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Understanding space and habitat use of the Near Threatened Eurasian curlew to inform the value of habitat restoration schemes for the species' conservation

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Dedication

I would like to dedicate this thesis to wildlife enthusiasts who I have met during the study and have contributed to the work.

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Publications and Conferences

Chapter 2: Mander, L., Scapin, L., Thaxter, C.B., Forster, R.M and Burton, N.H.K., 2021. Long-term changes in the abundance of benthic foraging birds in a restored wetland. Front. Ecol. Evol. 9:673148. doi: 10.3389/fevo.2021.673148. LM, LS, and NB: conceptualisation. LM: formal analysis, investigation, validation, and visualisation. LM, LS, and CT: methodology. NB and RF: supervision and writing—review and editing. LM and LS: writing—original draft. All authors contributed to the article and approved the submitted version.

Chapter 3: Mander, L., Nicholson, I., Green., R.M.W., Dodd., S.G., Forster, R.M and Burton, N.H.K., (2022). Individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Eurasian Curlew *Numenius arquata*. Bird Study, 69, pp 39–52. doi.org/10.1080/00063657.2022.2144129. Mander, L.— conceptualisation, methodology, field sampling, formal analysis, writing, reviewing, and editing— original draft. Nicholson, I.— investigation, funding acquisition, field sampling and reviewing. Green, R.M.W— field sampling and reviewing. Dodd, S.G.— field sampling and reviewing. Forster, R.M.— funding acquisition, review & editing and supervision. Burton, N.H.K.— investigation, conceptualisation, funding acquisition, validation, review & editing, and supervision.

Abstract

Intertidal habitats and terrestrial habitats connected to estuaries are subject to multiple anthropogenic pressures including the indirect effect of climate change (i.e., sea-level rise). To build sustainable coastal defences and create intertidal habitats in estuaries, managed realignment (MR) sites are created. These habitats are of potential value for wintering waders yet we know little about their long-term development and utilisation by waders (Charadriiformes; also referred to as shorebirds), for example, Eurasian curlew (*Numenius arquata*). The species is categorised as Near Threatened by the International Union for Conservation of Nature (IUCN) and uses both estuarine and non-estuarine habitats in winter. Understanding small-scale spatial patterns in the use of estuaries and of created intertidal habitats is essential in predicting the impact of habitat loss and designing effective compensatory sites for waders. In ecological models, e.g., individual-based models (IBMs), assumptions about animal movements are often made using *a priori* information on space use and habitat use. The first chapter of the thesis (Chapter 1) aims to provide background to the project and to review the use of modern telemetry and predictive modelling in assessing the success of estuarine habitat creation for waders. This thesis then examines the long-term suitability of managed realignment sites for waders in response to physical changes (i.e., in the elevation of created intertidal areas) (Chapter 2), and uses high-resolution tracking data to examine individual, sexual and temporal variation in the winter home range (Chapter 3) and habitat selection (Chapter 4) of Eurasian curlew. Furthermore, movement data – derived from GPS-tracked curlew – were incorporated to define parameters of an individual-based model, developed to predict the impact of managed realignment and other environmental changes. Using data on behaviour and fine-scale habitat use from the GPS-tracked Eurasian curlew, I also validated the model's predictions (Chapter 5). I found the foraging numbers of the four key waterbird species that colonised the MR site to decline above a certain elevation, and thus over time with accretion of the site, with this effect being most pronounced for the Eurasian curlew (Chapter 2). Using a sample of 21 GPS-tagged birds, I found Eurasian curlew to be faithful to foraging and roosting areas on their coastal wintering grounds, including a habitat creation site. Home range of Eurasian curlew was small (555.5 ha +/-SD 557.9 ha) and varied slightly in size through the non-breeding season (September to March). Home range sizes were greater at night than in the day, and showed high inter-individual variability which was not related to sex and thus potential differences in resource use (Chapter 3). I also found that Eurasian curlew's core ranges were restricted to one to two distinct patches on intertidal flats with some overlap. Eurasian curlew preferentially selected saltmarsh and the MR site at night, presumably for roosting (Chapter 4). Finally, I successfully parameterised an individual-based model (Chapter 5). The model was able to successfully predict the impact of habitat creation on the abundance of waders supported by a discrete area of the Humber Estuary. Our overall results provide a collective understanding of the responses of waders to the creation of the managed realignment site and of the space and habitat use of Eurasian curlew. The results have been crucial in informing and validating simulations from the individual-based model.

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Abbreviations

AFDM	Ash-free dry mass
BTO	British Trust for Ornithology
CD	Chart Datum
IBM	Individual-based model
GPS	Global Positioning System
LCT	Lower Critical Temperature
MR	Managed Realignment
OD	Ordnance Datum (at Newlyn, UK)
SPA	Special Protection Areas
Waders	Wading birds (Charadrii)
WeBS	Wetland Bird Survey

Chapter 1 The use of modern telemetry and predictive modelling in assessing the success of estuarine habitat creation for waders

1.1 Wading birds and their need for habitat creation

Waterbirds are defined as species of birds that are ecologically dependent upon wetlands (Ramsar Convention, 1971). They include a taxonomic group of 200 species known as waders (Charadriiformes; also referred to as shorebirds). Many waders breed in high Arctic regions and winter in the tropics (Van de Kam et al., 2004). They migrate along flyways – migration routes that connect their breeding sites to wintering sites. Flyways have been defined as “the entire range of a migratory bird species (or groups of related species or distinct populations of a single species) through which it moves on an annual basis from the breeding grounds to non-breeding areas, including intermediate resting and feeding places as well as the area within which the birds migrate” (Boere et al., 2006).

Along their flyways, waterbirds (including waders) interact with humans. It is evident that waterbirds have long been associated with human civilisations, providing valuable food sources and ornaments as well as being of sacred value to early civilisations (Figure 1.1), e.g., in ancient Egypt (Bailleul-LeSuer, 2012). However, as the human population expanded in range and numbers, its relationship with waterbirds has changed. In more developed countries, humans have become less reliant on wild birds as a food source, but bird populations have continued to provide direct or indirect benefits to human populations. Such links between biodiversity or natural capital and human societies are referred to as ecosystem services (Fisher et al., 2009; Luisetti et al., 2011; Turner et al., 2015).

Figure 1.1. “Three vignettes Thebes, Tomb of Queen, Nefretere, Ramesses ii, 1292–1225 b.c.”. Scene found on the west wall in the antechamber of the tomb of Nefertari, queen of Ramesses II, in the Valley of the Queens. Source: Bailleul-LeSuer (2012). The scene pictures a Bennu bird that resembles a heron which is worshipped in Egyption mythology.

Waterbirds provide a range of important services in the ecosystem: provisioning, cultural services, regulating services and supporting services (Green & Elmberg, 2014). Worldwide, waders are still harvested for food. For example, in Europe, an estimated minimum of 4,103,493 waders were shot annually across 27 European states by a total of six million licensed hunters (Hirschfeld & Heyd, 2005). The hunting of waders in Europe can be considered as a recreational activity (cultural services) rather than a necessity (provisioning of meat). As conservation concern for waders is increasing in western society, their cultural value has shifted in the last century. It is now widely accepted that waders provide ecosystems services that benefit human populations, and thus maintaining global wader populations is important for our society.

Most waders are obligate benthic invertebrate feeders in winter. Simple prey-predator relationships means that variation in the abundance and condition of prey can drive demographic changes through impacts on individual condition and thus survival and breeding productivity. In winter, the Eurasian oystercatcher (*Haematopus ostralegus*) (hereafter oystercatcher) relies chiefly on cockles and mussels in estuaries (Goss-Custard, 1996), and populations can respond directly to changes in the abundance of prey, e.g., through emigration (Bowgen et al., 2022) or increased mortality of oystercatchers (Atkinson et al., 2003). The presence of carry-over effects in shorebirds has also been found. For example black-tailed godwits (*Limosa limosa islandica*) from low-quality wintering sites had lower breeding success (Gill et al., 2001a). As a result, measures such as body condition or survival may potentially provide reliable indicators of environmental change. Through the use of an individual-based model (Goss-Custard & Stillman, 2008), Bowgen (2016) predicted how an invertebrate regime shift could impact the wintering survival of Eurasian curlew (*Numenius arquata*) (hereafter curlew), but also expressed doubts about the value of wader populations as an indicator of site health. Indeed, waterbirds do not always respond to environmental changes as we expect, raising doubts about their efficacy as effective bio-indicators (Amat & Green, 2010; Green & Elmberg, 2014).

Because waders are long-distant migrants (Figure 1.2) and use a range of habitats during their migration, measuring productivity and bird survival can also inform global environmental changes. Piersma and Lindström (2004) propose that waders may serve as 'integrative sentinels', given the dependencies between population processes of long-distant migratory waders and global environment features. With growing concerns for the impact of climate change on ecology, the effects of changes in climate and weather on birds have been extensively studied in recent years (Pearce-Higgins & Holt, 2013; van Gils et al., 2016; Burton et al., 2020) with these studies highlighting the value of long-distant migratory waders as valuable indicators to measure changes at a global scale. As changes in our ecosystems are rapidly occurring across the world due to climate change, waders can indeed be regarded as a bio-indicator or a sentinel of changes. Therefore, monitoring birds in lieu of other taxa (e.g., arthropods or plants) may be more cost-effective when assessing the overall health of the ecosystem and its response to change in environmental conditions.

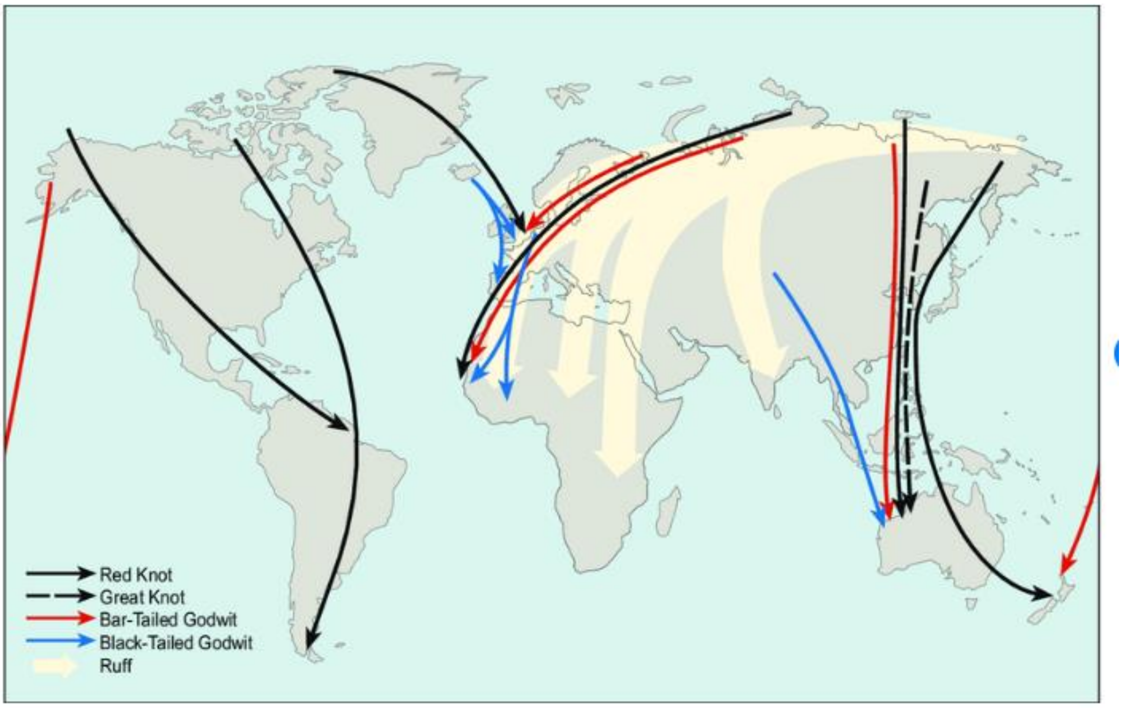

Figure 1.2. Map showing major southward migration pathways around the world of red knot, great knot, ruff, bar-tailed godwit, and black-tailed godwit. Different lines for red knots and bar-tailed godwits represent subspecies with differing migration patterns. Source: Helm et al. (2012).

There is little published evidence in the literature of other services provided by waders other than supporting services. For example, other waterbirds have been identified as a vector for the movement of other animals and plants (Green et al., 2002a; Santamaría & Klaassen, 2002; Green & Figuerola, 2005). They can disperse propagules via ingestion of seed (endozoochory; (Lovas-Kiss et al., 2018)) or carry seed or invertebrates on their plumage or feet (epizoochory; (Figuerola & Green, 2002)). The role of waterbirds as ecosystem engineers (supporting services) has been documented, with large birds such as swans and flamingos causing bioturbation of the sediment when feeding (Green & Elmberg, 2014). The repetitive probing action of waders (e.g., curlew) may also cause bioturbation, but experimental work on this has yet to be undertaken.

In addition to supporting a range of ecosystem services, waterbirds provide some regulating services in the ecosystems and those include disease surveillance and pest control. Waterbirds are hosts and vectors of pathogens, and are known to undertake some of the longest migration of the vertebrates (Gill Jr et al., 2009), moving between a pathogen-free or low pathogen environments in high Arctic regions to high pathogen environments, including limnic environments in the temperate and tropic regions. Because migratory waders from different breeding origins come together in wintering areas or stop-over sites and share resources with local and resident birds, they have the potential to act as vectors of pathogens along the species' flyways (Mihaela & Marina, 2014). Whilst a lot of information exists on the transport of pathogens by ducks, little is known about wader species.

Birds play an important role in regulating prey while contributing to pest control – a regulating service that can be economically quantified. In winter, waders feed almost exclusively on benthic invertebrates; they respond numerically and functionally to invertebrate abundance (Goss-Custard et al., 2006b). A number of studies have demonstrated the top-down effects of wader predation on invertebrates living on intertidal area (see review by Whelan et al. (2008)). However, none of the prey are considered as pests to human populations, although some benthic invertebrates are considered as alien species in estuaries and waders can exert a top-down control on those species (Ferreira-Rodríguez & Pardo, 2018).

The annual cycle of waders and their long distant migration make them ideal candidates to act as sentinels of global environmental change. Additionally, they are also used as conservation flagships by Non-Governmental Organization (NGOs) because of the cultural services they provide. The appeal of one particular cohort of waders – the Numeniini – has translated into global conservation efforts from a range of communities (from hunting association to NGOs) in the first instance, to examine the cause of their decline and set measure to reverse their decline. In the UK, the curlew is an iconic species which fascinates the public. The species provokes a range of emotions expressed in poetry, art and music (Colwell, 2018). Their conservation has been bolstered by public funding appeals (e.g., the British Trust for Ornithology (BTO) Curlew Appeal) and community initiatives, notably to protect local breeding populations. This PhD study is the result of a funding appeal launched by BTO to examine how curlew use the landscape around estuaries in winter and to inform measures to improve their survival.

1.2 Numeniini: A group of waders in peril.

Amongst the taxonomic group of waders, the Scolopaci sub-order (snipe-like waders) includes the large family of sandpipers (Scolopacidae) which itself can be divided further into several groups or tribes of similar species. One of those groups is the Numeniini, which includes 13 species of curlew and godwit. Because of changes in environmental and ecological conditions occurring across flyways, the Numeniini is a highly threatened group of wader species (Pearce-Higgins et al., 2017). In a horizon-scanning assessment of current and potential future threats to migratory shorebirds, Sutherland et al. (2012) indicated that some of the issues faced by waders were gradual (e.g., climate change on breeding grounds at high latitude and altitude), with responses at a population level difficult to predict (Table 1.1). Other current anthropogenic threats such as land-claim of tidal flats and marshes had already affected waders at a population level. In the Arctic and sub-Arctic regions, it is the effect of climate change (e.g., early snow melt) that presents the most significant threat to wader populations. In contrast, waders breeding in temperate regions face other threats of a more anthropogenic nature such as agricultural intensification and changes in grazing regime. As most wader species winter in temperate and tropical regions, the change of availability of estuarine wintering habitats in these regions – through anthropogenic sea-level rise or land claim of tidal marshes – will also impact non-breeding waders.

Table 1.1. List of current and potential future threats to migratory shorebirds derived from an horizon scanning assessment (Sutherland et al., 2012).

Punctuated threats	**Gradual changes**	**Current anthropogenic threats**	**Possible future threats**
Mega-tsunami	Climate change – major changes in weather patterns	Drainage of breeding and wintering habitats	Microplastics
Volcanoes	Changes in sediment flow	Agriculture intensification	Nanosilver
Earthquakes	Reduction in tundra habitat	Changes in grazing	New means of recreation
Asteroids	Anthropogenic sea-level rise	Changes in cutting date	Artificial meat
Hurricanes	Spread of algal species in intertidal habitats	Changes in flooding patterns of rice fields	Impact of global hydro-security and water wars
	Algal blooms	Abandonment of rice fields	High-latitude volcanism
	Botulism	Afforestation of temperate and sub-Arctic breeding habitat	Change in nitrogen fixing in high-latitude estuaries
	Infectious diseases	Land claim of tidal marshes	Changes in sediment with forest loss
		Restoration of coastal wetlands through managed realignment	Changing atmospheric circulation patterns
		Conversion of mangroves	Changes in primary productivity on wintering and migratory staging areas

Punctuated threats	Gradual changes	Current anthropogenic threats	Possible future threats
		Expansion of mangroves onto saltmarshes	Shutdown or slowdown of the thermohaline circulation
		Pollution from aquaculture	Impact of acidification on marine nitrogen cycles and shellfish
		Eutrophication of coastal systems	Increases in pharmaceutical discharges as human populations age
		Spread of Spartina and other angiosperms	
		Suppression of natural disturbance by river regulation	
		Disturbance	
		Harvesting and collection of shorebird prey	
		Hunting	
		Predators and predation	
		Invasive animals	

1.2.1 Effect of climate change

Wader populations can respond to climate change through changes in their phenology (e.g., timing of migration and/or breeding), their demography (i.e., productivity or survival) and their distribution (i.e., range shift, expansion or contraction). A number of studies have already shown evidence of the impact of climate change on wintering waders in the UK and northwestern Europe (Pearce-Higgins & Holt, 2013; Burton et al., 2020). There is also a growing body of evidence showing impacts on Arctic and sub-Arctic breeding grounds.

Both recruitment and survival, the key demographic processes that underpin changes in the size of populations, may be directly affected by climate change, but distributional changes may also occur because of spatial variation in these processes. Through demographic processes, the impact of mild winters in northwestern Europe and specifically the UK has resulted in shifts in the non-breeding distributions of waders towards their breeding grounds (Rehfisch et al., 2004; Austin & Rehfisch, 2005; Maclean et al., 2008), a process referred to as 'short-stopping' (Elmberg et al., 2014). Increased wintering numbers in the coldest locations may result from a changing pattern of movements, increased survival, or increasing numbers of juveniles choosing to settle at more northern or northeastern sites (Austin & Rehfisch, 2005; Pearce-Higgins & Holt, 2013).

Phenological changes in the timing of migration and breeding can lead to mismatch between prey and predators with far-reaching consequences for the bird's fitness (body condition, breeding success and survival). For example, early snow melt in the high Arctic region has a negative effect on the growth of the juvenile bill of red knot (*Calidris canutus canutus*) because of mismatch between hatching and peak abundance of arthropods (van Gils et al., 2016). Juveniles that have shorter bills as a result have a lower survival rate on their wintering ground in the tropics due to their inability to access deep buried bivalves (van Gils et al., 2016).

Waders have specific breeding habitat requirements making them susceptible to habitat changes. Despite other habitats at lower altitude offering similar food abundance in summer (e.g., lowland wet grassland), birds benefit from breeding in the high Arctic region because of lower nest predation (McKinnon et al., 2010) and the low numbers of pathogens and parasites which can be found. However, climate change is occurring particularly rapidly in Arctic and sub-Arctic regions (Rantanen et al., 2022) and thus habitats here are particularly susceptible to change. In fact, Virkkala et al. (2008) predicted that most land bird species in Fennoscandia will lose most of their climatic space by 2080, with species dependent on continental Europe (and thus not currently present on offshore Arctic islands) the most vulnerable to the threat of climate change. The sensitivity of waders to northward shrub and tree encroachment associated with global climate warming has been recently documented in breeding habitat requirement studies (Ballantyne & Nol, 2015; Miller et al., 2015; Swift et al., 2017). Predictions from an ecological niche model indicate that as a result of rising temperatures, suitable breeding conditions for Arctic shorebirds will decline dramatically by 2070 (Wauchope et al., 2017).

At more temperate latitudes where waders breed in open habitats (e.g., lowland wet grasslands, upland and moors), the consequences of recent warming are already evident, with significant changes in the range extent and abundance of breeding birds. In the UK, the distribution of curlew showed an upward altitudinal shift between 1994-2009 (albeit no latitudinal shift) (Massimino et al., 2015). Densities of breeding curlew in the UK have also declined dramatically since the mid-1990s (Balmer et al., 2013; Brown et al., 2015; Massimino et al., 2015) (Figure 1.3). Populations in the Republic of Ireland have declined even more dramatically with a 96–97% reduction in the last 30 years (O'Donoghue et al., 2019).

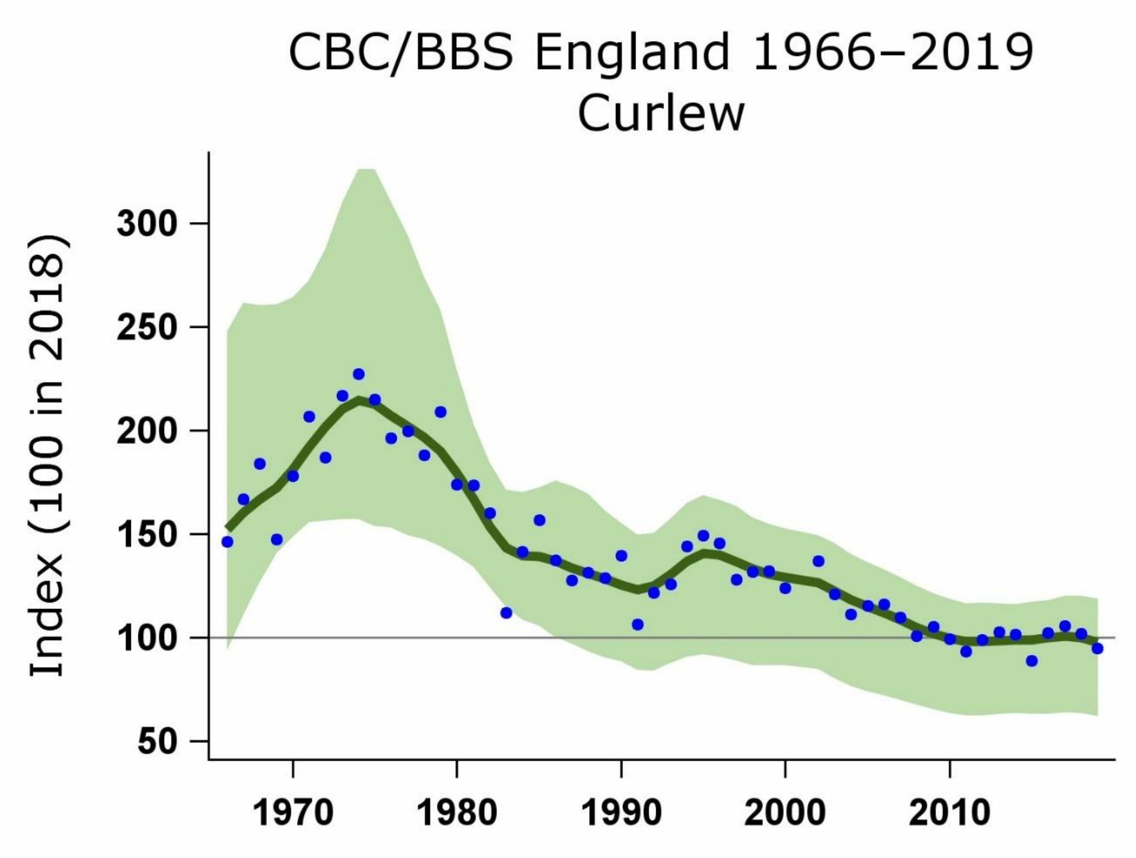

Figure 1.3. Smoothed population index of breeding curlew in England, relative to an arbitrary 100 in the year given, with 85% confidence limits in green. Source: Woodward et al. (2020)

Evidence points to low reproductive success as the likely demographic driver of population declines throughout Europe and the UK. In the UK, a large-scale analysis of Breeding Bird Survey (BBS) data shows the negative effect of intensive agriculture, forestry, increase in generalist predator populations and climate warming on breeding curlew (Franks et al., 2017).

Climate change caused by human activities is also indirectly impacting on coastal habitats through sea-level rise, with the magnitude of the loss of tidal flats depending on the topography of the estuary and the management approach to coastal flood defence. Models developed to predict wader densities in response to sea-level rise indicate that changes in morphology will bring a decrease in densities of waders favouring muddy sediments (Austin & Rehfisch, 2003) as increases in estuary width lead to sandier substrates. However, under a scenario that allowed land behind existing sea defences to be exposed to tidal inundation, this work showed that the resulting increase in intertidal area could potentially support more birds thus offsetting any predicted decreases from changes in morphology. In some estuaries, however, natural processes are no longer taking place as the landward migration of habitats is constrained by hard defences (Pethick, 1993), resulting in the possible loss and deterioration of habitats because of sea-level rise. Therefore, sea-level rise can directly affect the availability, quantity and quality of habitats suitable to waders (Rehfisch & Austin, 2006). In Poole Harbour (UK), the survival of five over-wintering shorebirds was previously predicted to decrease in response to a simulated sea-level rise (Durell et al., 2006). A more recent individual-based model similarly showed that simulated sea-level rise led to potential population declines in five wader species, with modelled birds responding to sea-level rise by increasing time spent feeding and shifting diets in response (Bowgen, 2016). In addition to sea-level rise, a further consequence of climate change is a long term increase in sea temperature. In a study predicting the indirect trophic effects of a future warm-water outflow on populations of shorebirds and wildfowl, Garcia et al. (2016) found that the clam (*Macoma balthica)* was the only potential benthic prey used by the birds suspected to be adversely affected by warm-water outflow.

1.2.2 Land claim and consequences for birds

Human activities are also directly impacting coastal habitats through land claim. Many coastal wetlands in Europe have been subject to the loss of habitats, with most countries estimated losses of coastal wetlands and seagrasses exceeding 50% of the original area (Gibson et al., 2007). Whilst the pace of habitat reclamation has slowed along some flyways, for example in northwest Europe along the East Atlantic flyway, land claim continues at an alarming rate at critical stop-over sites along the East Asian Australasian flyway (MacKinnon et al., 2012). For example, staging sites in the Yellow Sea in East Asia are subject to dramatic losses of habitat and pervasive degradation in quality: 28% of tidal flats existing in the 1980s in the Yellow Sea had disappeared by the late 2000s (Murray et al., 2014). Along the coast of Bohai Bay in the northwest part of the Yellow Sea, 218 km^2 of intertidal areas have been reclaimed between 1994 and 2010.

Habitat loss on estuaries could lead to emigration and reduce survival of displaced birds. As waders feed extensively on tidal flats on stop-over and wintering sites, the consequence of loss of habitat due to land claim could ultimately lead to demographic changes along the flyway. Through density-dependent processes, decreases in resources associated with habitat loss may lead birds to feed at higher densities in remaining areas, some of which will be of poorer quality. Burton et al. (2006), for example, found that the loss of intertidal areas in Cardiff Bay (UK) impacted on body condition and survival of the displaced common redshank (*Tringa totanus*), with a 44% increase in the winter mortality rate. At a larger spatial scale along the flyway, it is difficult to examine the fate of displaced birds. The construction of a sea wall in Saemangeum (Republic of Korea) in 2006 led to a decline in 130,000 waders between 2011 and 2013 with no reported increases at other sites, which suggested that the decline was driven by poor survival and represented a significant impact on species' populations (Moores et al., 2016). In contrast, there is evidence from the Yellow Sea that displaced birds from large land claim have moved to remaining intact areas in other parts of the Yellow Sea (Yang et al., 2011). Whilst the birds were able to re-settle in intact areas, the long-term consequences for the displaced birds are unknown, with possible consequences ranging from loss of body condition to higher mortality. It is possible that the loss of body condition on the non-breeding ground could be carried-over onto the breeding grounds – a process known as a carry-over effect. There is also evidence of decreases in survival rates linked to losses of habitats in stop-over sites (Baker et al., 2004; Piersma et al., 2016; Studds et al., 2017).

In northwest Europe, where land claim continued at a sporadic scale until approximately the late 1980s, there are a few empirical studies showing the effect of estuarine habitat loss on wader populations at small-spatial scale e.g., individual estuary level. Within the Tees and the Forth Estuaries (UK), counts of waders before and after habitat loss showed the crude effect on wader populations with most species experiencing a decline (Evans, 1981; McLusky et al., 1992). In the Tees Estuary, the effect of a loss of 60% of the most important intertidal habitat caused feeding time to be cut from 12 hrs to 8 hrs in every tidal cycle. As a result, waders were unable to meet their daily food requirement on the intertidal area and had to use supplementary non-tidal feeding area over the winter (Evans, 1981). The impact on survival was not determined in this instance, but foraging in sub-optimal habitats could lead to reduced survival or an increase in predation risk.

Elsewhere in Europe, the effects of estuarine habitat loss on waders have been documented on the Oosterschelde (southwest Netherlands), where 170 km^2 of intertidal area was lost between 1982 and 1987. Waders dispersed to adjacent intertidal areas but some suffered from increase mortality during the harsh winter following the reclamation (Schekkerman et al., 1994). In the lower Zeeschelde (Belgium), there was no change in overall waterbird numbers and the construction of a container terminal. However, the trophic composition of the bird population showed a major shift with herbivorous species increasing whilst the function for migrating benthivorous species became less important (Van den Bergh et al., 2005). More recently, in a study combining large-scale benthic mapping effort, long-term colour ringing, and regular bird counts in the Dutch Wadden Sea, Kraan et al. (2009) found that the 55% loss of suitable foraging areas for red knot led to a 42% decrease in that species, suggesting that available suitable habitat controlled red knot numbers. The survival of adult wintering oystercatcher was studied in response to the 1986–1987 partial closure of the Oosterschelde in the Dutch Delta. Bird survival decreased from the combined effect of habitat loss and with severe winters (Duriez et al., 2009).

In northwest Europe, although the pace of land claim has slowed down, intertidal habitats in low-lying estuaries are vulnerable to increase in sea-level rise, especially in estuaries where the landward migration is constrained by flood defence. Although the response of birds to climate change and land claim may differ in time, the long-term consequences are comparable, as subsequent changes in survival and carry-over effects on breeding productivity lead to population declines. To mitigate the effect of direct and indirect anthropogenic activities, conservation efforts targeting habitat creation for waders and the recovery of declining wader species are occurring along many flyways.

1.3 Conservation efforts undertaken to help wader populations.

To date, the main conservation effort for halting or reversing the decline of wader populations, particularly those at the greatest risk of extinction e.g., the tribe of Numeniini (Pearce-Higgins et al., 2017), has been focused on the breeding productivity. For curlew, whilst Cook et al. (2021) found that changes in breeding productivity were the principal cause of curlew population change, it was also important not to overlook potential impacts on survival across the year. For critically endangered species close to extension, boosting recruitment of young birds in the declining population is one of the most vital conservation measures. Increasing the recruitment of young in the population by ‘head-starting’ young birds (Clark et al., 2014) can lead to population recovery in the wild, although evidence of success is limited to species which are on the verge of extinction and inherently of a small population size. As a critically endangered species, the spoon-billed-sandpiper (*Calidris pygmaea*) with a population of 210–228 pairs in 2014 in the Arctic regions of Russia (Clark et al., 2018) is subject to a head-starting programme. In northwest Europe, conservation efforts to boost productivity of waders have also included head-starting programmes e.g., curlew and black-tailed godwit in the UK. On the breeding grounds, predator control measures can also be set to improve the breeding productivity of waders, although there is some evidence showing no overall effect of predator control on breeding performance (Bolton et al., 2007). Fencing large areas of meadows to protect nesting waders from mammalian predation can also boost productivity (Malpas et al., 2013). Generalist predators such as foxes have the potential to cause population decline. This was shown for lapwing (*Vanellus vanellus*) on lowland wet grassland in Britain (Ausden et al., 2009). Predator control and removal are mostly implemented at temperate latitudes where waders breed in heavily modified and fragmented habitats, such as lowland wet grasslands, which are maintained through human intervention.

Outside the breeding period, most waders spend the non-breeding season in coastal areas at lower latitudes. With few sites supporting a significant proportion of the biogeographic population, protecting these important habitats and controlling human activities there are essential measures to maintain population level, and many conservation actions take place on non-breeding grounds. In many instances, conservation efforts are driven by environmental legislation, in particular, designation of protected sites. Indeed, sites supporting large number of waterbirds are designated by the Ramsar convention and, depending on the environmental law of each country state, environmental jurisdiction addressing the effect of human activities exist at wetlands sites. In the European Union, important wetland sites are also designated as Special Protected Area (SPAs) as part of the Natura 2000 network (Stroud et al., 2001). At these sites, the statutory bodies have the responsibility to maintain population of waterbirds in a favourable condition. In the UK, following the country’s exit from the EU, SPAs have retained their protected status under UK legislation, including the Wildlife & Countryside Act 1981 and the Conservation of Habitats and Species Regulations (https://jncc.gov.uk/our-work/special-protection-areas-overview/). At designated sites, the UK Conservation of Habitats and Species Regulations 2017 aim to ensure that the economic growth does not occur at the detriment of the natural environment. Therefore, human activities may be regulated to preserve the integrity of the site and the assemblage of species it supports. When the loss of designated features is deemed to be of public interest (e.g., a large infrastructure project), the legislation imposes mitigation measures. In many instances, the likely adverse effect on bird populations from a development or an activity may be mitigated through measures such as the provision of compensatory habitats.

