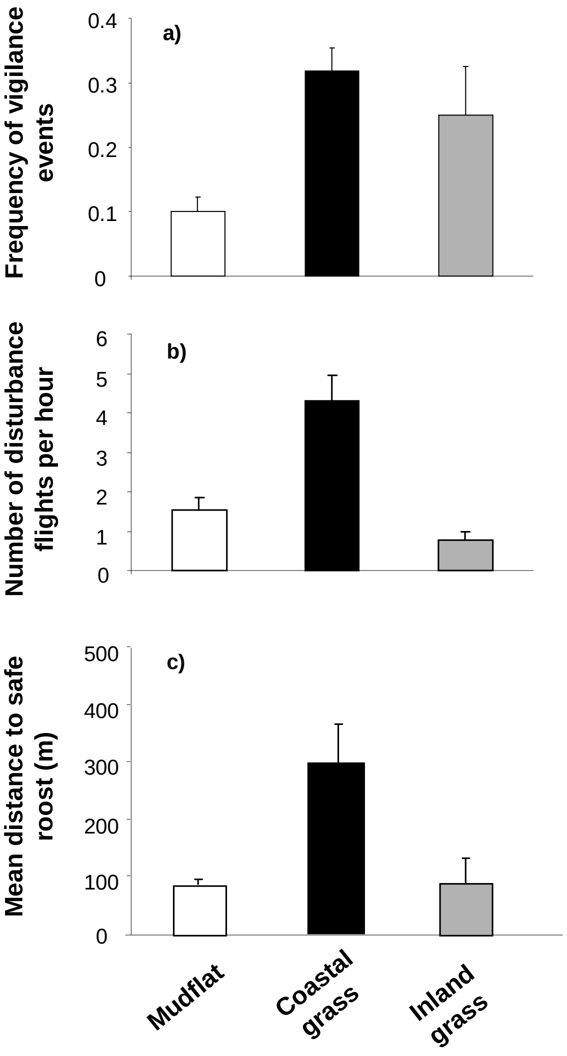

Figure 10. Variation in the behavioural and environmental costs associated with godwits foraging on different habitats: a) the number of disturbance flights per hour, b) the proportion of observations in which a vigilance event occurred c) the average distance (m) from foraging locations on each habitat type to nearest safe roosting site.

Discussion

Both freshwater and estuarine habitats are important for black-tailed godwits wintering throughout the coastal regions of western Europe, but the extent to which each is used is highly variable (Fig. 2). Ireland is unique in providing an abundance of freshwater grazing pasture surrounding most estuaries whereas, for wintering sites elsewhere in Europe, the availability of freshwater habitat is typically restricted to a small number of isolated inland wetlands. These fields are not typical bird watching sites so the percentage of sightings of colour-ringed birds on grassland in Ireland are likely to be an underestimate of the extent to which this habitat is used. In Ireland, godwits use mudflat and grassland habitats in the coastal zone on a daily basis throughout the non-breeding season. There is no strong seasonal or tidal pattern in the intensity of use of coastal mudflats and grasslands, but godwits make extensive use of inland grasslands when seasonal flooding results in areas of standing water to which godwits can retreat when disturbed. Similar instantaneous energetic intake rates are achieved on mud and grass throughout the winter, however, godwits foraging on coastal grasslands are disturbed significantly more frequently than on mudflats or on inland grassland, they have higher levels of vigilance and have to travel further to safe roosting sites when disturbed. However, while coastal grasslands may be more costly habitats in which to forage (as disturbance rates and vigilance levels are high), energetic intake rate on mudflats alone appear not to be sufficient for godwits to meet their energetic requirements throughout the winter, and thus grassland foraging resources are a critical part of the habitat matrix required to support the godwit population in southern Ireland.

The difficulties in meeting daily energetic requirements for godwits wintering in Ireland are also indicated by the large proportion of the day spent foraging (Fig. 6). In comparison, black-tailed godwits wintering in west Portugal can meet their energetic requirements in only *c.* 5 hours of foraging per day on mudflats and salinas (Alves 2009). In Ireland, continual use is made of grasslands despite the apparent cost of the high level of disturbance experienced, suggesting that food supplies for godwits on all habitats are limited, and thus that the matrix of mudflat and grassland habitats is very important in providing sufficient foraging opportunities throughout the winter months.

Interestingly, there was no strong evidence for changes in godwit behaviour reflecting seasonal depletion of prey resources, as both the proportion of time spent foraging and the instantaneous intake rates are maintained on all habitats throughout the winter. This may appear to contradict the idea that prey resources are limited, however, godwits wintering in Ireland move between habitats frequently (often several times per day), and flocks may therefore be regularly encountering new foraging patches. Prey depletion may therefore occur over small spatial scales and may result in localised changes in patch use and foraging effort which may not be picked up in large scale studies such as this. There is an indication that foraging effort increases in spring; on both habitats godwits increased peck rate significantly from autumn to spring. When foraging on grassland, godwit step rates and peck rates are consistently higher than on mudflats. Increased step rates may increase encounter rates with prey and higher peck rates may increase the chances of encountering prey even at low densities. Thus, increased foraging effort on grasslands may offset any declines in prey abundance. However, prey sampling on fields in autumn and spring suggested that earthworm abundance does not decline strongly over the winter, and the availability of earthworms does not appear to be greatly influenced by levels of rainfall (Fig. 5). Earthworm densities recorded here are comparable with those found elsewhere in Ireland on permanent pasture; densities ranged from 203 to 324 individuals.m^{-2} (Curry *et al.* 2007). Godwits are solely tactile foragers on grasslands, whereas prey on mudflats can be located visibly, which may make slower pacing worthwhile as it increases scanning time and may thus increase prey encounter rates (Speakman and Bryant 1993).

Although the energetic intake rates that can be achieved on grasslands are comparable to those on mudflats, the higher vigilance levels and greater rate of disturbance flights suggest that there may be significant costs to godwits of foraging on grasslands. In addition, the coastal grassland sites are typically 300 - 400 m away from roosting sites (usually the tide edge on adjacent mudflats), whereas godwits foraging on mudflats typically forage within 200 m of the tide edge (Fig. 10). This means that grasslands are potentially a more costly place to forage than mudflats. Although predator attacks and human disturbance incidents were rarely observed, grassland sites are clearly perceived to be riskier habitats than mudflats, warranting higher levels of vigilance and frequent escape flights even in the absence of an apparent cause. Perhaps as a consequence of the differing costs of habitat use, godwits on mudflats spend up to 35% of their time in non-foraging activities (preening, roosting etc) whereas godwits on grassland sites spend less than 5% of their time in these activities.

Grassland fields are all typically surrounded by hedges and trees, providing a level of cover which could contribute to the perceived level of risk. Godwits' ability to detect a potential predator attack could be reduced by the vegetation resulting in the reported levels of vigilance. The high levels of vigilance displayed by godwits on coastal fields could be influenced by differences in field area, as coastal fields are typically smaller (*c.* 15 ha) than inland grassland fields (*c.* 28 ha).

Legal protection of sites in Ireland for wintering waterbirds is varied; the inland 'callows' sites are listed as sites of national importance due to the large congregations of wintering water birds and therefore designated as Special Protection Area (SPAs), in accordance with the EU Birds and Habitats directive (No. 79/409/EEC). In contrast, on the coast, the current level of legal protection only designates the intertidal mudflat areas and the boundaries of these SPAs only include a very small number of coastal grasslands. However, to support the internationally important numbers of black-tailed godwits in S Ireland, all the components of the coastal estuarine and freshwater habitats as well as inland wetlands appear to be necessary (Hutchinson and O'Halloran 1994). Without the extensive use of coastal grasslands, godwits would have to meet their energetic requirements for the majority of the winter from mudflat prey resources, and the analyses presented here suggest that this is not likely to be possible.

The problem of limited legal protection of freshwater habitats in Ireland is mirrored across the non-breeding range in Europe, with most mudflat areas being protected under international agreements whereas the importance of freshwater habitats is less widely recognised. The extent of use of marine and freshwater habitats by godwits across the non-breeding range is clear from the distribution of colour-ring sightings (Fig. 2), and in Ireland the grazing pasture is an essential habitat throughout winter. Protection of these habitat complexes of grassland fields in combination with mudflats would therefore appear to be critical in order to maintain the wintering godwit population in Ireland.

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Chapter 3

Selection of grassland fields by foraging black-tailed godwits, *Limosa limosa islandica*

Abstract

1. Protected areas typically encompass rare or threatened habitats that are important for wildlife but they may exclude adjacent, more common, habitats which may be important for mobile populations. In coastal ecosystems, protected areas for waterbirds often only incorporate intertidal areas, with the boundaries coincident with the high water mark. However, waterbirds frequently use adjacent agricultural fields in addition to intertidal habitats, and these supratidal habitats often have no legal protection despite evidence for their importance in supporting populations of wintering birds.
2. Inclusion of agricultural lands within protected area boundaries would require identification of the factors influencing field choice by waterbirds. Grasslands are commonly used as foraging habitats by waders and waterfowl, and Ireland has permanent pasture surrounding many coastal estuarine areas which are important for wintering shorebirds. Ireland supports *c*. 20% of the flyway population of the Icelandic black-tailed godwit and previous studies have shown grasslands to be critical in supporting the godwit population throughout the winter. Identifying the factors influencing the selection and use of grasslands by foraging birds is therefore an important step in developing strategies for protecting these habitats.
3. In 2008, a large-scale survey of 112 pasture fields surrounding eight estuaries in southern Ireland was undertaken during January – March, the period when godwit use of pastures is most frequent. The presence of godwits on each field was recorded along with a suite of structural and landscape characteristics. In addition, monthly surveys of seven frequently used fields were undertaken during which the location of godwit flocks within each field was mapped, allowing comparison of the characteristics of the areas of fields selected and avoided by godwits.

4. Godwits avoided very small fields (< 1 ha) and were much more likely to use fields larger than 5 ha, but no other field structure or landscape features appeared to influence field selection. The selection of foraging patches within fields was restricted by the degree to which visibility was impeded; flocks were more likely to forage in areas further from field boundaries, where the boundary had more gaps and where the overall levels of visibility were higher.
5. The absence of legal protection for most grasslands despite the strong evidence for their importance in supporting waterbirds throughout the winter is an issue of conservation concern. High rates of urban expansion into agricultural landscapes in Ireland mean that identifying the sites in which protection may have the greatest influence on the populations that they support is of key importance. This study suggests that only small, enclosed fields in which visibility is hampered are actively avoided by foraging godwits, and thus that large fields with an open boundary structure are likely to be particularly important to protect.

Introduction

Establishing networks of protected areas in key locations has been a fundamental part of international policies to protect species and habitats in order to conserve biodiversity (Primack 1995, Chape *et al.* 2005, Sinclair and Byrom 2006). In the EU, under the Birds (1979) and the Habitats (1992) Directives, member states are required to protect threatened and vulnerable flora and fauna, migratory species and the habitats on which these populations rely. The development of a network of protected areas is the primary means by which these directives have been implemented, with Special Areas of Conservation (SACs) designated under the Habitats Directive, and Special Protection Areas (SPAs) designated under the Birds Directive, forming the basis of the Natura 2000 network (Donald *et al.* 2007). Member states of the EU have a legal requirement to maintain the species and habitats protected within Natura 2000 sites. However, while protected areas may encompass habitats of particular importance for nature conservation, they often exclude more common habitats which are also used by species for which a site was designated, particularly highly mobile species such as birds.

Recognition of this issue in Ireland has led to consideration of potential mechanisms for including common habitats adjacent to SPAs within the protected area boundaries (J. Fuller, SPA Designations Team Leader, National Parks and Wildlife Service, pers. comm.).

Wetland areas are afforded particular attention for protection of migratory waterbirds under the Birds Directive and the Ramsar Convention on Wetlands of International Importance (www.ramsar.org). Coastal wetlands can comprise a complex mixture of habitats (e.g. mudflats, sandflats, saltmarshes and rocky shores) and many mobile bird communities exploit a range of habitat types (Prater 1981). For most coastal wetlands, the protected area encompasses intertidal habitats and the boundaries are coincident with the high tide mark. However, many waterbirds wintering in coastal areas use a variety of intertidal and supratidal habitats, depending on factors including tidal cycles, prey abundance and the availability of adjacent habitats e.g. (Connors *et al.* 1981, Goss-Custard *et al.* 1996, Van Gils *et al.* 2005). Many supratidal habitats used by shorebirds as foraging and roosting sites are agricultural in nature, and include grazing marshes, pasture and arable fields (Goss-Custard 1969, Fuller and Lloyd 1981, Townshend 1981, Lovvorn and Baldwin 1996, Shuford *et al.* 1998). Understanding the relative importance of the different habitat types used by such species can provide important information about the potential effectiveness of protected areas. The relative importance of supratidal habitats for shorebirds may also vary among individuals. For example, immature Oystercatchers *Haematopus ostralegus* have been reported to forage on grasslands when excluded from foraging on intertidal mussel beds by more dominant adult birds (Goss-Custard and Durell 1983), and Townshend (1981) reported that male curlews *Numenius arquata* with shorter bills were significantly more likely to use pasture fields while large females were more likely to forage on intertidal mudflats, where deeply buried polychaetes were more accessible to larger birds. However, both studies also reported increases in the overall extent of field use by each species during periods of lower temperatures, high tides or intense rainfall, when the profitability of foraging on mudflats is reduced as prey are inaccessible or less active (Townshend 1981, Goss-Custard and Durell 1983).

Patterns of use of non-intertidal habitats by waterbirds have also been shown to be influenced by landscape-scale factors such as distance to roosts or safe refuges (Lovvorn and Baldwin 1996), and the presence of human features in the landscape. For example, several species of goose wintering in agricultural landscapes have been shown to avoid foraging close to roads (Madsen 1985, Sutherland and Crockford 1993, Gill 1996). In addition, the abundance and quality of alternative foraging sites in the locality has been shown to influence the distribution of dunlin *Calidris alpina*, as use of individual wetland patches is influenced by the levels of rainfall and flooding patterns which determine the amount of available foraging habitat (Taft 2006). These studies emphasise the potential importance of considering the distance between roosts, alternative foraging habitats and human features in the surrounding landscape when selecting sites for inclusion in protected areas.

Agricultural habitats are particularly widely used by shorebirds (Goss-Custard 1969, Hutchinson and O'Halloran 1994, Colwell and Dodd 1999, Evans Ogden *et al.* 2005, Lourenco and Piersma 2009), and the physical characteristics of agricultural fields can influence the extent to which they are selected and used by different species. For example, species such as lapwing *Vanellus vanellus* and golden plover *Pluvialis apricaria* frequently forage on coastal grasslands, and many studies describe preferred fields as being large, without enclosed boundaries and with short swards (Milsom *et al.* 1985, Shrubb 1988, Tucker 1992, Gillings 2007a), although sward height preferences are often less apparent in longer-legged species such curlew and black-tailed godwit (Milsom *et al.* 1998). In Ireland, a comparison of the relative profitability of foraging on mudflat and grassland habitats has shown that the grasslands surrounding estuarine complexes are critically important habitats for maintaining the internationally important Icelandic black-tailed godwit population (Chapter 2). However, only a very small number of these fields are currently included within protected areas, and high rates of coastal development mean that many fields are being lost to housing and urban development. Urban land cover increased by *c*. 30% across the whole of Ireland from 1990 to 2000, and the greatest land use change has been conversion of grassland and wetland habitat into urban developments (EPA 2008). Given the primary commercial purpose of agricultural habitats, it is likely that only small areas would potentially be included within protected area boundaries, thus identifying the specific characteristics of fields most likely to be important for shorebirds is essential. This study aims to understand the factors influencing the selection and use of grassland foraging locations by black-tailed godwits at a range of scales by (1) identifying whether godwits display a preference for specific physical characteristics of fields within the landscape; (2) quantifying variation in prey abundance between used and unused fields; (3) exploring variation in the frequency of use of fields in relation to their physical and landscape features and (4) comparing characteristics of used and unused foraging patches within fields.

Methods

Large-scale survey of field use by foraging godwits

The survey encompassed 112 individual pasture fields located across eight estuarine complexes located in County Cork and County Waterford, Ireland (Fig 1). The survey was carried out between January and March 2008 in order to maximize encounter rate with godwits, as previous surveys indicated that the use of grasslands by godwits is highest during these months (Chapter 2). Only fields for which the whole area could be observed from one location were included and surveys were carried out on blocks of one to eight fields, with each coastal complex containing one to seven blocks. Each block was visited once during the survey and observed for 30 minutes, during which the presence of any godwit flocks was recorded. All fields included in the survey were within 3 km of the nearest estuary, as previous studies (Chapter 2) indicate that this is the typical maximum daily distance that godwit flocks will travel from estuarine sites.

For each field, a suite of structural and landscape characteristics were recorded (Table 1A). On the survey visit to each field, the boundary structure was mapped and the state of tide and the number of cars passing on the nearest road during the 30 minute survey was recorded. As all the fields were managed as grazing pasture, sward height within each field was highly uniform, and thus the predominant sward height was estimated visually. Google Earth (2005) images were used to calculate the level of urbanisation in the landscape surrounding a field by overlaying a 1 km^2 grid divided into 100 m^2 cells centred on the middle of each field. A cell containing any urban or human features (buildings, roads, tracks or industry) was categorised as an urban cell and the percentage of urban cells within each grid was used as the level of urbanisation. The same images were used to measure the slope, from the maximum change in elevation across each field, the field area (ha) and the distance to nearest potential roost site (shallow pool or tide edge).