Through the process of habitat compensation, many wetland sites have been created or restored in northwest Europe (e.g., managed realignment in the UK (Morris, 2013)), particularly in estuarine systems subject to anthropogenic activities. Whilst directly offsetting for losses of habitats due to direct human activities, intertidal habitats are also created to offset for future losses due to sea-level rise. This is most relevant for low-lying estuaries where the landward migration of habitats is not possible due to hard defences protecting the areas inland. Efforts to improve the flood storage of wetlands, in order to alleviate impact of flooding on human populations, have also contributed to the creation of new wetlands in northwest Europe. In many instances, the newly created wetlands will support foraging or roosting waders during the non-breeding season. It is, however, unknown how these sites can contribute to maintaining or increasing the bird-carrying capacity (Goss-Custard et al., 2002) in estuaries, or how their resource availability compares with existing intertidal areas.

In low-lying estuaries where historical land claim has taken place, the reclaimed land is protected from tidal flooding by hard defences or soft embankments. In these circumstances, one of the techniques to create intertidal habitats is to realign the flood defences. In northwest Europe, the realignment of flood defences, also known as managed retreat or depolderisation, is one of the preferred engineering techniques (Esteves., 2014). The technique consists of setting back existing hard defences inland to create new habitats on the upper shore. It may be, however, questionable whether the created sites are at an optimal position in the estuary with resulting benefits for the wider ecology, or whether they are sub-optimal and merely fulfil management rather than ecological aims (Elliott et al., 2016). Indeed, these sites are often created where the marginal land is available to buy at a reasonable affordable price. Where intertidal habitats are created in response to a development, there are quantitative targets associated with the compensatory sites, e.g., in the number of birds an area can support, habitat types, and the sites are subject to medium-term ecological monitoring i.e., 5 to 15 years to assess whether ecological targets have been met. For waders, the assessment of success is based on the collection of bird counts (e.g., monthly bird counts throughout the tide) to compare abundance or assemblages between created and natural habitats (Atkinson et al., 2004; Mander et al., 2007). Though this information is of value, evidence of the function and efficacy of these re-created sites is sparse, partly because our understanding of small-scale spatial movements of waders in estuaries is still incomplete. With environmental concern growing in response to sea-level rise, the creation and restoration of new intertidal habitats is expanding to other flyways, where land claim has had a profound effect on wader populations e.g., East Asian Australasian flyways (Studds et al., 2017). Understanding small-scale spatial patterns in the use of estuaries and of created intertidal habitats is essential in predicting the impact of habitat loss and designing effective compensatory sites for waders and has been better enabled by recent technological advances in bird telemetry. High-resolution tracking data has already led to important discoveries in the field of ecology, but continuing development has allowed new questions to be explored e.g., through predictive modelling of animal movements and integration with other remote sensing data (Kays et al., 2015).

1.4 The development of the field of telemetry and its application to wader ecology studies

As bird movements underpin demographic processes in bird population studies, it is essential to characterise individual movements. Historically, studies of bird movement and survival have relied on bird ringing whereby a ring with a unique identification number is fitted to the bird's leg. With metal-ringing, it is, however, necessary to recapture or recover the bird to obtain information on the bird's movement (known as 'capture -mark-recapture'). Individuals can, though, also be fitted with colour-rings enabling individual identification without the need to recapture (mark-resighting). Mark-resighting studies have revealed a huge amount of information on the ecology of waders e.g., black-tailed godwit (Gill et al., 2001a; Gunnarsson et al., 2004; Gill et al., 2014). However, with the development of tracking devices, it is now possible to track bird movements without the need to recapture the bird or rely on observer effort for re-sightings. Tracking technologies range from radio telemetry, to Global Positioning System (GPS) or satellite (e.g., Argos) devices, to light-level geolocators (Table 1.2).

With any tracking study, it is important to consider what devices are appropriate for the research aims and the species being studied, and to understand any potential impacts of tagging on individual welfare, whether with respect to their body condition, breeding success or survival. Bridge et al. (2011) discusses the strength and weakness of tracking technologies, whilst the impacts of satellite telemetry on the study of animal migration are discussed by Perras and Nebel (2012). The effects of such devices on individual birds are also reviewed by Geen et al. (2019). The field of bird tracking has grown exponentially over the last decade due to a miniaturization of devices with complex electronics. It is the miniaturisation of GPS devices that gives the greatest opportunity to fit trackers to an increasing number of bird species occupying different environments, and to track birds for longer periods, providing that the welfare of the bird is carefully considered. The rule of thumb adopted around the globe recommends that the device should not exceed 3%-5% of an animal's body mass. In a meta-analysis of biologging effect on birds (based on 214 studies), Bodey et al. (2018) found a negative effect of tagging upon survival when tags were >1% of body mass, but no effect when tags were <1% of body mass, thus it is important to keep device weight to a minimum.

Table 1.2. Some key properties of bird tracking technology using devices attached to birds (adapted and updated from Bridge et al. (2011)).

Data retrieval system	Tracking technology	Minimum device (grams)	Maximum locations per days	Resolution /accuracy (best expected in meters)	Range of operation
Satellite relay systems (data collected by and retrieved from satellites)	Doppler PTTs	5	1	150	Global
Ground-based receivers (data retrieved by fixed or mobile antennas)	GPS logger with transmitter	2.6g	> 2,000 (depend on battery size)	5	Global
	GPS/GSM	7.2g	> 2,000 (depend on battery size)	5	Global
	Radio transmitter	0.3g	200	100	Local
Dataloggers (require recovery of the tracking device)	GPS	0.95	> 100 (depend on battery size)	5	Global
	Solar Geolocation	0.5	2	~ 200,000	Global

Within the field of telemetry, the study of bird movement has to date relied heavily on radio telemetry, whereby a radio transmitter attached to the animal tracks the signal to determine the animal locations (Cochran & Lord Jr, 1963). Because radio-marked birds can be relocated more frequently and consistently than those marked by other methods, radio telemetry can provide a history of detailed movements that is not possible with simpler capture-mark-recapture (e.g., bird ringing) or capture-mark-resighting studies (e.g., colour ringing). Therefore, telemetry has been widely used in the field of wader ecology to determine the site fidelity, home range, nocturnal activity and habitat preferences of wader species (Burton & Armitage, 2005; Leyrer et al., 2006; Taft et al., 2008; Lindström et al., 2010; Verkuil et al., 2010; Mittelhauser et al., 2012). Although radio telemetry has been used to track the routes and timing of migration of long-distant migratory waders which use a narrow and predictable corridors, e.g., bar-tailed godwit (*Limosa lapponica*) (Green et al., 2002b), other devices e.g., geolocators, Platform Transmitter Terminal (PTT) and GPS devices have been more widely used to look at long-distance seasonal movements.

Geolocators have remained the most commonly used device to track long distance migrants of waders since there were first deployed on small passerines (Stutchbury et al., 2009). Geolocator devices record time and light-level data enabling the reconstruction of latitudes and longitudes over time. The need to re-capture the birds to retrieve the device and the inherent difficulties caused in determining latitude from recorded light-levels for high Arctic-breeding species posed the greatest challenges for the use of geolocators in wader studies. Nevertheless, geolocators have been used to determine the location of breeding and wintering sites and their connectivity (i.e., use of stop-over sites) as well as the timing of migration and site fidelity of long-distant migratory waders (Giunchi et al., 2015; Johnson et al., 2015; Lislevand & Hahn, 2015; Lisovski et al., 2016a; Lisovski et al., 2016b). Recent studies using geolocators have, for example, given new insights into the transoceanic non-stop flight undertaken by waders ranging from 4,100 km to 8,700 km for Pacific golden plover (*Pluvialis fulva*) between Alaska and wintering grounds in Oceania (Johnson et al., 2015). Geolocators have also been used to examine the movement of short-distant migrants in response to temperature e.g., cold weather movements in wintering European golden plover (*Pluvialis apricaria*) (Machín et al., 2015). In addition to tracking the full annual cycle, breeding activity (incubation and chick brooding) can be inferred from geolocators, e.g., great knot (*Calidris tenuirostris*) study (Lisovski et al., 2016b).

Satellite tags (also referred to as Platform Transmitter Terminal (PTT)), which have a higher spatial precision than geolocators, have also been used to study wader migration. They are typically heavier and their use has been limited to larger species. Implanted in the bird or attached to a harness, they have been widely used in Numeniini to examine migration strategies e.g., Eastern curlew (*Numenius madagascariensi*s) (Driscoll & Ueta, 2002), black-tailed godwits (Hooijmeijer et al., 2013), bar-tailed godwits (*Limosa lapponica baueri)* (Gill Jr et al., 2009), winter habitat use e.g., long-billed curlew (*Numenius americanus*) (Olalla-Kerstupp et al., 2015b) and site fidelity to wintering, stop-over and breeding sites (Olalla-Kerstupp et al., 2015a).

The space and habitat use of waders is increasingly being examined using GPS devices which can transmit the data automatically to a receiver or a mobile network. For example, the use of GPS tags on oystercatcher during the breeding season in the Wadden Sea showed that habitat use was strongly dependent on abiotic factors: individuals preferred muddy and low-lying tidal flats with short exposure times close to their breeding sites (Schwemmer et al., 2016b). Using glue-mounted GPS loggers on six breeding curlew in southern Scotland, Ewing et al. (2017) demonstrated differences in activity patterns and habitat uses for different stages of the breeding cycle. Habitat use and site fidelity of wintering curlew have also been examined on the Humber Estuary based on a small sample of GPS-tagged individuals (Cook et al., 2016). Using a different type of attachment (i.e., harness), the migration routes of four curlew were tracked using GPS loggers in the Wadden Sea (Schwemmer et al., 2016a). In addition to showing temporal and spatial patterns during migration, the study showed high site fidelity of curlew to roosting sites in winter, confirming findings of mark-recapture studies e.g., Rehfisch et al. (2003).

Whilst telemetry work to date on wintering curlew has shown a high level of site fidelity, the studies have been based on small samples of birds. GPS tracking of a greater number of individuals offers the possibility of examining variation in individual wintering strategies, as well as variation in habitat use between sexes and over time. Tracking data on curlew thus have the potential to fill the gaps in knowledge on wintering ecology of curlew. Currently, assumptions about bird movements and the value of different habitat types are made without strong evidence. Furthermore, as we try to predict the impact of habitat mitigation and habitat loss in the estuarine environment, it is crucial that we gain a better understanding of animal movements to predict the fitness consequences for waders. For example, such data can be incorporated in ‘agent-based models’ (ABMs) or ‘individual-based models’(IBMs) developed to predict the consequences of environmental changes on individual fitness.

1.5 The development of individual-based models (IBM) to predict the consequences of environmental changes on fitness of waders.

At designated sites across Europe, bird populations should be maintained or restored to a favourable condition (i.e., with respect to their size). Understanding and predicting the effect of environmental changes on the fitness (body condition, survival and breeding success) of wintering waders in estuaries is therefore a key challenge to address in the conservation of their populations. Prey availability is a key factor that determines the distribution of estuarine waders in winter (Prater, 1981). On estuarine tidal flats, wader species are continuously making foraging decisions, with their benthic prey varying in availability and accessibility across the mudflats. Despite an abundance of organisms on the tidal flats, the prey selected might not be accessible to waders for a large portion of the day because of tidal and temperature influences on burying depths. Furthermore, shallow and accessible prey often have a relatively poor body condition (Zwarts & Wanink, 1991). Handling efficiency is an important factor that drives foraging strategies of waders e.g., a bird will not target small size animals because of the low handling efficiency (Zwarts & Blomert, 1992). Paradoxically, waders must consider other factors than simply maximising their food intake rate e.g., risk of choking on large prey items or damage to the bill when increasing feeding rate (Van de Kam et al., 2004).

Knowing the densities, mass and rate of depletion of waders' invertebrate prey over the winter is also crucial to understand the prey-predator relationship. The asymptote in the functional response between intake rate, measured as the ash-free dry mass (AFDM) per second of active foraging, and prey abundance (Goss-Custard et al. (2006b) is critical (Figure 1.4). Crucially, the asymptote of the functional response of a shorebird can be predicted only using two variables (i.e., bird and prey sizes) providing the birds are not breeding and are not oystercatchers eating mussels (Goss-Custard et al., 2006b). As such, the asymptote can be reliably predicted from just four easily measured variables. The foraging decisions that the birds make are underpinned by the 'Optimal Foraging Theory' (MacArthur & Pianka, 1966) and the 'Game Theory' (Smith, 1982). These theories are the foundation in the development of a generation of models that can predict the impact of environmental changes on individual bird fitness (e.g., survival). Models – underpinned by these theories – have evolved from 'habitat association models' to 'agent-based models' or 'individual-based models'. Whilst 'habitat association models' can examine changes in bird abundance, the functional relationships between predators and prey is not considered. In contrast, ABMs/IBMs includes the functional relationships between predators and prey and thus capable of predicting the impacts on demography.

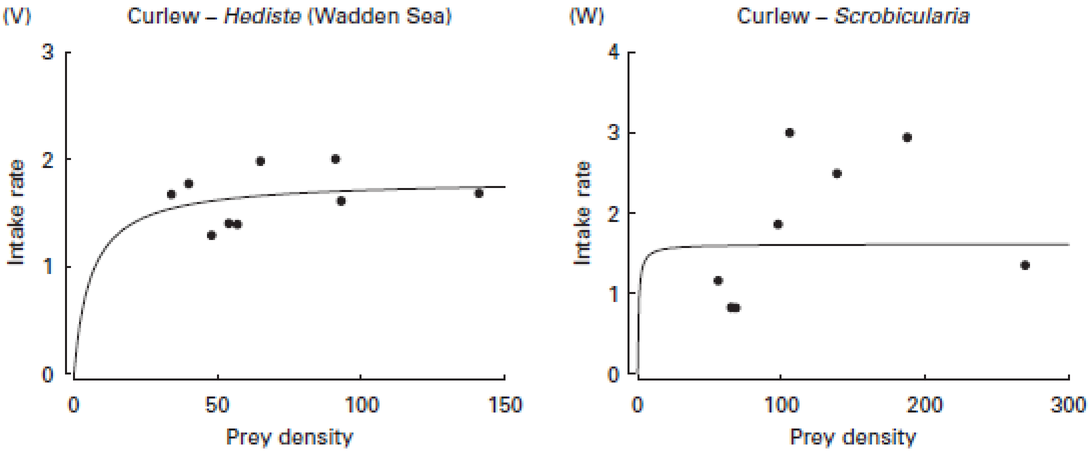

Figure 1.4. Functional responses of curlew eating *Hediste* and *Scrobicularia*: intake rate (mg ash-free dry mass sx1) against numerical density of the prey (number mx2). The solid lines show the fitted asymptotic hyperbolic functions (equation 1) either for prey of all sizes or just for large prey, the data points for which are filled circles (Goss-Custard et al., 2006b).

Work on assessing the impacts of environmental change on waders has evolved since an early 'habitat association model' was developed in response to a proposed tidal barrage on the Severn Estuary (Goss-Custard et al., 1991). By examining the relationship between bird abundance and non-static (e.g., prey abundance) and static environmental variables (e.g., sediment parameter) in six estuaries, a ‘habitat association’ model attempted to derive an equation to predict invertebrates’ densities following the barrage construction. Since then, more complex ‘habitat association models’ have been constructed by establishing the empirical relationship between environmental predictor variables (e.g., shore-width and sediment composition) and bird abundance e.g., see Yates et al. (1996); Burton et al. (2010). However, the main drawback of these simplistic approaches is the uncertainty of the predictions as the empirical relationships on which the model is developed may not hold under new conditions (West & Caldow, 2006).

In addition to ‘habitat association models’, ‘spatial depletion models’ or ‘ration models’ have also been developed to examine the response of waders to habitat management (Gill et al., 2001b). Although ‘spatial depletion models’ are based on the components of the functional response, these models are limited because they do not take account for the interference between individuals, the variation in foraging abilities between individuals and the birds’ physiology (i.e., body condition). Moreover, similarly to ‘habitat association models’, they cannot predict how environmental change influences the body condition and thus survival of birds (Stillman & Goss-Custard, 2010a).

Because of a growing awareness of the limitations of these approaches in predicting the impact of environmental changes on bird populations (West & Caldow, 2006; Stillman, 2008), alternatives have been developed. The field of individual-based ecology has provided a new framework for scientists to simulate animal behaviour in realistic environments (Grimm & Railsback, 2005). IBMs/ABMs have become an established approach with numerous platforms available (DeAngelis & Diaz, 2019); the IBMs/ABMS simulate the interactions of autonomous organisms (referred to as ‘agents’) with other organisms and their environment. The development of IBM/ABM platforms in ecology along with the realisation that individuals amongst a population behaved in different ways has contributed to the numerous implementations of decision-making rules in IBMs/ABMs, from simple rules to highly complex ones (DeAngelis & Diaz, 2019).

Thirty years of research has gone into developing a modelling platform for waders: the MORPH model (Stillman, 2008). The model simulates how birds obtain their food across patches to meet their daily energy requirement; the model is based on the key principle that individuals continuously make fitness-maximising decisions. The MORPH model allows the prediction of feeding time, distribution of birds, body condition and mortality – the latter two being measures of individual fitness. Details of the MORPH model are presented in Stillman (2008), and a recent user-friendly version of the MORPH model is also presented in West et al. (2011). There exists extensive literature detailing the development of the MORPH model and its application to address shorebird conservation issues (West & Caldow, 2006; Goss-Custard & Stillman, 2008; Stillman & Goss-Custard, 2010b; 2010a).

MORPH is based on earlier work on 'behaviour-based models' (synonymous for IBM). The first behaviour-based models developed for waders used an empirical game theory distribution model to simulate bird-decision making processes in estuaries; game theory assumes that birds vary in their competitive ability and foraging efficiency. The game theory model was first developed on the Exe Estuary (UK) on oystercatcher to predict intake rates (Goss-custard et al., 1995a) and a similar approach was used to predict the consequences of winter habitat loss on oystercatcher (Goss-custard et al., 1995a; Goss-Custard et al., 1995b) and the strength of the interference between foraging oystercatcher (Stillman et al., 1997).

Building on from the work in the Exe Estuary where the first IBM was tested and parametrised for oystercatcher (Stillman et al., 2000), it was recommended that the model could be applied to predict the impact of a range of environmental effects. Since then, the model has been used to explore the effect of shellfisheries management and human disturbance (Stillman et al., 2001; West et al., 2002; Stillman et al., 2003) on the survival and on the numbers of oystercatchers in the Exe Estuary; it has also been used to examine the relationship between over-wintering mortality of oystercatcher and the amount of food available in autumn (West et al., 2005). Within the IBM modelling framework, the functional response is a key parameter derived from extensive field observations (e.g., oystercatcher in the Exe Estuary), and thus this parameter limited the application of the model to other species and sites. However, an extensive review of intake rates found that the functional response of waders could be predicted (Goss-Custard et al., 2006b). From this equation, it became possible to apply the IBM developed on the Exe Estuary to other sites and species.

The MORPH model has become an important tool to predict waders' response to environmental changes (West & Caldow, 2006) and has been applied to a range of scenarios looking at the following effects: environmental changes on site quality for waders (Stillman et al., 2005; Durell et al., 2006); the impacts of habitat loss and mitigation on shorebird mortalities (Durell et al., 2006; Goss-Custard et al., 2006a), disturbance on coastal birds (Stillman et al., 2007); hunting and disturbance (Durell et al., 2008), warm-water flows in estuary (Garcia et al., 2016), regime shifts of invertebrates (Bowgen et al., 2015) and oyster reefs as supplementary foraging habitats for waders (Herbert et al., 2018).

The impacts of the loss of intertidal habitats due to anthropogenic activities on shorebird survival rates has been predicted using IBMs in the Seine Estuary (France) and in the Severn Estuary (UK) (dit Durell et al., 2005; Goss-Custard et al., 2006a). Both studies also predicted the efficacy of proposed mitigation measures though findings differed between the two studies. In the Severn Estuary, a mitigation area equivalent to 10% of the area lost due to barrage development was sufficient to maintain the survival of common redshank displaced after habitat lost whilst in the Seine Estuary a mitigation area equivalent to the one lost was necessary to maintain the fitness of dunlin (*Calidris alpina*) pre-port extension.

The predictions of the IBMs in these two studies show the response to habitat loss may vary between species and sites. On the Seine Estuary, curlew were not affected by habitat loss whereas dunlin and oystercatcher were, presumably because the latter two species were present in higher densities (dit Durell et al., 2005). Furthermore, the model on the Seine Estuary did not account for the possibility of curlew foraging on non-estuarine habitats, which influence the ability of birds to maintain fitness in the event of habitat loss on intertidal areas. Feeding strategies may also explain the differences in the species' response to habitat loss. Bowgen et al. (2015) in a study of invertebrate regime shifts occurring in estuaries found that species such as curlew – which have a more specific foraging strategy – will be first affected, with the species having to shift to terrestrial resources which are less profitable. Curlew is one of the few wader species that frequently feed on terrestrial habitats; however, to date IBMs have seldom incorporated terrestrial foraging patches as a parameter (Stillman et al., 2000). Stillman et al. (2005) found that terrestrial fields around the Humber Estuary (UK) were critical to maintaining high curlew survival in winter. Simulations in which curlew were able to feed in fields during the hours of daylight predicted survival rates of 90–100% – assuming an intake rate of 0.5 to 1 mg AFDM s^{-1} when feeding in the fields (Stillman et al., 2005).

It is apparent that terrestrial habitats play an important role as a supplementary foraging resource for curlew in estuaries. Information is however lacking on terrestrial food resources, especially where the hinterland of the estuaries is dominated by arable land, as in the Humber Estuary. Where foraging patches resources become available, simulations with an IBM make it possible to determine the effect of terrestrial habitat provision on curlew winter survival; it is also possible to determine whether sexual differences in survival exist – as male curlew as most likely to feed on terrestrial habitats (Townshend, 1981).

In parallel, new mitigation measures (i.e., managed realignment sites) designed to offset for the loss of intertidal areas have been created in the Humber Estuary. Understanding the impact of mitigation measures is also crucial as these schemes are created to maintain populations of waders in favourable condition in estuaries. The Humber Estuary, with several existing realignment sites and others in planning, provides a good opportunity to examine the impact of these schemes on wader fitness, particularly on curlew which has a Near Threatened status on the IUCN Red-list (BirdLife International, 2021); the species is also Red-listed in the UK Birds of Conservation Concern (Stanbury et al., 2021). The ecological success of re-created intertidal habitats is assessed based on changes in bird numbers, their food resources (e.g., halophyte plants and benthic invertebrates) and abiotic factors (e.g., sedimentation processes), but to date, studies have not addressed the consequences for individual bird fitness e.g., body condition and survival. A better mechanistic understanding of the impacts of habitat re-creation on wader populations is needed, especially given that these schemes are being created in response to major environmental changes (e.g., sea-level rise) across estuaries in northwest Europe.

1.6 Project aims and objectives

Through complementary packages of work, the overall aim of the study is to examine the effectiveness of compensatory habitats for waders, and in particular for a Near Threatened wader species: the curlew. This thesis first aims to examine changes in wader abundance according to geomorphological changes at an existing managed realignment site (Chapter 2). I then use GPS tracking data to determine the home range (Chapter 3) and resource use (Chapter 4) of curlew in an area featuring an estuarine habitat restoration scheme. Finally, I aim to parameterise an individual-based model by considering movement data from GPS-tracked curlew and validate the model with data on behaviour and fine-scale habitat use (Chapter 5). The model aims to predict the effect of habitat creation on curlew survival.

The following hypotheses will be tested:

- The abundance of waders within a managed realignment site is driven by change in elevation;
- Home range size may change through the non-breeding season as a function of resource depletion and between winters, reflecting changes in resource availability;

- Home range size may be driven by individual strategies related to sexual dimorphism, and thus that home range sizes may differ between males and females;
- Home range might be smaller at night because of the greater risk of predation in intertidal and terrestrial habitats;
- Habitat selection may reflect the individual strategies of curlew; and
- Curlew winter survival is positively influenced by the provision of compensatory habitats during the non-breeding season.

1.7 Thesis structure

Chapter 1: The use of modern telemetry and predictive modelling in assessing the success of estuarine habitat creation for waders.

Chapter 2: Long term changes in the abundance of benthic foraging birds in a restored wetland.

Chapter 3: Individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Eurasian curlew (*Numenius arquata*).

Chapter 4: GPS tracking of Eurasian curlew (*Numenius arquata*) to examine non-breeding habitat selection in coastal habitats modified by shoreline management.

Chapter 5: Using Eurasian curlew (*Numenius arquata*) GPS tracking data to inform an individual-based model at an estuarine restoration scheme.

Chapter 6: Discussion and concluding remarks.

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Chapter 2 Long term changes in the abundance of benthic foraging birds in a restored wetland

2.1 Abstract

Estuaries have historically been subject to considerable habitat loss, and continue to be subjected to such in areas where the natural landward migration of intertidal habitats is constrained by hard coastal defences. Thus, in estuaries where direct (e.g., port development) or indirect (e.g., sea-level rise) processes are predicted to threaten intertidal habitats and associated waterbird species, there is a regulatory requirement to produce compensatory intertidal habitats. Managed realignment (MR) is a shoreline management practise that is undertaken to build sustainable coastal defences and create intertidal habitats in estuaries. This nature-based solution brings multiple benefits in the form of carbon storage, increased resilience to flooding, and, potentially, the formation of new habitats, which is the topic of this study. A 75-ha site at the Paull Holme Strays (Humber Estuary, United Kingdom) was monitored over a 10-year period following MR to examine the change in the abundance of waterbirds in the chosen site in response to the physical processes occurring there. Using digital terrain models (DTMs) collected via light detection and ranging (LiDAR), we examined how four compensatory target species responded to changes in elevation after the creation of the site. It was shown that the very rapid accretion of estuarine sediment occurred in the first decade of the new re-created intertidal, which, over time, led to changes in the numbers of benthic foraging birds supported. Furthermore, elevation change was also driven by this sediment accretion, the rate of which depended on the initial bed elevation of the sectors within the site. Ten years after the recreation of the habitat, the spatial heterogeneity in the bed elevation remained high; however, the sectors with the lowest elevations accreted the most over the 10-year period. The foraging number of the four waterbird species that colonised the MR site significantly declined above a certain elevation, with this effect being most pronounced for the Eurasian curlew (*Numenius arquata*). The number of common shelduck (*Tadorna tadorna*), dunlin (*Calidris alpina*), and common redshank (*Tringa totanus*) declined significantly after initial peaks 5–7 years after the creation of the site, reflecting the ongoing elevation changes. Thus, this study highlighted the need for long-term studies to understand how species respond to large-scale habitat construction. It can also aid in predicting the suitability of an MR site for waterbirds in the medium and long term.

2.2 Introduction

Historically, large intertidal areas have been claimed from the sea. Estuarine wetlands, however, continue to be lost at an alarming rate across the globe. For example, in the Yellow Sea (East Asia), the rate of loss of intertidal areas has risen dramatically over the last decades (Yang et al., 2011). In Europe, most countries have estimated the losses of coastal wetlands and sea grasses as exceeding 50% of the original area (Airoldi & Beck, 2007). In the United Kingdom (UK), the land claims for agricultural, residential, and industrial developments have historically affected at least 85% of estuaries (Davidson et al., 1991), with an overall estimated loss of 913 km^2 of estuary area and 550 km^2 of saltmarsh area by the end of the twentieth century (Davidson et al., 1991). With the implementation of greater site protection (Stroud et al., 2016), large-scale intertidal land reclamations for agricultural and residential developments have eased; however, small expanses of intertidal areas continue to be claimed for infrastructure projects that are deemed to be of public interest, such as port developments and coastal protection.

Waterbird species that rely heavily on intertidal areas during the non-breeding season may be significantly affected by habitat loss. By reducing the carrying capacity of an estuary, habitat loss can increase the potential for interference competition among waterbird species in remaining areas (Goss-Custard et al., 2002). While waterbirds can respond to estuarine habitat loss by emigrating to another estuary (Yang et al., 2011), many of them are site-faithful and, thus, may only move locally in response to a loss of habitat (Burton & Armitage, 2008), which increases local densities and, consequently, competition for resources (Stillman et al., 1997). This may affect individual fitness, i.e., body condition and survival rates (Burton et al., 2006), while effects can also be carried over to impacts on the breeding productivity of birds, with ultimate impacts on population size (Baker et al., 2004; Piersma et al., 2016; Studds et al., 2017). In response to these observations, the creation or restoration of intertidal habitats can help to mitigate the effects of non-breeding habitat loss and the deterioration of intertidal habitats (Atkinson, 2003). By increasing the overall carrying capacity of estuaries, the creation of new intertidal habitats may reduce the effects of interference competition on the individual fitness of waterbirds.

With the loss of intertidal habitats being of growing conservation concern to wader populations across the globe (Sutherland et al., 2012; Pearce-Higgins et al., 2017), the re-creation of intertidal habitats offers a solution to mitigate impacts on waterbird populations and other benefits for carbon and nitrogen storage and increased flood protection. Habitat restoration and creation are driven either directly or indirectly by environmental policies (e.g., Clean Air Act in the United States of America, USA) and the European Union Habitats Directive (92/43/EEC) in European Union (EU) countries. In northwest Europe, where tidal flats in estuaries are often constrained by flood defences, the realignment of flood defences is the preferred shoreline management practise to re-create intertidal areas (Esteves, 2014). This shoreline management practise is also known as managed realignment (MR), managed retreat, or depolderisation. It consists of moving the flood defences landward while breaching the existing defences and allowing the tidal flooding of terrestrial habitats to increase the intertidal area. Of a total of 98 MR sites across the globe, 51 are located in the UK, equating to a total of 24 km^2 of intertidal habitats (ABPmer, 2021). These sites were created to offset the loss of intertidal habitats due to port developments, flood defence work, and environmental changes, e.g., sea-level rise.

The ecological success of re-created intertidal habitats is difficult to measure, although it is usually based on the broad principle that the re-created intertidal areas should exhibit processes that are found in natural intertidal flats (Atkinson, 2003). Geist and Hawkins (2016) emphasised the need to define a clear target state in an aquatic restoration scheme. However, when creating intertidal habitats, outcomes can be unpredictable and may not match the desired goals, for example, as waterbird communities evolve over time in response to physical and biological processes (Evans et al., 1998; Brusati et al., 2001; Armitage et al., 2007).

In the United Kingdom, monitoring studies at MR sites have been short-term but have focussed on both physical and biological developments (Garbutt et al., 2006; Mazik et al., 2007; Garbutt & Boorman, 2009) with some examples of studies on waterbird colonisation (Evans et al., 1998; Atkinson et al., 2004; Mander et al., 2007). The re-created intertidal habitats monitored for wintering waterbirds in the UK have been small in size, but the studies at these sites have shown that natural waterbird communities may be successfully reproduced in just a few years (Atkinson et al., 2004; Mander et al., 2007). In these studies, the ecological state of the MR was judged against ‘reference’ or ‘control’ sites.

The use of newly created intertidal areas by foraging waterbirds depends primarily on the colonisation of benthic invertebrates, which themselves are driven by the deposition of sediment. This could be rapid in highly turbid environments where siltation rates are high (Mazik et al., 2010). However, over time, these high siltation rates may also result in the increase in the elevation of mudflats through accretion and eventual colonisation by saltmarsh vegetation, consequently lessening the suitability of re-created intertidal habitats for foraging waterbirds (Morris, 2013; Pontee, 2014). Thus, there needs to be a better understanding of the physical factors that control the abundance of waterbirds in MR sites and their long-term sustainability.

At Paull Holme Strays MR (Humber Estuary, UK, Figure 2.1), 0.75 km^2 of intertidal areas were re-created through the realignment of flood defences. Initially, the aim was to create ~ 0.32 km^2 of mudflat (42%) and 0.43 km^2 of saltmarsh (56%) (Edwards and Winn (Edwards & Winn, 2006). Besides habitat creation, specific biodiversity targets were set by the stakeholders in the form of minimum population targets: the site was to support the foraging populations of a total of 30 individuals consisting of the common shelduck (*Tadorna tadorna*), Eurasian curlew (*Numenius arquata*) (hereafter curlew), dunlin (*Calidris alpina*), and common redshank (*Tringa totanus*). These species were affected by habitat losses resulting from flood defence improvements in the Humber Estuary (Edwards & Winn, 2006; Environment Agency, 2007). In winter, all four target compensatory species rely on intertidal benthic prey in estuaries and, thus, expected to forage on the developing mudflat in the MR site. Across the Humber Estuary, moderate (25–50%) decreases in the abundances of curlew and common redshank were recorded by the national Wetland Bird Survey (WeBS) between 2000/2001 and 2015/2016, while common shelduck and dunlin numbers remained stable (Woodward et al., 2018).

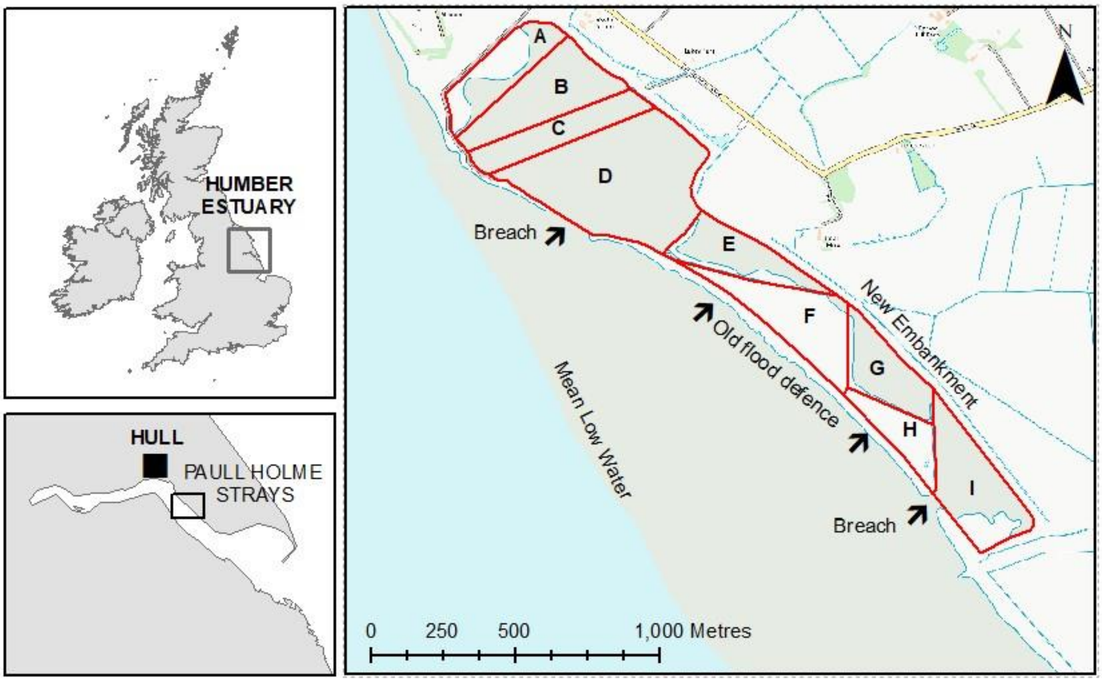

Figure 2.1. Location of the Paull Holme Strays managed realignment (MR) site on the Humber Estuary and sectors surveyed.

The MR site was created in 2003 and subjected to an 11-year monitoring programme on waterbirds. A previous study at the site indicated a rapid change in the waterbird community structure in the first 3 years of habitat creation following the transition from agricultural land to intertidal areas (Mander et al., 2007). High accretion rates, low elevation, and a lack of compaction in created borrow pits resulted in rapid colonisation by estuarine invertebrates (Mazik et al., 2007).

This study extended this temporal and spatial dataset to assess the long-term trends of waterbirds and changes in bird abundance in response to geomorphological changes occurring in the re-created intertidal habitats. The focus was on the four benthivorous species that were listed as compensatory requirement targets at the Paull Holme Strays MR: the common shelduck and three waders, namely, the curlew, dunlin, and common redshank. A generalised additive modelling approach was then followed, aiming to investigate the hypothesis that the relative use of areas within the site by foraging benthivorous species is determined by differences in elevation, which are associated with the pre-breach natural landscape conditions of the MR site and driven by sedimentary processes taking place over time (i.e., change in elevation due to accretion). It was also predicted that foraging benthivorous species would favour the intertidal habitats of a given elevation range and that, above this shore level, usage would decrease.

2.3 Methods

2.3.1 Study area

The study was carried out at the Paull Holme Strays MR site (53º44´N, 0º16´W), in the Humber Estuary Special Protection Area (SPA) and Ramsar site, UK (Figure 2.1). The Humber Estuary is an important wintering and stopover site for several East Atlantic Flyway waterbirds, supporting over 150,000 waterbirds in the winter (Stroud et al., 2016; Frost et al., 2021). Although, historically, the site was a wetland habitat before being claimed for agriculture (in ca. 1,700), the Paull Holme Strays site was opened to the estuary through the realignment of the sea wall in September 2003. Two breaches were then created, allowing the tidal flooding of the site and the subsequent development of intertidal habitats (Figure 2.1).

The MR site provides compensation for direct and immediate habitat losses resulting from the tidal defence improvement works carried out in the middle estuary in 2003. Flood defence work improvement in the middle Humber Estuary produced immediate losses of 0.005 km^2 of mudflat and 0.003 km^2 of saltmarsh, with a compensation ratio of 3:1 then being applied to these direct losses. The estuary also aimed to provide compensation for future losses associated with coastal squeeze, with a further 0.056 km^2 of mudflat and 0.05 km^2 of saltmarsh predicted to be lost because of this phenomenon as a result of flood defence work improvements in the middle estuary (Environment Agency, 2007). Thus, a compensation ratio of 1:1 was applied to these indirect losses.

Following the breach of the existing seawall at the Paull Holme Strays in September 2003, both intertidal saltmarshes and mudflats developed in line with the predicted or desired habitat ratio before the breach, with a high proportion of saltmarshes established (58% in 2013) at the expense of mudflats (39% in 2013), with the rest (3%) being terrestrial habitats in 2013 (Brown, 2014). The mean high-water spring tidal height in the area was 3.7 m, while the neap tidal height was 2.1 m [measured at King George Dock, 6 km upstream from the Paull Holme Strays site and heights are given above UK ordinance datum (OD, the mean sea-level)]. The MR site was high in tidal frame, as the elevation of the sediment surface varied between 2.78 and 3.65 m above OD in 2013. Because of its position on the tidal frame, the site remained dry on neap tides.

Nine areas (sectors) were defined within the site, delimited by remnant drainage channels from the former agricultural landscape (Figure 2.1). The size of the sectors varied between 0.07 (sector A) and 0.18 km^2 (sector D), with each sector being associated with distinct geomorphological characteristics (e.g., different geometry and bed elevations) and dominant habitat types at the pre-breach stage (Table 2.1). Before habitat creation, the MR site consisted of arable fields intersected by drains. The site also featured a soak dyke beyond the existing wall. A site intervention before the breach further modified the site through the creation of a series of borrow pits/pools, which resulted in sectors of the MR site varying considerably in initial elevation (Figure 2.2).

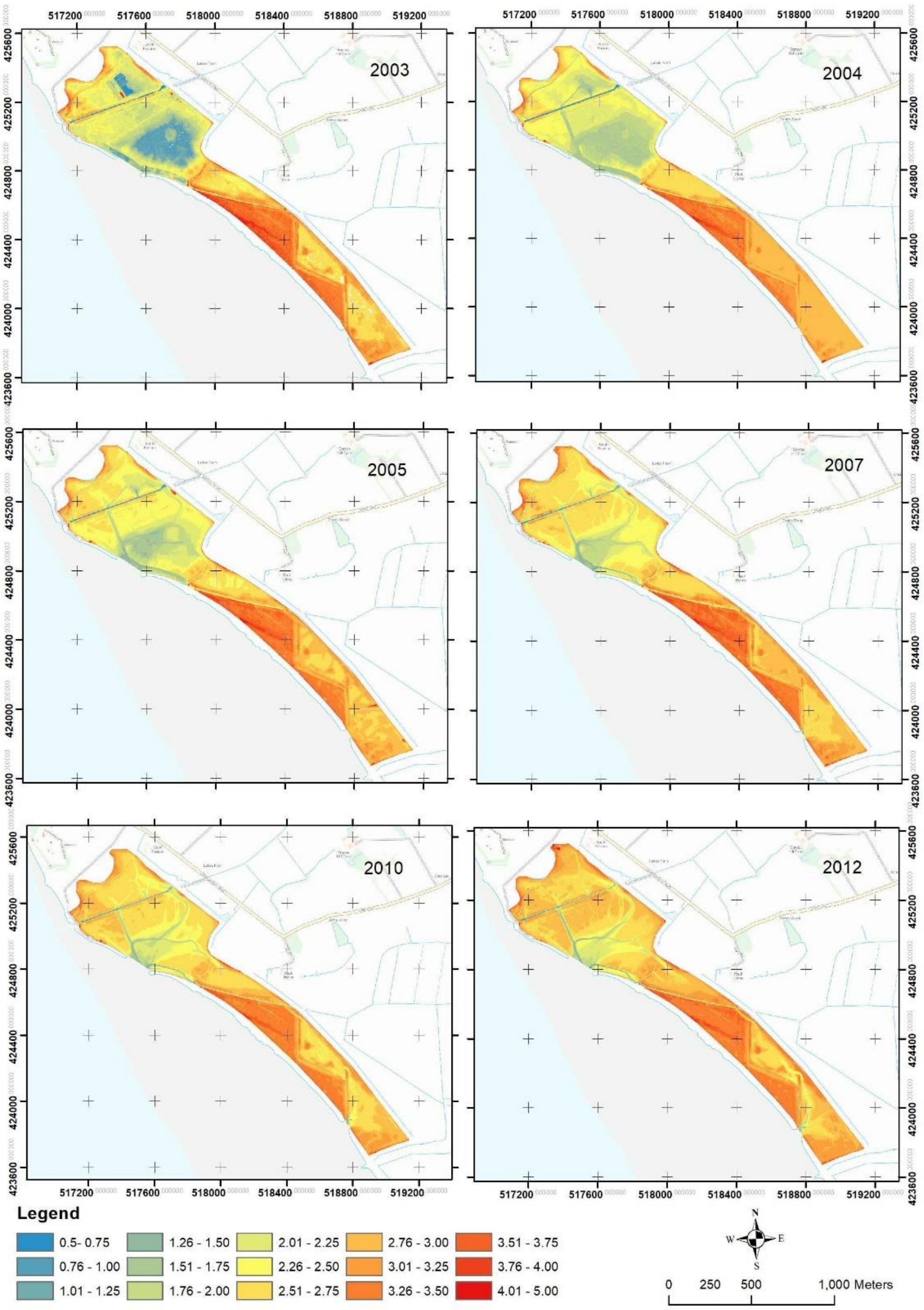

Figure 2.2. Elevation in the MR site between 2003 (Year 1) and 2012 (Year 10) derived from a digital terrain model (DTM). For the dates of the measurements, see Table 2.1.

The MR site was well connected to established intertidal habitats, as it was fronted by an extensive mudflat and sandflat supporting an assemblage dominated by foraging waterbirds during tidal emersion, such as common shelduck and waders such as curlew, dunlin, and common redshank. Other foraging wildfowl such as teal (*Anas crecca*), wigeon

(*Anas penelope*), and mallard (*Anas platyrhynchos*) were also present, albeit in lower numbers (Mander & Cutts, 2005; Calbrade, 2013).

Table 2.1. Size and dominant habitat prior habitat creation of sectors within the Paull Holme Strays MR.

Recording sectors	Area (km^2)	Dominant habitat types pre-breach
A	0.07	Arable fields
B	0.11	Arable fields and excavated pools
C	0.06	Arable fields and excavated pools
D	0.18	Arable fields and excavated pools
E	0.07	Arable fields and excavated pools
F	0.08	Arable fields and dykes
G	0.06	Arable fields and excavated pools
H	0.03	Arable fields and dykes
I	0.09	Arable fields and excavated pools

2.3.2 Geomorphological changes in the MR

We used digital terrain models (DTMs) collected via light detection and ranging (LiDAR) to investigate the temporal geomorphological changes following the tidal inundation of the site. LiDAR is an airborne mapping technique that uses a laser to measure the distance between the aircraft and the ground, allowing highly detailed terrain models to be generated at spatial resolutions of between 25 cm and 2 m. All LiDAR data have a vertical accuracy of ±15 cm root mean square error (RMSE). The LiDAR data in this study are open-source and can be obtained from environment.data.gov.uk. Digital terrain model (DTM) data were processed in ArcGIS to examine changes in elevation on a sectoral basis over the years.

2.3.3 Waterbird counts

Following the breach of the flood defence in September 2003, waterbird abundance was monitored at the MR site between the winters of 2003/2004 (Year 1) and 2013/2014 (Year 11). Over half a tidal cycle (either on the flood or ebb), counts were undertaken at low, mid, and high tide once a month each winter from October to March. For the first five years, counts were undertaken all year round but reduced in frequency after five years to cover the over-wintering period (October to march). As such, it was not possible to include the spring and autumn passage counts. While the survey dates coincided with the half tidal cycle during hours of daylight, they were also determined by weather conditions (heavy rain and strong winds were avoided). In total, 174 counts were made over an 11-year period.

Sectors of the MR site (A to I, (Figure 2.1)) were used as recording units. The counts of sectors A to H were made from vantage points located along the new and old flood embankments, with each sector surveyed consecutively from one or two specific vantage points (depending on wind, glare, and tidal state). The counts of sector I were undertaken from a single vantage point (a bird hide located on the old flood embankment). A single observer carried out the counts on foot using a telescope with 25× and 60× eye pieces and 10 × 50 binoculars. Counts of the site took approximately 2 hrs. Disturbance to the avifauna was minimised by accessing the vantage points from below the bank. Species abundance and behaviour (foraging and non-foraging) were recorded within each sector of the MR site from Year 2 to Year 11. Counts were recorded for the MR site as a whole in Year 1, with bird recording sectors not being defined until Year 2. Waterbirds were categorised as foraging when actively looking for food or non-foraging when they were roosting, loafing, preening, etc.

2.3.4 Describing changes in bird abundance and elevation

The temporal changes in the abundance of functional groups and individual species over the 11-year monitoring period were assessed by analysing counts of foraging birds alone, as this was reflective of the quality of the intertidal habitat, with low-, mid-, and high-water counts for each monthly survey considered in the analysis.

While assemblages can be defined according to the taxonomic identities and abundances of those species, it has been increasingly viewed as valuable for defining communities according to species functional characteristics (Mendez et al., 2012). Accordingly, waterbird species were grouped into five trophic guilds based on their winter diet preferences on UK estuaries (Cramp & Simmons, 1983): (i) herbivorous geese, swans, and ducks; (ii) benthivorous ducks; (iii) omnivorous ducks and rails; (iv) piscivorous grebes, cormorants, and herons; (v) benthivorous waders (Appendix 1). The annual abundance of each functional group (i.e., foraging guild) at the MR site was calculated by summing the monthly counts undertaken between October and March and the relative abundance of each functional group considered as the proportion of the abundance of the overall waterbird assemblage.

Temporal changes in the monthly foraging abundances of the four target benthivorous species associated with the MR compensatory requirement site, namely, common shelduck, curlew, dunlin, and common redshank, were also examined using box plots.

Finally, the annual changes in the elevation of sectors, which were used as a proxy for the geomorphological changes in the MR site, were examined between 2003 (Year 1) and 2012 (Year 10). The mean elevation (in mm) was calculated for each recording sector for the following years: 2003, 2004, 2005, 2007, 2010, and 2012. Data for the years 2006, 2008, 2009, and 2013 were excluded from the analysis because they only had partial LiDAR coverage of the MR site (Table 2.2).

Table 2.2. Bird count periods with their corresponding light detection and ranging (LiDAR) periods.

Bird count	Year	LiDAR Year	Date of LiDAR image taken
Oct 03 to Mar 04	1	2003	12th and 15th July
Oct 04 to Mar 05	2	2004	18th and 31st July
Oct 05 to Mar 06	3	2005	16th and 22nd Sep
Oct 06 to Mar 07	4	n/a	
Oct 07 to Mar 08	5	2007	10th and 29th Sep
Oct 08 to Mar 09	6	n/a	
Oct 09 to Mar 10	7	n/a	
Oct 10 to Mar 11	8	2010	31st Jan and 2nd March
Oct 11 to Mar 12	9	n/a	
Oct 12 to Mar 13	10	2012	16th Dec
Oct 13 to Mar 14	11	n/a	

2.3.5 Modelling bird responses to geomorphological changes in the MR site

The effects of elevation on the foraging abundances of dunlin, curlew, common redshank, and common shelduck were tested using generalised additive models (GAMs) in the mgcv package (R Core Team., 2021). These GAMs were selected in order to account for the potential non-linearity in the responses of the birds to elevation changes (Wood & Augustin, 2002). The analysis considered the monthly winter counts of each species at low, mid, and high water in each sector. The dataset used for the analysis included Years 2, 3, 5, 8, and 10. Year 1 was excluded because bird counts were not undertaken at an individual sector level, while Years 4, 6, 7, 9, and 11 were excluded because the elevation data from the LiDAR were incomplete. Measurements of elevation for each year were included as a predictor using thin-plate regression splines as the smoothing function (Wood, 2003). Assuming that the state of the tide would influence the use of MR habitats by foraging birds, tidal height at the time of observation was included as a continuous predictor in the model structure. We also fitted a factor-smooth interaction between tide height and elevation to account for variable relationships between the two variables. Furthermore, year was included to account for the possible annual differences in the overall numbers of birds using the site, reflecting the development of the habitat of the site following its creation in 2003 and wider patterns across the estuary. To disentangle absolute elevation and elevation change, an interaction between sector and year was included, with sector being used as a random factor. Day within the winter (since October 1) was also included to account for seasonal variations in numbers. A Poisson distribution in the GAM structure was initially performed and tested for over-dispersion using the DHARMa package. Since the results indicated the model to be mis-specified, we chose to perform a negative binomial distribution to model bird abundance, as negative binomials are used for count data when the variance is much larger than the mean (Zuur et al., 2009). In the dataset, the mean number of birds was 10.48 and the variance was 1702.22. The significance of each variable included in the models was tested using Wald tests (Wood, 2013a; 2013b), and the importance of the model terms was assessed accordingly.

Correlations in the residuals from the models were examined using the autocorrelation function (ACF) and partial autocorrelation function (PACF) in R (R Core Team., 2021). A model diagnostic was undertaken (gam.check in the mgcv package); this command provided graphical model outputs that examined the homogeneity and normality of the unstandardised residuals (Appendix 3).

2.4 Results

2.4.1 Changes in elevation

There was a steady, year-on-year increase in the annual elevation across the MR site as a whole, but the greatest increase in elevation occurred in parts of the site with the lowest elevations at the times of breach, namely, sectors B, C, and D (Figure 2.3). In these sectors, the increase in elevation varied between 0.51 and 0.57 m. In comparison, the sectors with the highest elevations (F and H) at the times of the breach showed some inter-annual variability in subsequent elevations, but there was no clear increasing trend in elevation since the creation of the site (Figure 2.3).

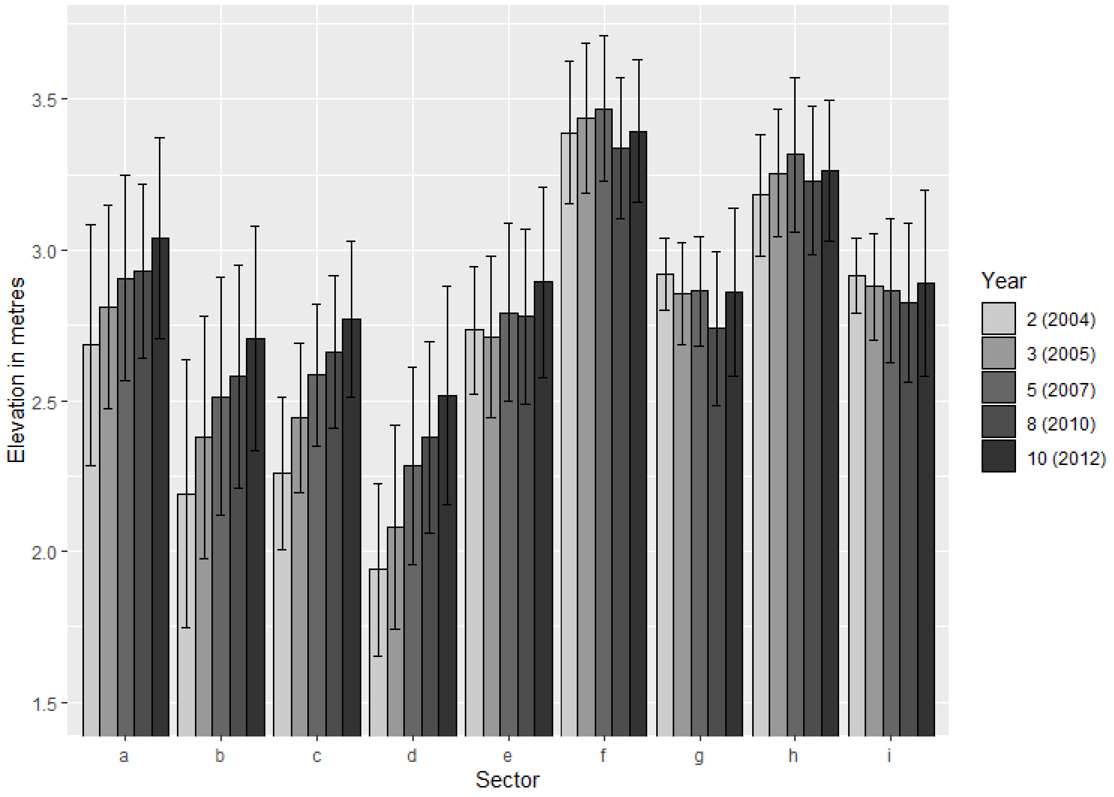

Figure 2.3. Changes in the mean elevation (+/- SD) of each sector of the Paull Holme Strays MR site over the study period.

2.4.2 Waterbird assemblage in the MR

Of the total 49 species recorded at the site between 2003/2004 and 2013/2014, 45 were recorded during the winter months. Specialist benthivorous (waders and ducks) were well represented by a total of 12 species: Eurasian oystercatcher (*Haematopus ostralegus*), common ringed plover (*Charadrius hiaticula*), grey plover (*Pluvialis squatarola*), red knot (*Calidris canutus*), sanderling (*Calidris alba*), dunlin, black-tailed godwit (*Limosa limosa*), bar-tailed godwit (*Limosa lapponica*), curlew, common redshank, common shelduck, and northern pintail (*Anas acuta*) (Appendix 1). The proportion of benthivorous waterbirds at the MR site was lower during the first 3 years (<55% of the total assemblage). However, this guild became more important over time, and its proportion increased to over 80% in Years 5, 7, 9, and 11 (Figure 2.4). Omnivorous waterbirds represented a major component of the foraging assemblage at the MR site, especially in the first 3 years of habitat creation, whereas the herbivorous and piscivorous guilds contributed little to the foraging community (Figure 2.4).

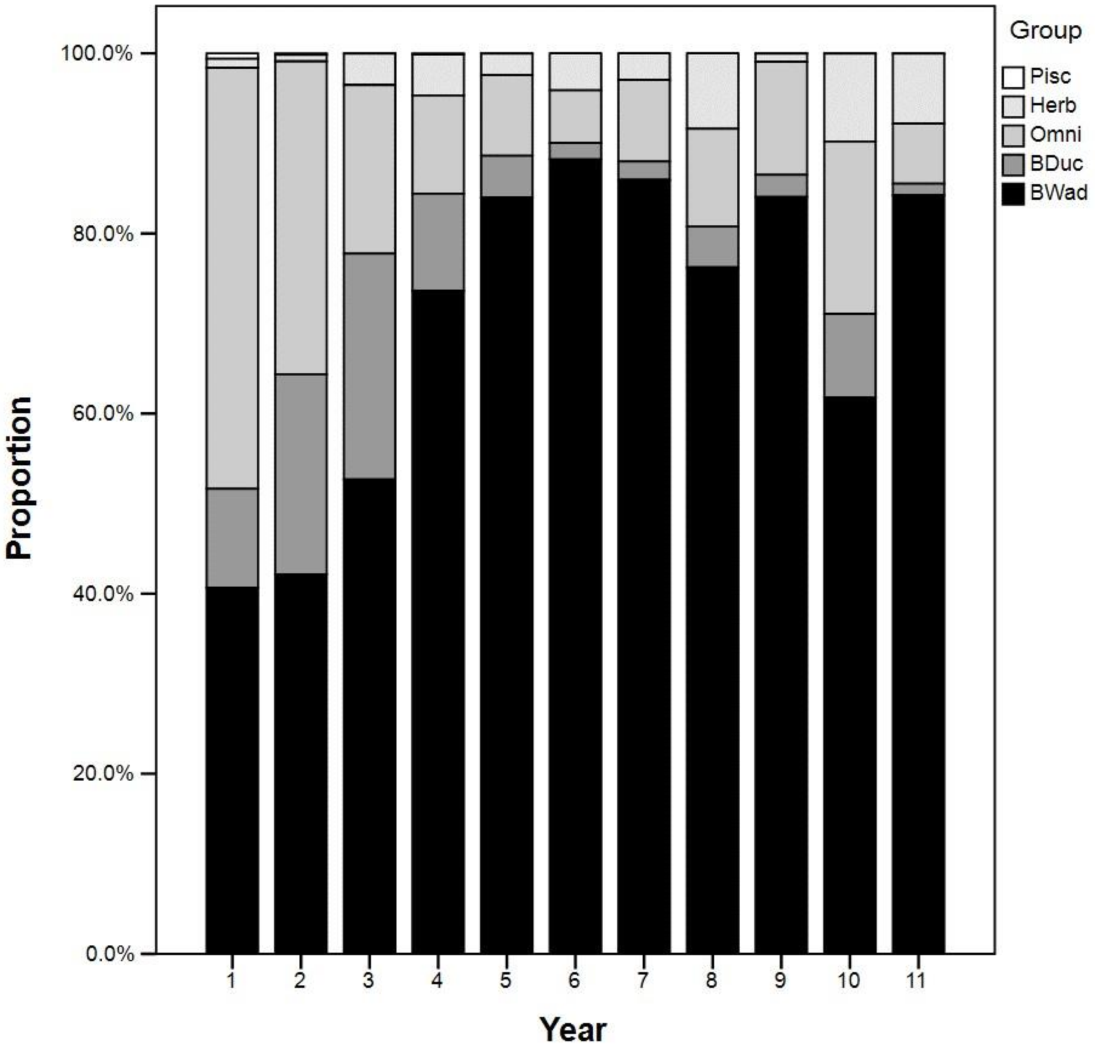

Figure 2.4. Temporal guild composition (% abundance) of the foraging assemblage at the MR site. Guilds are abbreviated as follows: BWad, benthivorous waders; BDuc, benthivorous ducks; Herb, herbivorous ducks, geese, and swans; Omni, omnivorous ducks and rails; Pisc, piscivorous grebes, cormorant, and herons.

Foraging benthivorous species (i.e., waders and sommon shelduck) exhibited markedly contrasting trends in abundance over the study period (Figure 2.5). Foraging dunlin numbers exhibited a gradual increase during the first 5 years of habitat creation at the MR site, followed by the relative stabilisation of numbers in the following years (Figure 2.5). In contrast, the abundance of common shelduck and common redshank rapidly increased in the first few years of habitat creation at the MR site, but their abundance decreased markedly after Years 5 and 7, respectively (Figure 2.5). Curlew, on the other hand, showed a marked rise in abundance in Year 2, with numbers being maintained at that level for the rest of the monitoring programme then on, although some inter-annual fluctuations were observed.

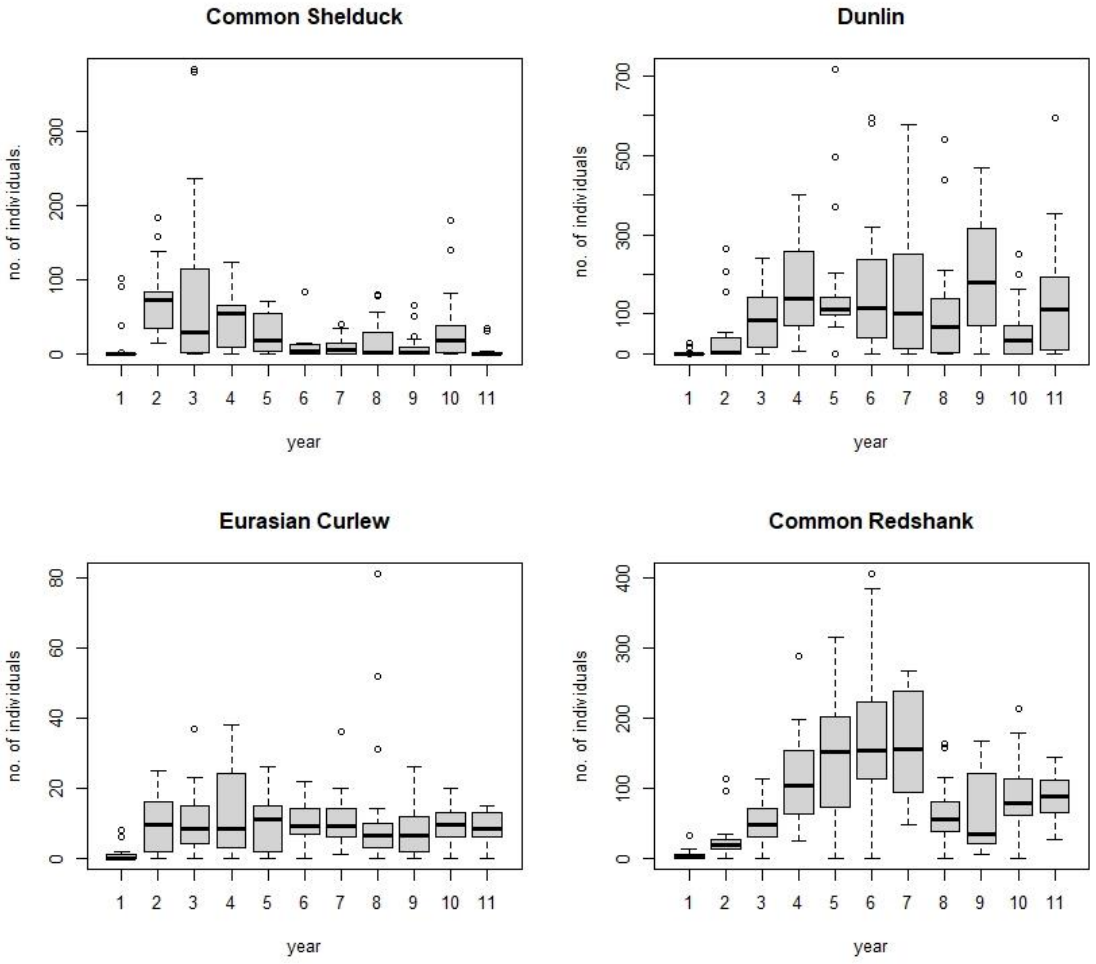

Figure 2.5. Boxplot of no. of individuals foraging per annum. Box plots represent the median values (horizontal line), interquartile distances (boxes), non-outlier range (whiskers), outliers (circles) and extreme values (asterisks).

2.4.3 Modelling bird response

For the four compensatory requirement target species, the results of the modelling conformed to the prediction of the study that increasing elevation had a negative effect on the abundance of benthivorous foraging birds (Table 2.3). ‘Day within the winter’ was also significant in models for all the species except for curlew, indicating a strong seasonal effect on bird abundance, while the effect of tide height was non-significant in all the models. The effect of ‘year since breaching’ was also significant, reflecting the rapid change in abundance that took place across the years.

The relationship with elevation indicated that birds avoided foraging at the highest elevations of the MR site. Results varied among the species: common redshank abundance decreased above elevations of 2.75 m (Figure 2.6), whereas curlew abundance decreased above elevations of 2 m and fell sharply above elevations of 2.75 m, although the model for this species explained a lower proportion of deviance (40.5%) compared with that for common redshank (48.3%) (Figure 2.6). The models for common shelduck and dunlin explained 57.7 and 53.6% of the deviance, respectively. A similar decreasing trend with increasing elevation was also noted in the abundance of other waterbirds (Appendix 2), with similar marked declines in the abundance of grey plovers and bar-tailed godwits being noted at elevations of 2.75 m and above.

As the models demonstrated, the suitable elevations for most foraging benthivorous species were found below 2.75 m at the MR site. After 10 years of sediment accretion, only two sectors of the Paull Holme Strays MR site featured a mean elevation below this level (sectors B and D). Interestingly, these two sectors were modified before the breaching of the original embankment. Sediment was excavated from these sectors to create a new defensive earth bank, and while these areas accreted the fastest since habitat creation, bed elevation continued to be the lowest of the whole site after 10 years. Based on sector size and average elevation in 2013, only 38% of the site featured an elevation suitable for most benthivorous species.

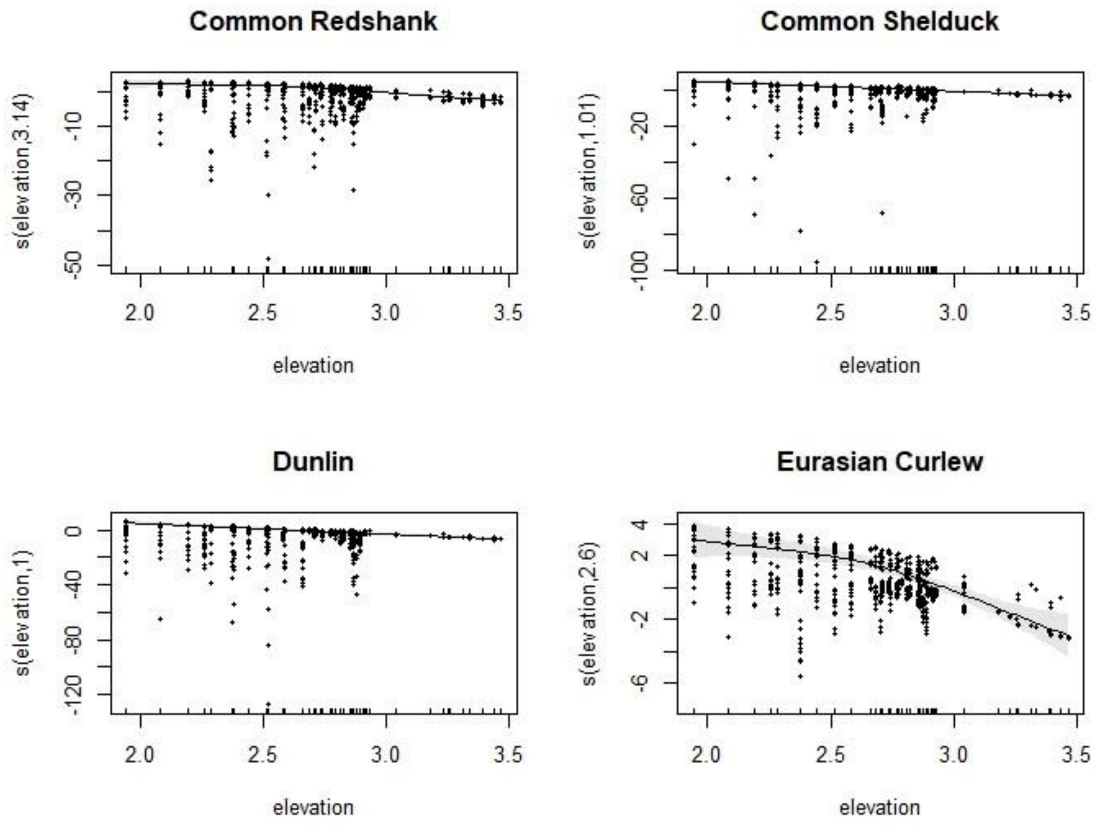

Figure 2.6. Generalised additive model (GAM) smoothing temporal terms (line) fitted to centre of gravity data for the four selected benthivorous species at Paul Holme Strays. Shaded areas and points represent point-wise confidence bands and partial residuals, respectively.