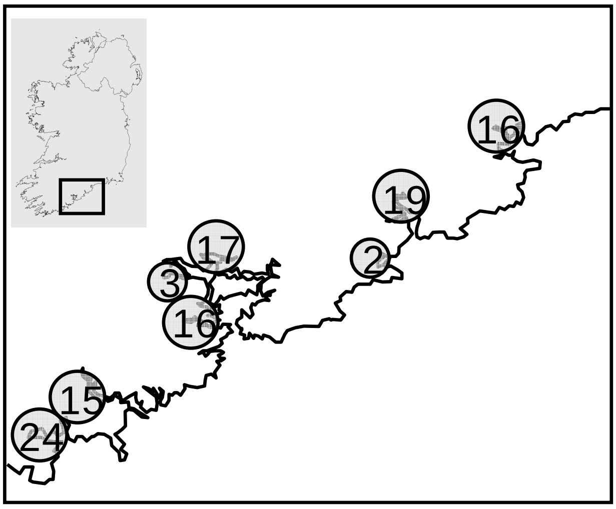

Figure 1. The distribution of the 112 fields included in the survey of field use by black-tailed godwits across eight estuarine complexes in the south of Ireland. Numbers indicate the number of fields in each site; from west to east: Timoleague & Courtmacsherry (24), Garranefeen (15), Cork Harbour - Owenabue & Loughbeg (16), Cork Harbour - Douglas Estuary (3), Cork Harbour North (17), Ballymacoda (2), Youghal (19), Dungarvan (16). Inset indicates the location of the complexes within Ireland.

Table 1. The names, units and descriptions of the variables recorded during the (A) large-scale survey of godwit use of grassland fields and (B) within-field survey of patch choice by godwits, in Co. Cork and Co. Waterford, Ireland. The analyses within which each variable was included (1 = logistic regression analysis of field use, 2 = regression analysis of frequency of field use, 3 = logistic regression analysis of within-field patch use) are also indicated.

Variable	**Unit**	**Analysis**	**Description**
A			
Level of urbanisation	%	1	Percentage of 100 cells in a 1 km^2 centred on each foraging location that contain any human features (buildings, roads, tracks, industry)
Field area	ha	1,2	Area of field
No. boundary segments	No.	1,2	Number of discrete sections of different types of boundary feature (tall (>9 m), medium trees (4-9 m) or short trees (2.5-4 m) trees, tall (> 2.5m), medium (1.3-2.5 m) or short (<1.3 m) walls, tall (1.3-2.5 m) or short (< 1.3 m) hedges, wire fence or nothing
Perimeter height	m	1	Average of the estimated height for each boundary segment
Slope	°	1	Estimated change in elevation from highest to lowest point of each field
Percent of field sloping	%	1	Proportion of field sloping (with an incline greater than 0°) estimated as a percentage of the whole area
Mud visible	Yes/No	1	Mudflats visible or not visible from within each field from godwit height
Nearest roost	m	1	Distance to nearest roost site where godwits alight after a disturbance event
Sward height	cm	1	Predominant sward height within field estimated visually to nearest 5 cm
Tide state	category	1	H = high & L=low tide (defined as two hours either side of published high or low tide times respectively) and R = rising & F = falling (defined as 2 hours before or after high or low tide time respectively)
B			
% visibility	%	2, 3	Average % sky visible recorded at each photo point
Mean number of boundary segments	n	3	Mean number of discrete boundary sections visible in each photo
Distance to edge	m	3	Distance to nearest boundary estimated from each photo point
Distance to mudflat	m	2, 3	Distance to nearest mudflat area estimated from each photo point

Resource characteristics of fields

Between December 2007 and March 2008, variation in prey abundance was explored on eight fields, four of which were regularly used by godwit flocks and four with the same environmental characteristics and location which godwits were never recorded using. On each field, 20 randomly distributed 8 cm diameter cylindrical soil cores were extracted and the contents were hand-sorted in the laboratory within 10 days of collection. Earthworms were the only invertebrates found that could be considered large enough to be potential godwit prey items (Hutchinson and O'Halloran 1994). Prey density was calculated in terms of no. of individual earthworms per m^2.

Frequency of field use and within-field patch selection by godwits

A subset of seven fields known to be used regularly by godwit flocks (Chapter 2) were selected and surveyed monthly (October 2007 – March 2008) in order to establish frequency of use by godwits. Between October and March, each field was visited four times in each of three seasons: autumn (October/November), winter (December/January) and spring (February/March). On each visit, 60 minutes was spent at each field and, if any godwit flocks were present, the locations were mapped. At the end of March 2008, these maps were then used to identify six used and six unused 30 x 30 m patches within each field, each of which was then visited and photographs were taken at five randomly located points (minimum distance between points = 10 m) within each patch. The camera was positioned on a horizontal plane on a tripod set to a height of 30 cm (the approximate height of an alert godwit), and four photographs were taken at each point with the camera being rotated 90 degrees between each photograph. A spirit level attached to the tripod ensured that the tilt of the camera on every plane was zero. The percentage of each photograph that comprised sky was then calculated using GLA imaging software (Frazer *et al.* 1999) and averaged across the four photographs to give a measure of the visibility at each point. Sward height was below the height of the camera in all cases so the visibility within each photograph describes the amount of sky not obscured by either the field boundary or the slope of field (referred to hereafter as % sky visible). An additional estimate of restrictions to godwit visibility at each point was calculated by recording the number of discrete segments in the section of boundary that was visible within each photograph, and averaging these numbers across the four photographs. The distance to the field boundary and the nearest mudflat were estimated in the field (Table 1B) for each photo point.

Statistical analyses

Variation in the characteristics of fields selected by godwits for foraging was explored using data was in the form of a presence/absence survey so a logistic regression analysis was the most appropriate method (Table 1). Block was retained in the model throughout to account for any variation caused by differences at each location. The best model was derived by manually removing the least significant variable in turn until only significant variables remained. To assess variation in prey density across four used and four unused fields, a Mann-Whitney test was used due to inequality of variances across fields. A paired t-test was used to determine whether there was any seasonal change in prey density between visits in winter (Nov/Dec) and spring (Mar/Apr). The factors influencing the percentage of visits on which godwits were present on a subset of seven fields was modelled in a linear regression (Table 1). The same 7 fields were divided into used and unused patched and the factors influencing within-field patch use were modelled using logistic regression (Table 1B).

Results

Field selection by foraging godwits

Godwit flocks were recorded using 20 of the 112 fields included in the large-scale survey. Used fields varied in area from *c*. 1 – 17 ha but godwits were significantly more likely to use larger fields from within this range (Fig. 2). The mean ± SE area of occupied fields was 6.2 ± 4.7 ha compared to the area of unoccupied fields of 3.6 ± 3.7

ha ($F_{1,110} = 7.34$, $p < 0.008$). The great majority of fields in the region are less than 5 ha in area but only 11 of the 82 fields in the survey that were < 5 ha were used, whereas four of the nine fields greater than 10 ha were used by godwits (Fig. 2).

A wide range of field types were occupied, encompassing almost the full range of variables described in Table 1. Godwits used fields up to 1.5 km from roost sites and field selection was not influenced by traffic levels, the extent to which fields sloped or the structure of field boundaries (Fig. 3). There is a slight suggestion that longer swards (> 20 cm) and steeply sloping (> 10°) fields may be avoided (Fig. 3), but these effects were not statistically significant.

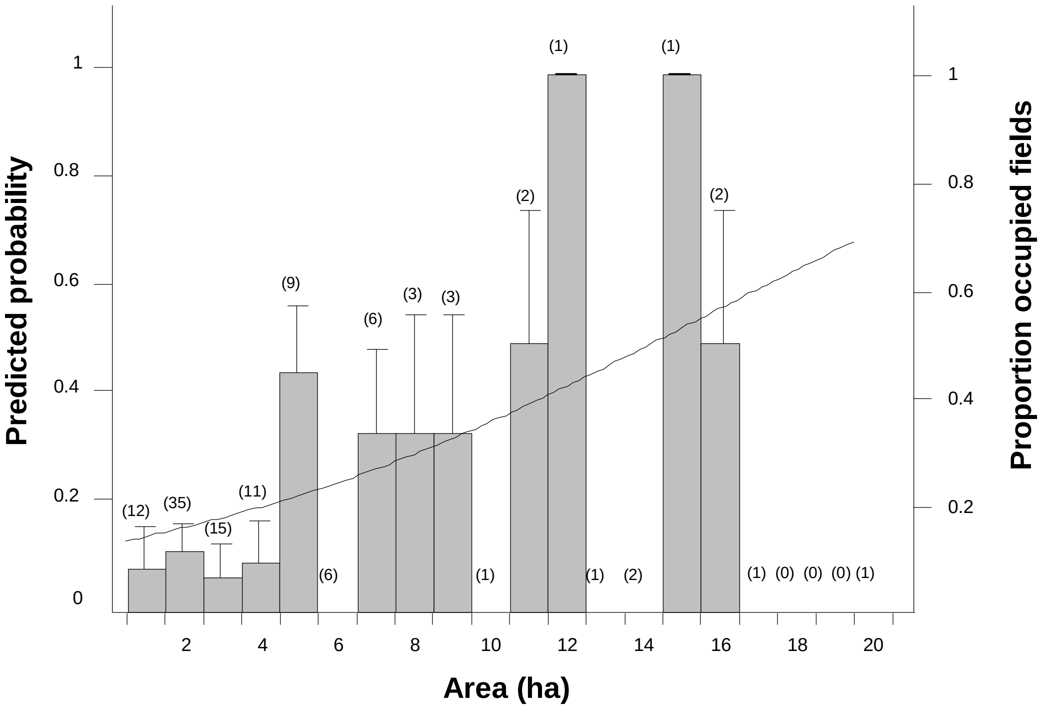

Figure 2. Variation in use of fields by foraging black-tailed godwits in relation to field area (Exp(B) = 1.2, Wald = 8.9, df = 1, p = 0.003). Bars show the mean (± S.E.) proportion of occupied fields of a given area (samples size in parentheses), and the line is the fitted logistic regression curve showing predicted probability of field occupancy.

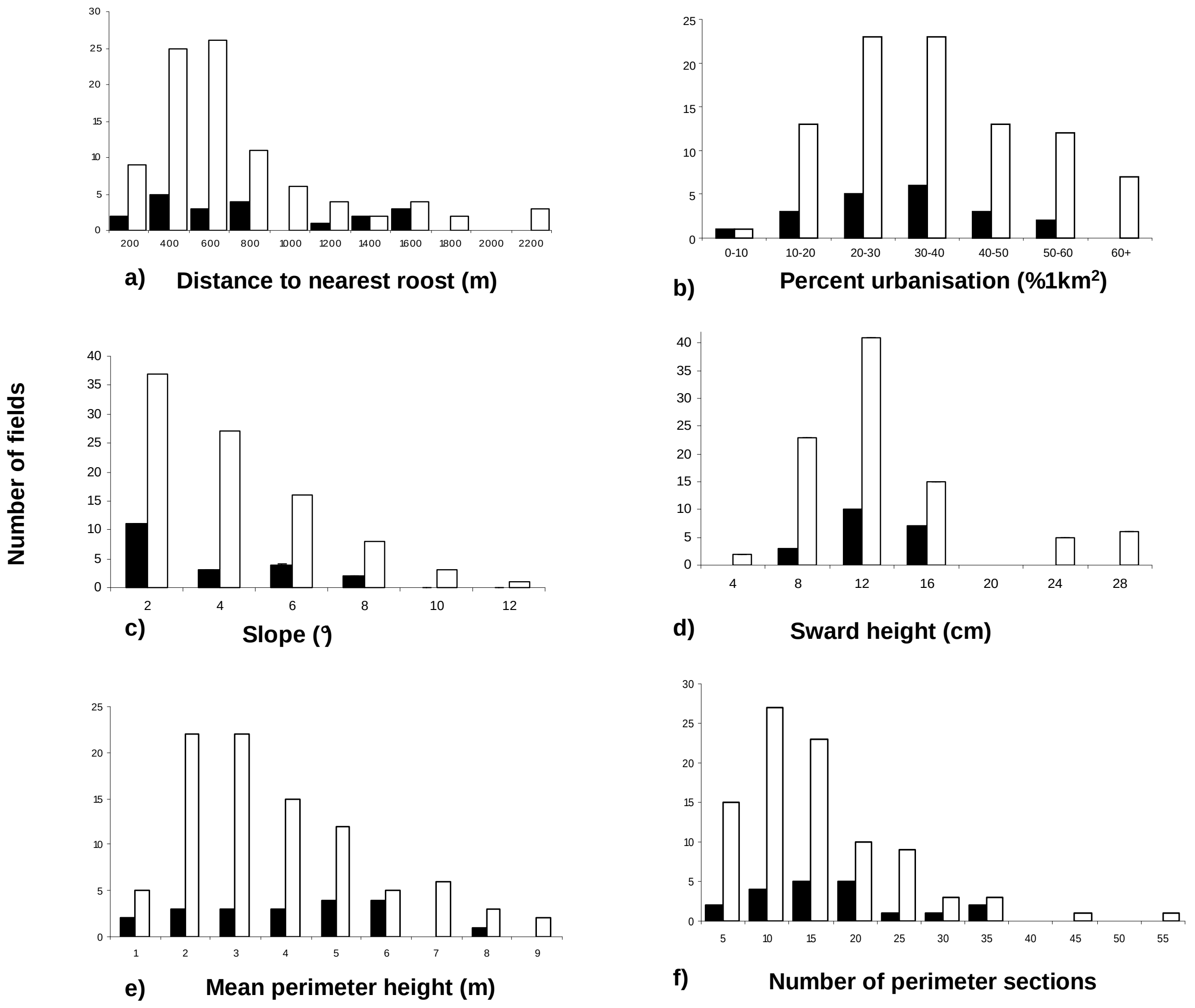

Figure 3. Variation in the location, structure and composition of fields occupied (filled bars) and unoccupied (open bars) by godwit flocks at grassland sites adjacent to estuaries in S Ireland (see Table 1 for details).

Effects of prey abundance on field use

Earthworms were the only potential prey types found in the soil samples, and they comprised 70% of all invertebrates found in soil cores across all eight fields surveyed. All other invertebrates were either smaller than the minimum sizes typically consumed by godwits (Gill *et al.* 2001); Enchytraeidae (22.4%) and earthworm cocoons (6.7%) or were too rare to be of significance in the diet (Diptera larvae = 0.5%). In the winter months (November and December), earthworm densities on used fields were higher than on unused fields but this difference was only of marginal statistical significance (Mann-Whitney: $U_{4,4} = 1.5$, $p = 0.06$); all used fields had earthworm densities of over 300 ind.m^2 compared to the unused fields which had lower densities ranging from 200 to 250 ind.m^2 (Fig. 4). By spring, there was no difference in prey density (Mann-Whitney: $U_{4,4} = 8$, $p = 0.99$) with all but one field containing earthworm densities of around 300 ind.m^2.

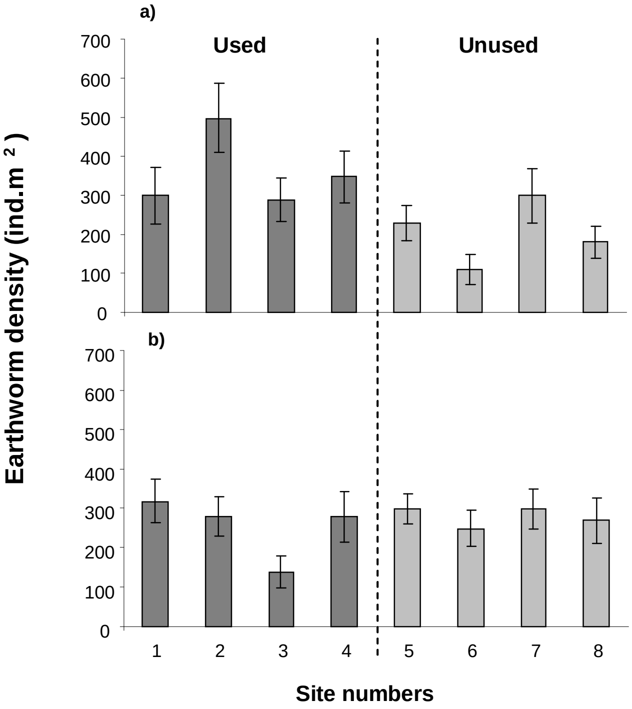

Figure 4. Mean earthworm density on grassland fields between fields that were used (dark bars) and unused (pale bars) by godwit flocks in a) November/December and b) March/April.

Frequency of use of fields by godwits

The seven fields that were regularly used by godwits were occupied on between 17 and 83% of the monthly visits (Table 3). Although the more frequently used fields were slightly closer to the estuary than the less frequently used fields (Table 3), the frequency of field use was not statistically significantly related to field area ($R^2 = 0.43$, $p = 0.65$), mean patch % sky visible ($R^2 = 0.13$, $p = 0.42$) or distance to the estuary ($R^2 = 0.54$, $p = 0.06$)

Within-field foraging patch selection by godwits

Areas of the field that were used by foraging godwits had distinct characteristics in comparison to areas that were never used (Table 4). Godwits selected foraging areas that had higher visibility (Fig. 5a), and that were closer to the mudflat (Fig. 5b). Patches with an enclosed boundary structure were significantly avoided; godwits selected patches in areas with an open boundary structure where more individual boundary segments (and hence more gaps in the boundary) were in view (Fig. 5c). In addition, patches further than 100 m from the field edge were much more likely to be used than those closer to the perimeter (Fig. 5d).