Table 2.3. Model results for the four key compensatory target species.

	Common redshank		Dunlin		Curlew		Common shelduck	
Parameter	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**	**Estimate (SE)**	**P-value**
Intercept	0.50(0.40)	0.212	-1.60(0.61)	0.009**	-0.58(0.28)	0.042*	-0.03(0.40)	0.933
Year3	1.01(0.68)	0.021*	2.15(0.91)	0.018*	0.33(0.37)	0.373	1.12(0.55)	0.042*
Year5	1.79 (0.44)	0.001***	2.55(0.96)	0.008**	0.11(0.39)	0.763	-0.30(0.48)	0.523
Year8	1.06(0.46)	0.029*	7.24(8.00)	0.001***	0.23(0.37)	0.521	-1.40(0.85)	0.100
Year10	1.39(3.65)	0.006**	1.83(0.85)	0.031*	0.98(0.37)	0.009**	0.09(0.63)	0.883
Tide_height	0.00(0.00)	NA	0.00(0.00)	NA	-0.06(0.18)	0.716	0.00(0.00)	NA
Smoother	**Df**	**P-value**	**Df**	**P-value**	**Df**	**P-value**	**Df**	**P-value**
S(elevation)	3.14	0.001***	1.00	0.001***	2.59	0.001***	1.00	0.001***
S(day)	3.72	0.001***	8.75	0.001***	2.57	0.087	8.73	0.001***
S(elevation): tide_height	2.00	0.001***	3.79	0.001***	3.04	0.383	4.21	0.019*
S(sector): year 2	6.72	0.001***	4.63	0.001***	3.46	0.017*	6.15	0.001***
S(sector): year 3	5.54	0.001***	7.23	0.001***	5.33	0.001***	6.83	0.001***
S(sector): year 5	5.06	0.004**	7.20	0.001***	4.90	0.001***	5.57	0.001***
S(sector): year 8	5.87	0.001***	7.24	0.001***	4.78	0.001***	6.20	0.001***
S(sector): year 10	6.82	0.001***	6.31	0.001***	5.50	0.001***	6.81	0.001***
R2 (adj)	48.3%		57.7%		40.5%		53.6%	

Significance of individual model predictors: *P < 0.05; **P < 0.01; ***P < 0.001.

2.5 Discussion

Alongside the protection of existing wetlands, the creation of new habitats is an important mechanism for supporting biodiversity and ensuring that ecosystems can support varied activities. The re-created intertidal site described here was undoubtedly successful in accreting and sequestering carbon-rich mud from the estuarine water column, with a first approximation of 100,000 tonnes dry weight of sedimented material, storing 3,000–8,000 tonnes of carbon [using conversion values from Kelleway et al. (2016)]. However, the main focus of this restoration site was the creation of new intertidal habitats for internationally important wading bird communities. In this study, we showed that newly created habitats can change with time and possibly diverge from their intended plan. This is because, where habitat creation is used as compensation, the resulting bird and plant communities may not match those of the natural sites that were lost (Campbell et al., 2002; Desrochers et al., 2008).

In this study, within the MR site, there was heterogeneity of elevation resulting from the pre-breach landscape and construction, which changed over the course of the study through sediment accretion (Clapp, 2009; Mazik et al., 2010; Brown, 2014). The topography of the MR site (i.e., bed elevation in the first year) influenced the rate of sedimentation (Mazik et al., 2010; Brown, 2014). The rate of sediment accretion inside MR sites like the one chosen in this study are also driven by tidal and sediment regimes (Garbutt & Boorman, 2009). At the Paull Holme Strays MR site, the intertidal habitats at the lowest initial elevation accreted sediments at the fastest rate over the study period. From the LIDAR data and derived change in elevation (the proxy for accretion), over time, we found the accretion to range from 0.51 to 0.57 m between 2004 and 2012 in sectors B, C, and D of the MR site (which all featured a mean initial elevation of lower than 2.25 m OD in 2004).

Intertidal areas with higher elevations have shorter exposure times to water during tidal immersions, with lower food supplies, higher temperatures, and desiccation stresses for benthic invertebrate prey species. We included elevation in the models given the known relationships between the food resources of benthivorous species and cumulative accretion at MR sites (Evans et al., 1998; Atkinson et al., 2004; Garbutt et al., 2006), including the Paull Holme Strays site (Mazik et al., 2010). The models demonstrated that elevation was a major source of variability in the abundance of benthivorous species as the new habitat matured and accumulated sediment. Of the four compensatory requirement target species, curlew showed the sharpest reduction in abundance in response to increasing elevation, while common redshank abundance started to decline at elevations above ~2.75 m. Elevation also had a significant effect on the abundance of foraging dunlin, common shelduck, and other benthivorous waterbird species that colonised the site (Appendix 2). Nevertheless, the decline in the abundance with increasing elevation across the MR site was more linear for dunlin and common shelduck, with a steady decline being noted (Figure 2.6).

Once elevation reached 2.75 m, the models indicated that the abundance of most of the waterbird species (except for dunlin and common shelduck) would start to decline sharply. In the Humber Estuary, tidal flats above ~2.75 m of elevation were not typically reached by neap high tides. However, Mazik et al. (2010) found the lower density and abundance of benthic invertebrates above this height at the site. Conversely, it was also found that the highest abundance of invertebrates was at the lowest elevation at the MR site. Furthermore, as sediment deposits and accretes, halophyte vegetation begins to colonise mudflats very rapidly in MR sites (Mossman et al., 2012b). While elevation within the tidal range is a primary driver of saltmarsh plant distribution, oxidation-reduction (redox) potential also affects the colonisation and distribution of saltmarsh plants in MR sites (Davy et al., 2011; Mossman et al., 2012a). Across the Paull Holme Stray MR site, saltmarsh vegetation coverage across the whole site increased over the years, with estimates of 36% in 2007, 54% in 2010, and 58% in 2013 (Brown, 2014). As a result of lower prey item density, those higher areas may not be longer profitable for the majority of benthivorous species to feed. However, the magnitude of the effect of elevation observed among the waterbird species may be linked to the species daily energy requirement and resource availability at the MR site. Dunlin and common shelduck foraging abundance, for example, did not decline sharply above a 2.75 m elevation. As small waders, such as dunlin, actively forage 80–95% of the time in the winter to meet their high daily energy requirements (Van de Kam et al., 2004), they may continue to feed across the tidal cycle, typically feeding on mobile prey associated with an incoming tide line. Additionally, they could also be feeding on microphytobenthos biofilms, which are of importance for dunlin and other small Calidris species (Mathot et al., 2010; Drouet et al., 2015). Common shelduck also continue to forage on submerged tidal flats by upending and dabbling in the shallow water; therefore, the effect of increasing elevation on abundance might be dampened.

While the elevation of intertidal habitats is one of the main abiotic factors that drive ecological processes in estuaries, other biotic factors such as predation may also control the abundance and spatial distribution of waterbirds in MR sites. Birds may avoid feeding in areas with high risks of predation despite an abundance of food (Newton, 2013). The use of these areas may, however, vary according to the fitness and ability of an individual bird to meet its daily energy requirement. In intertidal habitats, Cresswell et al. (2010) found that adult common redshank shunned available food-rich habitats close to concealed cover (e.g., bushes) from which Sparrowhawks (*Accipiter nisus*) were able to attack. Conversely, juvenile birds and individuals with low fitness and close to starvation may take greater risks. Because of this predation risk, a degree of confinement may be especially important in affecting how a bird uses the different areas of an MR site. Intertidal habitats re-created through realignment sites, however, are often small in size, enclosed, and located high on the tidal frame because the land availability for shoreline management practises is limited. The presence of footpaths on embankments may also affect bird distribution, as recreational human activities taking place there (e.g., dog walking, birdwatching) may deter birds from foraging (Collop et al., 2016).

The success of habitat creation through MR for waterbirds is based on re-creating hydro-ecological processes, with the deposition of sediment from tidal inundation being a driving factor (Wolanski & Elliott, 2015; Elliott et al., 2016). Garbutt et al. (2006) showed that marine macrofaunal colonisation occurred only in newly accreted sediments and not in the original, consolidated agricultural substratum. As new MR sites are opened to tidal inundation, ecological and geomorphological changes take place in response to sediment accretion (Garbutt et al., 2006). Atkinson et al. (2004) and Evans et al. (1998) indicated rapid, positive changes in bird indicators in response to sediment accretion within the first five years of habitat creation. Atkinson (2003) also found that an adequate supply of sediment was the main constraint in successfully creating mudflats that might support natural avian communities. By considering a relative change in elevation over time and absolute elevation in areas of the MR site in the models, this study highlighted that increasing elevation eventually has a negative effect on the abundance of benthivorous species. While the accretion of sediments contributes to increased elevations in MR sites, the long-term provision of food-rich, self-sustained mudflats for foraging benthivorous birds is a key challenge in MR sites.

However, understanding the relationship between habitat development indicators and benthivorous birds can aid us in designing and implementing future MR site projects. For example, bed elevation and predicted current speeds within an MR site need to be considered at the project design phase to improve the effectiveness of MR for benthivorous bird species (also for intertidal fish, see Burgess et al. (2020)). Furthermore, areas with higher pre-breach elevations are likely to be flooded less frequently, therefore limiting their estuarine sediment deposition (and consequent accretion and habitat change). This may be an important limitation in providing suitable foraging habitats for wading birds. It may also affect the ability of the site to achieve ecological targets that are related to compensation. Although bird and benthic communities may colonise MR sites very rapidly (Atkinson et al., 2004; Mander et al., 2007; Mazik et al., 2007), long-term monitoring is crucial in looking beyond the short-term development of sites and determining whether ecological compensatory targets have been met.

While the effect of environmental change on waterbirds at MR sites was the focus of this study, it is necessary to separate the role of habitat development within the site from the effect of any wider natural changes in order to effectively assess the development of re-created habitats. Waterbird populations may respond to wider environmental changes; however, it is unclear whether the changes in the waterbird numbers within the studied site reflected the wider estuary-level changes observed between 2000/2001 and 2015/2016 as there were no increases noted in the four compensatory target species across the Humber Estuary (Woodward et al., 2018). Furthermore, natural intertidal areas near MR sites are commonly used as a 'reference' or 'control' sites to assess the success of these sites in providing effective compensation for the loss of natural intertidal habitats (Atkinson et al., 2004; Mander et al., 2007). However, in this study, the 'reference' site, which was established as the one immediately fronting the MR sites (i.e., further downshore of the MR site), could not strictly be treated as a "control site" given the potential for knock-on effects from the habitat re-creation. Therefore, it is recommended that monitoring should focus on neighbouring sites presenting similar habitat characteristics and encompassing similar topographies, although it has already been acknowledged that finding adequate control sites might be difficult in heterogeneous estuarine systems. Pre-construction bird data were also not available for this study, but a Before-After-Control-Impact (BACI) approach should be considered in future studies to effectively assess the development of re-created habitats.

The main focus of the study was the creation of mudflats for foraging benthivorous waders and ducks. While the development of saltmarsh vegetation due to the accretion of sediment had a negative effect on the abundance of the focal species, saltmarshes provide many ecosystem services (Turner & Schaafsma, 2015). For example, saltmarshes support roosting/feeding and nesting birds and contribute organic matter to the base of the food chain in estuaries (Hughes, 2004). Furthermore, saltmarshes containing sufficiently deep creeks and lagoons can be an important habitat for fish in estuaries (Whitfield, 2017), while colonising saltmarshes in MR sites have the potential to store carbon in the long term (Burden et al., 2013; Burden et al., 2019). Lastly, saltmarshes provide effective physical barriers to coastal erosion (Zhu et al., 2020). Thus, when setting up ecological targets for MR sites, it is important to consider the ecosystem services and goods/benefits that saltmarshes and mudflats provide and take a broader view of these ecological targets. Specifically, these targets should be about creating habitats that provide ecosystem services similar to those provided by neighbouring natural intertidal habitats

2.6 Conclusions

In this study, within the MR site, there was heterogeneity of elevation resulting from the pre-breach landscape and construction, which then changed over the following 10-year through sediment accretion. Waterbird abundance was also closely related to elevation when the decreases in the numbers of foraging birds were at elevations above 2.75 m (OD) bed elevation. The modelling of the responses of benthic foraging birds to physical characteristics indicated that the long-term suitability of the MR site for these species was uncertain because of increasing elevation, which was a result of sediment accretion. Thus, this study recommends that the design and implementation of future projects should recognise the effects of accretion on waterbird abundance. It also highlights the need for long-term monitoring at MR sites (a minimum of 10 years) in determining whether bird targets related to habitat compensation have been met. While foraging benthivorous birds were the focus of this particular study, there are many facets to ecosystem responses to MR sites, with responses to physical changes varying among taxa and habitats. MR remains a nature-based solution that creates intertidal habitats with successive benefits as mudflats accrete and are colonised by saltmarsh vegetation.

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Chapter 3 Individual, sexual and temporal variation in the winter home range sizes of GPS-tagged Eurasian curlew (*Numenius arquata*)

3.1 Abstract

We examined individual, sexual and temporal (day/night, seasonal and annual) variation in the size of the home range of 18 GPS-tagged Eurasian curlew (*Numenius arquata*) captured at two sites on the Humber Estuary (UK). Eurasian curlew home ranges were small (555.5 ha +/- SD 557.9 ha) and varied slightly in size through the non-breeding season (September to March). We found some annual differences in home range size, and there was some evidence that home range size was greater at night compared to daytime. There was strong inter-individual variation in home range size, which was not related to the species sexual size dimorphism and thus potential differences in resource use. Our results highlight that wintering Eurasian curlew on the Humber Estuary maintain small home ranges which vary strongly between individuals. Knowledge of the home range size of wintering waders is vital to informing management responses to the potential impacts of environmental changes such as sea-level rise and improving the efficacy of compensatory habitats.

3.2 Introduction

Waders are facing long term declines because of the direct and indirect effects of human activities (Sutherland et al., 2012). The Numeniini, which include curlews and godwits, are the focus of both scientific research and conservation efforts because of rapidly declining trends across several flyways (Pearce-Higgins et al., 2017). This group contains 13 species, of which two are possibly extinct and several others endangered or threatened. In the United Kingdom (UK), the population and breeding range of the near-threatened Eurasian curlew (*Numenius arquata*) (hereafter curlew) have declined dramatically since the mid-1990s (Balmer et al., 2013; Brown et al., 2015; EBCC, 2020; Harris, 2020). There is also evidence of declining trends in some parts of northwest Europe (EBCC, 2020). Evidence points in the UK to low reproductive success as the likely demographic driver of these population declines (Brown et al., 2015). In the UK, a large scale analysis of Breeding Bird Survey (BBS) data showed adverse effects of intensive agriculture, forestry, the increase in generalist predator populations and climate warming on breeding curlew (Franks et al., 2017).

While UK birds are generally resident, the UK over-wintering population is inflated by the arrival of birds from Fennoscandia in winter, particularly along the East Coast of the UK (Bainbridge & Minton, 1978; Wernham et al., 2002). With an over-wintering population of

210,000 curlew, the UK plays a vital role in the species' conservation across the East Atlantic flyway. Numbers wintering in the UK increased during the 1980s, following the cessation of hunting, although they have declined since the 1990s, reflecting UK and European breeding population trends (Massimino et al., 2019; EBCC, 2020). There has been evidence that wintering survival was reduced by mechanised cockle harvesting and hunting in North Wales (UK) (Taylor & Dodd, 2013). Recent analyses showed that increases in winter survival in some areas of the UK appeared to coincide with the hunting ban (Cook et al., 2021).

With increasing sea-level rise due to climate change, there has been considerable effort to create new intertidal habitats to compensate for the current and future losses of intertidal habitats in estuaries, but the approaches used remain in development and sites largely confined to northwest Europe (ABPmer, 2021). In the process of managed realignment, farmland habitats adjacent to the estuary can be converted into intertidal habitats by lowering or breaching the sea walls (Esteves, 2014). Managed realignment has proved to be a successful approach for the re-creation of intertidal habitats for waders (Atkinson et al., 2004; Mander et al., 2007; Mander et al., 2021). Where existing farmland is already extensively used by curlew as a foraging ground, the effect of habitat creation can be a double-edged sword. Whilst suitable foraging terrestrial habitats (e.g., agro-ecosystems) are lost to the estuary, new intertidal habitats are created.

Curlew predominantly feed on estuarine intertidal flats during the non-breeding season, but also use terrestrial fields. It has not been demonstrated whether all birds in a population use both intertidal and terrestrial habitats or if individuals specialise in certain habitat types. However, this information is crucial to understanding the balance in value between terrestrial and intertidal habitats, and determining the extent of the areas in which birds reside (i.e., home range), forage and rest and the factors affecting this is key. Measuring home range, which is used to define the vital space that the animal uses over a given time (Burt, 1943), is key to many ecological studies. Knowledge of the space and habitat underpins effective conservation measures for a range of taxa (Zeale et al., 2012; Godet et al., 2018; Pop et al., 2018). In ecological modelling (e.g., using individual-based models: IBMs), assumptions about animal movements are often made using *a priori* information on space use and habitat use. Where IBMs are used to predict the effect of environmental changes and human activities on waders (Stillman et al., 2000), determining the home range size and making realistic assumptions about movements are crucial to accurately predicting the effect of environmental change on wader populations.

The foraging decisions that curlew make on their wintering grounds aim to maximise their food intake rate to maintain their fitness (i.e., body condition and ability to survive) (Stillman et al., 2000). For example, waders may forage at night on intertidal flats if they have been unable to meet their daily energy requirements during the day (supplementary feeding hypothesis of McNeil et al. (1992)). Conversely, they may prefer foraging at night because it is more profitable or safer from predators (preference hypothesis of McNeil et al. (1992)). The curlew is one of a number of wader species that uses both intertidal flats and non-estuarine habitats to forage over the wintering period (Townshend, 1981a; Milsom et al., 1998; Navedo et al., 2013). Non-estuarine habitats such as coastal pasture close to intertidal areas can be used as an alternative foraging ground or a supplementary foraging area (Navedo et al., 2013). For example, curlew have the ability to feed in terrestrial habitats to supplement their diet when the intertidal habitats are covered at high tide. Alternatively, they may switch to feed in terrestrial habitats when it is more profitable to do so (Bowgen, 2016). There is evidence from colour-ringing studies that individual curlew within the same population may have different habitat use patterns (Townshend, 1981a; Townshend, 1981b). The pattern of habitat use could be driven in part by sexual dimorphism.

Some waders, especially godwit and curlew species, exhibit differences between males and females such as bill length and body size (Van de Kam et al., 2004). Sexual dimorphism in black-tailed godwits (*Limosa limosa*) has been shown to drive spatial segregation on the intertidal flats in estuaries, linked to the accessibility of prey between individual males and females (Alves et al., 2013). Based on colour-ringing work, Townshend (1981a) found previously a difference in foraging habitat use and rate of foraging in cold weather between male and female curlew, with longer-billed female curlew preferentially feeding on intertidal flats and shorter-billed males on grassland.

To date, studies of the local winter movements of waders have been based on radio telemetry and/or ringing and colour-ringing. Such studies have been used to determine site fidelity, home ranges and the habitat preferences of several wader species (Leyrer et al., 2006; Taft et al., 2008; Lindström et al., 2010; Verkuil et al., 2010; Mittelhauser et al., 2012). Radio telemetry has also shown differences in the diurnal and nocturnal use of intertidal habitats (Burton and Armitage (Burton & Armitage, 2005; Leyrer et al., 2006). Recently, advancements in modern telemetry (e.g., GPS tracking technology) have enabled researchers to follow waders for more extended periods and obtain data remotely. One such study, deployed GPS tags to follow a small sample of curlew through their annual cycle, and their movements between breeding, staging, and over-wintering sites, demonstrating the species strong site-fidelity (Schwemmer et al., 2016), and confirming findings of mark-recapture studies (Rehfisch et al., 2003). High-resolution GPS devices have also been recently used on curlew to examine the factors affecting the timings of their departure from and arrival at their wintering sites (Schwemmer et al., 2021).

Through GPS tracking, there is potential to gain far more comprehensive information on the scale of animal space use, i.e., an individual's home range size, through the day and night and across seasons. Whilst colour-marking studies have focussed on the influence of sexual dimorphism on curlew movements (Townshend, 1981a), home range variation in response to sexual dimorphism has not been examined. Furthermore, although GPS tags equipped with accelerometers have also been used to determine the behaviour of waders (van der Kolk et al., 2019), studies have not evaluated behaviour from the GPS data alone. It is possible to infer bird behaviour from path track characteristics (e.g., step length and the angle of direction) using state-space models such as Hidden Markov Models (HMMs); such approaches have been used extensively to identify the behaviours of seabirds (Dean et al., 2013; Trevail et al., 2019; Zhang et al., 2019).

Here, we assess individual, sexual and temporal variation in the winter home range sizes of GPS-tagged curlew wintering on the Humber Estuary Special Protection Area (SPA), and use GPS tracking data alone to examine the main pattern of activity. We hypothesised that (i) home range size may change through the non-breeding season as a function of resource depletion and (ii) between winters, reflecting changes in resource availability. Home range size may increase in response to prey depletion on intertidal flats which may force the birds to explore other patches. We also hypothesised (iii) that home range size may be driven by individual strategies related to sexual dimorphism, and thus that home range sizes may differ between males and females. We further hypothesised that (iv) home range might be smaller at night because of the greater risk of predation in intertidal and terrestrial habitats.

3.3 Method

3.3.1 Catching and GPS tagging curlew

The work was carried out at two sites on the Humber Estuary: Welwick Saltmarsh (53.64°N; 0.02°E), which is contiguous to the Welwick managed realignment site (53.64°N; 0.00°E), and Long Bank Marsh (53.62°N; 0.12°E) (Figure 3.1). The Welwick managed realignment site was created in 2007 through a breach of the flood defence. The 54-hectare site was designed to offset the loss of habitats due to port development in the Humber Estuary. Adult curlew are present on their wintering sites, such as the Humber Estuary from early July to mid-April (Frost et al., 2021; authors pers. obs.). According to the Wetland Bird Survey (WeBS), 2,787 curlew (latest five-year average) over-winter in the Humber estuary (Frost et al., 2021). Long Bank Marsh and Welwick Saltmarsh (including the managed realignment site) support regular roosts of ~300 and ~700 individuals (Mander & Stone, 2020; Spurn Bird Observatory, 2022). Curlew were caught in the winters of 2015/2016, 2017/2018, 2018/19 and 2019/20, between late September and late February. At the Welwick Saltmarsh site, curlew were caught using mist-nets in saltmarsh pools, used as night-time roosts. At Long Bank Marsh, a wet grassland with standing water used by roosting birds, birds were caught using mist-nets at night and with cannon nets at dawn. A total of 22 curlew were captured on nine catches over the four winters (Appendix 4). Ageing of curlew was based on plumage characteristics as described in Baker (2017). The bill-length (mm), wing-length (mm) and mass (g) of all individuals were measured and the sex of adult birds determined based on the bill-length equation derived by Summers et al. (2013). Adult birds were positively assigned to a category (male or female) above a probability of 95%. A total of five males, eight females, five adult birds of unassigned sex, and four first-winter birds were included in the sample of 22 birds (Appendix 4).

All birds caught were fitted with a numbered metal-ring, a unique set of colour-rings for subsequent re-identification in the field, and a GPS/UHF tag. The Pathtrack nanoFix® GEO+RF tag used nano Fix® technology with low power UHF technology (Pathtrack, Otley, UK) for downloading data to a base station. To test their accuracy, eight of the tags were activated prior to deployment on curlew to record hourly GPS position for a period of up to 24 hrs. The tags were placed at a height of approximately 0.20 m above ground in a range of habitats (e.g., bare, exposed mud in small pools, low saltmarsh vegetation and high saltmarsh vegetation) across the upper shore. To produce a sample location error, the distance between observed and actual location of the tags was averaged (with a SD). We found the sample location error to be 25 m (+/- SD 13 m). According to the manufacturer, GPS xy position for these tags has an error of up to 20 m in good conditions (G. Brodin, Path track pers. comm.).

The GPS/UHF tags were glue-mounted to feathers (trimmed to 5 mm) on the bird's back between the scapulars (following Warnock and Warnock (1993)). Glue-mounting was preferred over the use of harnesses for welfare reasons. While the use of harnesses may provide long-term data over different stages of birds' annual cycles, their use may potentially have impacts on the birds' condition, their breeding success or even survival, depending on the method used and species (Geen et al., 2019). In contrast, there appears to be little if any long term effect from glue mounted devices which fall off at, or prior to, the next body moult. Long-term deployments beyond the wintering period were not required for this study, but at least one individual was observed without its tag three months after deployment.

The tags were set to record the position of the bird every 90 min and to attempt to download data to a field-based base station every 60 min, using a one-way remote UHF data communication. This sampling regime gave an expected battery lifespan of at least 28 days (and 448 fixes) for tags deployed in 2016, which covered two spring-neap-spring tidal cycles. Battery lifespan increased to at least 56 days (896 fixes) from 2017 as a result of manufacturing improvements. However, we found that battery lifespan declined if the deployment was delayed for more than a year from manufacturing, resulting in a reduction in the number of fixes obtained for six individuals. Field-based base stations were positioned within a maximum distance of 200 m from the roosts. The field-based base stations were checked weekly to retrieve the data and ensure regular downloads. All tags successfully downloaded fixes to the field-based base stations, with the exception of one tag deployed at the Welwick Saltmarsh for which no data fixes was recorded. The tags weighed between 4.9 g and 5.1 g which was below the 1% threshold of the average weight of known female and male captured in our study, respectively 922 (± 65 g) and 792 (± 77 g). Ringing and GPS tagging activities were undertaken under licence from the Special Methods Technical Panel of the British Trust for Ornithology Ringing Scheme. All fieldwork activities were subject to ethical approval from the University of Hull.

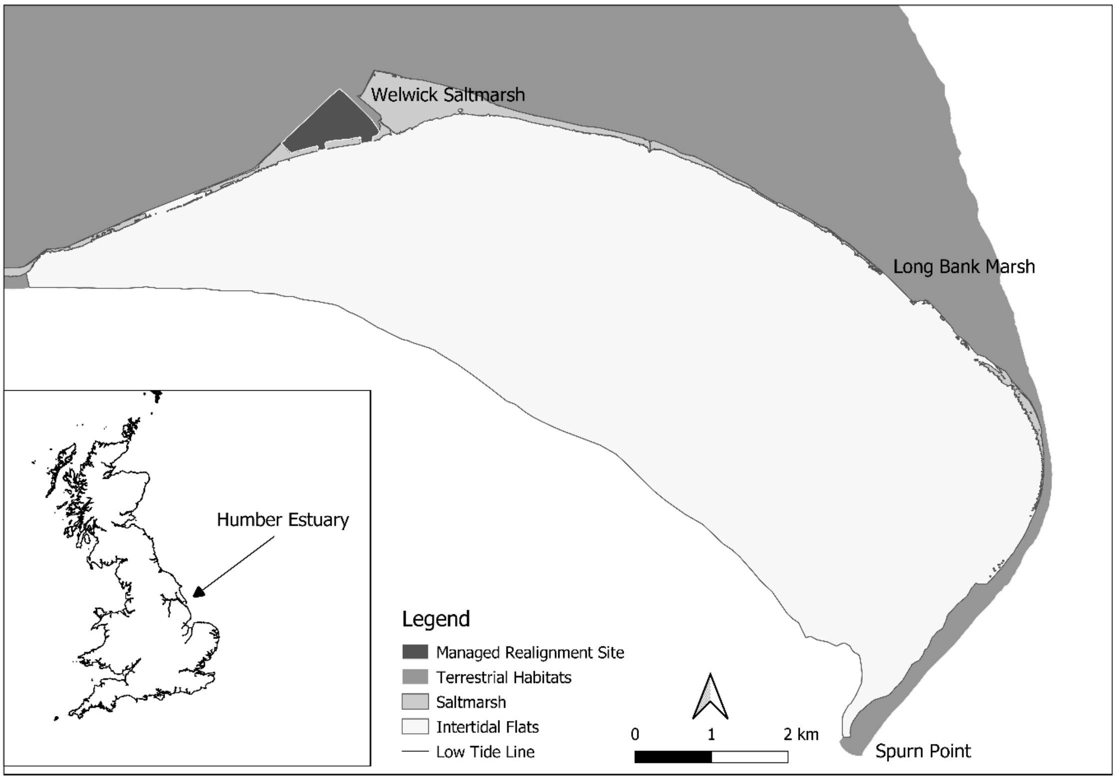

Figure 3.1. Study site showing the capture sites at Welwick Saltmarsh and at Long Bank Marsh.

3.4 Data analysis

R version 3.6.0 (R Core Team., 2021) was used for all analyses.

3.4.1 Home range estimation

Comparing estimates of home ranges between studies can be problematic due to differences in data collection and analytical methods. Here, therefore, we initially explored two approaches – Kernel Density Estimator (KDE) and Kernel Brownian Bridge (KBB). The techniques are described in the 'adehabitatHR' package (Calenge, 2019). The KDE is a commonly applied home-range estimator in which a kernel distribution (i.e., three-dimensional hill or kernel) is placed on each location. An estimation of the Utilisation Distribution (UD) is then generated across the area of interest (Worton, 1989). The calculation of the UD is sensitive to the bandwidth selection (i.e., smoothing parameter) of the kernels, which determines the resolution of the UD. Errors resulting from over-smoothing or under-smoothing can occur when estimating home-range sizes. There are standard methods to compute the smoothing parameter: 'reference bandwidth' and Least Square Cross Validation (LSCV). As curlew can spend several hours at the same position while roosting at high tide, many duplicates fixes in the data prevented the use of the LSCV. Instead the smoothing was determined by a 'reference bandwidth'.

This Kernel Brownian Bridge approach is an extension of the Kernel method which considers the time dependence between successive locations. The Kernel Brownian Bridge method places a kernel function above each step (a straight line connecting two consecutive locations). As a result, the Brownian Bridge is conditioned by the start and end time of the step, the animal's speed and the precision of the tag (Horne et al., 2007). Therefore, the Brownian movement model requires the input of sig1: a first smoothing parameter related to the speed of animals; sig2: a second smoothing parameter related to the imprecision of the location data. Sig1 was estimated from the data using a maximum likelihood estimate with the 'liker' function in the package adehabitatHR (Calenge 2019). Sig2 is similar to the smoothing parameter h of the classical kernel method, and is therefore related to the imprecision of the relocations (i.e., the spatial resolution of the tag).

Of 22 individuals GPS-tagged, core (50%) and total (90%) home ranges were estimated for a total of 18 individuals with data collected using an identical sampling regime (1 fix for every 90 min) but with a varying sampling duration. We excluded three individuals from the analysis for which fewer than 224 fixes were obtained (less than 14 days), and one individual for which no movement data was obtained from the tag. The low of numbers of fixes for two individuals could be explained by bird movements (i.e., use of other sites), device failure or mortality. An average of 691 fixes (range = 260 - 1,115) was obtained for the 18 individuals, equating to a period of 43 days (range = 16 - 69) (Appendix 5). There were no significant differences in core range sizes (one-way ANOVA, (F1,34) = 2.744, $P > 0.05$) or total home range sizes (one-way ANOVA, (F1,34) = 1.18, $P > 0.05$) between the two estimators. Because the two approaches provided similar estimates of both core (50%) and total (90%) home ranges, we chose to use the KDE to examine space use and variation in home range size.

3.4.2 Habitat use

We examined the proportions of different habitats in core and total home ranges for individuals captured at Long Bank Marsh (n = 4 individuals) and Welwick Saltmarsh (n = 14 individuals) assuming that broad habitat types did not change between years. Individual core (50%) and total (90%) home ranges were calculated using the Kernel Density Estimator (KDE). Using open-source layers on saltmarsh extent from environment.data.gov.uk, and boundary-lines for high and low tide from digimap.edina.ac.uk, we determined the extent of broad habitat types in QGIS. Boundary-lines of the managed realignment site were sourced from Associated British Port (ABP). Broad habitats were categorised into four categories. The land behind the sea defences which bordered the study area was classed as the 'terrestrial habitat'. Terrestrial habitat was dominated by arable land with rotation and therefore crops were likely to change between winters. Some fields were left fallow in winter 2019/20 due to preparation work for two proposed additional managed realignment sites near the Welwick Saltmarsh. Three broad habitat types were identified on the intertidal areas: 'intertidal flats', 'saltmarsh', and the 'managed realignment site', the latter was created in 2007 through the breaching of flood defence. We calculated for each individual the proportions of core and total home ranges which overlapped with broad habitat types. Finally, we averaged the proportions of different habitats in core and home range for individuals captured at Long Bank Marsh and the Welwick Saltmarsh.

3.4.3 Examining factors driving home range size

We examined the factors affecting variation in home range size by producing total (90%) KDE home range estimations for periods of 14 days, starting from the highest spring tide and finishing on the subsequent highest spring tide in the next spring tidal cycle. This standardisation enabled us to account for the effect of the variation of the tidal amplitude. Home range estimations were produced for day and night – based on civil twilight – and calculations were made using the R package 'suncalc'. A total of 48 periods (each 14 days) were considered in the analysis for 18 individuals. The home range estimation from the KDE method was used as a dependent variable in in a Generalised Additive Model (GAM) ('gam' function in mgcv) that evaluated the influence of date (number of days from 1st September), diurnal cycle (i.e., day and night), age/sex, winter and site. Number of days from 1st September was included as a predictor using thin-plate regression splines as smoothing function (Wood, 2003). The date was calculated from the 1st September for the start of each 14 days period. Diurnal cycle, age/sex, winter were included as fixed effects while individual (tag) ID was included as a random effect. Although we could not properly assess annual changes, given that individuals were 'nested' within year, we included winter of capture as a fixed-effect in the model. Following assessment of residual diagnostics using simulated residuals (DHARMa package (Hartig & Lohse, 2021) we chose to use a Gamma distribution to model home range size. We found no evidence of auto-correlation (DW = 1.8543, *P*-value = 0.4691) and over-dispersion (dispersion = 0.86236, *P*-value = 0.76) in the simulated residuals. The full model is presented with each term assessed on level of significance.

3.4.4 Determining movement behaviour

We used a HMM to identify the movement behaviour of curlew using the package move 'HMM' in R (Michelot et al., 2016). We used a two states model with state 1 defined as 'roosting' and state 2 defined as 'other' behaviour (including travelling and foraging). We used the gamma structure for the step length, the turning angle distribution was von Mises and we employed the Viterbi algorithm to define the states (Michelot et al., 2016). Tidal height (as metres above Chart Datum) was incorporated as a covariate in the model. Tide height data for Immingham were sourced from the British Oceanographic Data Centre (BODC) at a 15 min interval which matched with our GPS sampling frequency. Model fit was assessed through inspection of pseudo-residuals. Both pseudo-residuals of step and angle were tested for normality using the Jarque–Bera tests for normality.

The daytime feeding intensity of curlew was measured to verify the HMM predictions. Monthly scan sampling was undertaken over a half-tidal cycle between October 2019 and March 2020 at the Welwick managed realignment site which supports roosting flocks of curlew, and on the fronting intertidal flats where the birds forage. Scan sampling was also undertaken on nearby agricultural land, which supported flocks of 100 or more + curlew over the winter of 2019/20 to account for the field feeding activity. We recorded individual bird behaviour (categories: foraging, roosting and loafing/preening) every 20 min. Scan sampling was undertaken at least twice per month and covered rising and falling tides during spring and neap conditions to account for the variability in feeding intensity over a range of tidal heights. On rising tides, scan sampling started at low tide when the mudflat fronting the realignment site was fully exposed and finished at high water when the tide covered the area, and all birds had joined the roost in the realignment site. Conversely, on falling tides, scan sampling covered the high to low water period and finished when the mudflat was fully exposed. The percentage of time spent foraging (number feeding/total numbers) was averaged across the scan samples collected (n = 147) during the available feeding period.

3.5 Results

3.5.1 Feeding and roosting-site fidelity

Movement data of all 17 curlew captured and tagged at the Welwick Saltmarsh are presented. All individuals were faithful to the area during the non-breeding season (Figure 3.2; Appendix 6). In four winters of tracking, individuals did not switch roosts and remained faithful to their foraging areas on adjacent intertidal flats. While curlew used the Welwick Saltmarsh and the re-created intertidal areas of the Welwick realignment site to roost, they predominantly fed on the intertidal flats and in fields immediately contiguous to the Humber Estuary. Very occasionally individuals were tracked in farmland habitats at up to 3.5 km from the shoreline (Appendix 6). Six individuals only utilised intertidal habitats, while the remaining eleven individuals made movements between the intertidal and terrestrial habitats.

In two winters of tracking, the four curlew captured and tagged at Long Bank Marsh were predominantly site-faithful to their roosting site, but three individuals switched roosts intermittently to Welwick Saltmarsh and adjacent fields (Figure 3.2; Appendix 6). For one bird (Tag 17150), the switch coincided with an exceptional cold weather event in March 2018 (the ‘Beast from the East’). Two further birds (Tag 17582 and Tag 17590) captured in January 2020 regularly switched roosts to the Welwick Saltmarsh site through February and March 2020, predominantly using fields that had been flooded following periods of heavy rain. Inland movements were more prominent in individuals captured at Long Bank Marsh, with fields within 2 km from the intertidal flats regularly used (Appendix 6). All four individuals made movements between the intertidal and terrestrial habitats during the non-breeding season.

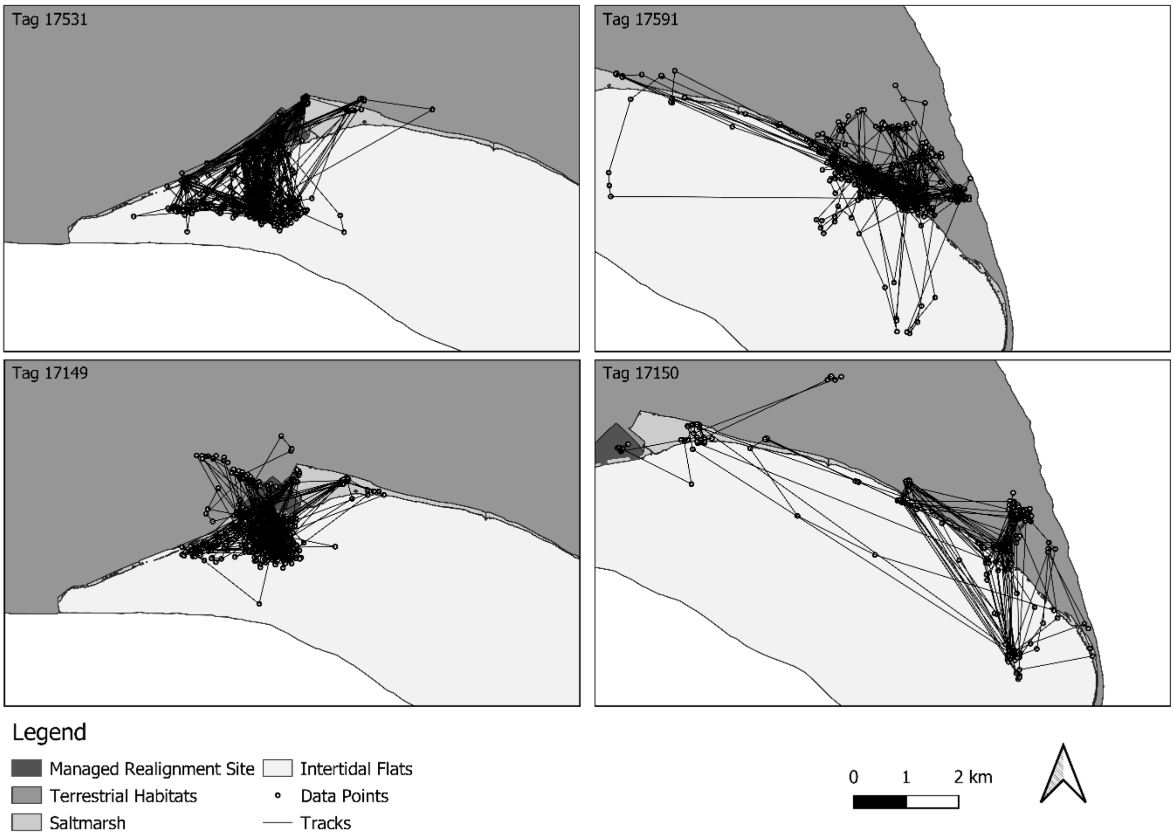

Figure 3.2. Example of GPS tracks of wintering curlew captured at Welwick Saltmarsh (tag 17531 and tag 17149) and Long Bank Marsh (Tag 17591 and Tag 17150).

3.5.2 Home range size estimates

Core (50%) and (90%) home ranges were estimated for a total of 18 individuals for which there were sufficient data. Both core (50%) range and total (90%) home range sizes varied markedly between individuals. For example, the estimated total home range size produced with the KDE varied between 60.0 ha (260 fixes) and 802.3 ha (521 fixes). The average home range size was 555.5 ha (691 fixes) and 76.1 ha, respectively, at the 90% and 50% level (Appendix 5). Examples of the spatial extent of the curlew home ranges are given in Figure 3.3

Figure 3.3. Examples of Kernel Density Estimator (KDE) estimated core (50%) and total (90%) home range sizes for individual curlew captured at Welwick Saltmarsh (Tag 17578 and 17602) and Long Bank Marsh (Tag 17590 and 17582).

3.5.3 Habitat use

The proportions of different habitats in core and total home ranges varied between the capture sites, i.e., Long Bank Marsh (n = 4 individuals) and Welwick Saltmarsh (n = 14 individuals) (Table 3.1). The home ranges of individuals captured and tagged at the Welwick Saltmarsh predominantly overlapped with the intertidal flats of the Humber Estuary, and curlew showed little use of the terrestrial habitat, with respectively 15% and 17% of their total home and core ranges overlapping with this habitat. By contrast, individual GPS-tagged curlew from Long Bank Marsh made more extensive use of the terrestrial habitat (Table 3.1). This habitat made up 55% and 52% of their core and total home ranges, respectively. Long Bank Marsh, which is a wet grassland with standing water, is a key roost for curlew on the outer Humber Estuary.

Table 3.1. Percentage of averaged curlew home ranges overlapping with broad habitat types (range is given in brackets).

Capture Site	Home Range	Terrestrial Habitat	Realignment Site	Saltmarsh	Intertidal Flats
Welwick Saltmarsh	Core	15% (0-53)	17% (0-36)	16% (5-38)	52% (0-75)
	Total	17% (5-38)	13% (4-25)	17% (8-39)	52% (31-64)
Long Bank Marsh	Core	55% (43-68)	0% (0-0)	1% (0-3)	43% (31-57)
	Total	52% (38-65)	0% (0-2)	7% (2-12)	41% (24-59)

3.5.4 Individual, age/sex and temporal variation in home range size estimates

Results of the full model that included all factors affecting variation in estimated total (90% KDE) home range sizes (ha) of wintering curlew are shown in Table 3.2. The full model explained 56.1% of the deviance. The estimates from this model indicate that total (90% KDE) home range sizes were typically greater during the night than in the day. No evidence was found for a difference in ranges between sites. There was, however, a difference between years, with smaller home range sizes found during the third winter of tracking. Variation in home range sizes across individuals (and thus between sexes and winters) and between the day and night is shown in Appendix 7, with example of individual movements shown in Appendix 8. There was a slight relationship between the number of days since the start of the wintering season and home range sizes, suggesting that home range sizes slightly decrease through the non-breeding season (Figure 3.4). We rejected the hypothesis that home range size was linked to sexual dimorphism: we could not identify any differences in home range size between adult males, adult females, adult birds of unassigned sex, and first-winter birds.

Table 3.2. Model coefficient estimates for the full model assessing factors affecting variation in estimated total (90% KDE) home range sizes (ha) of wintering curlew. Standard errors, T-values and *P*-values for the MGCV gam.

Parameter	Estimates	Std. error	T value	*P*-value
Intercept	6.55	0.46	14.41	0.001***
Nycthemeral (night)	0.21	0.10	2.08	0.040*
Site (Welwick Saltmarsh)	-0.54	0.37	-1.45	0.150
Winter 2	-0.12	0.42	-0.28	0.779
Winter 3	-1.42	0.47	-2.99	0.003**
Winter 4	-0.33	0.34	-0.95	0.344
Adult (male)	-0.05	0.32	-0.16	0.869
Adult (unassigned)	0.23	0.35	0.67	0.504
First Winter (unassigned)	0.67	0.36	1.87	0.065
Smoother	df	F	*P*-value	
S(days)	1	6.727	0.011*	
S(id)	6.39	4.631	0.001***	

Significance of individual model predictors: $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

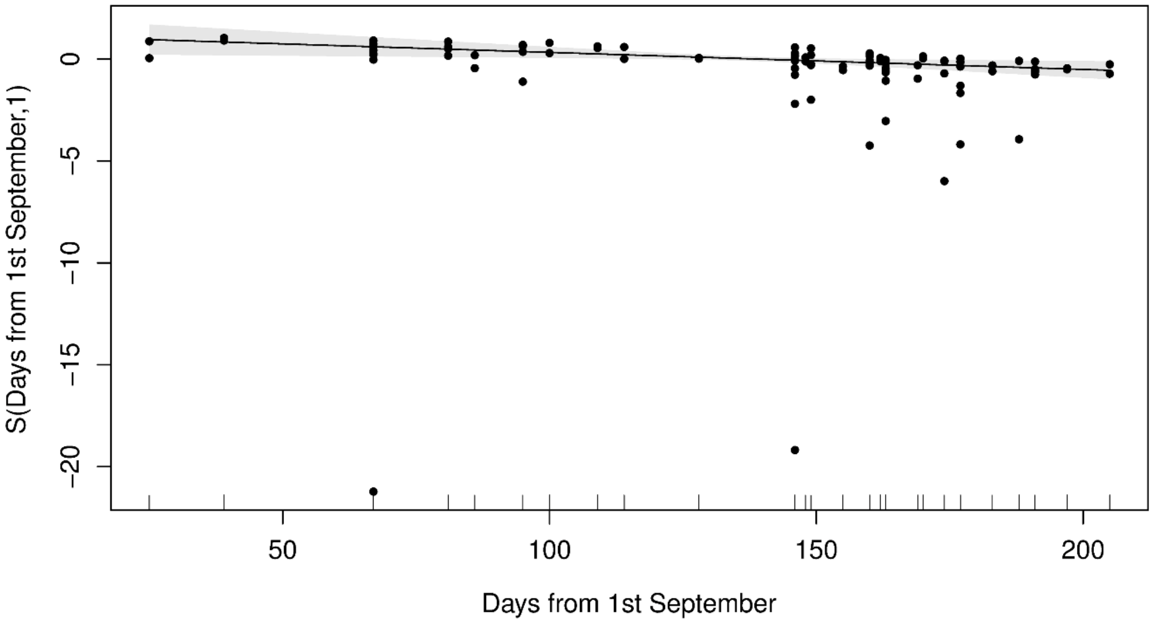

Figure 3.4. The relationship between (90% KDE) home range sizes (ha) of individual wintering curlew and date within the winter (days from 1st September) as shown by GAM smoothing temporal terms (line) fitted to centre of gravity data. Shaded area and points represent pointwise confidence bands (SE) and partial residuals respectively.

3.5.5 Movement behaviour

HMMs distinguished two distinct behaviour modes, which equated to resting (overall mean step length: 20.8 m +/- SD 14.9 m) and other behaviours (579.6 m +/- 660.0 m). According to the most likely state sequence under the fitted model, curlew spent 22% of their time resting and 78% engaged in other behaviours. At night, curlew spent 31% of their time resting versus 13% of the time during the day. This means that a greater proportion of curlew were undertaking other behaviours in the daytime, presumably foraging. Visual observations carried out across the intertidal flats (including the managed realignment site) and the terrestrial habitats between October 2019 and March 2020 indicated that curlew spent 62% of the time foraging during hours of daylight. As expected, the visual observations indicated the proportion of foraging curlew varied during the tidal cycle. The median was below 70% around 2 hours on either side of high water, but there was considerable variation in the range of values. By contrast, there was little variation three hours on either side of low water with a median between 80% and 100% (Figure 3.5).

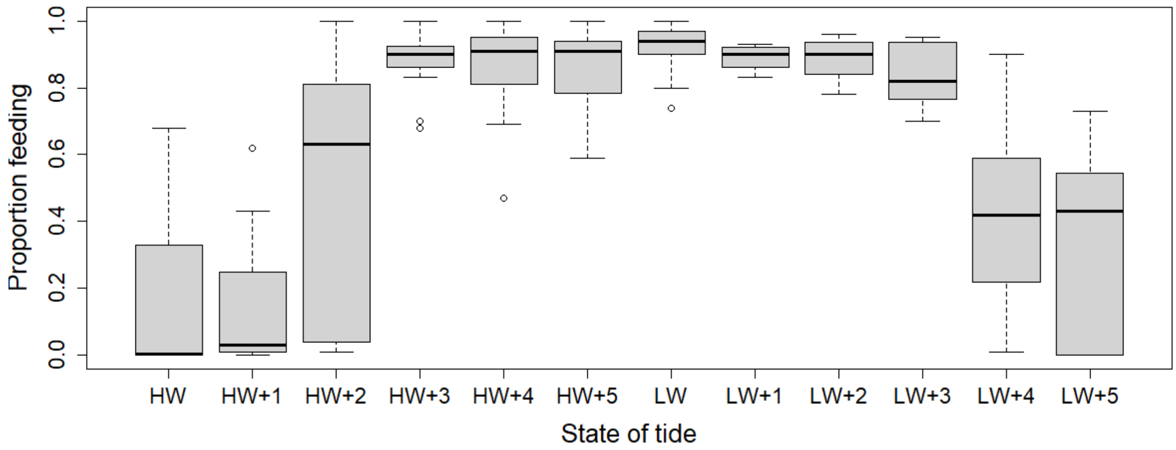

Figure 3.5. Medians representing the proportion of wintering curlew foraging across the tide during the day, as derived from monthly scan sampling undertaken over a half-tidal cycle between October 2019 and March 2020 at the Welwick realignment site, on the fronting intertidal flats and adjacent terrestrial fields.

3.6 Discussion

Our understanding of the habitat and space use of non-breeding waders that is needed to set effective conservation measures is limited. Here, we focus on the space use of the Near Threatened curlew which uses both intertidal and terrestrial habitats of estuaries in winter. Previous work has documented that curlew are very faithful to roosting areas during the non-breeding season (Rehfisch et al., 2003; Schwemmer et al., 2016), and are known to make extensive use of land surrounding the estuary, especially coastal grasslands (Townshend, 1981a; Milsom et al., 1998; Navedo et al., 2013). We examined individual, sexual and temporal (day/night, seasonal and annual) variation in the home range size of 18 curlew tagged over four winter seasons at two sites on the Humber Estuary (UK). This is the first study to our knowledge to investigate the variation in home range size of curlew throughout the non-breeding season.

3.6.1 Seasonal and annual variation

We hypothesised that home range size may change through the non-breeding season as a function of resource depletion on the intertidal flats. We detected only slight variation in home range size through the winter period. There were, however, small annual differences in home range size, but it must be acknowledged that we tracked different individuals in each winter, at different times during those winters. Number of birds tagged per winter were variable and dependent on successful catches. For most birds, home range size varies through the annual life cycle and food availability regulates home range dynamics (Rühmann et al., 2019). However, variation in home range size during the non-breeding season has not been well studied in wader populations. Townshend (1981a) found seasonal changes in the use of tidal flats and terrestrial habitats by individual colour-ringed curlew wintering on the Tees Estuary, UK. In radio-tracked Western sandpipers (*Calidris mauri)*, Warnock and Takekawa (1996) found no evidence of seasonal variation in overall home range size through the winter and spring in the San Francisco Bay Estuary, USA, but core areas were smaller in spring than in early or late winter. In our study, the lack of expansion or retraction of the home range in winter is likely to reflect the high-quality of resources on the intertidal habitats.

Our study shows that curlew (the largest European shorebird) occupied very small home and core ranges in comparison of waders of lower body mass. Small wader species such as red knot (*Calidris canutus*) may occupy larger home ranges, and show large variability in wintering home range size along the East Atlantic flyway. Although core and home ranges were not calculated in the following studies, the size of area used by radio-tagged red knot ranged from 1,600 ha or less at a tropical wintering area along the Sahara coast, the Banc d'Arguin in Mauritania (Leyrer et al., 2006) to 80,000 ha in the Western Wadden Sea, The Netherlands (Piersma et al., 1993). Radio-tracking studies found large home ranges for dunlin (*Calidris alpina)*, with home range calculated as a 95% Minimum Convex Polygon (MCP) or fixed kernel 95% Utilisation Distribution (UD) varying between 1,290 and 56,500 ha depending on geographical areas and habitats (Sanzenbacher & Haig, 2002; Shepherd & Lank, 2004; Taft et al., 2008; Choi et al., 2014). Within the Numeniini group, there is evidence of small (<600 ha) feeding core ranges (KDE) for GPS-tagged bar-tailed godwit (*Limosa lapponica)* (n = 6) (Jourdan et al., 2021) as bar-tailed godwits tended to specialize in their habitat use and thus in prey at an individual scale. In comparison, our study found the mean core range to be even smaller for curlew (<100 ha). Among other species of curlew, the home range (95% Minimum Convex Polygon) of a single radio-tagged long-billed curlew (*Numenius americanus)* was estimated to be 2,441 ha along the Gulf of Mexico, Florida, USA (Gabbard et al., 2001). In our study, only one individual had a home range size exceeding 2,400 ha (90% KDE) and mean home range size was 555.5 ha (+/- SD 557.9 ha). Although there is an allometric relationship between home range size and body mass in mammals (McNab, 1963) and such relationships also exist in birds (Newton, 1979; Ottaviani et al., 2006), the relationship may differ between the non-breeding and breeding season.

3.6.2 Variation in relation to sexual dimorphism

We also hypothesised home range size may be driven by individual strategies related to sexual dimorphism, and thus that home range size may differ between males and females. In our study, the sex of adult curlew did not account for variability in the home range size at the individual level. During the non-breeding season, intersexual competition in dimorphic wader species such as godwits drives small scale spatial segregation on tidal flats (Both et al., 2003; Alves et al., 2013), which might result in differences in home range. Townshend (1981a) found colour-ringed males and females curlew to distribute differently between terrestrial and intertidal habitats. Males moved to fields in winter because of decreasing feeding rates on tidal flats, resulting from the decreased availability of *Nereis* worms (Townshend, 1981a). Rolando (2002) argued that food availability is the only true factor controlling home range ecology in birds, and that intraspecific competition cannot be considered as a controlling factor. To maximise their access to resources and reduce intraspecific competition on the intertidal flats, waders adopt different feeding strategies, typically either actively defending a feeding territory or moving in flocks while maintaining their distance with other individuals to reduce interference competition (Goss-Custard, 1980; Van de Kam et al., 2004). Territoriality has been observed in curlew during the non-breeding season (Ens, 1979; Ens & Zwarts, 1980; Townshend, 1981b; Colwell, 2000; Colwell & Mathis, 2001). Although we did not detect difference between males and females in our study, the high inter-individual variation in home range size observed may reflect feeding strategies (e.g., territoriality) or individual specialisation (Durell, 2000). Individual variation makes populations and species less susceptible to environmental changes, and contributes to promoting ecological success (Forsman & Wennersten, 2016).

3.6.3 Diurnal variation

We further hypothesised that home range might be smaller at night because of the greater risk of predation. Although the nocturnal activity of waders has been investigated using radio telemetry (Burton & Armitage, 2005) and more recently using GPS tags (Jourdan et al., 2021), little is known about the nocturnal home range of curlew in winter. Our study provided evidence that nocturnal ranges were greater than diurnal ranges, although there was much individual variation. Differences in the nocturnal and diurnal use of feeding and roosting areas by wintering waterbirds may be linked to the density/activity of prey, disturbance and predation (Sitters et al., 2001; Piersma et al., 2006). Burton and Armitage (2005) found that individual wintering common redshank (*Tringa totanus)* had larger home ranges at night than in the day. However, that study focused solely on the areas used during the intertidal foraging period. In contrast, Jourdan et al. (2021) found that nocturnal feeding core areas (50% isopleth) of bar-tailed godwit to be even more restricted and mostly spatially distinct from the daytime ones on the tidal flats. Whilst there was evidence that nocturnal ranges were greater, we did not investigate habitat use in relation to diurnal cycle. As curlew feed by sight and touch (Davidson et al., 1986), the difficulty in visually detecting earthworms – the primary food source for curlew in coastal grassland (Navedo et al., 2020) – might influence the use of terrestrial fields at night. As artificial illumination has a positive effect on the nocturnal foraging of wader (Santos et al., 2010), lunar phase may also influence nocturnal foraging activity in terrestrial habitats. Using GPS data alone we found curlew spent 22% of their time resting and 78% engaged in other behaviours during the non-breeding season, but only 69% of their time feeding at night compared to 87% during the day. Large waders usually forage for 70-85% of the time (Van de Kam et al., 2004). To our knowledge, it is the first study to infer wader behaviour from path track characteristics (e.g., step length and the angle of direction) using state-space models such as Hidden Markov Models (HMMs).

3.6.4 Limitations

The biggest limitations in this study related to the tag attachment, the battery lifespan and the distribution of the capture sites in the outer estuary. Firstly, in this study, we did not consider harnesses to deploy tags to minimise welfare concerns. As an alternative, it is now possible to use leg loops which support the GPS tag for a longer period (Jiguet et al., 2021), although it is important to evaluate the potential effects of such deployments. As we were principally interested in movement data solely from within the winter period and not across other times of the birds' annual cycles and due to limited battery life of the GPS tags used, we used glue-mounting to deploy the tags that then detached from the birds after approximately three months. Hence, we were only able to track the same individual over a single winter. Thus, we could not examine the individual inter-annual variability in home range sizes. The relatively short battery life of the GPS with UHF download also meant that a trade-off had to be made between the sampling regime and the tracking duration to cover the tidal rhythm and ensure representative coverage of the non-breeding season. At least 56 days of data were expected with the trade-off, but performance of the tag over the four winters was not equal and thus resulted in a variable number of fixes per individual. With the continuous miniaturisation of tags, GPS/GSM technology is now available for birds the size of curlew and therefore individuals can be tracked over the full non-breeding season (from early July to early April) and for up to several years (Schwemmer et al., 2021). In this study, we only sampled individuals from roosts in the outer estuary where the large intertidal flats offered a long feeding window compared to the intertidal flats of the upper and middle estuary, which are narrower and thus quickly submerged. The decreasing availability of intertidal flats in other parts of the estuary could drive differences in movement behaviour or habitat use (i.e., habitat functional response) and could ultimately affect the distribution of birds within the estuary.

3.7 Conclusions

Using fine-scale GPS tracking data, this study provides new insight into the winter home ranges of curlew. To our knowledge, there are no published studies examining the home range size of curlew and highlighting the inter-individual variation. The relatively small home range size and its lack of variation through the non-breeding season are relevant for the conservation of this Near Threatened species. Knowledge of the home range size and movements of wintering waders in relation to the diurnal cycle is vital to informing management responses to environmental changes such as sea-level rise, and thus in improving the efficacy of compensatory habitats such as coastal grasslands and managed realignment sites. Furthermore, knowledge of home range area and behaviour patterns can improve mechanistic models of survival (e.g., IBMs, Stillman et al. (2000), which themselves can inform management decisions in the estuary. However, it is important to note that our results may be site-specific and reflect the birds' available habitats and resources on the Humber Estuary. Variation in home range size through the non-breeding season might occur at sites where the available intertidal resources are insufficient for individuals to meet their daily energy requirements, forcing some to switch to terrestrial fields feeding activity more frequently. The unexplained inter-individual variability in home range size thus requires further attention

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Chapter 4 GPS tracking of Eurasian curlew (*Numenius arquata*) to examine non-breeding habitat selection in coastal habitats modified by shoreline management.

4.1 Abstract

For species of conservation concern, understanding space use and the utilisation of resources is vital to implementing effective conservation measures. During the non-breeding season, the Eurasian curlew (*Numenius arquata*) (Red-listed in the UK Birds of Conservation Concern) uses intertidal flats, saltmarsh and terrestrial fields for foraging and roosting. New intertidal habitats created through a shoreline management practice known as managed realignment may also provide an important habitat for over-wintering waders such as Eurasian curlew. Through GPS tracking of a sample of 14 Eurasian curlew on the Humber Estuary (UK), we assessed factors affecting the species' selection of these habitats. We examined core areas (50% Kernel Density Estimates) to determine whether individuals might show territoriality and derived habitat selection ratios to examine individual, sexual and temporal (day/night, seasonal and annual) variation in habitat selection. We found that Eurasian curlew's core home ranges were restricted to one to two distinct patches on intertidal flats with some overlap, suggesting a low level of intraspecific competition and thus territoriality. By examining variation in habitat selection across four broad habitats, we found that Eurasian curlew preferentially selected saltmarsh and the managed realignment site at night compared to daytime, presumably for roosting. Sex did not explain variation in the habitat selection ratios, but our study revealed that first-year Eurasian curlew showed lower selection for intertidal flats than adults. It is the first study to our knowledge to investigate the day/night variation in habitat selection of Eurasian curlew through the non-breeding season.

4.2 Introduction

Waders wintering on estuaries have to balance their energy gain and costs, and they are faced with choices that may ultimately impact their fitness, i.e., survival or breeding success (Evans, 1976). Habitat selection is an important decision-making process for waders. Whilst the selection of habitats is driven by food availability and the risk of predation (Piersma, 2012), habitat preferences may not be consistent within populations and variation has been reported between individuals (Jourdan et al., 2021a). For waders wintering on estuaries, there may be a high level of feeding specialisation between individuals associated with different payoffs (Durell, 2000). This high level of specialisation might mean that less generalist individuals are less able to switch between different resources and are consequently more sensitive to environmental changes.

During the non-breeding season, most Eurasian curlew (*Numenius arquata*) (hereafter curlew) populations move to the coast where they predominantly forage on intertidal mudflats. Still, it is also one of the few wader species to make extensive use of non-estuarine habitats (Townshend, 1981a; Milsom et al., 1998; Navedo et al., 2013) as individuals complement or supplement their diet (Navedo et al., 2013) by foraging on terrestrial land close to the estuary. The curlew has received much attention in recent years due to its conservation status (Brown et al., 2015; Pearce-Higgins et al., 2017; Young et al., 2020; Douglas et al., 2021). It is listed as Near Threatened on the IUCN Red-list (BirdLife International, 2021) and is also Red-listed in the UK Birds of Conservation Concern (Stanbury et al., 2021). In the UK, although the decline is principally attributed to poor productivity on the breeding grounds, maintaining high levels of survival is key to implementing effective conservation strategies (Cook et al., 2021).

The miniaturisation of tags equipped with Global Positioning System (GPS) receivers enables the movement of birds to be followed for long periods without the need for recapture. Using GPS deployments, it has been possible to investigate many aspects of bird movement ecology previously only studied through more limited radio telemetry and visual observations, e.g., home range size (Mander et al., 2022), territoriality and habitat use (Jourdan et al., 2021a). Territoriality in non-breeding waders can be defined as the defence of a fixed location by an individual for a variable duration (Colwell, 2000). It differs from the home range, the vital space that the animal uses over a given time (Burt, 1943). Territory and home range size may differ between individuals (Jourdan et al., 2021a), reflecting resource selection. Individuals within a population can vary considerably in how they exploit food resources, and thus distribute in the landscape. Accounting for individual variation is essential in animal studies and has potential conservation implications (Durell, 2000; Bolnick et al., 2003). By comparing usage and the availability of resources, a measure of resource selection can be obtained (Johnson, 1980; Manly et al., 2002). Such measures have been widely used in animal studies to inform conservation strategies.

Non-breeding waders are subject to a number of pressures related to human activities, including loss of intertidal flats, disturbance from recreational activities, and land-use change. In response to the loss of intertidal flats, managed realignment has proved a successful approach for the re-creation of intertidal habitats for waders (Atkinson et al., 2004; Mander et al., 2007; Mander et al., 2021). Farmland habitats border most low-lying estuaries in northwestern Europe, and there is evidence that curlew rely on these habitats to forage in winter (Navedo et al., 2013). Understanding the selection of habitats is critical for setting effective conservation measures to protect agro-ecosystems functionally linked to estuary.

The movement ecology of curlew has been studied at the flyway scale, and these studies have highlighted the site fidelity of birds to non-breeding areas (Rehfisch et al., 2003; Schwemmer et al., 2016). Recent work has also highlighted that curlew home range size was relatively consistent through the non-breeding season (Mander et al., 2022). There was, however, high individual variability in home range size which was not related to the species sexual size dimorphism and that may have reflected differences in resource use (Mander et al., 2022). In waders, individual variability in resource use may reflect individual feeding specialisations (Durell, 2000). Within the tribe Numeniini, individual specialisation also exists because of size dimorphism. During the non-breeding season, intersexual competition in dimorphic wader species such as godwits drives small scale spatial segregation on intertidal flats (Both et al., 2003; Alves et al., 2013). Specialisations may nevertheless also exist within sexes, which are unrelated to size (Catry et al., 2011).