Table 3. Details of the seven fields used regularly by foraging godwits; **A** Frequency of use (% of visits flock present) and whole field characteristics: distance to estuary (m), area (ha) and mean % sky visible. **B** details of within-field variation between used and unused patch characteristics: mean ± SE % sky visible, the number of boundary segments visible, the distance to the estuary and the distance to the boundary from each patch.

Field	**A** **% visits flock present**	**Estuary (m)**	**Area (ha)**	**% sky visible**	**B** **% sky visible**		**No. boundary segments**		**Estuary (m)**		**Boundary (m)**	
					Used	**Unused**	**Used**	**Unused**	**Used**	**Unused**	**Used**	**Unused**
Cork Harbour N Slatty's	0.83	50	10.35	51.62 ± 1.7	59.0 ± 1.5	44.2 ± 2.4	4.5 ± 0.2	4.1 ± 0.2	147.7 ± 8.1	179.5 ± 12.4	66.8 ± 4.9	23.5 ± 1.5
Cork Harbour Owenabue	0.5	34	2.62	36.97 ± 0.78	41.0 ± 0.5	33.0 ± 1.1	5.9 ± 0.1	5.36 ± 0.2	18.4 ± 1.3	38.5 ± 3.3	13.0 ± 1.4	15.7 ± 1.7
Timoleague S	0.5	92	5.87	33.5 ± .67	34.5 ± 0.9	32.5 ± 1.0	5.5 ± 0.2	4.6 ± 0.2	172.0 ± 6.0	182.7 ± 9.2	42.1 ± 7.4	27.7 ± 2.46
Cork Harbour Loughbeg	0.33	196	14.89	57.03 ± 0.56	58.8 ± 0.6	54.9 ± 0.8	4.7 ± 0.3	4.4 ± 0.3	157.2 ± 9.6	177.5 ± 13.3	62.7 ± 8.6	48.2 ± 6.8
Ballymacoda	0.33	97	11.69	39.04 ± 1.4	31.9 ± 0.8	46.1 ± 1.9	2.4 ± 0.2	2.1 ± 0.1	85.0 ± 9.4	152.8 ± 7.5	49.0 ± 3.6	39.9 ± 2.8
Dungarvan	0.17	537	13.15	27.68 ± 0.72	29.3 ± 0.8	26.0 ± 1.1	4.3 ± 0.3	4.6 ± 0.2	192.0 ± 8.7	181.0 ± 9.4	57.1 ± 6.9	21.0 ± 2.2
Timoleague W	0.17	294	5.92	42.53 ± 0.62	42.2 ± 1.0	42.9 ± 0.7	5.3 ± 0.3	4.9 ± 0.2	212.3 ± 17.5	222.2 ± 9.7	24.4 ± 3.1	34.5 ± 17.7

Table 4. Results of a logistic regression model of the effect of visibility and patch location characteristics on the probability of godwits foraging in particular areas within fields (comparison of 210 used and 204 unused points on seven fields).

Variable	**Wald**	**Exp(B)**	**df**	**Sig.**
Mean % sky visible	6.67	1.04	1	0.009
Mean boundary segments	16.82	1.48	1	0.001
Distance to edge	21.728	1.02	1	0.001
Distance to mudflat	32.802	0.99	1	0.001
Site	19.422		6	0.004

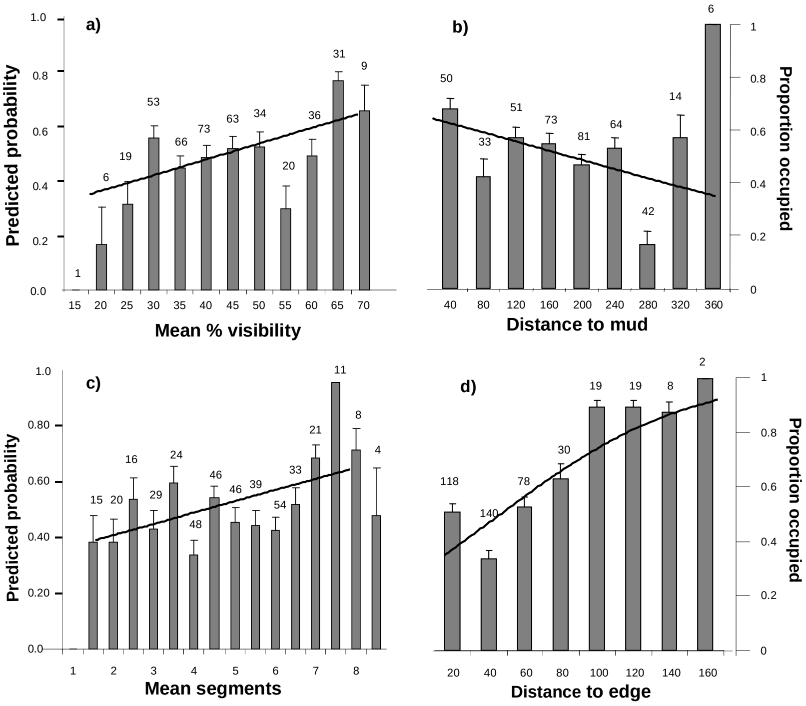

Figure 5. Variation in the use of patches within fields by foraging black-tailed godwits in relation to a) mean % sky visible from patch, b) distance to nearest mudflat, c) mean number of segments in nearest boundary to the patch and d) distance to the nearest field edge. Bars represent the mean (± SE) proportion of patches of each category occupied (sample sizes above each bar). Lines show the fitted predicted probability curves from logistic regression analyses.

Discussion

Godwits do not appear to be highly selective in the types of fields used for foraging, either in terms of the surrounding landscape structure or the characteristics of the fields themselves. Very small fields (< 5 ha) are avoided (Fig. 2) but a wide variety of field types were used in sites with a wide range of levels of surrounding urban development (Figs. 3a & b). Fields up to 1600 m from a safe roost site were occupied, and neither the structure of the field boundary (Fig. 3e & f). Sward heights taller than 20 cm and steeply sloping fields may be slightly more likely to be avoided but neither parameter significantly influenced field choice. Small pasture fields are very abundant around coastal areas of southern Ireland; 83 of the 112 fields surveyed were smaller than 5 ha, and only eleven of these were used. The analysis of godwit selection of foraging patches within fields highlights the likely reason for this preference for larger fields, as the patches that were used had significantly greater visibility, were further from the field boundary and the boundary in view had more gaps (Fig. 5). Thus, maintaining high levels of visibility appears to be an important component of the choice of foraging locations on grassland fields by godwits. Godwits foraging on grassland fields frequently take flight, and their levels of vigilance are higher than when foraging on mudflats (Chapter 2), thus grassland fields appear to be perceived as a risky habitat by godwits. A greater proportion of a large field is further from the boundary therefore avoidance of enclosed areas is likely to be the main reason for the preference for large fields.

Avoidance of small, enclosed fields has also been described in foraging flocks of golden plover and lapwing on agricultural fields (Milsom *et al.* 1998, Gillings 2007b). In addition, factors affecting prey abundance and availability, such as levels of manure application, time since reseeding and levels of rainfall have been shown to influence field use by foraging shorebirds (Tucker 1992, Colwell and Dodd 1999). In this study, earthworm abundance in used and unused fields did not vary either in winter or spring (Fig. 4). The similarity of earthworm densities and sward structures on the fields is likely to be a consequence of the majority of grassland fields in southern Ireland being managed as grazing land with similar types and densities of livestock (Curry *et al.* 2007). In addition, variation in rainfall appears to have little influence on earthworm availability in the south of Ireland (Chapter 2, Fig. 5a).

The agricultural landscape on the south coast of Ireland is rather uniform in terms of field area, the structure of perimeter boundaries and sward heights; this could mean that there are few restrictions on godwit use of fields in the current environment. However, high rates of urban development across Ireland in the last two decades have led to many areas of farmland being developed as residential or industrial areas (EPA 2008). As these commercially farmed grasslands typically receive no protection, despite their importance for maintaining populations of migratory waterbirds in southern Ireland (Chapter 2), identifying suitable areas for protection is of likely to be of importance for conservation. Recent discussions regarding the inclusion of adjacent grasslands within the boundaries of Natura 2000 sites in this region have taken place (J. Fuller, SPA Designations Team Leader, National Parks and Wildlife Service, pers. comm.). Given the wide range of fields used by godwits, the findings presented here can potentially help to form the basis of recommendations for the particular types of fields most likely to be used and to be of greatest value for inclusion within protected areas. Across eight estuarine complexes in southern Ireland, the primary restriction on the use of grassland fields is an avoidance of small, enclosed fields. Thus any large fields (> 5 ha) with open boundary structures and within 1 – 1.5 km of estuaries are likely to be potential candidates for protection. These fields are used by several other waterbird species in addition to black-tailed godwits; during this study large numbers of curlew, oystercatcher, lapwing and wigeon *Anas penelope* were recorded foraging on the same fields as the godwits. On a few occasions several smaller wader species were also seen foraging on these fields, including redshank *Tringa totanus*, knot and dunlin. Agricultural fields are therefore likely to be important in supporting a wide range of the waterbird species wintering in Ireland, and protection of fields adjacent to the estuarine habitats from urban development may be critical in maintaining these populations, which is a legal requirement of signatories to the EC Birds Directive.

The most heavily populated areas in Ireland are in the coastal zone and the levels of urbanisation around the major estuaries and wetlands that godwits rely on throughout the winter vary greatly. Habitat selection and the distribution of godwit flocks does not appear to be influenced by the level of urbanisation in the surrounding landscape; godwits use fields in urban-dominated sites as well as rural areas. It is possible, however, that godwit behaviour within these fields could be altered by high levels of urbanisation in the surrounding area thereby influencing the capacity of the birds to exploit the available resources, which might influence the relative effectiveness of protecting fields in rural or urban areas. Thus, an assessment of the consequences of landscape urbanisation for the behaviour of foraging godwits would help to confirm the findings reported here, and to identify the grasslands sites of greatest importance for black-tailed godwits in southern Ireland.

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Chapter 4

Effects of urbanisation on foraging and vigilance behaviour in wintering black-tailed godwits

Abstract:

1. Urban development and human population growth are resulting in increasingly human-dominated landscapes in many areas of the world. Landscape urbanisation may influence species distribution, through direct habitat loss and avoidance of areas with high levels of human activity. However, many species continue to use urbanised landscapes. Human presence may have little impact on the distribution of such species but their capacity to use the available resources may be altered if human presence influences their behaviour.
2. In Ireland, since the 1990s there have been high rates of urban development, particularly in coastal areas. As Ireland’s estuaries support internationally important numbers of many species of wintering waterbirds, the rapid increase in coastal development could influence the capacity of sites to support these populations.
3. Ireland supports about 20% of the Icelandic black-tailed godwit flyway population in winter. Throughout the winter, black-tailed godwits in Ireland forage primarily on soft muddy estuaries but also on commercially farmed grassland habitats. Across the south coast of Ireland, the landscape around some estuarine-grassland complexes is now quite highly developed while other, more rural, sites are comparatively undeveloped. Black-tailed godwits use mudflats and grasslands throughout this gradient of urbanisation but the presence of humans in the landscape could influence their capacity to use the resources in these sites if their behaviour varies in relation to levels of urbanisation. This study therefore investigates the behaviour of Icelandic black-tailed godwit on ten estuarine complexes in southern Ireland, in order to explore whether key components of the foraging behaviour of the birds vary in relation to levels of urbanisation, and whether these effects vary between mudflat and grassland habitats.

4. The ten complexes varied greatly in levels of urbanisation, with human development of the surrounding landscape ranging from 0 – 78% and the frequency of observed disturbance events of godwit flocks ranging from 0 – 15 per hour. However, there were no clear differences in godwit foraging or vigilance behaviour in relation to levels of urbanisation on either habitat across the ten complexes. However, clear differences in foraging and vigilance behaviour are apparent between the two habitats, with vigilance levels and frequency of disturbance flights on grasslands being consistently higher than on mudflats across all complexes.
5. Levels of urbanisation vary greatly across these sites but most components of godwit foraging behaviour vary between but not within habitats, suggesting that godwits perceive risks to be higher on grasslands than mudflats irrespective of levels of urbanisation. The rate of urban development in southern Ireland has been very high in recent years and many grassland sites have been converted to urban or industrial uses. As godwit behaviour on grasslands does not vary with levels of urbanisation, protecting grassland foraging habitats is likely to be equally important in urban and rural areas, and maintaining the availability of the habitats would appear to be a far more important strategy than limiting the effects of disturbance on existing sites.

Introduction

As human populations grow over most of the world, the areas of co-occurrence of humans and wildlife are increasingly of conservation concern (Marzluff et al. 2001, McKinney 2002). Urban areas are expanding rapidly in developed countries; there has been particular growth of low density housing on the outskirts of cities (Theobald 2001, Grimm et al. 2008). The resulting urban sprawl leads to an increase in the area of the interface between urban and rural habitats (Alberti and Waddell 2000, 2003). Where wildlife does persist in the natural or modified habitats that remain in the human dominated landscape, their distribution and behaviour may be affected by human presence and activities. From a site conservation perspective it is important to establish whether changes in distribution impact adversely on wildlife using that area (Gill 2007, McKinney *et al.* 2009).

Over a range of spatial scales, studies have described how the distribution of species of a range of taxa has been impacted by different levels of human activity. For example, songbirds (Blair 1996) and lizards (Germaine and Wakeling 2001) have shifted species composition in relation to levels of urbanisation when studied on a landscape scale covering 28 km^2 and 1158 km^2 respectively. Human presence and activity may impact animal distribution within an area; restricting human access to an area of foreshore resulted in a 50% increase in the number of bar-tailed godwits *Limosa lapponica* feeding there (Furness 1973). Similarly, areas with high levels of human activity may be used less frequently than expected; for example several species of goose in agricultural landscapes have been shown to avoid foraging close to roads (Madsen 1985, Sutherland and Crockford 1993, Gill 1996). This avoidance of areas with high levels of human activity can constrain the capacity of a species to use the available resources, for example, pink-footed geese, *Anser brachyrhynchus*, avoid areas of fields close to roads, which significantly reduces the number of bird-days that are supported on these fields (Gill 1996).

Although avoidance of disturbed areas does not necessarily mean that individual fitness or population processes are influenced by human presence (Gill et al. 2001, Beale and Monaghan 2004), behavioural responses to disturbance can be a tool to indicate whether a species' ability to use a site has been affected (Sutherland 1996, Gill 2007). Disturbance could reduce a species' ability to find food by reducing foraging efficiency thereby effectively reducing habitat quality; this could operate through increased vigilance levels or time lost to foraging engaged in disturbance flights. A comparison of a populations' foraging behaviour, foraging success and levels of vigilance between undisturbed habitats and habitats with high human presence will allow the response to be quantified (Caro 1999). Studies across a gradient of levels of disturbance can inform policy makers decisions as to which sites are most valuable to protect and can aid the design of buffer zones to ensure that sites can be effectively used by target species (Fox and Madsen 1997, Yasué 2006).

Recent rapid economic growth and development in the Republic of Ireland, in part as a consequence of the funds available through EU membership (OECD 2000), has resulted in increasing levels of urbanisation in some areas. Over 60% of Ireland’s population lives on the coast and consequently rates of urban and sub-urbanisation in the coastal zone have been particularly intense in the last 20 years; the greatest land use change in Ireland has been conversion of grassland and wetland habitat into urban sites (EPA 2008). Many estuaries now have adjacent housing and industrial developments, while others are still surrounded by the traditional pastoral rural landscape, which comprises more than half of the land area of Ireland (EPA 2008). Ireland is particularly important for migratory waterbirds due to abundance of wetland habitat and mild climate, and several shorebird species take advantage of the mixture of estuarine and freshwater habitats that make up many coastal complexes (Crowe 2005). However, freshwater habitats are particularly threatened by habitat loss due to urbanisation, but there is no legal protection for the conservation value of these habitats, as their primary purpose is commercial grazing.

Ireland supports about 20% of the flyway population of Icelandic black-tailed godwits (calculated from Gunnarsson et al. (2005) and Crowe et al (2008)). In Ireland, the main foraging habitats used by godwits are mudflats and grasslands, and insufficient food resources on the mudflats means that the grasslands are essential in maintaining the wintering godwit population (Chapter 2). Godwits use mudflats and grasslands in urban and rural areas, and they therefore experience varying degrees of urbanisation and levels of human activity in the local landscape. This chapter investigates variation in the behaviour of black-tailed godwits foraging on mudflats and grassland sites across ten estuarine complexes in southern Ireland, which range from urban sites adjacent to a large city with high levels of human activity to rural sites with low levels of human presence and activity. Specifically we (i) quantify the variation in levels of urbanisation across grasslands and mudflats used by godwits, and (ii) assess the extent to which levels of urbanisation affects the levels of disturbance and godwit foraging and vigilance behaviour both within and between the two habitats.