On the intertidal flats of northwest Europe, the curlew's diet consists mainly of lugworms (*Arenicola marina*) and ragworms (*Hediste diversicolor*), sand gaper (*Mya arenaria*) and common shore crabs (*Carcinus maenus*) (Townshend, 1981b; Zwarts & Esselink, 1989; Rippe & Dierschke, 1997; Van Gils, 2018). Individuals select prey, and thus habitats, in order to maximise their rate of biomass intake. Through the course of the winter, short-billed male curlew may switch from mudflat-feeding to feeding in terrestrial habitats, especially grassland (Townshend, 1981a). On coastal grassland, earthworms are the primary food source for curlew, which preferentially select the smallest size class (<32.5 mm) of epigeic earthworms (Navedo et al., 2020). Large waders such as curlew usually forage for 70-85% of the time in winter (Van de Kam et al., 2004). Using GPS data alone, Mander et al. (2022) found that curlew spent 22% of their time resting. Waders may be forced or prefer to feed at night to maximise their intake rates. Studies have demonstrated nychthemeral variations in the utilisation of foraging resources (Jourdan et al., 2021b). Waders typically roost over the high-tide period, but may use different day and night roosts e.g., Conklin and Colwell (2007), although see Van Gils and Piersma (1999). Differences in nocturnal and diurnal area and habitat use by wintering waterbirds are also linked to disturbance and predation risk (Sitters et al., 2001; Piersma et al., 2006).

Although the site fidelity and home ranges of curlew have been demonstrated recently through GPS tracking, little attention has been paid to the species' resource selection. As a long-lived species which is present on non-breeding grounds for most of the year, curlew might adopt different strategies to maximise their intake rate. Furthermore, little is known about the level of individual and day/night variation in the species use of estuarine and non-estuarine resources.

Through GPS tracking data of a sample of curlew on the Humber Estuary (UK), we aimed to examine how individuals utilised intertidal foraging patches and so investigate the territoriality of curlew during the non-breeding season. Understanding space use on the intertidal flats is crucial to implementing effective conservation measures and predicting the impact of environmental changes. Furthermore, we examine the individual, sexual and temporal (day/night, seasonal and annual) variation in habitat selection between estuarine and non-estuarine resources.

We hypothesised that variability in habitat selection ratios may reflect individual strategies of curlew and we, therefore, predicted that habitat selection would vary amongst individuals from the same population in response to sexual size dimorphism or age (i.e., adult and first-winter). We also hypothesised that habitat selection would differ between day and night in response to predation risk, and we predicted contrasting use of sites by day and night. Finally, we hypothesized that selection ratios may change through the non-breeding season and between winters.

4.3 Method

4.3.1 Study site, GPS tagging and data collection

Fieldwork was carried out on the Humber Estuary (UK) at the Welwick Saltmarsh (53.64°N; 0.02°E), which is contiguous to the Welwick managed realignment site (53.64°N; 0.00°E) (Figure 4.1). The Welwick managed realignment site was created in 2007 through a breach of the coastal flood defence. The 54-hectare site was designed to offset the loss of habitats due to port development in the Humber Estuary (ABPmer, 2021). At the Welwick Saltmarsh site, curlew were caught at night using mist-nets in saltmarsh pools, used as tidal roosts. The mist-net catches took place between late September and late February during the period when curlew are over-wintering on the Humber Estuary (Frost et al., 2021). A total of 18 curlew were captured on eight catches over four winters (Table 4.1). The bill-length (mm), wing-length (mm) and mass (g) of all individuals were measured, and the sex of adult birds was determined from the bill-length equation derived by Summers et al. (2013). Adult birds were positively assigned to a category (male or female) above a probability of 95%. A total of three males, eight females, five adult birds of unassigned sex, and two first-winter birds were included in the sample of 18 birds (Table 4.1)

All birds caught were fitted with a numbered metal-ring, a unique set of colour-rings for subsequent re-identification in the field, and a GPS/UHF tag. The Pathtrack nanoFix® GEO+RF tag used nano Fix® technology with low power UHF technology (Pathtrack, Otley, UK) for downloading data to a base station. The tags weighed between 4.9 g and 5.1 g which was below 1% of the average weight of the known females and males captured in our study, respectively 922.4 (± 65.3 g) and 791.9 (± 77.5 g). To test the accuracy of the tags, eight of the tags were activated to record hourly GPS positions for a period of up to 24 hours prior to deployment on curlew. The location errors of eight tags deployed for 24 hours at the same position was found to be 25 m (+/- SD 13 m).

The GPS/UHF tags were glue-mounted on the bird's back between the scapulars (following Warnock and Warnock (1993)). Because of the small battery inside the GPS tag, a trade-off was made between fix rate and tracking duration. The tags were set to record the position of the bird every 90 min to give an expected lifespan of at least 28 days for each tag, which would cover two spring-neap-spring tidal cycles. Tags were set to start recording at slightly different times from each other (with 5 minute intervals between tags) so that there were not several tags attempting to communicate with the base station at the same time, which can increase the time taken to download data and therefore the power consumption by the tags, reducing their lifespan. The base stations were positioned within a maximum distance of 200 m from the roosts, and checked weekly to retrieve the data and ensure regular downloads. Fixes were successfully downloaded from all tags, with the exception of one tag for which no data fixes were recorded.

Ringing and GPS tagging activities were undertaken under licence from the Special Methods Technical Panel of the British Trust for Ornithology Ringing Scheme. All fieldwork activities were subject to ethical approval from the University of Hull.

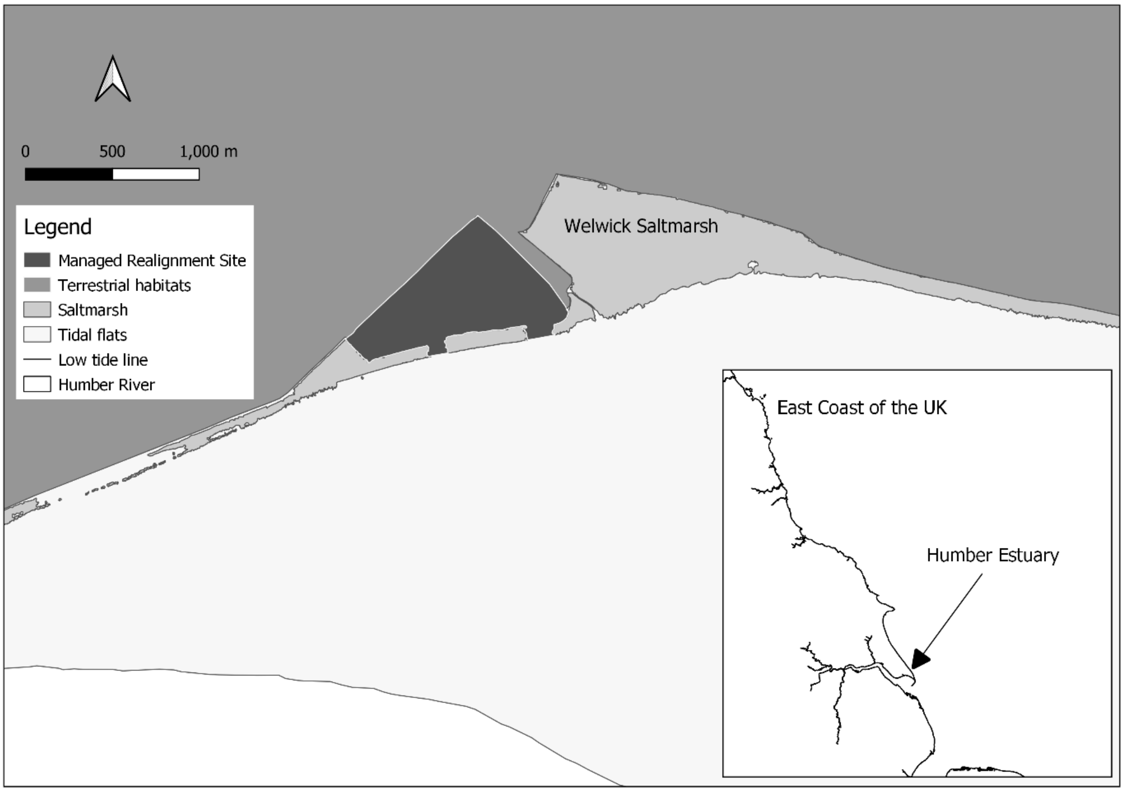

Figure 4.1. Study site showing the capture sites at Welwick Saltmarsh and habitat maps.

Table 4.1. Number (by age and sex) of curlew caught at Welwick Saltmarsh on the Humber Estuary and date of capture. The four individuals excluded from the analysis are italicized.

Winter	Device ID	Date deployment	Last day	No. days	Age	Sex
1	13701	24/01/16	26/02/2016	33	adult	female
1	13751	24/01/16	25/02/2016	32	adult	unassigned
1	13760	24/01/16	01/03/2016	37	adult	unassigned
2	17149	03/02/18	05/04/2018	61	adult	unassigned
3	17151	26/09/18	30/10/2018	34	adult	male
3	*17152*	*26/09/18*	*26/09/2018*	*0*	*adult*	*unassigned*
3	*17153*	*25/10/18*	*27/10/2018*	*2*	*adult*	*male*
3	17154	06/11/18	27/11/2018	21	adult	female
3	*17155*	*06/11/18*	*10/11/2018*	*4*	*adult*	*female*
3	17156	06/11/18	22/11/2018	16	adult	female
3	*17157*	*06/11/18*	*07/11/2018*	*1*	*first winter*	*unassigned*
3	17160	06/11/18	25/11/2018	19	adult	female
3	17531	06/11/18	28/12/2018	52	adult	female
3	17570	06/11/18	06/01/2019	61	adult	male
4	17602	26/11/19	23/01/2020	58	adult	female

4	17608	25/01/20	05/03/2020	40	adult	female
4	17571	25/01/20	17/03/2020	52	first winter	unassigned
4	17578	27/01/20	03/03/2020	36	adult	unassigned

4.4 Data analysis

4.4.1 Home range estimation

R version 3.6.0 (R Core Team., 2021) was used for all home range estimation computations. We estimated home range sizes using the Kernel Density Estimator (KDE) described in the 'adehabitatHR' package (Calenge, 2019). The KDE is a commonly applied home-range estimator in which a kernel distribution (i.e., three-dimensional hill or kernel) is placed on each location. An estimation of the Utilisation Distribution (UD) is then generated across the area of interest (Worton, 1989). The calculation of the UD is sensitive to the bandwidth selection (i.e., smoothing parameter) of the kernels, which determines the resolution of the UD. Errors resulting from over-smoothing or under-smoothing can occur when estimating home-range sizes. There are standard methods to compute the smoothing parameter: 'reference bandwidth' and Least Square Cross Validation (LSCV). As curlew can spend several hours at the same position while roosting at high tide, many duplicates fixes in the data prevented the use of Least Square Cross Validation. Using the default bandwidth (href) as the smoothing parameter resulted in considerable over-smoothing. As such, we used a fixed bivariate normal kernel (smoothing factor h of 25) with the grid size set at 200 m as these parameters provided the best fit to our data. Core (50%) home ranges were estimated for a total of 14 individuals with data collected using an identical sampling regime (1 fix for every 90 min) but with a varying sampling duration. We excluded three individuals from the analysis for which fewer than 224 fixes were obtained (less than 14 days) and did not obtain any movement data from one tag. An average of 640 fixes (range = 260 – 1027) was obtained for these 14 individuals, equating to a period of 40 days (range = 16 – 69). Using the tidal height (as metres above Chart Datum), we estimated KDE home range sizes for the low tide and high tide period to reflect foraging and non-foraging activity (i.e., roosting). To produce KDE home range size at low tide, we excluded GPS points collected above a tidal height of 3.3 m CD. At high tide, we excluded GPS points below a tidal height of 5.3 m CD. Using the British Oceanographic Data Centre (BODC), we sourced the tide height data (available at a 15 min interval) from the Immingham tidal gauge (53.63° N 0.19° W), and matched each GPS point to the actual tide height.

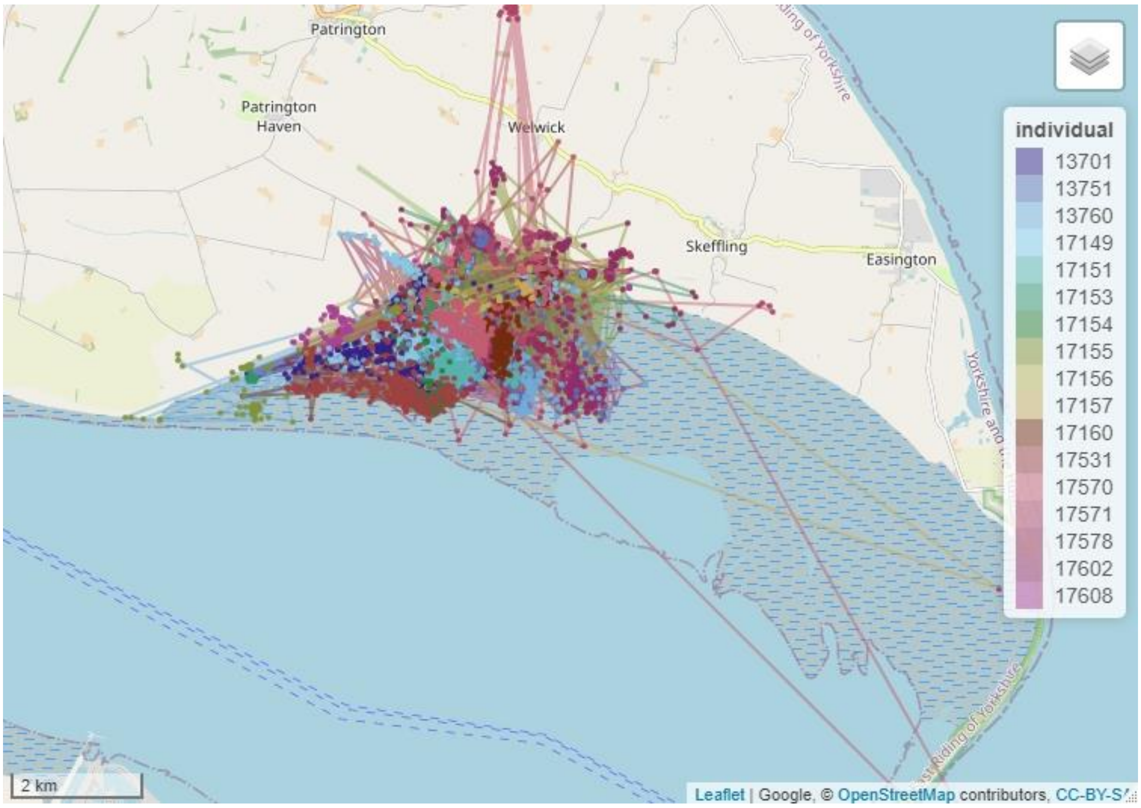

Figure 4.2. GPS tracks of wintering curlew captured at Welwick Saltmarsh and included in the habitat selection analysis (n = 14).

4.4.2 Habitat selection

To examine habitat selection, habitat selection ratios (Manly et al., 2002) were calculated using the R package ‘adehabitatHS’ (Calenge, 2015) in the R version 3.6.0 (R Core Team., 2021). Manly’s Selection Ratios rely on the following hypotheses: (i) that there is independence between animals, and (ii) that all animals are selecting habitat in the same way (Manly et al., 2002). To compute the selection ratios, we followed the design II which assumed the same availability for each animal, but with use unique to each individual (i.e., use is measured for each one). Using open-source layers on saltmarsh extent, high tide and low tide lines from environment.data.gov.uk, we determined the extent of broad habitat types in QGIS. Broad habitats were categorised into four categories. The land behind the sea defences which bordered the study area was classed as the ‘hinterland’. Three broad habitat types were identified on the intertidal areas: ‘mudflats and sandflats’, ‘saltmarsh’, and the ‘managed realignment site’, the latter was created in 2007 through the breaching of flood defence. The extents of broad habitat types were translated into a high-resolution habitat map (10 m x 10 m). Using the Kernel Density Estimator (KDE) described in the ‘adehabitatHR’ package (Calenge, 2019), we estimated a single (90%) home range based on the fixes for all 14 individuals. We overlaid the KDE 90% home range estimate over the broad habitat map to calculate the availability of habitats. The design II (second order selection) was used to determine if individual curlew selected habitat during day- and night-time in the same proportion as was available in the 90% home range estimate. Using the ‘over’ function in package ‘sp’ (Pebesma & Bivand, 2005), we placed the 90% KDE home range estimate around all animal locations and define this as ‘available’ to all. We assumed that availability of habitats was the same for all individuals between day and night. To estimate Manly Selection Ratios, home range habitat availability was combined with used points, which we identified using the ‘join’ function in ‘adehabitatMA’ (Calenge, 2020). Points outside of the 90% home range boundary were excluded. We performed the analysis of habitat selection using the wides function in the ‘AdehabitatHS’ R package (Calenge, 2015). Whilst a selection ratio <1 indicated habitat avoidance, a selection ratio with a value > 1 indicated that the habitat was being selected for. Selection ratios for each habitat were computed for each individual for both the day and night.

4.4.3 Modelling habitat selection

The Manly Selection Ratio was used as a dependent variable in a Generalised Linear Mixed Effect Model (GLMER) (‘GLMER’ function in lme4) that evaluated the influence of age/sex, day/night cycle and other temporal factors (winter of capture and no. days since the start of the winter). Day/night cycle, age/sex, winter were included as fixed effects while individual (tag ID) was included as a random effect. We included the KDE home range size (90%) as a fixed effect to account for sampling bias. The number of days since the start of the winter, calculated from 1st September to the tracking period median, was included as a predictor to investigate potential seasonal variation in selection of habitats. The full model for each habitat is presented with each term assessed on level significance. Following assessment of residual diagnostics using simulated residuals (‘DHARMa’ package (Hartig & Lohse, 2021)) we chose to use a Gamma distribution to model home range size estimate.

4.5 Results

4.5.1 Core areas (50%) and territoriality

The size of core areas varied amongst individuals at low tide (Figure 4.3), and some individuals held several distinct core areas whilst others held a single, but large core area. Figure 4.3 showed individuals using one to three discrete core areas on the intertidal flats, often of very small size. Two individuals (tags 17571 (first-winter) and 17578 (adult male)) had large core areas, which overlapped with the saltmarsh (including the managed realignment site) and the hinterland at low tide. For individuals tagged simultaneously in January 2016, individual core areas on the intertidal flats overlapped. There was also little overlap in November 2018, when five individuals were tracked simultaneously (Figure 4.3). At low tide, results thus indicated that the majority of individuals used small discrete patches (up to three) and that core areas overlapped. Core areas at low tide were distributed from the mid to upper shore, with little utilisation of the low shore (Figure 4.3).

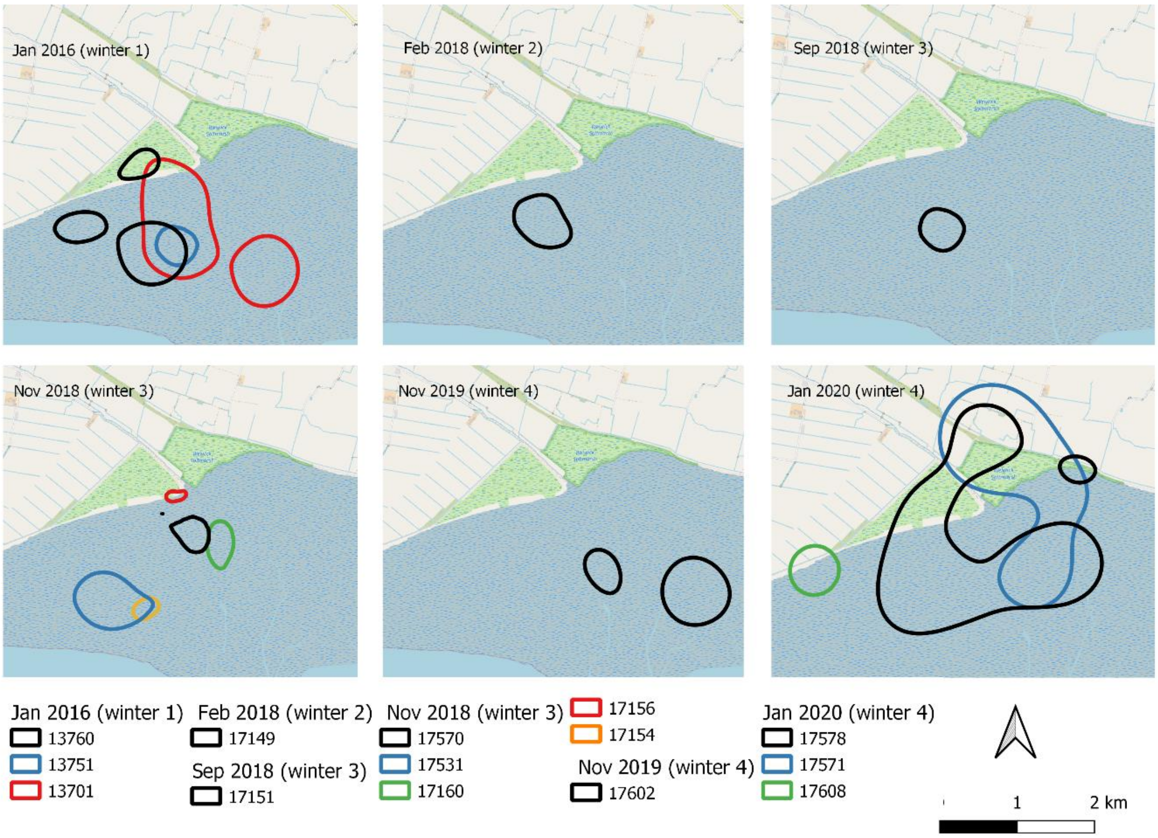

Figure 4.3. Low tide core areas (50% Kernel Density Estimates) of individual curlew captured and GPS-tagged at the Welwick Saltmarsh.

At high tide, the core areas overlapped predominantly with the managed realignment site and the saltmarsh, where the birds roosted at high tide (Figure 4.4). In some instances, the core areas overlapped with the terrestrial fields, which supported roosts of birds and foraging birds when the intertidal flats were submerged by the tide. Figure 4.4 suggested that there were several roosts used at high tide, which overall remained very close to their core areas at low tide (Figure 4.4).

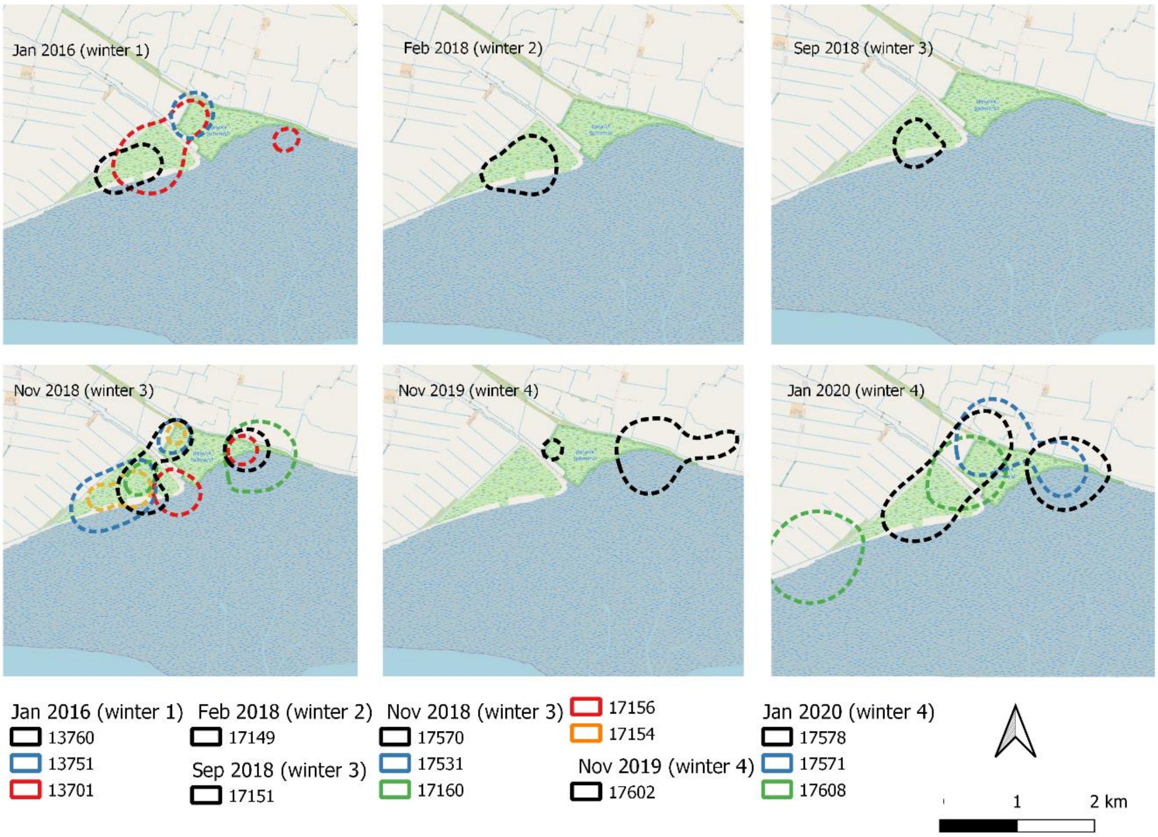

Figure 4.4. High tide core areas (50% Kernel Density Estimates) of individual curlew captured and GPS-tagged at the Welwick Saltmarsh.

4.5.2 Habitat selection (using 90% home range)

Median selection ratios for the curlew caught at the Welwick Saltmarsh across the four winters of study showed that the hinterland was the most avoided habitat, with ratios of < 0.09 in winters 1, 2 and 3 and 0.76 in winter 4 (Figure 4.5). In contrast, median selection ratios suggested that the managed realignment site was the most preferred habitat, with values > 3.5 in winters 1, 2 and 3. However, there was notable inter-individual variability in selection of the realignment site (Figure 4.5). Median selection ratios for saltmarsh were very close or above 1 in winters 1, 3 and 4. Similarly, the mudflats and sandflats had median ratios just above or close to one, with less inter-individual variability observed amongst individuals (Figure 4.5).

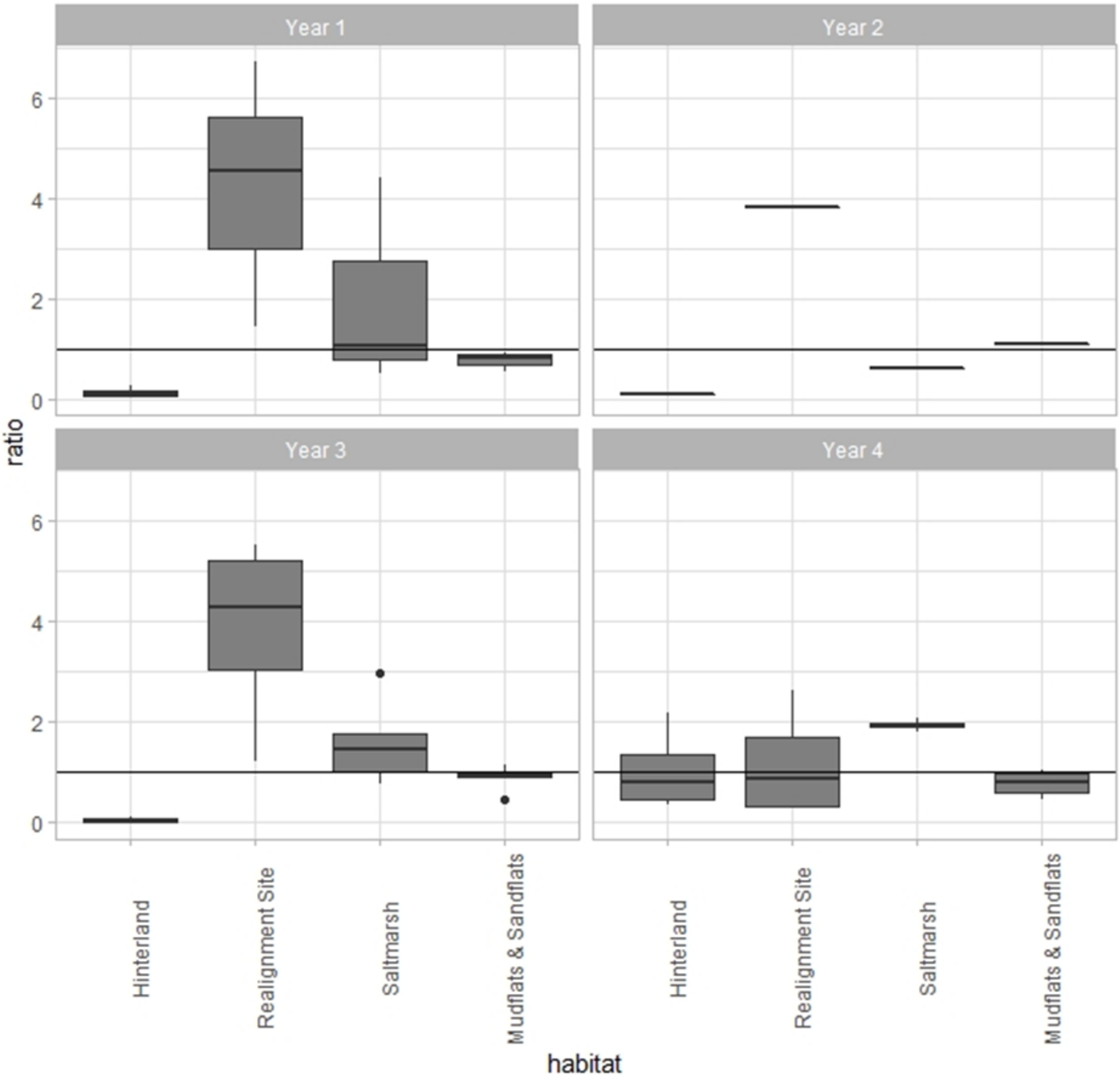

Figure 4.5. Selection ratios (using Manly's Selectivity Measure) for all habitat types of curlew caught in winter at the Welwick Saltmarsh on the Humber Estuary and each winter. Habitat type is on the x-axis and selectivity measure is on the y-axis. Black line at 1 represents line of selection (above = selected for; below = avoided).

4.5.3 Individual variation in habitat selection

Selection of different habitats did not differ significantly between adult males and females (Table 4.2). It is of note that the selection ratios were lower for individuals of unassigned sex (below 95% probability) in the realignment site and for the mudflats and sandflats. Age explained some variation in the selection ratios amongst individuals for mudflats and sandflats, with lower habitat selection shown by first-winter birds (Table 4.2). Overall, individual variation explained a large proportion of the overall habitat selection variation in our models but higher residual variation was also present (Table 4.2). Selection for each habitat by curlew for the most part did not change significantly between winters. Selection of the hinterland increased in winter 4, while selection of the managed realignment site decreased, suggesting a switch between the two habitats. The seasonal effect (measured as number of days since 1st September) did not explain variation in habitat selection, inferring that the selection ratio remained constant throughout the winter in our study. In contrast, the models showed a greater selection of saltmarsh and the managed realignment site at night, when curlew roost in these habitats, compared to the day. Conversely, selection of mudflats and sandflats was highest in the daytime. As overall selection for the hinterland was low, none of the factors could significantly explain the variation in the hinterland selection ratio amongst individuals, although habitat selection ratios of the hinterland appeared to be highest in daytime (Figure 4.7). The selection for the realignment site and mudflats and sandflats increased with larger home range size estimates. Therefore, individuals with the greatest home ranges were more likely to select both habitats.

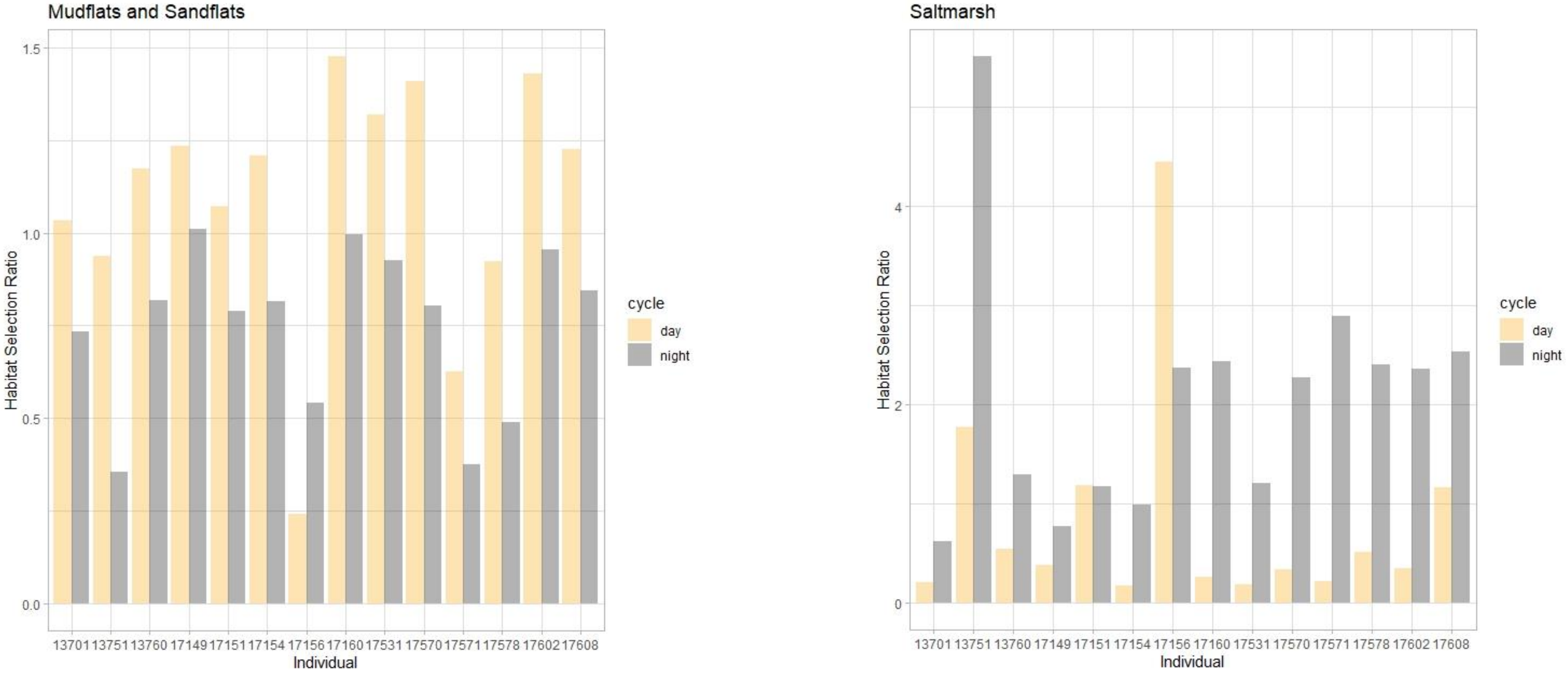

Figure 4.6. Selection ratios for each habitat type in the day and night of curlew caught in winter at the Welwick Saltmarsh on the Humber Estuary. Individual (Tag ID) is on the x-axis and the Manly Selection Ratio is on the y-axis. A selection ratio with a value >1 indicates habitat use away from random, a value <1 indicates habitat avoidance.

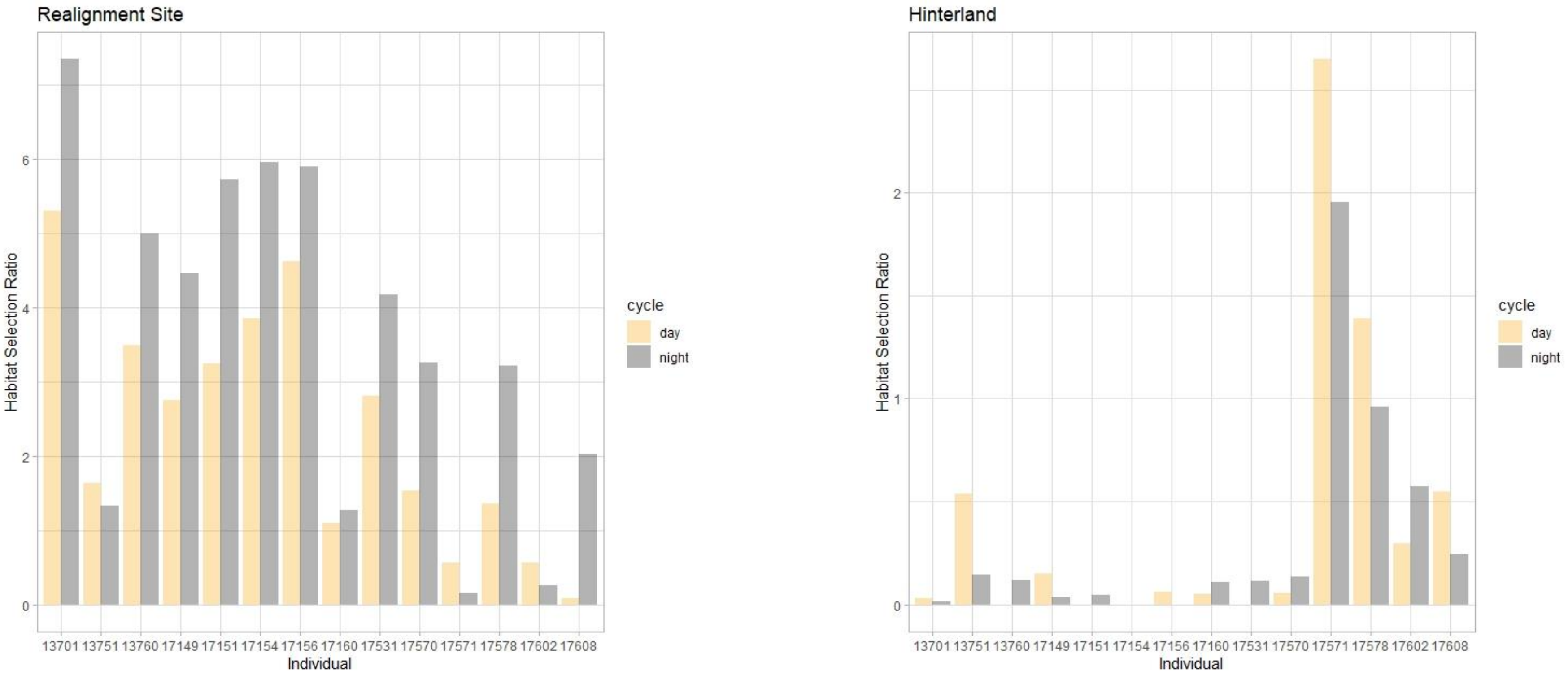

Figure 4.7. Selection ratios for each habitat type in the day and night of curlew caught in winter at the Welwick Saltmarsh on the Humber Estuary. Individual (Tag ID) is on the x-axis and the Manly Selection Ratio is on the y-axis. A selection ratio with a value >1 indicates habitat use away from random, a value <1 indicates habitat avoidance.

Table 4.2. Model coefficient estimates and random effect variance parameters for model assessing all factors affecting variation in the Manly Selection Ratio for each of the habitats of curlew caught in winter at the Welwick Saltmarsh on the Humber Estuary. Estimate (beta), Standard errors (SE), T-values (T) and P-values for the fixed effects. Variance (VAR) and standard deviation (SD) are presented for the random effects. Significance of individual model predictors: * P < 0.05; ** P < 0.01; *** P < 0.001.

	Hinterland				Realignment Site				Saltmarsh				Mudflats and Sandflats			
Parameter	Beta	SE	T	P	Beta	SE	T	P	Beta	SE	T	P	Beta	SE	T	P
Intercept	-3.784	0.682	-5.545	0.001***	0.708	0.775	0.914	0.360	-0.912	0.619	-1.472	0.140	0.132	0.277	0.479	0.632
Home range	0.220	0.246	0.898	0.369	0.778	0.196	3.970	0.001***	-0.352	0.227	-1.546	0.122	0.191	0.088	2.158	0.030*
Cycle (night)	-0.033	0.300	-0.111	0.912	0.305	0.147	2.075	0.038*	1.285	0.196	6.538	0.001***	-0.398	0.077	-5.116	0.001***
Days	0.509	0.556	0.915	0.360	0.594	0.645	0.921	0.356	-0.531	0.544	-0.975	0.329	0.164	0.242	0.679	0.497
Winter 2	-0.307	0.883	-0.348	0.728	0.783	0.994	0.788	0.431	-1.093	0.870	-1.257	0.208	0.661	0.373	1.773	0.076
Winter 3	1.187	1.094	1.085	0.278	1.324	1.272	1.041	0.297	-0.492	1.066	-0.462	0.644	0.188	0.476	0.396	0.691
Winter 4	2.515	0.619	4.064	0.001***	-1.813	0.740	-2.451	0.014*	0.557	0.579	0.961	0.336	-0.033	0.255	-0.130	0.896
Adult (male)	0.403	0.594	0.678	0.498	0.255	0.692	0.369	0.712	-0.035	0.587	-0.061	0.951	0.220	0.256	0.861	0.389
Adult (unassigned)	1.153	0.725	1.591	0.112	-0.735	0.759	-0.969	-0.332	1.283	0.658	1.949	0.051	-0.588	0.284	-2.070	0.038*
First winter (unassigned)	1.388	0.889	1.560	0.119	-1.441	1.030	-1.399	-0.161	0.497	0.851	0.584	0.208	-0.972	0.379	-2.561	0.010*
Random effects	VAR	SD			VAR	SD			VAR	SD			VAR	SD		
Intercept/Individual	0.110	0.332			0.254	0.254			0.200	0.447			0.020	0.144		
Sigma (Resid.var)	0.503	0.709			0.202	0.449			0.339	0.582			0.039	0.198		

4.6 Discussion

Wader species such as curlew use both estuarine and non-estuarine habitats, and both habitats are vulnerable to environmental changes in estuaries. Understanding habitat selection and the distribution of important areas for roosting and foraging is thus vital for species conservation. By analysing the movements of 14 individual curlew over four winters, we found evidence that individual area use was focused on one to two distinct patches (50% core areas). The saltmarsh and the managed realignment site were selected at night over the mudflats and sandflats, with the latter habitat preferred in daytime. There was no evidence of day/night variation in habitat selection of the hinterland. Whilst sex did not explain any variation in the habitat selection ratios, our study revealed that age was important in explaining variation in habitat selection of mudflats and sandflats. The lower selection of this habitat by first winter birds may relate to intraspecific competition in winter, leading to the exclusion of first-winter birds from foraging areas.

Our study highlighted that individuals showed distinct foraging patches on the intertidal flats. In winter, waders may adopt varying strategies to maximise their access to resources, typically either actively defending a feeding territory or moving in flocks while maintaining their distance with other individuals to reduce interference competition (Goss-Custard, 1980; Van de Kam et al., 2004). Curlew are an interference-sensitive species (like Eurasian oystercatcher (*Haematopus ostralegus)* and grey plover (*Pluvialis squatarola*) that maintain large minimal distances from conspecifics and only form occasional, sparse flocks when foraging (Folmer et al., 2010). Using core areas (50%), Jourdan et al. (2021a) found that bar-tailed godwit (*Limosa lapponica*) showed extreme fidelity to restricted feeding areas during winter, with low overlap between individual feeding home ranges. Whilst there was evidence that curlew had small foraging patches in our study, these were not exclusive on the intertidal flats. There was some overlap between feeding areas of curlew which were captured and tracked together for a similar period of time, indicating a low level of intraspecific competition. In a study of Long-billed curlew (*Numenius americanus*) distribution on the intertidal flats, Mathis et al. (2006) speculated that the uniform distribution found was the consequence of the species' territorial social system. Territoriality has been observed in curlew during the non-breeding season (Ens, 1979; Ens & Zwarts, 1980; Townshend, 1981b; Colwell, 2000; Colwell & Mathis, 2001), but according to Ens (1979) and Townshend (1981b), the proportion of curlew defending territories on the intertidal flats in winter is small. In our study, the overlap between core areas (50% KDE) at low tide suggested the lack of territoriality for most individuals with aggregations found on the mid shore of the intertidal flats. There was, however, evidence of some territoriality for at least two individuals with core areas below seven hectares. Ens (1979) estimated territory size of 0.5 – 0.8 ha on the mudflat based on daytime visual observations. In our study, the core areas are based on nocturnal and diurnal GPS points, and territory size may differ between day and night due to feeding method and prey availability.

Mander et al. (2022) found that the 90% home range estimates of wintering curlew showed little overlap with the hinterland of the Humber Estuary (UK). Although the use of the hinterland was not extensive or widespread between individuals, we investigated the influence of factors on the variation in habitat selection. We found that the sex of individual curlew did not influence the selection of the hinterland although birds of unassigned sex showed a weak selection of the sandflats and mudflats. Based on observations of colour-ringed birds, Townshend (1981a) previously found a difference in foraging habitat use between male and female curlew, with longer-billed females preferentially feeding on intertidal flats and shorter-billed males on grassland.

Individual curlew varied in their habitat selection between the day and night, with greater selection of the saltmarshes and the managed realignment site at night, and conversely, a lower selection of mudflats and sandflats. In addition to differences in the activity and thus availability of prey, disturbance and predation risk might explain differences in the nocturnal and diurnal use of feeding and roosting areas by wintering waterbirds (Sitters et al., 2001; Burton & Armitage, 2005; Piersma et al., 2006). Several studies have shown that roost sites may also differ between day and night (see in Rogers (2003)). One possible explanation is that waders are more likely to be vulnerable to ground predators at roost sites at night than in daytime and consequently avoiding predation risk may have a greater influence on roost selection at night (Rogers et al., 2006). Jourdan et al. (2021b) highlighted differences in habitat selection between day and night in bar-tailed godwit. Although we could not detect any difference in use of the hinterland due to the low utilisation of this habitat in our study, the activity of prey is likely to influence the use of terrestrial habitats at night. Indeed, curlew feed by sight and touch (Davidson et al., 1986), and earthworms, the primary food source for curlew in coastal grassland (Navedo et al., 2020), might be difficult to detect at night.

Using GPS, our study helps to fill a gap on the habitat selection of curlew in winter and better understanding variation between the day and night. The study highlighted the importance of saltmarsh and the managed realignment site at night for roosting curlew. On the intertidal flats, overlaps between core areas reflected the reduced level of intraspecific competition in curlew. The lack of sex-specific variation in habitat selection suggested that intersexual competition was not occurring in our study site, although individuals of unassigned sex show a lower selection of the mudflats and sandflats. Intersexual competition in dimorphic wader species such as godwits has been shown to drive small scale spatial segregation on intertidal flats (Both et al., 2003; Alves et al., 2013). For curlew, the evidence of spatial segregation is limited to a colour ringing study on the Tees Estuary (UK) showing that males and females curlew distribute differently between terrestrial and intertidal habitats (Townshend, 1981a). Longer-billed females are able to access deeper prey than males on the intertidal flats (Ferns & Siman, 1994). Conversely, the prey selected by short-billed males may become less accessible as invertebrates bury deeper in winter and thus they may be forced to select prey in other habitats e.g., earthworms in agro-ecosystems. Amongst the tribe of curlew, short bill length species such as the little curlew (*Numenius minutus)* and formerly the Eskimo curlew (*Numenius borealis)* were associated with foraging on grasslands in winter (Cramp & Simmons, 1983). Davidson et al. (1986) provided evidence that the increased length of the curlews' bill had evolved for probing on mudflats on the non-breeding ground.

The study was based on a sample of 14 birds captured from two areas within the Welwick Saltmarsh. The biggest limititations of this study related to the relatively small size because of the difficulty and constraints in catching curlew at the same site throughout the winter. Furthemore, we could not examine inter-annual variability amongst individuals because we were only able to track individuals over a single winter. Indeed, glue-mounted GPS devices detached from the birds after approximately three months. Finally, capturing birds at night from the same roost might introduce a bias in the sampling of individuals if birds from different cohorts display varying strategies. There is evidence that curlew feeding inland during the day come to roost at night on the Tees Estuary (UK) (Townshend, 1981a). Our study reveals consistent habitat selection ratios across the four broad habitats throughout the non-breeding season and little inter-annual variability. The only notable difference in habitat selection ratios related to day and night variation. Variation in habitat selection is likely to reflect the quality and availability of habitats. In this instance, it can be hypothesised that the availability of intertidal habitats, including saltmarsh and habitats created through the realignment of flood defence, reduces the need for curlew to prospect on the hinterland to fulfil their daily energy requirement. Designing managed realignment sites close to foraging areas is crucial as the created intertidal habitats can support diurnal and nocturnal roosts, potentially reducing energetic expenditure for birds commuting between roosting and foraging sites. Furthermore, the colonising saltmarsh vegetation within the managed realignment site is a source of organic matter that might benefit the macrobenthos community on the sandflats and mudflats contiguous to the managed realignment site. Whilst saltmarsh colonisation of realignment sites can have a detrimental effect on the abundance of foraging benthivorous species within those areas (Mander et al., 2021), the saltmarsh within managed realignment site can support roosting birds at high tide. As sea-level rises, the long-term strategy of realigning flood defences is becoming a widely adopted shoreline management practice to provide sustainable coastal defences and create intertidal habitats in estuaries. Understanding how the creation of intertidal habitats might mitigate the loss of terrestrial habitats and benefit individual fitness needs to be addressed for this species of high conservation status.

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Chapter 5 Using Eurasian Curlew GPS tracking data to inform an Individual-Based Model (IBM) at an estuarine restoration

5.1 Abstract

Intertidal habitat creation is an important mechanism to maintain populations of waders on protected sites in the face of environmental changes, such as sea-level rise. The Eurasian curlew (*Numenius arquata*) is of high conservation status and is one such species that can benefit from the creation of intertidal habitats through the realignment of flood defences. Using individual-based models we can simulate animal behaviour in a realistic environment and quantify the impact of environmental changes on wader fitness (i.e., body condition, survival). The aim of this study was to parameterise an individual-based model, built using the open-access MORPH software, to examine the effect of environmental changes on wader populations. The model was specifically parameterised for Eurasian curlew in an area of the Humber Estuary (UK) featuring a managed realignment site. LiDAR-based elevation data and benthic ecological survey point data was used to define patches in order to define the terrestrial and marine food resources across the site. To enable real-world predictions, the model was validated using data on behaviour (proportion of time spent feeding) and fine-scale habitat use from 16 GPS-tracked Eurasian curlew. The model predicted both the proportion of time spent feeding for Eurasian curlew and their distribution across the modelled area to be in line with observed values. The MORPH predictions showed the value of the managed realignment site. Indeed, the numbers of birds supported at the end of the non-breeding season (relative to those at the start) were greater when including the managed realignment site in the modelled area. At such a small within-estuary spatial scale, knowledge of bird movements to define patches and resources is essential to enable real-world predictions and the study showed that the model could be parameterised at this scale. In response to anthropogenic pressure (e.g., sea-level rise), nature-based solutions in estuaries play an increasing role in maintaining bird populations, and assessing the effectiveness of habitat restoration schemes is critical for estuarine bird conservation.

5.2 Introduction

Together with breeding productivity, annual mortality is one of the key demographic rates that control the overall size of animal populations. For many species, such as migratory waders, mortality rates may vary through their annual cycle, through the breeding and non-breeding (migration and wintering) seasons. Quantifying the impact of environmental changes on mortality is thus crucial to predicting the impact of future environmental changes, e.g., of sea-level rise, on their populations.

Many estuaries in northwest Europe are designated as Special Protection Areas (SPAs) under the EU Bird Directive (2009/147/EC) or national legislation (e.g., under the Wildlife Countryside Act 1981 Act in the UK), with conservation objectives that populations of feature bird species should be maintained in a favourable condition. To offset for the loss of intertidal areas on estuaries due to sea-level rise or direct anthropogenic activities, new schemes have thus been designed to create new intertidal habitats. Understanding the efficacy of such mitigation measures on wader mortality is thus also crucial if these schemes are to meet their objectives.

After centuries of land claim in estuaries in northwest Europe (Gibson et al., 2007), new intertidal habitats have recently been created through a shoreline management practice known as managed realignment (MR) site (Esteves, 2014). Where arable land is returned to the estuary and new intertidal habitats created, there is potential for the change in land use to affect the survival of over-wintering waders, notably species that use both terrestrial and intertidal habitats e.g., Eurasian curlew (*Numenius arquata*) (hereafter curlew), thereby potentially benefitting the numbers of birds that might be supported. The development of animal GPS tracking has provided new insights into the habitat and space use of birds, including the use of mitigation sites such as managed realignment sites. Knowledge of the habitat and space use of birds can improve mechanistic models of bird survival, e.g., individual-based models (IBMs), which provide a valuable basis for informing understanding of environmental change on estuaries and thus conservation decision making (Wood et al., 2015).

Individual-based models have become an established approach to simulating animal behaviour in a realistic environment (Grimm & Railsback, 2005). Numerous platforms are available (DeAngelis & Diaz, 2019), and in particular a flexible platform – called MORPH – has been developed over the last 30 years to be used with a wide range of species, particularly birds, and environmental issues (Stillman, 2008). The MORPH model simulates how birds obtain their food across patches to meet their daily energy requirement. The model is based on the key principle that individuals make fitness-maximising decisions (Grimm & Railsback, 2005). MORPH provides predictions of the time spent feeding by individuals, the distribution of birds and their body condition and survival, i.e., their individual fitness. However, assumptions about animal movements in designing an IBM are often made using *a priori* information on habitats available to birds and the extent of the foraging ranges.

The MORPH platform has become an important tool to predict waders' responses to environmental changes (West & Caldow, 2006) and has been applied to a range of scenarios looking at the potential impacts of, for example: environmental changes (Stillman et al., 2005; Durell et al., 2006), recreational disturbance (Stillman et al., 2007); hunting (Durell et al., 2008), warm-water flows into estuaries (Garcia et al., 2016), regime shifts of invertebrates (Bowgen et al., 2015) and the development of oyster reefs as supplementary foraging habitats for waders (Herbert et al., 2018). The impact of the loss of intertidal habitats and proposed mitigation measures on waders has also been studied using MORPH (Durell et al., 2005; Goss-Custard et al., 2006a). These studies have found the responses to loss and gain of intertidal habitats to differ between species, potentially due to differences in species' diet and foraging strategies. Bowgen et al. (2015) found that birds such as curlew – which have a more specific foraging strategy – will be first affected by a regime shift of invertebrates, with the species having to shift to terrestrial resources which are less profitable.

Wader IBMs seldom incorporate the terrestrial foraging patches as a parameter in an estuarine environment (Stillman et al., 2000) because of the lack of information on habitat use and space use of terrestrial habitats. Curlew is one of the few wader species that frequently feeds on terrestrial habitats (Townshend, 1981; Milsom et al., 1998; Navedo et al., 2013). Using an individual-based model, Bowgen et al. (2015) predicted that terrestrial habitats play an important role as a supplementary foraging resource for curlew. Furthermore, Stillman et al. (2005) predicted that terrestrial fields around the Humber Estuary were critical to maintaining high survival of curlew in winter. However, the assumptions of movement underpinning these predictions were based on a general pattern of movements between terrestrial and intertidal habitats observed in other estuaries, not site-specific movements. Because of the development of GPS tracking, we have gained a greater understanding of home range size and resource selection of waders. This information can help us to refine assumptions about movements used in individual-based models.

This study focuses on investigating the use of movement data of curlew in an estuary to define foraging patches and subsequently parameterise an IBM. For over-wintering waders that use both intertidal and terrestrial habitats in estuaries, defining the vital space used by birds and making realistic assumptions about ranging movements are crucial to accurately predicting the effect of environmental change on wader populations. In this study, an individual-based model is parameterised by considering foraging patches on the terrestrial habitats which have been used by GPS-tracked curlew. Using data derived from 16 GPS-tracked curlew on the Humber Estuary, we aim to validate the model with data on behaviour and fine-scale habitat use. Using the validated model, the effect of the managed realignment site on over-winter survival of curlew will be quantified and then used to predict the numbers of birds supported at the end of the non-breeding season (relative to those at the start).

5.3 Method

5.3.1 Study site

The research was carried in an area of the outer Humber Estuary, which included the Welwick managed realignment site (53.64°N; 0.00°E), the Welwick Saltmarsh (53.64°N; 0.02°E) and adjacent intertidal and terrestrial areas (Figure 5.1). The Welwick managed realignment site was created in 2007 through a breach of the flood defence (ABPmer, 2021). The 54-hectare site was designed to offset the loss of habitats due to port development in the Humber Estuary. The managed realignment site is high in the tidal frame, as the sediment surface elevation varies between 1.3 m and 5.8 m above UK Ordnance Datum (OD) (i.e., sea-level) in 2018 (LiDAR data from environment.data.gov.uk). Prior to habitat creation, the land had an approximate elevation of 2.8 m above OD (Pontee et al., 2004). Because of the position of the managed realignment site on the tidal frame, the intertidal habitats remained dry on neap tides. The managed realignment site is fronted by an extensive mudflat and sandflats used by waterbirds during tidal emersion (Mander & Stone, 2020). The site is also contiguous to the Welwick Saltmarsh, which is a high saltmarsh grazed by sheep outside the winter period. The Welwick Saltmarsh features a small number of pools and flashes, where waders roost at high tide. Mean High-Water Spring (MHWS) measured at Sunk Channel was 3.40 m above OD, whilst Mean Low Water Spring (MLWS) was below 3.00 m OD [measured at the Sunk Dredged Channel, < 1 km from the Welwick managed realignment site], giving a maximum tidal range of 6.4 m. The area is of importance for over-wintering and passage waterbirds, including foraging and roosting curlew, with the area supporting at least 25% of the Humber curlew population in winter (Mander & Stone, 2020). The Humber Estuary is one of the top 10 sites in the UK for over-wintering curlew with 2,787 individuals (five-year average) (Frost et al., 2021).

5.3.2 Characterising space of curlew using home ranges

We obtained movement data from 16 GPS-tagged curlew. Capture of curlew took place during the winters of 2015/16, 2017/2018, 2018/19 and 2019/20, between late September and late February at the Welwick Saltmarsh. Roosting curlew were caught at night using mist-nets in saltmarsh pools. All birds caught were fitted with a numbered metal-ring, a unique set of colour-rings for subsequent re-identification in the field, and a GPS/UHF tag. The tag type was a Pathtrack nanoFix® GEO+RF tag, which employed nano Fix® technology with low power UHF technology (Pathtrack, Otley, UK) for downloading data to a field-based base station. Field-based stations were located approximately 200m from the roost to help with data downloading. The tags were set to record the position of the bird every 90 min and to attempt to download data to a field-based base station every 60 min. The methodology is described in

Mander et al. (2022). To determine home range size, we use Kernel Density Estimation (KDE), described in the 'adehabitatHR' package (Calenge, 2019) and all fixes from the 16 individuals were combined to produce a total home range size (90% KDE). An estimation of the Utilisation Distribution (UD) was generated across the area of interest. Number of fixes varied between 260 fixes and 1,115 fixes (mean = 691, n = 16).

5.3.3 Individual-based model

We used a pre-existing model of the Humber Estuary (Bowgen, 2016) designed in MORPH (Stillman, 2008) which predicts the numbers of birds supported at the end of the non-breeding season. The model was updated to focus on the use of the specified study area by waders and with revised environmental datasets as outlined below. Further details of the parameters are given in Appendix 10.

5.3.3.1 Environmental parameters

The model simulations were run from 1st September 2019 to 31st March 2020, to match with contemporary data on bird abundance, foraging intensity, and movements, as well as on prey resources collected over this period. The September to March period encompasses the major over-wintering period of most shorebirds in the UK. The time step was set to one hour and environmental conditions (i.e., daylight, tidal height and air temperature) were assumed to vary between each time step. Using an online source of sunrise and sunset for Kingston-upon-Hull on the Humber Estuary (https://www.timeanddate.com/sun/uk/kingston-upon-hull), each time step was categorised by the presence of daylight or not. We determined the tidal height of each time step using the observed tide height (recorded at a 15 min interval) from Immingham Port on the Humber Estuary (sourced from the British Oceanographic Data Centre (BODC) https://www.bodc.ac.uk). Hourly air temperature data was obtained for each time step from the station South Killingholme on the Humber Estuary from the Met Office Integrated Data Archive System (MIDAS) archived in CEDA (https://archive.ceda.ac.uk/).

5.3.3.2 Patch parameters

An overlap was made of the total home range for all 16 individuals over the intertidal and terrestrial habitats to define patches of resources used by GPS-tracked curlew. Using digital terrain models (DTMs) collected via light detection and ranging (LiDAR) from environment.data.gov.uk, we categorised in QGIS the intertidal flats into four areas according to tidal elevation (very low, low, mid or high). Using site-specific information on the resources available (i.e., benthic sampling station, described in the next section) over the study area, we defined discrete patches on the intertidal flats and terrestrial habitats. Our study area was thus divided into 27 feeding patches on the intertidal flats (including the managed realignment site); the terrestrial habitats were defined as one patch. The Welwick Saltmarsh was included as a high tide roosting patch, used by the birds when the tide covered the foraging area on the intertidal flats (Figure 5.1).

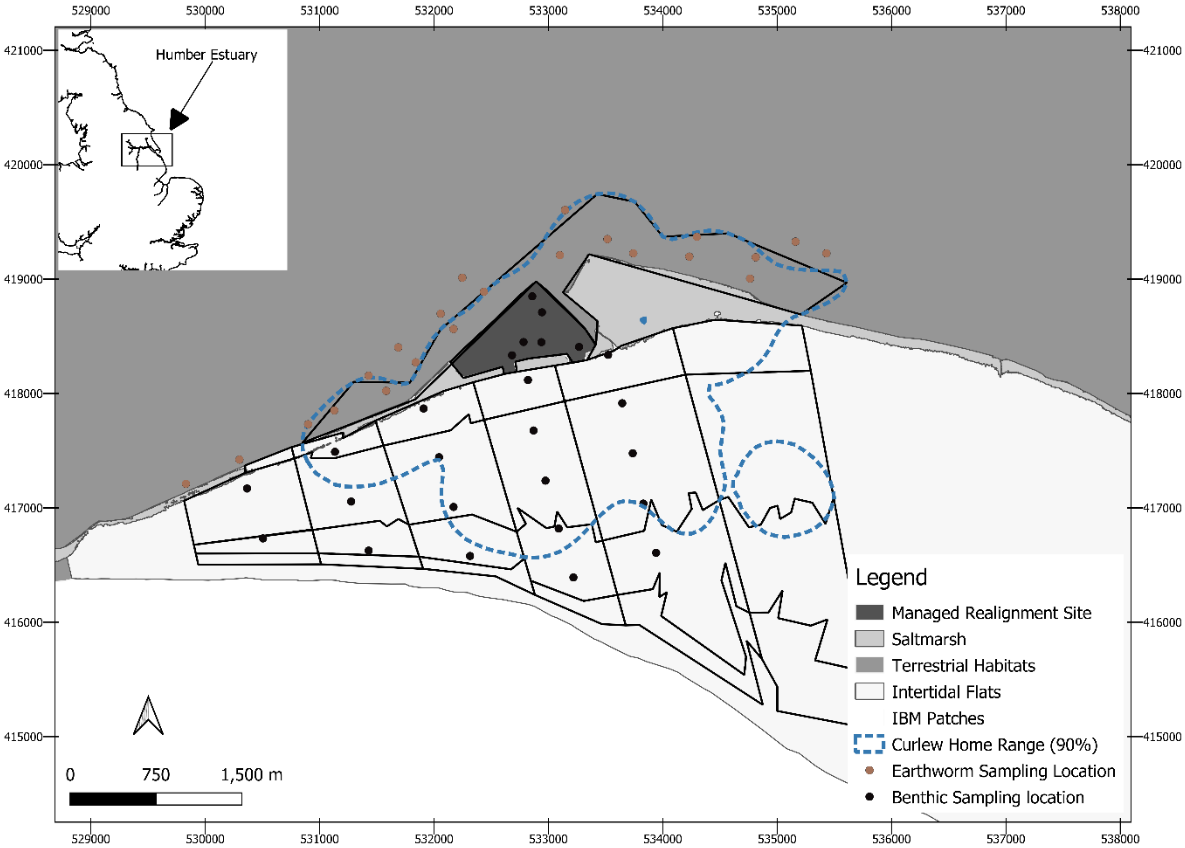

Figure 5.1. Study area showing discrete model patches.

5.3.3.3 Food resource parameter

A survey of the intertidal benthic community at 25 sample sites was conducted in September 2019 and repeated in March 2020 using triplicate cores at approximately the central point of each patch (Figure 5.1). The invertebrate sampling was undertaken using a 11.5 cm diameter corer (0.01 m^2 area). Sediment was cored to a depth of approximately 15 cm and subsequently stored in pre-labelled heavy-duty polythene bags with an internal label. Once retrieved, the benthic samples were kept cool and returned to the laboratory within a 12-hr period for sieving and preservation. Sediment samples were gently washed through a 0.5 mm sieve and the animals retained for microscopic analysis. The faunal samples were then sorted and identified to species level (where practicable). Total length/shell length in mm were measured for each individual of the worm, crustacean and mollusc taxa collected. For each species, we measured ash-free dry mass (AFDM) by pooling all individuals from the same core. To determine food resources in the terrestrial habitats, we surveyed earthworms using a method adapted from Bouché and Gardner (1984) and Bouché and Aliaga (1986). The method consisted of a physical extraction by hand-sorting soil cores (30 cm X 30 cm X 10 cm) to collect earthworms. We sampled earthworm densities from October to November 2019 at 22 stations spread across a range of terrestrial habitats overlapping with the total home range of curlew. The earthworm sampling could not be repeated in March 2020 due to the first Covid-19 lockdown. Total length (in mm) and biomass of each earthworm was measured. All benthic species and earthworms recorded during the survey were arranged into resource groups (Table 10). For each resource group, we used specific size-classes based on published information on the size range of prey handled by different bird species (Goss-Custard et al., 2006b). The initial density of each resource group was calculated using the October 2019 abundance data.

5.3.3.4 Bird parameters

Although the study was designed to primarily examine curlew survival, an additional 10 wader species were included in model to account for indirect interspecific competition through loss of resources: dunlin (*Calidris alpina*), sanderling (*Calidris alba*), common ringed plover (*Charadrius hiaticula*), ruddy Turnstone (*Arenaria interpres*), red knot (*Calidris canutus*), common redshank (*Tringa totanus*), grey plover (*Pluvialis squatarola*), black-tailed godwit (*Limosa limosa*), bar-tailed godwit (*Limosa lapponica*) and Eurasian oystercatcher (*Haematopus ostralegus*). Each of the 11 species had specific physiological and behavioural parameters that remained constant (Appendix 10). The numbers of individuals considered in the IBM were based on through the tide counts (half tidal cycle) carried out between September 2019 and March 2020 at the Welwick managed realignment site and on the adjacent intertidal areas (Mander et al., 2022).

5.4 Results

5.4.1 Food resources and distribution

There was a high spatial variation in the distribution and abundance of food resource across the intertidal habitats of the study area (Figure 5.2). The abundance of benthic invertebrates was the highest in the high shore patches. Abundance declined markedly further down the mid and low shores, and was very low for the terrestrial patch. The abundance of food resource in the managed realignment site was low compared to the mid shore, although the managed realignment site was positioned higher in the tidal frame. In terms of abundance, the benthic assemblage was dominated by *Peringia* whilst other molluscs and marine worms accounted for the rest of the assemblage on the high and mid shores (Figure 5.2). In the managed realignment site, *Peringia* was the most abundant food resource. As expected, food resources declined markedly between October 2019 and March 2020 as the result of mortality due to predation, including birds.