Methods

Habitat characteristics of black-tailed godwit foraging locations

Locations were selected to represent the gradient of rural- to urban-dominated landscapes used by black-tailed godwits on ten estuarine and grassland complexes on the south coast of Ireland (Fig 1). Within these complexes, regularly used mudflat (n = 29, mean ± SE area = 16.3 ± 3.7 ha) and grassland (n = 20, area = 6.8 ± 1.7 ha) foraging locations were identified and a range of local landscape characteristics and indicators of human presence were collated using Google Earth^{TM} 2005 (Table 1). On grasslands, the boundaries for each location were defined by field boundaries while on mudflats boundaries were defined by the low tide mark, coastline and boundary features such as large water channels and jetties. The landscape surrounding these foraging locations typically comprises mudflats and grasslands (all of which are potentially available foraging habitats for godwits) and urban developments (roads, footpaths, and buildings including farms, housing developments and factories). The proximity of each location to roads and footpaths was measured from the centre of each location (Table 2), and the percentage of the perimeter of each location that was immediately adjacent to mudflat or grass fields was used as a measure of the availability of adjacent alternative foraging habitat (Table 1). The level of local urbanisation was estimated by overlaying a 1 km^2 grid sectioned into ten 100 x 100 m cells onto each location, centred on the central point of each location, using Google Earth^{TM} 2005. All cells containing any building, road, track, jetty, car park or playground were classified as urban cells and the percentage of urban number of vehicles passing on the nearest paved road during a 30 minute survey was recorded.

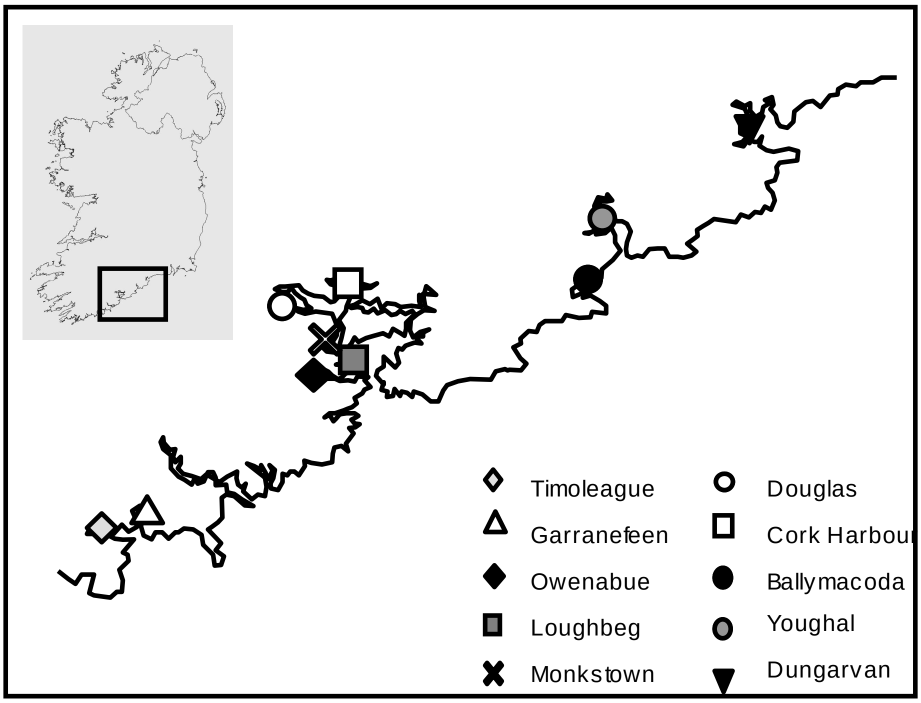

Figure 1. Location of the ten estuarine complexes (County Cork and County Waterford) included in this study. Symbols for each site correspond to symbols used in other figures. Inset shows the location of the study area within southern Ireland.

Table 1. Name, unit of measurement and description of the components of landscape structure recorded on the 29 mudflat and 20 grassland locations, and the components of foraging behaviour recorded during observations of black-tailed godwit flocks on these locations.

Variables	Unit	Description
Landscape structure		
Urban land cover	%	Percentage of the surrounding hundred 100 x 100 m cells centred on each foraging location containing any human features
Adjacent habitat	%	Percentage of the cells adjacent to the perimeter of each field or mudflat that contain mudflat or grass fields
Distance to nearest footpath	m	Distance from the centre of each foraging location to the nearest footpath
Distance to nearest road	m	Distance from the centre of each foraging location to the nearest road
Vehicles per minute	n.min^{-1}	No. of cars on nearest road during 30 minute survey
Mudflat area	ha	Area of each mudflat used by foraging godwit flock
Components of behaviour		
Disturbance flight rate	.hour^{-1}	No. of occasions on which each flock took flight during each observation period at each foraging location
Vigilance frequency	%	Percentage of individual foraging observations in which one or more vigilance scans were recorded
Vigilance intensity	%	Percentage of individual foraging time spent vigilant
Prey intake	n.sec^{-1}	No. prey items consumed per second by foraging godwits at each location
Peck rate	n.sec^{-1}	No. of pecks per second by foraging godwits at each location
Step rate	n.sec^{-1}	No. of steps per second by foraging godwits at each location
Intake rate	mg AFDW.sec^{-}	Biomass of prey consumed per second by foraging godwits at each location

Table 2. The number and structure of mudflat and grassland foraging locations in each estuarine complex (see Table 1 for definitions of each structural component).

Estuarine complex	Mud/ Grass	No.	Mean (± SE) site area (ha)	Mean (± SE) urban land cover (%)	Mean (± SE) adjacent habitat (% boundary)	Mean (± SE) distance nearest road (km)	Mean (± SE) distance nearest path (km)
Timoleague	mud	3	19.08 ± 16.46	30.0 ± 8.74	53.33 ± 12.02	0.10 ± 0.02	0.24 ± 0.11
	grass	4	5.8 ± 1.54	26.75 ± 3.33	58.75 ± 11.79	0.16 ± 0.05	0.31 ± 0.1
Garranefeen	mud	2	3.92 ± 1.52	46.5 ± 3.5	5 ± 5	0.11 ± 0.01	0.13 ± 0.03
	grass	1	1	38.0	75	0.05	0.31
Owenabue	mud	3	13.81 ± 8.50	55.33 ± 18.81	30 ± 16.07	0.17 ± 0.05	0.33 ± 0.18
	grass	1	1.66	17.0	80.0	0.44	0.44
Loughbeg	mud	1	8.27 ± 2.27	38.5 ± 0.5	52.5 ± 12.5	0.35 ± 0.07	0.49 ± 0.2
	grass	2	17.86 ± 3.0	29.0 ± 1.0	55.0 ± 5.0	0.24 ± 0.005	0.41 ± 0.18
Monkstown	mud	2	5.68 ± 0.56	39 ± 5	15 ± 0	0.16 ± 0.08	0.32 ± 0.08
	grass	0					
Douglas	mud	3	27.19 ± 15.69	40.67 ± 13.37	56.67 ±21.86	0.17 ± 0.04	0.17 ± 0.06
	grass	1	5.07	52.0	0	0.04	0.08
Cork Harbour	mud	5	7.38 ± 2.12	41 ± 9.94	52 ± 11.14	0.10 ± 0.02	0.28 ± 0.12
	grass	3	5.46 ± 2.60	49.0 ± 10.58	40.0 ± 11.55	0.11 ± 0.06	1.0 ± 0.57
Ballymacoda	mud	1	25.08	0	100	0.6	0.31
	grass	3	8.49 ± 1.70	24.67 ± 8.25	80.0 ± 11.55	0.44 ± 0.12	1.55 ± 0.37
Youghal	mud	3	14.22 ± 1.98	23.33 ± 6.96	71.67 ± 23.51	0.43 ± 0.06	2.51 ± 0.89
	grass	2	4.1 ± 2.6	15 ± 15	95.0 ± 5.0	0.18 ± 0.07	2.74 ± 1.88
Dungarvan	mud	5	41.26 ± 18.48	27.6 ± 12.48	74 ± 11.66	0.48 ± 0.18	0.81 ± 0.39
	grass	3	10.89 ± 3.56	44.0 ± 5.57	20.0 ± 11.55	0.13 ± 0.015	1.6 ± 0.76

Foraging behaviour

Foraging godwit flocks consisting of a minimum of 20 birds (flock size range: 25 - 435) were observed for between 10 and 121minutes (depending on the length of time that flocks stayed within a site). The mean number of disturbance flights per hour was calculated for each observation period (disturbance flights were defined as occasions when over 80% of the flock simultaneously took flight). Focal sampling was used to record the foraging behaviour of individual godwits within flocks. Instantaneous prey intake rates were measured by observing randomly located individuals for the time taken to make ten paces, during which the number of successful and unsuccessful pecks was also recorded. In addition, the time each individual spent being vigilant (head and bill above the level of the body) or in aggressive interactions was also recorded, and subtracted from the total observation time in order to calculate time spent actively foraging. A minimum of 25 individual intake rates (range = 28 - 80) were recorded within each flock and averaged to give a mean intake rate per foraging flock. These data allow direct calculation of peck rate (pecks per second of foraging time) as a measure of foraging effort, and step rate (steps per second of foraging time) as a measure of effort expended in foraging. All variables recorded during these surveys are detailed in Table 1. The prey type (bivalve or polychaete (on mudflats) or earthworm (on grassland)) was recorded and prey size taken was estimated in the field as small, medium, large, or very large. The number of each prey size consumed by each focal bird was multiplied by the estimated ash-free dry mass (g) of the median of each prey size category and summed and averaged across all focal individuals to give a mean biomass intake rate (mg.AFDM.sec^{-1}) for each flock (see Chapter 2, Table 2 for prey sizes and biomass calculations).

Data analyses

Variation in levels of urbanisation across the 29 mudflat and 20 grassland locations were quantified by incorporating the components of landscape structure (Table 1) within two separate PCA analyses for mudflat and grassland locations (Table 3). The resulting PCA scores were then used as predictors in general linear models with different components of godwit foraging and vigilance behaviour of godwits on mudflat and grasslands separately. In all models, estuary complex was included as a random factor and retained regardless of statistical significance, in order to account for variation resulting from differences between complexes. Variation in godwit foraging behaviour between habitats was explored within general linear models in which habitat type (mudflat or grassland) was included as a fixed factor and estuary complex was included as a random factor.

Results

Levels of urbanisation on coastal habitats used by foraging black-tailed godwits

Across the ten estuarine complexes, the amount of urban land cover surrounding both mudflat and grassland foraging locations varies from 0 – 78%, the amount of adjacent foraging habitat varies from 0 – 100% and, while some locations have roads and footpaths adjacent to them, others are hundreds of meters to kilometres from such features (Table 2). Mudflat foraging locations tended to be larger than grass fields and slightly, though not significantly, further from footpaths (Fig. 2, Table 2), as many estuaries have adjacent amenity walks. However, mudflats and grassland foraging locations were otherwise similar with both habitats having a similar range of surrounding urban land cover, surrounding potential godwit foraging habitat and distances to the nearest road (Fig. 2, Table 2).

To explore variation in levels of urbanisation between foraging locations, the landscape factors (Table 2) were incorporated into separate principal component analyses for grasslands and mudflats. These analyses each produced a component explaining 49.5% and 54.1% of the variation in among locations for grasslands and mudflats respectively (Table 3). Each component was then used as an urbanisation gradient which was plotted against each habitat characteristic that was included in PCA analysis for each foraging location (Fig 3). The urbanisation gradient described by the PCA factor scores followed the same pattern for both habitat types, with low values indicating higher levels of local urban land cover, lower amounts of adjacent foraging habitat and closer proximity to footpaths and roads (Fig. 3). On grasslands, traffic levels were included in the PCA because of the fields' close proximity to roads, and low factor scores indicated higher traffic levels (Fig. 3). Traffic intensity was not included in the mudflat PCA because it correlated poorly with other landscape variables and resulted in creating a separate component where traffic intensity explained most of the variation. Patch area was included as smaller locations tended to be at the head of the estuary and therefore likely to be in more urban areas (Fig. 3). Field area was excluded from the grass PCA as it did not improve the amount of variation that was explained by the resulting component.

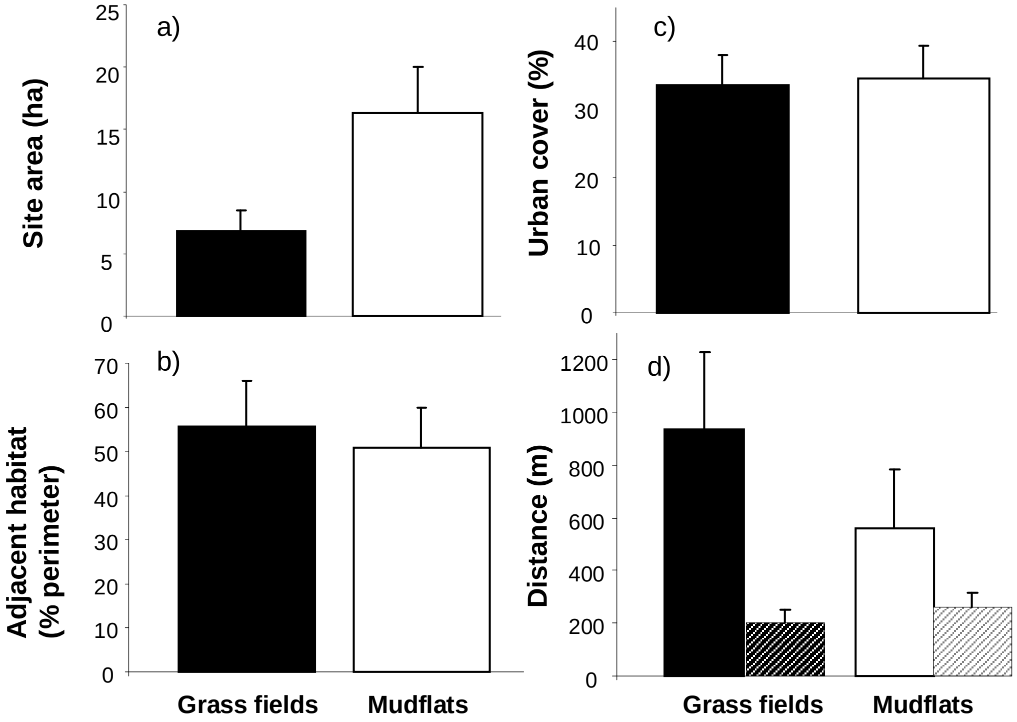

Figure 2. Variation in the mean (±SE) (a) area (t = 1.82, df = 47, p = 0.08), (b) percent of the adjacent land suitable for godwit foraging (t = 0.18, df = 47, p = 0.86), (c) percent cover of urban features in the surrounding 1 km^2 (t = 0.84, df = 47, p = 0.41) and (d) distance to the nearest footpath (solid bar, t = 1.67, df = 47, p = 0.10) and road (hatched bar, t = 0.63, df =47, p = 0.53) of grassland field (filled bars) and mudflat (open bars) foraging sites.

Table 3. Correlation coefficients and proportion of variance explained in principal components analyses of landscape features on 20 grassland and 29 mudflat foraging locations used by flocks of black-tailed godwits in southern Ireland. See Table 1 for definition of variables.

Principal components analysis	Coefficients
Grassland variables	
Urban land cover (%)	-0.879
Adjacent habitat (%)	0.883
Distance to nearest road	0.665
Distance to nearest footpath	0.411
Vehicles per minute	-0.558
% of variance	49.46
Mudflat variables	
Urban land cover (%)	-0.729
Adjacent habitat (%)	0.795
Distance to nearest road (km log)	0.844
Distance to nearest footpath (km log)	0.761
Mudflat area (ha)	0.500
% of variance	54.12

Behavioural responses of black-tailed godwits to different levels of urbanisation

Vigilance and disturbance levels

Across all ten coastal complexes godwit flocks foraging on grass fields displayed a significantly higher frequency of vigilance behaviour (c. 18% of observations) and spend significantly more time being vigilant (c. 4%) than those foraging on mudflats (Fig 4a,b). In addition, the number of disturbance events, when the flock is forced to take flight, is nearly three times higher on grasslands than on mudflats (Fig. 4c). Although levels of urbanisation vary greatly between grassland locations, godwit vigilance behaviour and levels of disturbance were not related to levels of urbanisation (Fig4b,c).

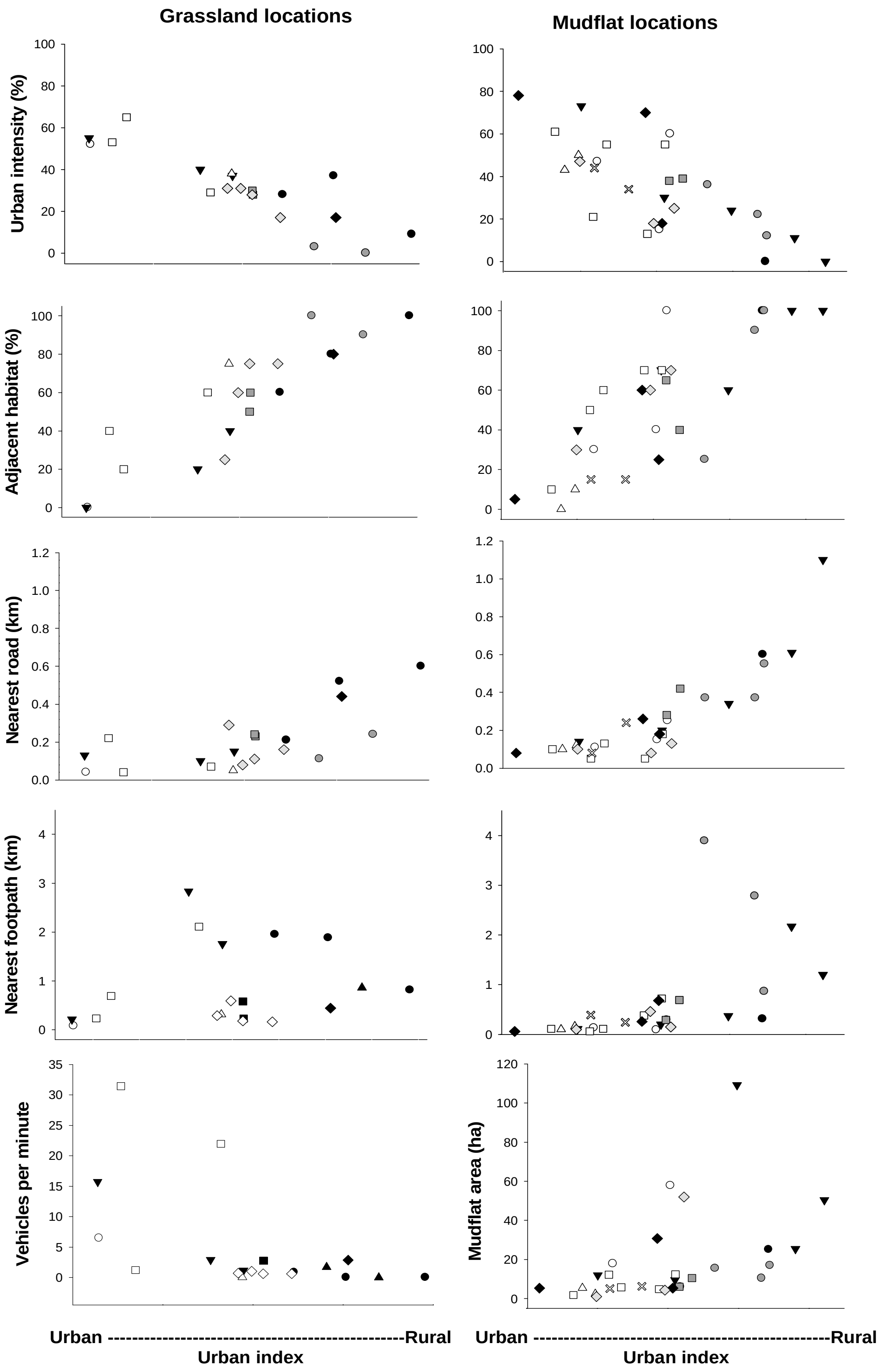

Figure 3. The correlations between the factor scores from PCA analyses describing an urbanisation gradient for grasslands (left column) and mudflats (right column) on ten estuarine complexes, and the five habitat characteristics included within each PCA analyses. Symbols represent different complexes (see Fig. 1) and Table 1 gives definitions of the habitat structure components.

On mudflats, on most locations fewer than 5% of observations of foraging godwits included any vigilance events, and there was no trend for increasing vigilance rates with urbanisation (Fig 4a). Similarly, godwits foraging on mudflats spend only about 1% of foraging time being vigilant, and this also does not vary with levels of urbanisation (Fig 4b). The frequency of disturbance flights on mudflats is also unrelated to levels of urbanisation (Fig 4c).

Components of foraging behaviour

Different components of godwit foraging behaviour vary depending on whether godwits are foraging on grasslands or mudflats, but there is little evidence of changes in any of these components in relation to levels of urbanisation on either habitat (Fig. 5). Peck rates on mudflats decline slightly as levels of urbanisation increase, but this is only marginally statistically significant (Table 2). Thus, while foraging effort appears to be higher for godwit flocks on grass fields, with step rates and peck rates being 26% and 47% higher on grasslands than mudflats respectively (Table 4), these behavioural differences are consistent across the range of levels of urbanisation. Despite prey consumption rates (in terms of numbers of prey consumed per second) on grass fields being lower than on mudflats (Table 4), instantaneous biomass intake rates on grasslands are consistently around 0.4 mg AFDM.sec^{-1}, while on mudflats they vary between 0.1 and 0.7 mg AFDM.sec^{-1}. However, in neither case is there any variation in intake rate in relation to levels of urbanisation (Fig. 5d).

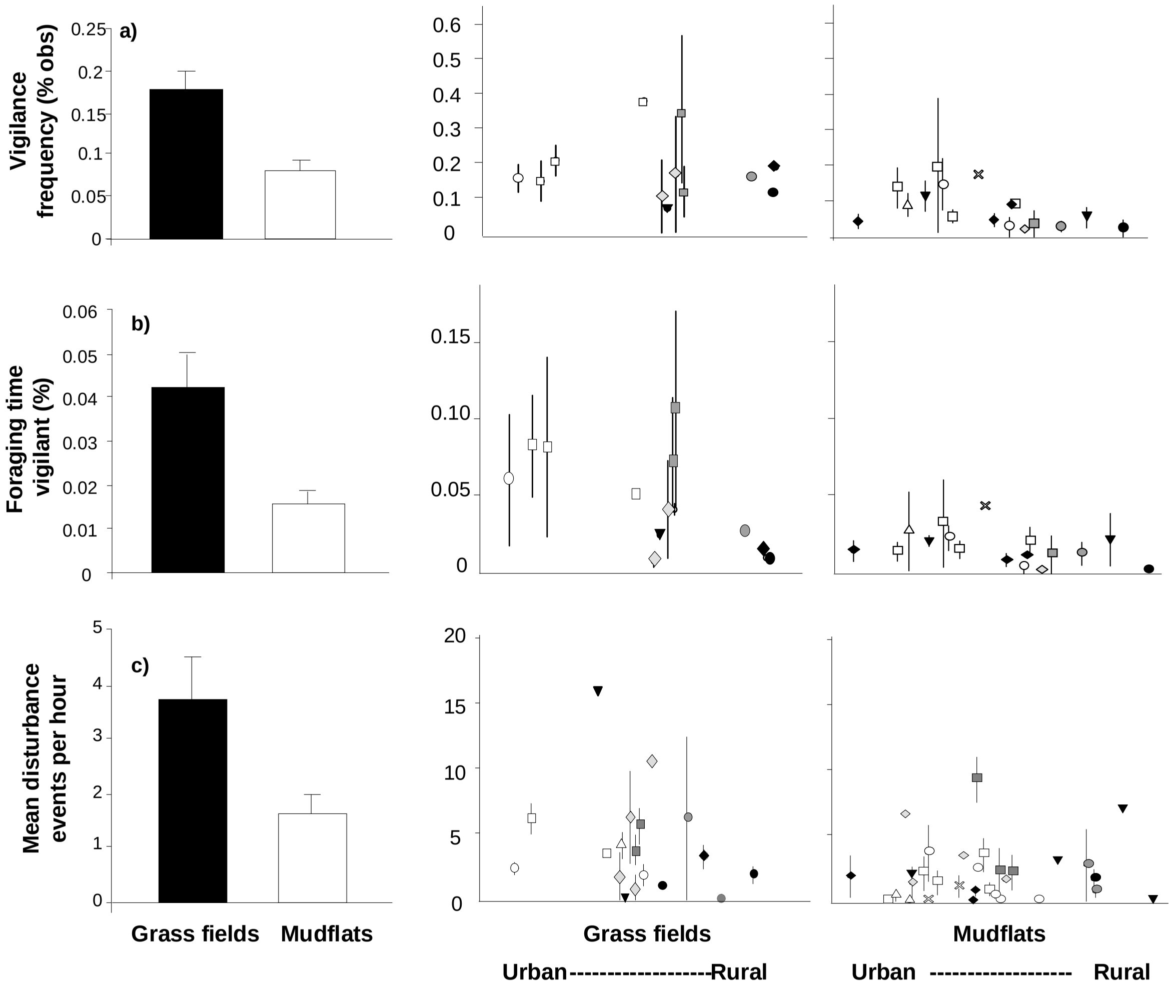

Figure 4. Variation in the mean (± SE) (a) frequency of vigilance events, (b) time spent vigilant and (c) rate of disturbance of foraging black-tailed godwits on grassland fields and mudflats across ten estuarine complexes, and in relation to the PCA urbanisation index on individuals grassland fields and mudflats within the ten complexes Symbols represent different complexes (see Fig. 1), Table 1 gives definitions of the behavioural components and see Table 4 for statistical analyses.

Table 4. Results of general linear models of the differences in components of foraging behaviour of black-tailed godwits (see Table 1 for definitions) on grassland fields (g) and mudflats (m) within ten estuarine complexes, and regression analyses of the relationships between each component and an urbanisation index within grasslands and mudflats. Significant relationships are highlighted in bold.

		Comparison between habitats				Relationships with urbanisation index			
Dependent variables		Mean±SE	F	DF	p	intercept	slope	R^2	p
Disturbance flight rate	g	4.09±0.54	23.58[a]	1,170	< **0.001**	3.13	-1.28	0.075	0.059
	m	1.48±0.28				1.03	-0.24	0.004	0.578
Vigilance frequency	g	0.17±0.03	4.14	1,65	**0.046**	0.177	0.007	0.001	0.874
	m	0.08±0.01				0.091	-0.030	0.105	0.067
Time spent vigilant	g	0.05±0.01	7.73	1,65	**0.007**	0.054	-0.011	0.038	0.430
	m	0.02±0.002				0.015	-0.004	0.034	0.236
Step rate	g	1.94±0.1	18.99	1,65	< **0.001**	1.690	0.151	0.151	0.248
	m	1.31±0.04				1.355	0.070	0.032	0.239
Peck rate	g	0.68±0.03	6.14	1,65	**0.016**	0.776	-0.011	0.048	0.819
	m	0.56±0.03				0.622	-0.079	0.166	**0.043**
Prey intake	g	0.04±0.002	33.39	1,65	< **0.001**	0.030	0.003	0.196	0.364
	m	0.08±0.005				0.066	-0.010	0.078	0.098
Intake rate	g	0.42±0.03	12.77	1,65	**0.001**	0.288	0.013	0.139	0.721
	m	0.24±0.03				0.139	-0.035	0.122	0.277

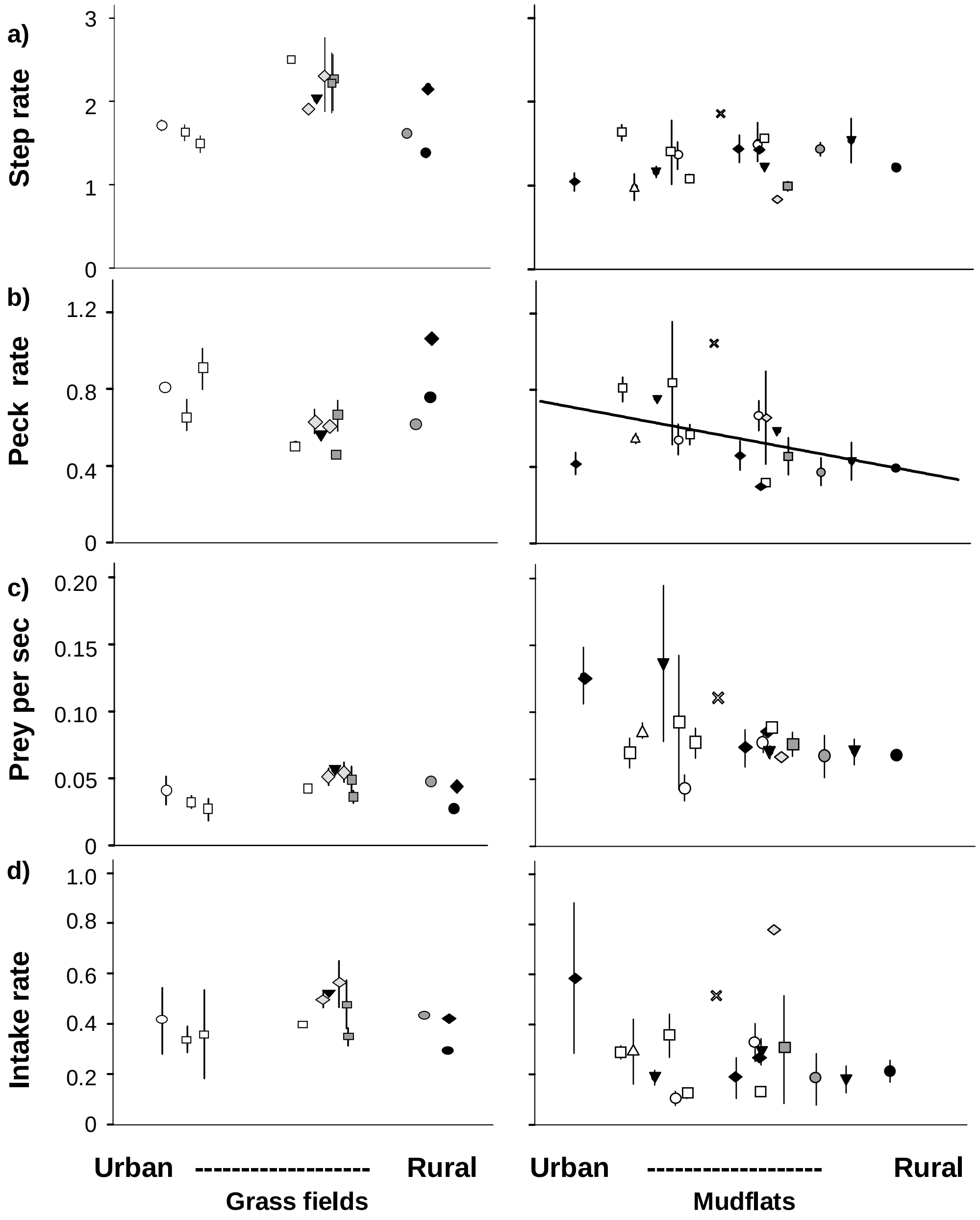

Figure 5. Variation in the mean (± SE) (a) step rate, (b) peck rate, (c) prey intake rate and (d) biomass intake rate of foraging black-tailed godwits on grassland fields and mudflats across ten estuarine complexes, and in relation to the urbanization gradient on individual grassland fields and mudflats within the complexes. Symbols represent different complexes (see Fig. 1). Definitions of the behavioural components are given in Table 1 and see Table 4 for statistical analyses.

Discussion

The coastal mudflats and grasslands of the south coast of Ireland provide important foraging locations for a wide range of shorebirds and wildfowl (Crowe 2005). This area comprises areas of intense urban development around cities and towns and highly rural areas with small villages and farming communities. Much of the literature focussing on disturbance and predation risk has considered the degree to which habitats are avoided or abandoned as a result of perceived risk (Lima and Dill 1990). Such non-lethal effects are described detail in redshank, *Tringa totanus*, shown to avoid highly profitable foraging habitat except in times of high starvation risk due to high predation risk from sparrowhawks, *Accipiter nisus*, in these areas (Yasue *et al.* 2003). The scale at which these non-lethal effects operate is predicted to be larger in heterogenous fragmented habitats such as European farmland dissected by hedgerows (Cresswell 2010). The level of human presence and activity can have similar implications for the perception of 'risk' of a habitat as predation and can also impact on population distribution. If however, as had been shown in southern Ireland that godwit foraging distribution does not appear to be impacted by the level of human presence (as quantified by urban intensities surrounding a foraging location, Chap 3); then comparing behaviour across a range of sites with varying levels of 'disturbance' can illuminate whether non-lethal affects can operate more subtly. Using detailed analysis of habitat components to create a gradient of urban intensity this chapter show that despite the high levels of urbanisation surrounding some of these sites (<78%) do not appear to influence key components of vigilance and foraging behaviour of godwits, showing that their capacity to exploit the available resources is not adversely affected. At high levels of urban intensity, godwits on grassland fields exhibited no changes in foraging behaviour in terms of energetic intake rate or foraging effort in comparison to fields in predominantly 'low risk' rural areas. Feeding rate can also be reduced when vigilance behaviour is elevated in high-risk environments (Lima and Dill 1990).There was no significant difference in levels of vigilance behaviour across the urban gradient either; however variance in the percentage of time spent vigilant during foraging bouts appeared to be greater in more urban environments. This study may suggest that godwits display a level of habituation to human presence because in the most urban sites vigilance frequency and disturbance rates were as low as on the mudflats whereas in the sites in the middle of the urban gradient, where unexpected human activities might occur, vigilance behaviour appears to be elevated.

Disturbance levels are highest on grassland fields, in comparison to mudflats, indicating that godwits perceived this to be a more risky habitat, especially as they seem to avoid using very small enclosed fields where it is presumably more difficult to see approaching predators or humans (Chapter 3). A high frequency of disturbance flights can increase energy expenditure and therefore increase the energetic consumption required for survival (Bélanger and Bédard 1990), but there was no evidence for increased foraging intensity on fields with higher levels human presence and urbanisation (Fig 5). Frequent disturbance flights have been suggested to reduce fitness in some systems; for example, oystercatchers foraging on cockle beds in France were disturbed up to 1.7 times per hour (Goss-Custard et al. 2006), which the authors suggest is likely to increase mortality in years with poor environmental conditions. However, flight responses to human presence do not necessarily indicate significant costs as individuals may be more likely to take flight when the costs of moving are low and/or alternative locations are available (Gill et al. 2001).

Within Ireland, the grasslands used by foraging godwits are typically managed as commercial grazing pasture, with very few recognised for their conservation value by any legal protection. Ireland still has a greater area of grassland pasture than any other northern European country (OECD 2000). Land use changes over the last two decades have resulted in the largest conversion of land area being from pasture and wetland to urban (housing services and recreation) and other artificial surfaces (industry and commercial sites, mines, quarries and waste disposal, and transport infrastructure) (EPA 2008). Land claim of intertidal areas has also resulted in the loss of mudflat habitats in many major estuaries (Crowe 2005). This study indicates that, despite the fact that levels of urbanisation vary greatly across all mudflat and grassland sites, godwit foraging behaviour and vigilance behaviour does not seem to vary with increasing human presence and activity. However, both the frequency of disturbance incidents and godwit vigilance levels are higher on grass than mudflats, even in the most rural areas. As godwit behaviour on grasslands does not vary with levels of urbanisation, protecting grassland foraging habitats is likely to be equally important in urban and rural areas, and maintaining the availability of the habitats would appear to be a far more important strategy than limiting the effects of disturbance on existing sites. If urbanisation of coastal zones continues in Ireland, providing protection for grasslands to maintain their availability to foraging shorebirds in the face of continued development is likely to be very important (Chapter 2). Small and enclosed fields are not extensively used by godwits (Chapter 3) but beyond that there appear to be few constraints on field preferences. As grasslands are important foraging areas throughout the coastal areas of southern Ireland, and as the field choices and behaviour of godwits on these fields does not appear to vary with level of urbanisation, inclusion of some fields within as many intertidal SPAs as possible even in the most urban dominated sites is likely to be of great value in maintaining the large numbers of wintering godwits in Ireland.

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Chapter 5

Changing use of an inland wetland by an expanding shorebird population

Abstract

1. The availability of habitats of varying quality can be a key driver of population size and distribution. In expanding populations, exploring patterns of habitat use can help to illuminate the relative importance of different habitats and their role in driving population change and patterns of distribution.
2. The Icelandic population of black-tailed godwits has been increasing in number, particularly in the last three decades. During the non-breeding season, godwits forage on mudflats and grasslands, with the extent of use of grasslands varying greatly between winter sites. Numbers of godwits wintering in the east of England have increased particularly rapidly since the 1970s and, while these godwits used to be restricted to mudflat habitats, in recent years increasing numbers have been reported on two inland areas of grassland in E England, the Ouse and Nene Washes. This changing pattern of habitat use and distribution may result from (a) improved foraging conditions on the grasslands, (b) resource constraints on mudflats requiring the use of additional habitats, (c) increased awareness of grassland foraging opportunities or d) changing patterns of migratory behaviour if the birds using these grasslands are from other winter sites.
3. The availability of inland grasslands to godwits is typically determined by water levels, as godwits forage in soft sediments and roost in areas of shallow floods. Here, long-term monitoring of godwit numbers on these sites and records of water level data on the Ouse Washes are used to explore the relationship between environmental conditions and numbers of godwits over the last three decades. In addition, colour-marking of individual godwits is used to explore changes in the proportions of godwits arriving on the grasslands from different winter locations throughout the range.
4. Icelandic black-tailed godwits have been recorded on the Ouse and Nene Washes since the early 1990s, when flocks of a few hundred individuals were present in

March and April. Since then, numbers have steadily increased to flocks of over 3000. In addition, godwits have been arriving on the sites progressively earlier in the winter, with first flocks now appearing between November and January. Although water levels fluctuate on the Ouse Washes, suitable conditions for godwits appear to have been available in virtually all winters, and there is no clear correlation between numbers of godwits and water levels over the period of the population increase.

5. Between 60 and 85% of the individually marked godwits recorded on the Ouse and Nene Washes between 1997 and 2009 came from winter locations on the east coast of England, but godwits from Ireland, France, Portugal, Spain and elsewhere in England also use these sites in spring. However, the increasing use of grasslands earlier in the winter is primarily a consequence of birds from the E England coast moving inland earlier each year, while timing of arrival of birds from more distant winter locations, particularly France and Iberia, does not appear to have changed.
6. The rapid increase in numbers of godwits using the Ouse and Nene Washes in late winter and early spring in recent years does not appear to be related to changing water levels at this time of year. The earlier arrival of godwits from local winter sites in recent years is therefore likely to indicate more rapid depletion of resources on mudflats by the increasing population size and/or increased awareness of foraging opportunities on these grasslands.

Introduction

When populations expand in size and range, identifying the causes and consequences of those changes can be complex. Increases in population size can result in density-dependent constraints on resource use and consequently expansion into new sites (Sutherland 1996, Newton 1998). For example, during a period of increase of the grey plover (*Pluvialis squatorola)* population wintering in Britain, Moser (1988) showed that estuaries were filled sequentially, suggesting that density-dependent processes constrained occupied estuaries from supporting further increases. Expansion into poorer quality habitats has been reported in a number of studies, for example, breeding ospreys, *Pandion haliaetus*, (Lõhmus 2001) and Spanish imperial eagles, *Aquila adalberti*, (Ferrer and Donazar 1996) have been shown to expand into habitats where breeding success is lower, and wintering cormorants, *Phalacrocorax carbo*, have expanded into progressively poorer quality water bodies in Switzerland (Suter 1995). If there are fitness consequences of occupying poorer quality habitats then this can result in a buffer effect (Brown 1969), which can ultimately be a mechanism for population regulation (Panek 1997, Gill *et al.* 2001a, Soutullo *et al.* 2006). However, expansion into new sites can also be as a result of changing environmental conditions. For example, increased use of new sites or habitats could occur if conditions in those sites improve as a result of increased food abundance (Sutherland 1996), discovery of novel food sources (Gill *et al.* 1997) or reduced disturbance on a site (Madsen 1998). In contrast to buffer effects, expansion into sites or habitats in which environmental conditions have improved could facilitate population growth, if these sites provide fitness benefits (Yeh and Price 2004, Urban *et al.* 2007).

The Icelandic population of black-tailed godwits has been increasing in number and range for over a century (Gill *et al.* 2007). The winter range of this population extends from Britain and Ireland to Iberia, and the population wintering in Britain increased four-fold between 1970 and 1999 (Gill *et al.* 2001a). This population increase has not been uniform throughout Britain; the estuaries of the south coast of England have supported large and stable numbers of black-tailed godwits since the 1970s but the estuaries on the east coast of England were first occupied by godwits during the 1970s, and numbers on these sites increased very rapidly through the next two decades (Gill *et al.* 2001a). Comparison of conditions on east and south coast estuaries indicated that this pattern of expansion followed a buffer effect, as both prey intake rates and adult survival rates were significantly lower on the recently occupied east coast estuaries than on the traditionally occupied south coast estuaries (Gill et al. 2001a). As godwits from the east of England sites also arrive later on the breeding grounds (Gill et al. 2001b), and as later arrivals tend to have lower breeding success (Gunnarsson *et al.* 2005b), the population expansion into the east coast of England was likely to result in a decline in *per capita* survival and breeding success, which could ultimately limit population size and growth (Gill *et al.*

2001a, Gunnarsson *et al.* 2005b, Gunnarsson *et al.* 2005c). Since 1999, high rates of population growth have continued on east coast estuaries; comparison of WeBS counts in the 1990s and 2000s have shown that numbers have more than doubled in the last decade on the Wash, Breydon Water & Berney Marshes in Norfolk and on the Alde and Orwell estuaries in Suffolk (Musgrove *et al.* 2001, Austin *et al.* 2008).

Godwits are known to use a mixture of estuarine and freshwater foraging habitats across the non-breeding range (Chapter 2, Figure 1). During the 1990s on the east coast of England, godwits foraged almost exclusively on mudflats, and rapid depletion of the invertebrate prey resources on these mudflats resulted in very low prey intake rates by the end of the winter (Gill *et al.* 2001b), which was likely to be the cause of the low survival rates among these birds at this time (Gill et al. 2001a). Recent comparisons of the energetic trade-offs associated with different godwit wintering locations confirms that the intake rates achieved by godwits in east England at this time were not likely to be sufficient to meet their energetic demands (Alves 2009). Use of grassland by godwits in the east of England was very rare during the 1990s but, since 2001, increasing use of grasslands has been reported, and grassland use in this region is now quite common (Austin *et al.* 2008). In comparison to Ireland, where godwits can make use of the abundant grass fields surrounding many estuaries, godwits in the east of England have to travel some distance inland to the flooded grasslands on which they now forage. The main grassland sites now used by godwits in the east of England are the Ouse and Nene Washes in Cambridgeshire.

This changing pattern of habitat use by the expanding population of black-tailed godwits wintering in the east of England may have resulted from resource constraints on the mudflats requiring additional, even poorer quality, habitats to be used. However, if increased use of grasslands is as a result of improved foraging conditions on these sites or increased awareness of good foraging opportunities on the grasslands, then the shift inland may have reduced the fitness inequality between birds in the traditional and recently occupied winter sites. Alternatively, the increasing use of these grasslands may be a consequence of godwits from elsewhere in the winter range using them as stop-over sites, in which case the shift inland would have no influence on the godwits wintering on the east coast estuaries. In order to explore these different options, long-term survey data on numbers of godwits, locations of individually colour-marked godwits and water levels on grasslands were used to explore; (i) whether numbers of godwits on the Washes have changed in recent years, (ii) the timing of use of the Washes by godwits, (iii) environmental conditions on the Ouse Washes and (iv) the winter site origins of godwits using the Washes.

Methods

Study Sites

The Ouse Washes and Nene Washes in the fenlands of Norfolk and Cambridgeshire (Fig 1) are extensive areas of seasonally flooded wet grassland habitat (2469 ha and 1517 ha respectively). Originally constructed in the 17th Century as flood storage areas to protect the surrounding farmland from riverine flooding, both sites comprise linear areas of unimproved grassland between retaining river banks. In times of flooding, and when peak flow coincides with high spring tides, river water is diverted through sluices into the channels that run within the Washes, which then fill and overflow to flood the washlands. The Ouse and Nene Washes lie in different river catchment areas, so flooding of each site is independent beyond the influences of regional rainfall and tide levels (Ratcliffe *et al.* 2005). Both Washes are designated as Ramsar sites and a large proportion of each site comprises nature reserves, which are primarily managed by NGOs, including the Royal Society for the Protection of Birds, the Wildfowl and Wetlands Trust and Cambridgeshire Wildlife Trust, primarily to benefit breeding waders and wintering wildfowl.

Sources of data

Large-scale waterbird censuses

Since 1969, the number of waterbirds on many British wetlands has been counted monthly by volunteers, as part of the BTO Wetland Birds Survey (WeBS) (Austin *et al.* 2008). Co-ordinated counts are conducted once per month, primarily from September to March. The Ouse and Nene Washes have been counted from 1970 to the present, but no Icelandic godwits were recorded on the site until the winter of 1991/92, and not in significant numbers (> 50) until the winter of 1993/94. The numbers of black-tailed godwits recorded on each site during the WeBS counts were used to examine changes in extent and timing of use of these sites during the months November - April inclusive (as no godwits have been recorded earlier than November in any year). Data were available for all years from 1991/92 to 2005/06. Peak annual numbers on each site were used to explore long-term trends in numbers of godwits using these wetlands. To assess changes in the timing of use of the Washes by godwits, average bi-monthly (November and December, January and February, March and April) peak counts were calculated for the Ouse and Nene Washes combined.

Water levels on the Ouse Washes

Use of inland grasslands by black-tailed godwits typically does not occur until rainfall has been sufficient to create areas of shallow flooding around which the birds can forage and roost (Chapter 2). On the Ouse Washes, water levels have been recorded daily by RSPB staff on the Delph River Channel since 1970 (J. Reeves, RSPB site manager pers. comm.). Mean monthly water levels (± SD) were calculated from these data in order to explore whether godwit numbers were related to water levels. To explore whether timing of flooding or mean monthly water levels have changed during the period of increasing godwit numbers on the Ouse Wash, the time series was divided into 3 periods (1991/92 to 1996/97, 1997/98 to 2002/03 and 2002/03 to 2008/09), univariate analysis of variance was used; mean monthly water level as the dependent variable and time period and month as fixed factors with a month x time period interaction to see if flooding patterns had changed seasonally over time. RSPB reserve staff have also mapped the relationship between the water depths in the Delph and the extent of flooding on the grasslands; below water depths of 0.9 m there are no floods present on the grassland and thus the site is likely to be too dry for foraging godwits. Consequently, the percentage of days in which water levels exceeded 0.9 m in (a) November and December, (b) January and February and (c) March and April of each year was calculated as a measure of variation in availability of suitable conditions for godwits on the Ouse Washes. In addition, at water depths above 1.7 m, flooding is continuous between the retaining banks and the whole site is under water (J. Reeves, pers. comm.). Although it is likely that some foraging areas are still available in the shallower parts of the Ouse Washes at these water levels, the percentage of days in which water levels were between 0.9 and 1.7 m in each bi-monthly period of each year was also calculated as a measure of the likely minimum availability of suitable foraging conditions for godwits. Pearson correlation analyses were used to assess the relationship between the peak number of black-tailed godwits recorded on the Ouse washes and the percentage of days suitable foraging habitat was likely to be available.

Winter origins of colour-ringed black-tailed godwits recorded on the Ouse and Nene Washes

Icelandic black-tailed godwits have been caught and ringed during autumn migration on the east coast of England since 1995 (Gill *et al.* 2001a), and on the Icelandic breeding grounds since 1999 (Gunnarsson *et al.* 2005a, 2006). Colour-ringing of these populations has taken place over several years, so the number of colour-ringed godwits estimated to be alive in each winter was calculated from the annual totals (between 16 and 284 colour-ringed each year between 1995 and 2007) and published estimates of the survival rates during the first year of life (50%) and annual survival rates for adults (93%) (Gill *et al.* 2001a, 2007). With the help of several hundred volunteer observers, non-breeding godwit flocks throughout the range are regularly scanned for colour-ringed individuals, which has allowed the winter locations and migratory routes of more than half of these birds to be identified (Gunnarsson *et al.* 2004). Regular visits by colour-ring observers to the sites along the Ouse and Nene Washes that support black-tailed godwits have resulted in 294 different individuals being recorded between 1997 and 2009, and the winter location of 186 of these individuals is known. The proportion of colour-ringed birds from eachmajor wintering location was calculated in order to assess whether winter origins of individuals has changed as numbers have increased on the Washes.

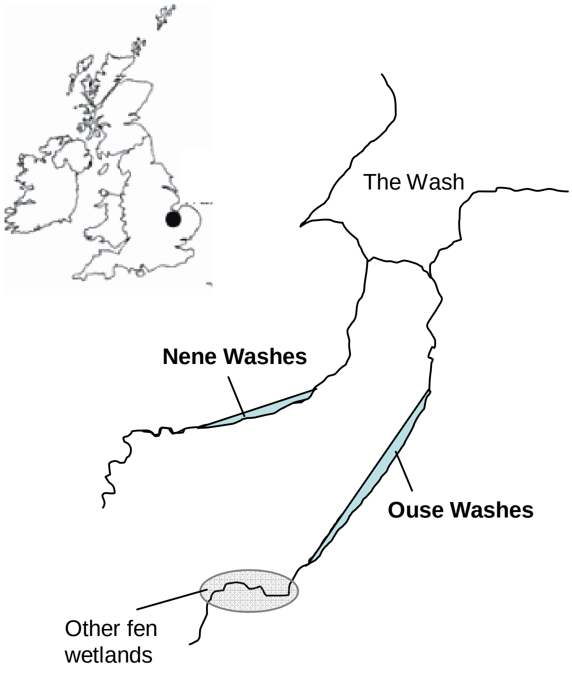

Figure 1. Location of Ouse and Nene Washes and the major rivers flowing through them and out to the sea at the Wash. Additional fen wetlands detailed upstream of the Ouse Washes are also used by godwits.

Results

Recent changes in numbers of black-tailed godwits on the Washes

No Icelandic black-tailed godwits were recorded on either the Ouse or Nene Washes before the winter of 1991/92. Since these first records of godwits on the Washes, numbers have increased dramatically (Fig. 2a), particularly on the Ouse Washes. In the early 1990s, only a few hundred godwits were ever recorded on the Ouse Washes, by the late 1990s, peak counts exceeded 1500 and, since 2002/03, peak counts in excess of 3000 have been recorded in most years (Fig. 2a). Use of the Nene Washes has also increased but less markedly; peak counts of around 500-1000 been recorded in several winters since 1993/94.

Timing of use of the Washes by black-tailed godwits

Increasingly large numbers of godwits have been recorded on the Ouse and Nene Washes earlier in the winter (Fig. 2b). Peak counts calculated over bi-monthly periods each year indicate that, in the early 1990s, the vast majority of godwits counted on the Washes were only present in March/April, with only a few hundred birds being recorded in January/February during these years. However, in the late 1990s, many more godwits were recorded on the Washes during January/February and, during the 2000s, the earliest arrivals of godwits occurred during November/December (Fig. 2b). Despite this trend for godwits to move inland earlier in the winter, the use of the Washes in early spring has also increased over time, thus both the numbers of birds and the length of time for which the Washes are used have increased dramatically over the last two decades.

Extent and timing of flooding on the Ouse Washes

Water levels on the Ouse Washes fluctuate greatly throughout the year (Fig. 3). The Ouse Washes begins to flood when water levels exceed 0.9 m, and this level is typically exceeded from October until April or May (Fig. 3). Thus, during the period when

Icelandic godwits use on the Washes (November – April), water levels are typically sufficient to create areas of flooding, and there is no indication that the timing of flooding has varied through the period of increasing godwit numbers or timing of use of the Washes (Fig 3). There is some indication that water levels between November and April have been higher in the more recent two time periods (Fig 3), but there is no significant difference in mean monthly water levels between all three time periods 1991/92 to 1996/97, 1997/98 to 2002/03 and 2002/03 to 2008/09 ($F_{2,130} = 1.34$, $p = 0.27$) (Fig. 3).

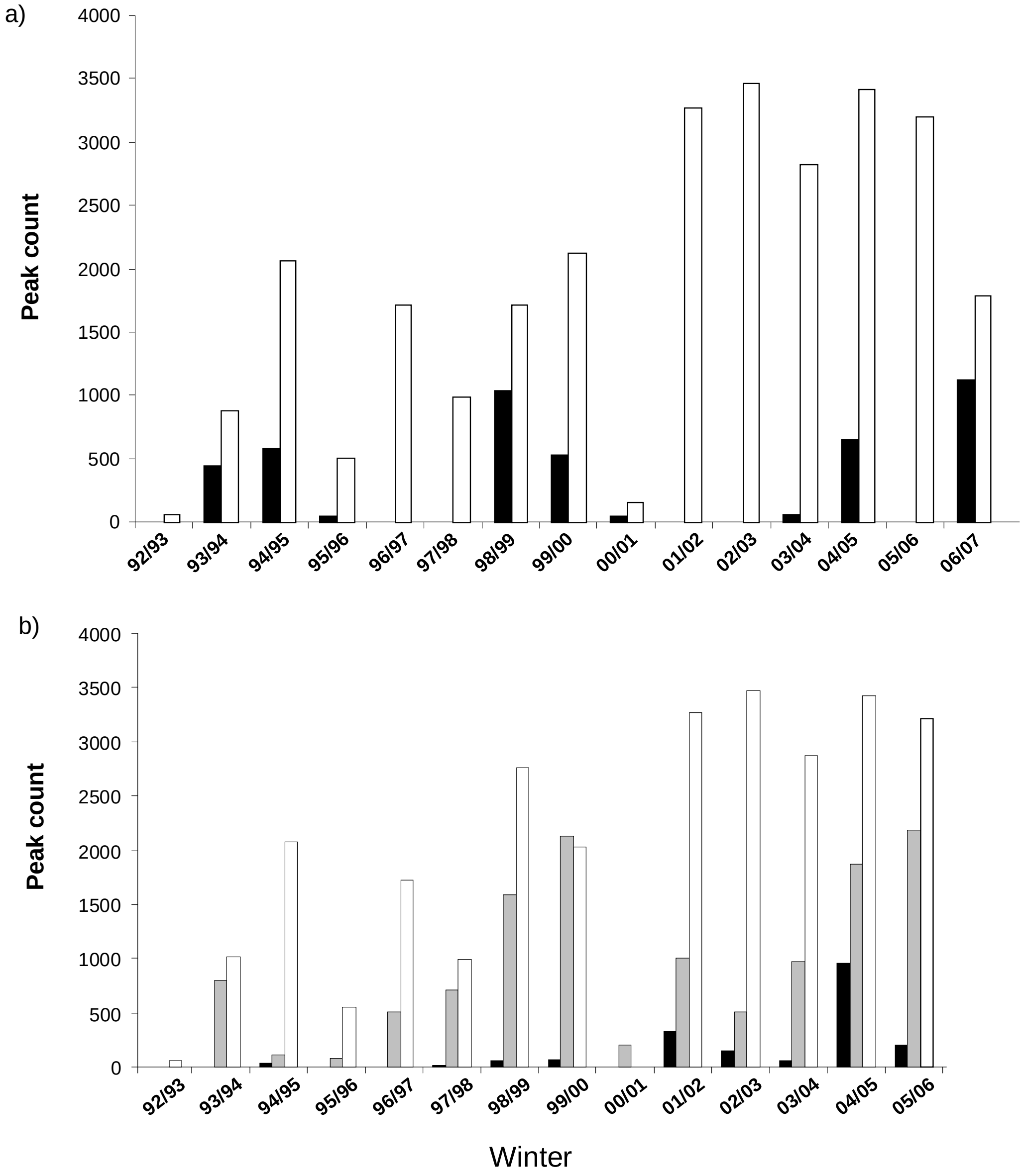

Figure 2. Annual variation in the peak number of black-tailed godwits recorded during Wetland Bird Surveys on (a) the Ouse (open bars) and Nene (filled bars) Washes between November and April and (b) both Washes combined during November and December (black bars), January and February (grey bars) and March and April (open bars) in each winter.

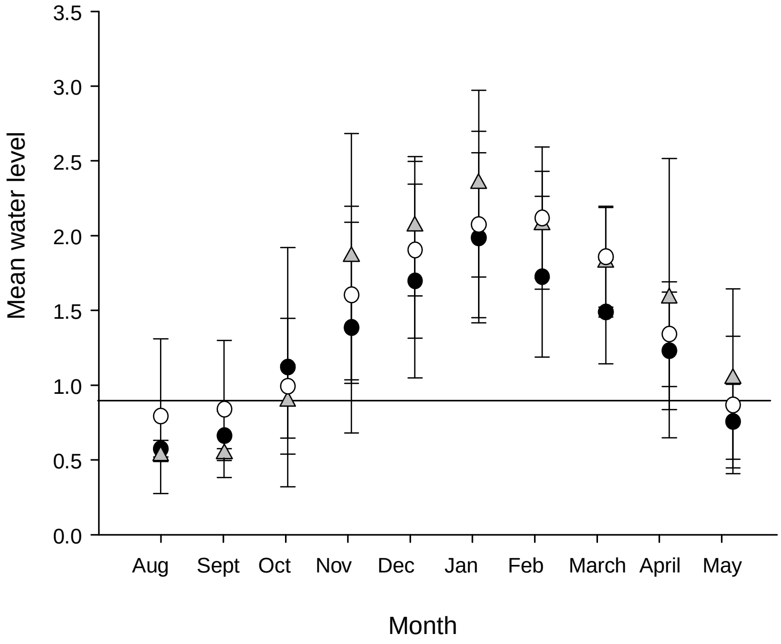

Fig 3 Variation in monthly mean (± SD) water levels recorded on the Delph River of the Ouse Washes throughout the non-breeding season for the years 1991/92 to 1996/97 (black circles), 1997/98 to 2002/03 (grey triangles) and 2002/03 to 2008/09 (white circles). The horizontal line indicates the 0.9 m level where the Ouse Washes starts to flood.

The length of time for which flooding is present on the Ouse Washes also shows no evidence of having changed over the last two decades. Since 1992/93, water levels have exceeded 0.9 m on 40 – 100% of days in November and December, 95 - 100% of days in January and February and 40 - 100% of days in March and April (Fig 4). However, high levels of rainfall can result in extensive flooding that is likely to restrict the availability of suitable foraging sites for godwits on the Ouse Washes. When water levels exceed 1.7 m on the Delph River, the Ouse Washes floods extensively between the two retaining banks and the majority of the site is under water. The percentage of days on which water levels were between 0.9 and 1.7 m in each bi-monthly period was therefore also calculated (Fig. 4). Even when the percentage of days is restricted in this manner, suitable foraging conditions would have been available to the godwits on *c*. 30 – 50% of days in all winters since the 1990s (Fig 4).

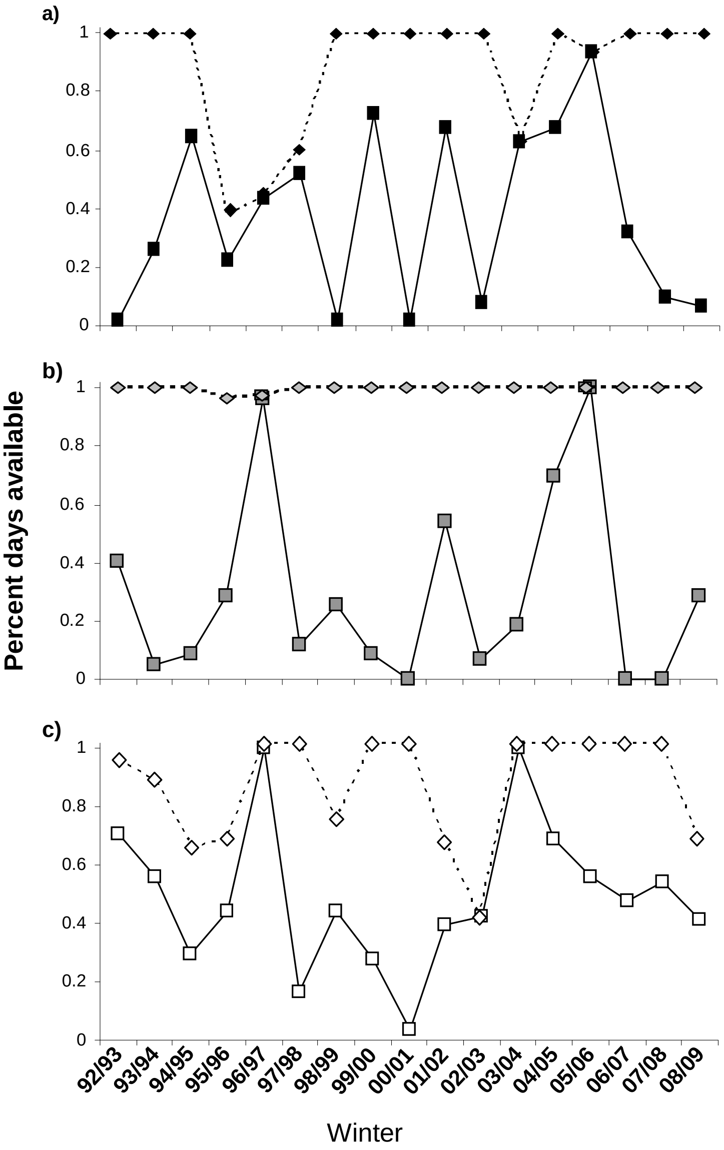

Figure 4. Percentage of days during each two month period a) November and December, b) January and February and c) March and April on which the minimum threshold for flooding to start (0.9 m) was exceeded (diamonds and dotted line), and on which water levels were between 0.9 m and 1.7 m (squares and solid line). See text for details.

The peak numbers of godwits recorded on the Ouse Washes in each bi-monthly time period between 1992/93 and 2008/09 were not significantly correlated with the percentage of days on which water levels were between 0.9 and 1.7 m or the mean water levels in the Delph River (Table 1). Maximum water levels were weakly, negatively correlated with the peak numbers of godwits recorded in March/April (Table 1), but no other significant correlations were apparent..

Table 1. Results of Pearson correlation analyses of the peak numbers of black-tailed godwits recorded in WeBS counts on the Ouse Washes and the percentage of days when suitable foraging habitat is likely to be available (water levels between 0.9 and 1.7 m), mean water levels and maximum water levels in bi-monthly periods in each year between 1992/93 and 2008/09.

	% days habitat available		**Mean water depth (m)**		**Maximum water depth (m)**	
Peak count	r	p	r	p	r	p
Nov/Dec n = 13	0.37	0.217	0.23	0.456	- 0.04	0.990
Jan/Feb n = 13	0.43	0.140	- 0.39	0.188	- 0.54	0.058
Mar/April n = 13	0.41	0.163	- 0.47	0.106	- 0.58	0.037

Winter origins of colour-ringed black-tailed godwits recorded on the Washes

A total of 294 different individually colour-marked godwits were recorded on the Washes between 1996/97 and 2008/09, and the numbers of individuals recorded on the Washes in each year has increased in line with the increasing population using the Washes (Fig 2a), and with the number of colour marked godwits estimated to be alive in the population (Fig 5a). Since 1999, the number of individuals recorded on the Washes has been between 50 and 150 in most years. Prior to 2000/01, more than 70% of all individuals were recorded in March/April (Fig. 5b), but since then the number sighted earlier in the winter has increased, with nearly half of all first sightings now occurring in January/February, and some birds being seen even earlier in November/December (Fig. 5b).

The winter locations are known for 186 of the individual godwits recorded on the Washes since 1996/97. The majority (between 60 and 85%) are known to winter on the east coast of England, but godwits from Ireland, France, Portugal and Spain as well as other locations in Britain are also recorded each year (Fig. 6a). The proportion of birds from different wintering locations using the Washes each year has changed very little since1996/97 (Fig 6a). The earlier winter use of the Washes by godwits in recent years is largely a consequence of birds moving inland earlier from the east England estuaries (Fig. 6b). Prior to 2000/01, only *c*. 20% of birds from the east coast of England arrived in January/February, but in recent years this has increased to *c*. 60% with a small number being recorded even earlier in November/December. Timing of arrival on the Washes of birds from more distant wintering locations, particularly Iberia and France, does not appear to have changed; godwits from these southern wintering locations appear to use this as a stop off site on spring migration and have not been recorded earlier than January. There is some indication that godwits are arriving slightly earlier from other UK winter locations and from Ireland (Fig 6b); between 2005/06 and 2008/09 over 50% of birds from these locations were recorded in January or February as opposed to fewer than 10% in the late 1990s.

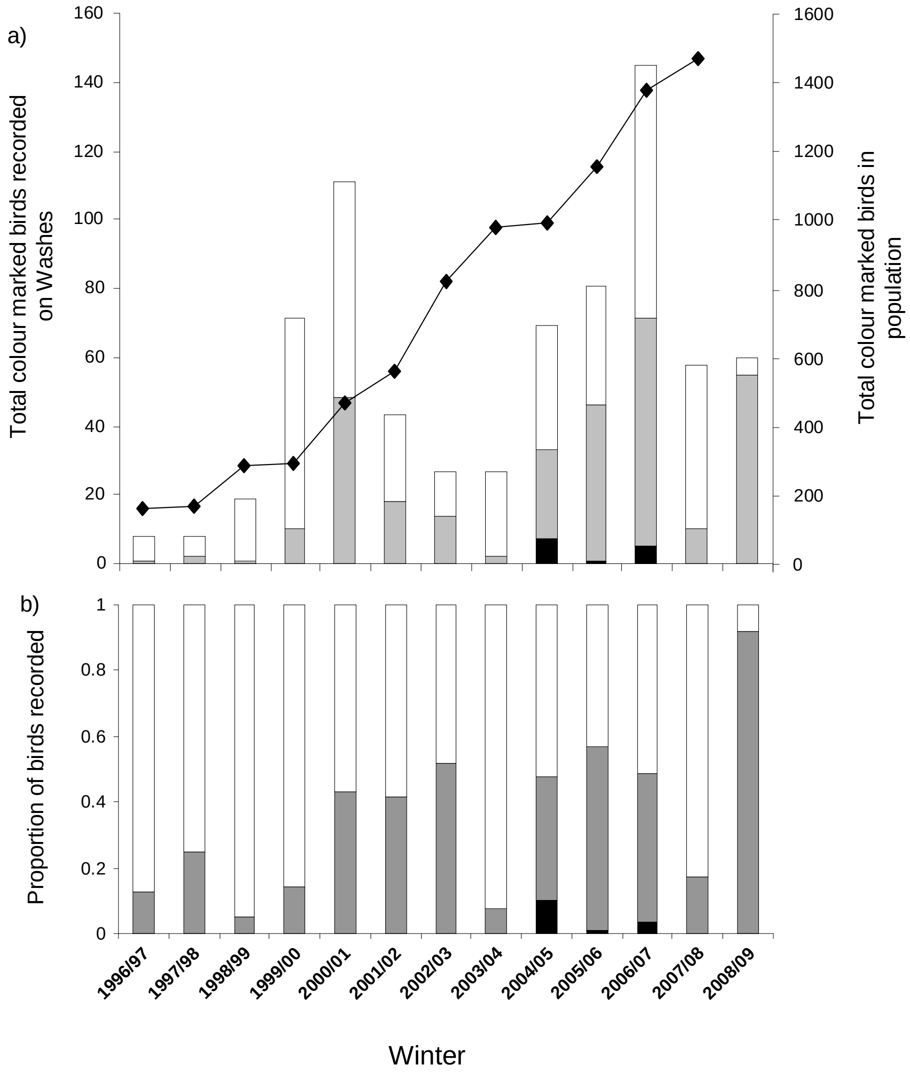

Figure 5. Annual variation in the (a) numbers of individually colour-marked black-tailed godwits recorded and b) proportion of first sightings of individuals in November/December (black bars), January/February (grey bars) and March/April (white bars) on the Ouse and Nene Washes, and the total number of colour-marked godwits estimated to be alive in the population (diamonds and line) between 1996/97 and 2008/09.

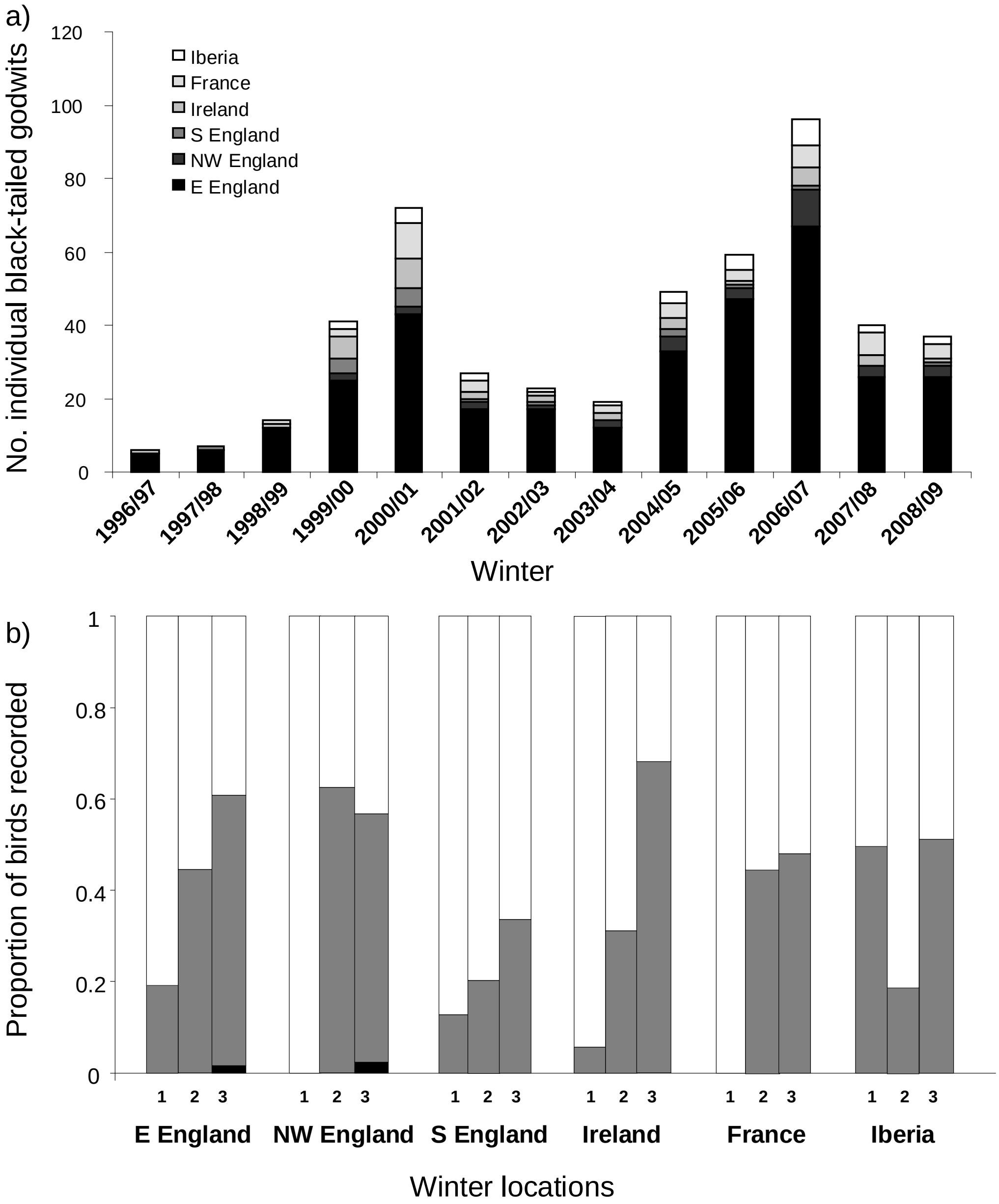

Fig 6. Variation in (a) the number of individually colour-ringed black-tailed godwits from different winter locations recorded on the Ouse and Nene Washes and (b) the proportion of colour-ringed birds from each winter location recorded in November/December (black bars), January/February (grey bars) and March/April (white bars) in (1) 1996/97 – 1999/00, (2) 2000/01 – 2003/04 and (3) 2004/05 – 2008/09.

Discussion

Use of inland grasslands by godwits in the east of England has increased dramatically in the last two decades, from a few hundreds in the early 1900s to several thousand in the 2000s. This increase has not just been in spring; godwits are arriving earlier in the winter with first flocks being recorded in November in most recent years. Godwits remain on the site and can now be found on the Washes between January and April in much larger numbers than in the 1990s. This change in distribution and the extent to which the new habitat is being used is unlikely to be a result of improving conditions on the Washes. Godwits rely on areas of shallow water in which to feed and roost, however, water levels on the Ouse Washes have not changed over the last two decades, Management of both the Ouse and Nene Washes has been consistent throughout the last two decades, with the primary change being an increase in the frequency and extent of flooding in late spring (Ratcliffe *et al.* 2005). However, the Icelandic godwits have departed for their breeding grounds by this time and are therefore unlikely to be affected by these changes. This suggests that sufficient water levels on the site have been available in all winters since the early 1990s, and thus that the availability of foraging conditions are unlikely to have changed. As black-tailed godwits are a long-lived species with high site-fidelity (Gill *et al.* 2002), the pattern of increasing use of the Washes over the last two decades may represent increasing awareness of additional foraging opportunities.

Increasing use of the Washes in spring could also have been as a result of more birds from distant wintering locations using the site as a stop-over on spring migration. However, the proportion of birds from different wintering locations using the Washes has not changed since the 1990s; the vast majority of birds (*c*. 70%) are from estuaries on the east coast of England. Previous studies have indicated that the prey resources on mudflats of the east of England are very limited through the winter (Gill *et al.* 2001a, Gill *et al.* 2001b), and that rapid depletion of these resources results in prey intake rates that are not always sufficient to meet energetic demands on these estuaries (Alves 2009). The increasing timing and extent of exploitation of inland grasslands each year may therefore be an indication that the Washes play a key role in supporting the increasing population of godwits in this region.

Like many wading birds, godwits prefer to roost in shallow water and will alight on pools or at the tide edge after disturbance flights (Chapter 2). The availability of inland grassland habitats for godwits may therefore rely on the presence of shallow floods. Godwits wintering in Ireland have been shown to respond rapidly to the presence of shallow floods on inland grasslands after sufficient rainfall, and that godwits rapidly depart from these sites when flood levels decline (Chapter 2). On the Ouse Washes, however, the recorded water levels suggest that suitable foraging and roosting condition are available to godwits from October until April in every winter. As water levels on inland grasslands are likely to be very important drivers of their availability for foraging godwits, changes in winter rainfall patterns could influence the availability of suitable conditions. Records of colour-marked godwits indicate that the use of freshwater grasslands is important across the non-breeding range (Chapter 2). Flooded inland grasslands are particularly important during late winter and early spring; sites such as the Blackwater Callows and Little Brosna Callows in Ireland and the Ouse Washes and Nene Washes in England often support flocks of several thousand Icelandic godwits. As the entire population of Icelandic godwits is estimated to be around 50,000 individuals (Gill *et al.* 2007), this suggests that a very large proportion of the population uses these grasslands at this critical time of year. Records of colour-marked birds also suggest that there is significant turnover of individuals on the Washes, so it is likely that many more than recorded in the peak counts use these sites each year.

The change in timing of use of the Washes is being primarily driven by more birds moving from east coast estuaries earlier in the year. Studies of resource availability and conditions on the east coast estuaries over the time that the godwit population has been increasing indicate that prey depletion significantly reduces intake rates for godwits on all major estuarine sites by the end of the winter (Gill *et al.* 2001b). The energetic costs of living for godwits are also higher on the east coast of England than on winter sites in Portugal and Ireland, primarily because of higher wind speeds and lower air temperatures in east England (Alves 2009). Analyses of the survival rates of black-tailed godwits wintering in east England between 1995 and 2000 indicated that average adult annual survival was 0.87 ± 0.02 se (Gill *et al.* 2001a). However, in more recent years, the survival rates of godwits wintering in east England appear to have increased (average adult annual survival, 1995-2006: 0.96 ± 0.01 se, J.A. Gill unpublished data). This increase in survival is coincident with the increase in numbers of using the inland grassland sites, which suggests that the foraging opportunities available on the grasslands are sufficient to overcome the shortfall in intake that was experienced by godwits foraging only on the mudflats in the 1990s (Gill et al. 2001b).

Inland grassland sites may provide suitable resources for foraging godwits but they are also likely to be more sheltered from wind chill effects than coastal habitats, as a consequence of being enclosed by river banks and having tall vegetation within which the birds can forage and roost. Wind chill has a very strong influence on the energetic costs of living of shorebirds (Wiersma and Piersma 1994). Large areas of flooded grasslands also provide an abundance of foraging and roosting sites in the same location without having the travel costs imposed by tidal cycles. Thus, the continued increase in the numbers of godwits wintering in the east of England (Austin *et al.* 2008) may be a consequence of increased use of these grassland foraging sites at the key times of year when resources on the mudflats are not sufficient to meet energetic demands.

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Conclusions

Conclusions

Understanding the habitat requirements of a population is essential for effective conservation and design of protected areas. Many species can occupy a variety of habitat types, and the use of different habitats may vary spatially and/or temporally. Different habitat types may also vary in their relative quality for the populations that they support. When variation in habitat quality is sufficient to influence the fitness of individuals occupying those habitats, habitat quality has the potential to also influence population-scale processes (Orians and Wittenberger 1991, Rosenzweig 1991, Sutherland 1996, Newton 1998, Sibly and Hone 2002, Johnson *et al.* 2006). In such cases, the protection of habitats in which fitness is highest may be considered preferable. However, poorer quality habitats can also play a key role in supporting populations, particularly when individuals occupy different habitats types at different points in time, and may thus require resources from all habitats irrespective of their relative quality.

In migratory species, identifying the relative importance of different habitats is particularly complicated because of the huge spatial scales across which individuals can travel within the migratory range. The widespread and growing evidence of carry-over effects in migratory species, in which the conditions experienced in one season can influence fitness in subsequent seasons, highlights the complex manner in which habitat quality can impact on individuals (Ebbinge and Spaans 1995, Marra 1998, Gill *et al.* 2001a, Bearhop *et al.* 2004, Norris *et al.* 2004, Gunnarsson *et al.* 2005a, Studds and Marra 2007). Variation in the availability and occupancy of habitats of varying quality in the breeding and non-breeding seasons can therefore potentially restrict or facilitate population growth in migratory species.

Over the last two decades, studies of an expanding shorebird population, the Icelandic black-tailed godwit, have revealed a migratory system in which variation in habitat quality influences individual fitness and carry-over effects (Gill *et al.* 2001a, Gunnarsson *et al.* 2005a) and may also influence the rate of population growth, as the population is expanding into poorer quality habitats in both seasons (Gill *et al.* 2001a, Gunnarsson *et al.* 2005b). The inspiration for this study came from the finding that the extent of use of saline and freshwater habitats by individual godwits in winter appeared to be a key component of habitat quality that varied across the winter range and was related to survival (Gill *et al.* 2001a), the type of breeding habitat occupied and subsequent breeding success (Gunnarsson *et al.* 2005a). However, the reasons for this difference in quality between saline and freshwater habitats, and hence the mechanisms underpinning the carry-over effects and demographic consequences, were not known. Consequently, the main purpose of this thesis was to explore the implications of using saline and freshwater habitats in winter for black-tailed godwits. Ireland was chosen as the study location both because it supports large numbers of godwits in winter, and because the grasslands which are the primary freshwater habitat used by godwits are abundant throughout Ireland. Over the course of three winters, I studied godwit distribution and behaviour across nine habitat complexes in southern Ireland, each of which comprised an estuary surrounded by grassland fields. These data clearly show that grassland habitats are not simply a supplementary foraging site used when mudflats are unavailable. The matrix of mudflats and grassland fields provides a wide variety of foraging patches and godwit flocks regularly move between the two habitats within a tidal cycle. Prey intake rates are comparable on both habitats but the high levels of vigilance displayed on grasslands indicate that godwits perceive them as ‘risky’ foraging locations, which is likely to be a consequence of the higher rates of disturbance and reduced visibility on grasslands, coupled with their greater distance from safe roosting locations (Chapter 2). Critically, however, the energetic intake rates achieved by godwits on mudflats in southern Ireland are not sufficient to meet daily energetic requirements. The coastal grasslands therefore appear to be essential in supporting the godwit population wintering in southern Ireland.

These finding are supported by a recent study of the energetic costs of wintering in three different parts of the winter range for Icelandic black-tailed godwits (Alves 2009). This study used the energetic intake rates reported in this thesis for south Ireland together with similar information for west Portugal and east England, and showed that godwits in Ireland need to forage for twice as long as those in Portugal to maintain a positive energy balance (Alves 2009). Maintaining this energy balance in Ireland can only be achieved through the additional use of grasslands as well as estuarine resources (Chapter 2). In contrast, energetic intake rates for godwits wintering on the east coast of England were found to be lower than both south Ireland and west Portugal (Alves 2009), primarily because estuarine food supplies were insufficient to meet the high thermoregulatory costs of this location (Gill *et al.* 2001b). However, the energetic intake rate data used for these calculations for east England were collected during the 1990s, at a time when only mudflats were used by this population. In Chapter 5, I describe how godwits wintering on the east coast of England have shown a rapid increase in use of the inland wetlands since the 1990s, which may have contributed to the apparent increase in survival rates for this region in recent years. Thus grasslands appear to provide key resources for godwits in both Ireland and the east of England, two areas which together may support *c.* 30-40% of the world population of Icelandic black-tailed godwits in winter (Austin *et al.* 2008, Crowe *et al.* 2008).

The lack of any substantial increase in the numbers of godwits wintering in Ireland (Chapter 1) despite the recent overall population increase, which has been especially apparent in some parts of the UK (Austin *et al.* 2008), indicates that the mudflat and grassland resources in Ireland may be limiting the size of the wintering population in this part of the range. Despite this apparent limitation, Ireland still supports a large proportion of the godwit population, and their arrival dates in Iceland are not significantly later than the earliest birds which arrive from Portugal (Alves 2009). The analyses presented in this thesis suggest that this is in large part due to the abundance of grasslands that remain in Ireland. In particular, inland wetlands (callows) are potentially a key part of the mechanism by which Ireland has continued to supports such large numbers of godwits over the last 40 years (Chapter 1). The large flocks that congregate on inland sites in late winter and early spring may benefit individuals by reducing predation risk and levels of vigilance (Pulliam 1973, Clark and Mangel 1986). The benefits accrued on the callows in Ireland will likewise apply to godwits congregating on inland wetlands throughout the range; particularly on the Washes in East Anglia (Chapter 5) and on flooded river valleys in the Netherlands (Gerritsen and Tijsen 2003) which are primarily used as stop-over sites by godwits that have wintered further south in France and Portugal (Alves 2009). Use of both the Washes and the Dutch grasslands by Icelandic godwits has increased rapidly since the 1990s (Chapter 5, Gerritsen and Tijsen 2003), and both regions now regularly support flocks of several thousand godwits in spring. Therefore a large proportion of the godwit population is supported on inland grasslands at some point during the non-breeding season.

Given the importance of grasslands for godwits and recent high levels of urbanisation of coastal zones in Ireland, the lack of protection for grasslands is of concern. Urbanisation has been shown to impact on wildlife through built developments resulting in direct habitat loss, but distribution and behaviour can also be influenced by animals avoiding areas of high human activity (Blair 1996, Clergeau *et al.* 1998, Bock and Jones 2004, McKinney *et al.* 2009). During my field research, some of the fields used by godwits the previous year were building sites when I returned the following year. The greatest land-use change in Ireland has been from pastoral farmland and wetlands to urban development, especially in the coastal zone where *c*. 60% of the population lives (EPA 2008). Despite this, Ireland is in a unique position as it retains a larger proportion of grassland habitat than any other northern European country (OECD 2000). Recently, interest has been shown in incorporating some of the fields in the estuarine habitat complexes that are used by waterfowl within the SPA boundaries that provide protection for the intertidal habitats (J. Fuller, SPA Designations Team Leader, National Parks and Wildlife Service, pers. comm.). Chapters 3 and 4 therefore set out to identify the types of fields used by godwits and where those fields would best be located. Only very small and enclosed fields are avoided by godwits. A wide variety of larger, more open fields with good visibility are used by godwits and, although fields up 1500 m from the estuary were used, the majority were adjacent to the mudflats, which allowed flocks to retreat to the tide edge when disturbed. In addition, there is no evidence for changes in godwit distribution or behaviour in relation to local- or landscape-scale urbanisation (Chapter 4). Consequently, candidate fields for inclusion within protected areas could include any large, open fields close to the estuary throughout the urban and rural areas of the south coast of Ireland.

For Icelandic godwits, a range of habitats appear to be essential during the non-breeding season. Prey resources on mudflats may be preferred but grasslands provide an important food source when estuarine resources are limiting, and particularly during spring migration when a large proportion of the population makes use of inland grasslands in Ireland, England and the Netherlands. This illustrates the dynamic nature of habitat use and relative habitat importance; two very different habitat types that are essential in supporting different parts of the wintering population of a single species at distinct points throughout the non-breeding season.

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