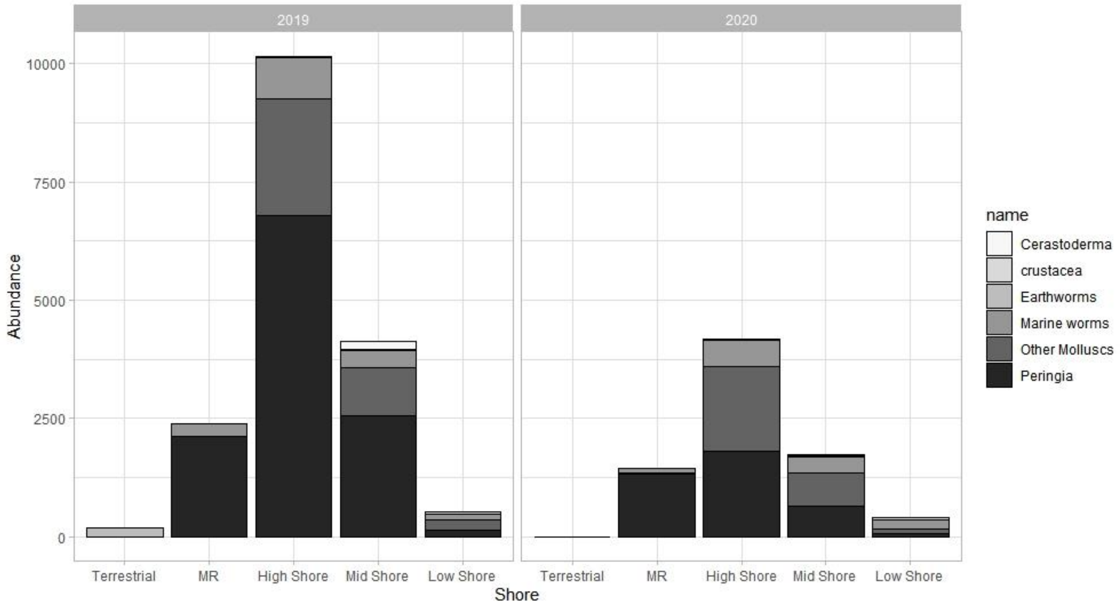

Figure 5.2. Abundance of food resources (animals per m^2) in each zone at the start (October 2019) and end of the winter (March 2020).

5.4.2 Calibration of the present day model

As the model predicted no mortality of curlew over the winter period, we calibrated the model by increasing the size of the population using the modelled area. Starting with the mean count recorded two hours either side of low water, we applied an incremental increase (+ 10%) in the population size of curlew and other species until a mortality threshold of 9% was reached for curlew. Annual survival of waders is high (Méndez et al., 2018), with adult annual survival estimates of 0.714 ± 0.045 (CI 0.618-0.794) for the genus Numenius. As with most waders, curlew do experience over-winter mortality. In Britain, Taylor and Dodd (2013) found a stable annual survival rate of 90% for curlew wintering in North Wales (UK). More recently, Cook et al. (2021) estimated over-wintering mortality of 0.884 (0.875–0.893) based on UK ringing data between 1970 and 2018.

By increasing the size of the wader populations by 3.4, an overall mortality of 14.7% across all species was obtained. Although it is possible to calibrate the model using day and night feeding efficiency, we decided that population size was more appropriate given that count data were collected over the winter period. The calibrated model predicted no mortality of red knot and common redshank whilst mortality of grey plover and dunlin was below 10%. Black-tailed godwit had a mortality exceeding 65% in the calibrated model. This might be because the model was primarily parameterised for curlew in terms of space use and resources, and, therefore likely be more effective at predicting mortalities for this species than other species.

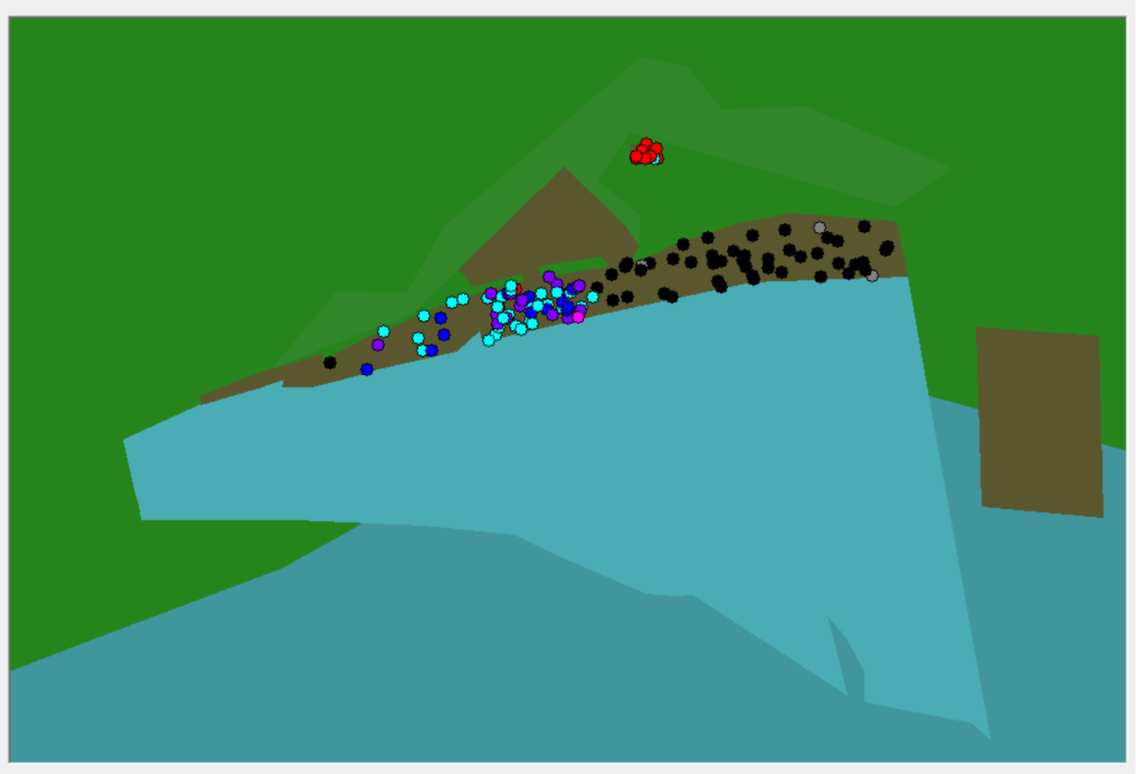

Figure 5.3. Screenshot of the MORPH viewer at Welwick for the last time step in the model. The area in light blue area indicate that habitat is currently unavailable as submerged by the tide. The area in grey are intertidal habitats available to the birds whilst lighter green areas are terrestrial fields available to the birds. The foragers are represented by colour circles.

5.4.3 Validation of the MORPH model

MORPH predicted the time spent feeding by an average bird over a tidal cycle. The measure is a good indicator of the effort required by the birds to meet their daily energy demands (Goss-Custard and Stillman, 2008). By comparing predicted values from MORPH with observed values, we were able to conclude that the model performed well at predicting the observed behaviour of birds. For curlew, we considered the proportion time feeding derived from daytime visual observations and from GPS tracking data carried out in the study area (Mander et al., 2022). For curlew, the predicted MORPH value (75% of time spent feeding) was very close to observed values. Using GPS data alone in the study area, Mander et al. (2022) found that curlew spent 22% of their time resting and 78% engaged in other behaviours during the non-breeding season whilst visual observations carried out across the tidal flats and the hinterland between October 2019 and March 2020 indicated that curlew spent 62% of the time foraging during hours of daylight. For other species in our study area, we did not obtain visual observation of the proportion time spent feeding and therefore could not validate the MORPH values. However, the general literature indicates that large waders usually actively forage for 70-85% of the time and smaller waders for 80-95% (Van de Kam et al., 2004), which appeared to be in line with our MORPH predictions. We also compared predicted values with observed estimates of the time spent feeding by waders collected from Poole Harbour (Collop, 2017). With the exception of Eurasian oystercatcher, the predicted values were above the visual observations suggesting that birds feed longer than seen from the observational data (Table 5.1).

Table 5.1. Proportion time spent feeding from MORPH compared to visual observations from Poole Harbour (Collop, 2017).

Species	MORPH	Visual observations from Poole Harbour
Dunlin	0.74	0.41
Red knot	0.74	N/A
Common redshank	0.73	0.49
Grey plover	0.79	0.29
Black-tailed godwit	0.88	0.47
Eurasian oystercatcher	0.35	0.59
Curlew	0.75	0.61

The predicted habitat use from MORPH was compared with the observed proportional habitat use from the GPS-tracked curlew (Figure 5.4). It was clear that the predictions from MORPH matched the observed tracking data on the low shore and very low shore, indicating that a small fraction of the curlew population used these zones of the intertidal areas. Predicted and observed use also matched on the managed realignment site. However, there were marked differences between observed and predicted values on the high shore and mid shore. Except for the high shore, we found the observed use of these habitats to be higher than the MORPH predictions. The discrepancy may be because the observed data is based on the home range of curlew, which included all birds regardless of their activity (i.e., feeding and non-feeding). In contrast, MORPH predicted well the number of feeding birds per patch. This value was subsequently converted into proportional habitat use to allow validation with observational data. Because the terrestrial habitat was used by both feeding and roosting birds (Mander et al., 2022), the observed proportion of terrestrial habitat use was higher than the predictions from MORPH. Whilst it was not possible to validate habitat use for other species, the model replicated the real world for curlew with predicted values for proportion of time spent feeding mostly matching observed values, although there were notable differences between the high shore and the mid shore.

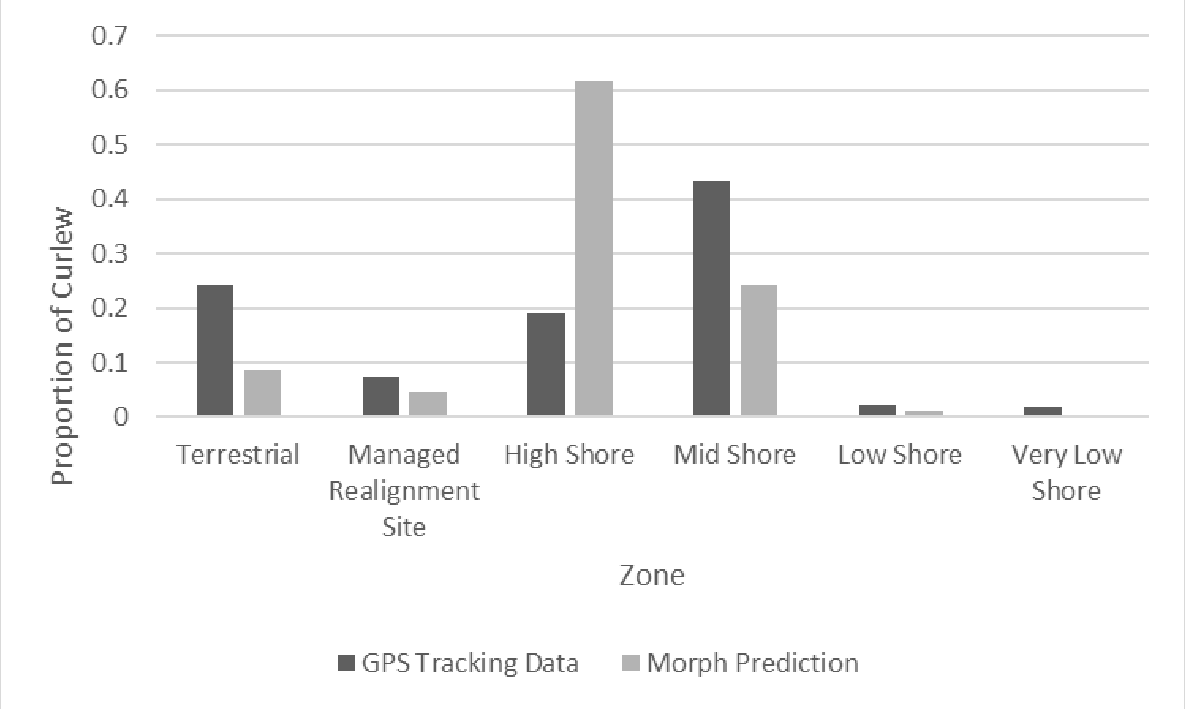

Figure 5.4. Predicted proportions of curlew using each zone versus proportion of curlew home range (KDE) overlapping with each zone.

5.4.4 Effect of habitat creation

The removal of the ‘managed realignment site’ patch from the modelled area resulted in fewer birds being supported at the end of the non-breeding season, especially curlew (Table 5.2). With a starting population of 440 birds on 1st September 2019, 400 individuals were predicted to be supported by the model (with the managed realignment site) at the end of the winter (31st March 2020). In comparison, the model without the managed realignment site only supported 340 individuals at the end of the breeding season, an 18% reduction in population supported overall by the system. To a lesser extent, other species were also adversely affected by the removal of the patch ‘managed realignment site’, with fewer dunlin (-18%), red knot (-10%), grey plover (-23%) and no black-tailed godwit supported by the system. Only Eurasian oystercatcher and common redshank remained unaffected by the removal of the managed realignment site from the system. The managed realignment site (13 years after habitat creation) had a significant positive effect on waders and in particular curlew, as the modelled area containing the managed realignment site was able to support a larger population size of curlew and other waders.

Table 5.2. Prediction of the present day model.

Species	Present in system on 1st September 2019	Present in system on 31st March 2020 (including realignment site)	Present in System on 31St March 2020 (excluding realignment site)
Dunlin	700	650	550
Sanderling	0	0	0
Common ringed plover	0	0	0
Ruddy turnstone	0	0	0
Red knot	1700	1700	1550
Common redshank	140	140	140
Grey plover	170	160	130
Black-tailed godwit	30	10	0
Bar-tailed godwit	0	0	0
Eurasian oystercatcher	30	30	30
Curlew	440	400	340

5.5 Discussion

Making realistic assumptions about ranging movements is crucial in being able to accurately predict the effects of environmental changes on wader populations. Here, we parameterised an individual-based model by considering the space use of GPS-tracked curlew in a discrete area of the Humber Estuary. The site features an estuarine restoration scheme fronted by extensive intertidal flats and backed by terrestrial habitats. The curlew is a Near Threatened wader species known to forage on terrestrial habitats in winter, especially coastal grasslands (Townshend, 1981; Milsom et al., 1998; Navedo et al., 2013). To our knowledge, this is the first study that has incorporated movement data – derived from 16 GPS-tracked curlew – to validate parameters for an individual-based model in an estuarine environment. Using data on behaviour (proportion of time spent feeding) and fine-scale habitat use from the GPS-tracked curlew, the model's predictions showed a good match to four years of observations. The validated model was able to predict the effect of habitat creation on curlew.

5.5.1 Using GPS tracking data to parameterise and validate an individual-based model

Except for a study by Herbert et al. (2018), MORPH has been chiefly used to predict the impact of environmental changes and human activities across entire systems e.g., at a full estuary scale (Stillman et al. (1997); Durell et al. (2005); Stillman et al. (2005); Durell et al. (2008); Bowgen et al. (2015)). In this study, we used MORPH at a finer spatial scale, i.e., a discrete area of the Humber Estuary featuring a managed realignment site. At such a small spatial scale, knowledge of bird movements to define patches and resources is essential to parameterise IBMs and enable real-world predictions in response to environmental changes. When applying MORPH at an estuary scale, all potential patches (at least intertidal habitats) of the estuary are included in the parameterisation of the model. Birds are assumed to move freely between patches, i.e., amongst feeding patches and between roosting patches. Waders are very mobile within estuaries, and distances travelled between roosting sites vary greatly amongst species (Rehfisch et al., 2003). As such, information on fine-scale habitat use of roosting and feeding sites is often not necessary when parameterising MORPH. However, at a finer spatial scale (e.g., with discrete areas of less than 1 km^2), knowledge of space use is essential to parameterise the model. This is particularly relevant for species which use both intertidal and terrestrial habitats to forage.

The validation of simulation models such as MORPH against real observations is crucial in being able to entrust the outcome of predictions (Grimm & Railsback, 2005; Goss-Custard &

Stillman, 2008). Most IBMs have been validated against observed data on the behaviour (such as proportion of time feeding) and distributions of birds (usually using count data from the UK Wetland Bird Survey (WeBS) Low Tide Counts scheme: https://www.bto.org/our-science/projects/wetland-bird-survey/taking-part/low-tide-counts). However, feeding intensity data rely on the observation of behaviour in the field, and those observations can only be carried out in daytime. Yet, MORPH predicts the average feeding intensity over day and night and across the winter (e.g., 1st September to 31st March). Recently, advancements in modern telemetry (e.g., GPS tracking technology) have enabled movement data collection at a greater GPS sampling rate than in previous GPS tracking studies. This has opened the possibility of inferring bird behaviour (e.g., feeding and resting) from path track characteristics (e.g., step length and the angle of direction). In this study, the observed value of the % of time spent feeding across day and night for curlew from the GPS tracking data was in line with the prediction from MORPH.

In our study, MORPH is used both at a small spatial scale and with a fine resolution (i.e., with multiple patches spread down the shore). Validating predictions (e.g., of the number of birds) on the low and very low shore may be problematic because counts of birds are difficult to carry out on wide intertidal habitats, where observation distances can be great. In our study we used GPS tracking data to validate habitat use across the shore. To our knowledge, this is the first time that GPS tracking data has been used in the validation of MORPH outputs. Here, we make the point that as restoration schemes are created in estuaries in response to sea-level rise, the impact on wader mortality will need to be investigated at the local scale to verify that these schemes are effective. Here, we showed that with the help of GPS tracking data we can successfully parameterise an individual-based model at a small spatial scale.

5.5.2 Model predictions

Model predictions showed that habitat restoration scheme can be valuable in supporting curlew populations. Previously, the MORPH model was used to assess long term changes in the quality of the Humber Estuary for waders (Stillman et al., 2005). That study suggested that intertidal habitat loss of up to 50% had no influence on the survival rates of any species, except for curlew. Although simulations did not include terrestrial fields because the food supply was not surveyed, Stillman et al. (2005) found – by assuming an intake rate of 0.5 to 1 mg AFDMs^{-1} – that terrestrial habitats were critical to maintaining high survival (90%-100%). We found no mortality (100% survival rate) of curlew in our present model by including food resources surveyed on the terrestrial habitats. Despite adjusting the count of birds modelled (inflated by 3.4), the predicted survival rates remained high in the present model. The population modelled was based on the adjusted mean count recorded two either side of low water over the winter period. However, predictions using the peak count recorded over the half tidal cycle surveyed resulted in a reduced survival rate. This might be because the peak count was recorded at high water, and might have included birds that do not feed on the intertidal habitats but occasionally roost at Welwick.

5.5.3 Limitation of the input variables and recommendations

One of the main limitations of the model relates to its application to other waders. Indeed, the model was parameterised for curlew and we specifically used movement data from a sample of 16 individuals to define patches and sampling resource. The model can be used as a basis from which to develop models for other species, but refinements (in particular the consideration of species-specific home ranges) to the existing model are required in order to improve the accuracy of the predictions for other species. There is evidence that large wader species, for example curlew (Mander et al., 2022) and bar-tailed godwit (Jourdan et al., 2021) occupied very small home and core ranges in comparison of waders of lower body mass. Indeed, small wader species such as red knot or dunlin may occupy larger home ranges, exceeding 1,000 hectares (e.g., Piersma et al. (1993) and Choi et al. (2014)). Therefore, using movement data from the literature (e.g., home range size) or by collecting movement data (e.g., site-specific home ranges derived from tracking studies), we can better define the extent of patches of the species modelled and refine predictions. Furthemore, whilst we treated the realignment site as a foraging ground, it is also used by roosting birds (as shown by the GPS tracking). The realignment site is dominated by saltmarsh where the birds predominantly roost. Splitting the managed realignment site into several patches to distinguish feeding to roosting areas might improve the predictions regarding the effect of the habitat creation on waders.

In our model, resource parameters were derived from benthic and earthworm sampling surveys. Determination of invertebrate energy values is time-consuming and difficult to perform. As a method, ash-free dry mass (AFDM) to determine energy value is often used however, development stage, food conditions, local environment, reproductive stage, season and taxonomic group can, among others factors, affect the measurements obtained (Brey et al., 1988). Although AFDM was measured, we decided to use equations from the literature to convert size of invertebrates into AFDM because of a discrepancy between the size of invertebrates and measured AFDM, in particular for the marine worm resource. Indeed, when coring in the sediment to collect benthic samples, large oligochaetes and polychaetes can be accidentaly sectioned and body parts unaccounted for. During the processing of the sample in the laboratory, the length of marine worms is estimated from the size of the head to give a true reflection of the abundance and biomass of marine worms. However, the confidence in the ash-free dry mass value is low as the latter is based on a worm part (e.g., head) rather than the estimated length of the worm. In order to get matching abundance and AFDM, it would be necessary to collect whole undamaged worms from each size class and combine them up to a set weight, and then subsquently ash them as a whole to give an accurate reference. The values could then be used to calculate more accurate ash weights from the abundances in the samples. Relationships between such a dataset and remotely-sensed environmental variables such as salinity and elevation can then be used to predict food resources for areas of the estuary which surveyors cannot reach, such as mid-channel tidal flats (van der Wal et al., 2008).

5.5.4 Potential application of the model (futher research)

To our knowledge, it is the first study that incorporates such movement data to define parameters of an individual-based model in an estuarine environment. We sucessfully developed a model that predicted the impact of habitat creation in the discret area of the Humber Estuary. The approach for evaluationg the success of MR sites can be replicated in other estuaries. However, it must be noted that our approach was made at a certain point in time (13 years after habitat creation) and we know from the literature that the habitats created within MR sites and thus their effectiveness can change over time (Mander et al., 2021). To date, the in-combination impact of several existing re-created sites on bird fitness at an estuary level has yet to be tackled. The Humber Estuary, with several existing realignment sites, and other large areas in planning, provides a good opportunity to examine the impact of these schemes on wader fitness, particularly on curlew.

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Chapter 6 General discussion and concluding remarks

Conservation efforts for threatened or endangered species rely on extensive knowledge of the species' ecology. Study of space and habitat use is critical to set effective conservation measures for a range of taxa (Zeale et al., 2012; Godet et al., 2018; Pop et al., 2018). Many wader species using coastal habitats in winter are declining along their migratory flyways, with environmental changes (directly or indirectly associated with human activities) contributing to population declines (Sutherland et al., 2012). Despite environmental laws protecting the coastal environment, increasing anthropogenic pressures on the estuarine ecosystem are of concern, including the indirect effects of climate change. The greatest threat here is sea-level rise, but increases in air and water temperatures, and reduction in pH, will also be important factors in coastal ecology of the 21st century (Pörtner et al., 2019).

The loss of intertidal habitats in estuaries due to sea-level rise has the potential to affect the survival and breeding success of over-wintering waders and consequently drive population changes. Conversely, as we mitigate for the loss of habitats by shoreline management, there is the potential for habitat restoration schemes to alleviate the consequence of intertidal habitat loss (Davidson & Evans, 1987; Mander et al., 2021). To understand the consequences of habitat loss and gain for waders, it is vital to understand species behaviour and space use, data on which individual-based models that can predict the impacts of environmental change can be built and tested. The need for robust data on behaviour and space use will only increase as the impact of climate change exacerbates and nature-based solutions are sought. With the development of modern telemetry (e.g., GPS tagging), the movement of birds can be followed for long periods without the need for recapture. It is now possible to investigate many aspects of bird behavioural ecology previously only studied through more limited radio telemetry and visual observations.

In this thesis, I sought to examine the movement ecology of wintering curlew – a Near Threatened wader species and thus of high conservation status – in the Humber Estuary (UK). Over-wintering curlew use both intertidal flats and terrestrial habitats, with the latter habitat used either as an alternative or a supplementary foraging ground (Navedo et al., 2013). Chapter 2 examined how curlew and other waterbirds responded to environmental changes occurring in a habitat restoration scheme (i.e., managed realignment site) in the Humber Estuary. At two other sites of the Humber Estuary, I assessed the over-wintering space use of curlew and individual, sexual and temporal (day/night, seasonal and annual) variation in home range size using high-resolution data from 21 birds fitted with GPS tracking devices (Chapter 3). In the next chapter (Chapter 4), I further aimed to examine individual, sexual and temporal variation in habitat selection between estuarine and non-estuarine resources in an area of the Humber Estuary featuring a managed realignment site. Finally, in Chapter 5, an individual-based model at a habitat creation scheme was parameterised using data on space use collected through GPS tracking data together with food resources collected on the intertidal and terrestrial habitats. The model aimed to predict the effect of habitat creation on curlew survival.

Collectively, the findings from each chapter of the thesis provide an understanding of how waders respond to habitat creation schemes and how information on space and habitat use of over-wintering curlew can be used – through an – individual-based model (IBM) – to better inform the impacts of habitat restoration on wader survival and thus the conservation of populations. By examining the abundance of foraging birds at a managed realignment site in response to elevation changes, I highlighted the limitations of the long-term suitability of habitat restoration schemes for foraging birds and the need for a greater understanding of the function of these schemes for waterbirds. At another realignment site, I used a combination of movement analysis and resource selection measures to test several hypotheses regarding curlew behavioural ecology. This information was crucial to parameterising an individual-based model, built to accurately predict the effect of habitat creation on wader populations. Together, the results thus provide invaluable information to understanding the conservation implications of habitat change in estuaries and improving the efficacy of restoration schemes for waterbirds.

6.1 Understanding the impacts of habitat restoration on over-wintering waders

I highlighted that nature-based solutions such as managed realignment sites can deliver suitable intertidal habitats very rapidly, but it is important to understand their limits for foraging benthivorous species. Atkinson et al. (2004) and Evans et al. (1998) indicated rapid, positive changes in bird indicators in response to sediment accretion within the first five years of habitat creation. In Chapter 2, it was however found that increasing elevation (due to rapid accretion of sediment) in a managed realignment site had a negative effect over 11 years on the abundance of foraging benthivorous waders, including curlew. Once elevation reached 2.75 m, the models indicated that the abundance of most of the waterbird species (except for dunlin and common shelduck) would start to decline sharply. Mazik et al. (2010) found a lower density and abundance of benthic invertebrates above this height at the study site. It was chiefly the high rate of sedimentation, which added to the intrinsic elevation of mid-to high-shore mudflats (i.e., the position of the managed realignment site in the tidal range) which eventually led to a less favourable environment for foraging waders. Although bird and benthic communities may colonise MR sites very rapidly (Atkinson et al., 2004; Mander et al., 2007; Mazik et al., 2007), I recommended that long term monitoring (> 5 years) should be implemented at managed realignment sites, and the effect of accretion should be accounted for when designing compensatory sites

In Chapter 3, I found that curlew on our study sites displayed consistent space use throughout the non-breeding season and the birds predominantly exploited intertidal flats for foraging. There was a strong fidelity to feeding and roosting sites on the study sites in the Humber Estuary and some level of segregation between the groups that use the two sites. Ten of the 21 individuals only utilised intertidal habitats, while the remaining 11 individuals made movements between intertidal and terrestrial habitats. Previous work has documented that curlew are very faithful to roosting areas during the non-breeding season (Rehfisch et al., 2003; Schwemmer et al., 2016), and are known to make extensive use of land surrounding the estuary, especially coastal grasslands (Townshend, 1981; Milsom et al., 1998; Navedo et al., 2013). I found that curlew had a relatively small home range which only varied slightly in area throughout the non-breeding season. I found the mean core range to be small in comparison to other species within the Numeniini group (e.g., GPS tagged bar-tailed godwit (Jourdan et al., 2021)). There was also considerable variation in the size of home ranges (as determined by 90% KDE) between individuals (555.5 ha +/- SD 557.9 ha), which was not related to sex. Previous work, based on the observations of colour-ringed birds, has found males and females curlew to distribute differently between terrestrial and intertidal habitats (Townshend, 1981a). Small scale spatial segregations are known to occur on tidal flats occur as the result of intersexual competition in dimorphic wader species (Both et al., 2003; Alves et al., 2013), and this might result in differences in home range between males and females. Whilst we did not detect difference between males and females in our study, there was a high inter-individual variation in home range size observed which may reflect feeding strategies (e.g., territoriality) or individual specialisation. Although high-resolution GPS devices have also been recently used on curlew to examine migratory movements (Schwemmer et al., 2021), this is the first study to our knowledge to investigate the variation in home range size of curlew throughout the non-breeding season (Mander et al., 2022).

In Chapter 4, by analysing the tracks from 14 GPS-tagged curlew that used the managed realignment site, I found evidence that curlew used one to two distinct patches on the intertidal flats when foraging, with some overlap indicating a low level of intraspecific competition. Using GPS-tracked bar-tailed godwit, Jourdan et al. (2021) showed low overlap between individual feeding range, and extreme fidelity to restricted feeding areas during winter. Although territoriality has been observed in curlew (Ens, 1979; Ens & Zwarts, 1980; Townshend, 1981b; Colwell, 2000; Colwell & Mathis, 2001), the proportion of curlew defending a territory is low (Ens, 1979; Townshend, 1981b). In our study, there was only evidence of territoriality in two of the 14 GPS-tracked Curlew. Whilst curlew is one of the few wader species that frequently feed on terrestrial habitats, especially coastal grasslands (Townshend, 1981a; Milsom et al., 1998; Navedo et al., 2013), our study found that the terrestrial habitats had the lowest selection ratio compared to other broad habitats: intertidal flats, saltmarsh and the managed realignment site. Stillman et al. (2005) found that terrestrial fields around the Humber Estuary were critical to maintaining high curlew survival in winter. Within our study site, we argue that the availability of intertidal habitats, including saltmarsh and habitats created through the realignment of flood defence, reduces the need for curlew to prospect on the terrestrial habitats to meet their daily energy requirement. Bowgen et al. (2015) found curlew to be the first affected by loss of prey resource on the intertidal habitats, with the species having to shift to terrestrial resources which are less profitable. I found differences in nocturnal and diurnal habitat use: curlew preferentially selected saltmarsh and the managed realignment site at night compared to daytime, presumably for roosting. Using GPS-tagged bar-tailed godwit Jourdan et al. (2021) also highlighted differences in habitat selection between day and night. Differences in nocturnal and diurnal habitat use by wintering waders are linked to disturbance and predation risk (Sitters et al., 2001; Piersma et al., 2006). Some degree of inter-individual variation in habitat resource selection was found, which was attributed to the age of the curlew (adult/first-winter). Individual differences in habitat selection may result from intra-population competition for areas of higher resource (Goss-Custard et al., 2006a).

To my knowledge, this is the first study that has incorporated movement data – derived from 16 GPS-tracked curlew – to define parameters for an individual-based model in an estuarine environment. Assumptions about animal movement in designing an IBM are often made using *a priori* information on habitats available to birds and the extent of the foraging areas (e.g., Bowgen et al., 2015 using MORPH). Whilst the impact of the loss of intertidal habitats and proposed mitigation measures on waders has also been studied using MORPH (Durell et al., 2005; Goss-Custard et al., 2006a), this is the first study to examine the effect of the managed realignment site on the size of the population supported by the modelled area. The managed realignment site contributed to an increase in the population of curlew by 18% by the end of the non-breeding season. With the exception of red knot and common redshank, the numbers of other wader species supported at the end of the non-breeding season (relative to those at the start) were also greater when the managed realignment site was included as a resource. Durell et al. (2005) and Goss-Custard et al. (2006a) found the responses to loss and gain of intertidal habitats to differ between species, potentially due to differences in species' diet and foraging strategies.

6.2 Future research needs

Further research is required across several sites to more fully understand individual variation in space use, and the spatial segregation of curlew populations in estuaries, and consequently the potential impacts of habitat selection on fitness and survival. Previously, on other estuaries, curlew have been reported to exploit terrestrial fields because they are unable to fully meet their daily energy requirements on intertidal flats (Townshend, 1981a). Therefore, there is a need to compare results from across studies to understand better how habitat selection varies according to habitat availability. The results of this thesis are representative of birds using two particular roosts on the Humber Estuary and there may be variation both within the estuaries and between estuaries. With the high conservation status of curlew across Europe, curlew GPS tracking programmes have been undertaken at several sites across Europe to date (e.g., through the Limitrack project, University of La Rochelle, France; Institute for Waterbirds and Wetland Research e.V, Germany; the ECHOES project, UK and Ireland). With other datasets that have been collected elsewhere, there is an opportunity to share the data and explore this variation in habitat selection on wintering ground. Although curlew survival is high on the wintering grounds (Taylor & Dodd, 2013; Cook et al., 2021), variation in habitat selection due to habitat availability has the potential to impact bird the survival of individuals.

The effect of both age and sex in habitat selection during the non-breeding season is also worthy of further investigation. Curlew are long-lived species and very site-faithful in winter (Rehfisch et al., 2003), and through their familiarity with their wintering areas, they are likely to gain detailed knowledge of their feeding resources. Studies have already shown that juvenile and sub-adults have a larger home range (Rolando, 2002) as they actively prospect their foraging areas. They may also compete with others for finding suitable foraging patches. In birds, juvenile-adult differences in foraging result from both physiological constraints (e.g., immaturity of the beak) and the time required to learn foraging skills. As, such stronger competitors might be able to exploit higher-quality areas (Marchetti & Price, 1989). Thus, age could have an effect on resource selection and home range size. However, accurately ageing waders is very difficult without capturing known-aged birds (previously ringed as chicks or juveniles) or using invasive sampling techniques.

There is wide evidence of at least partial spatial segregation between sexes in waders and other species that relates to their morphology (e.g., bill-length and body size) and consequently differences in diet (Summers et al., 1990; Both et al., 2003; Alves et al., 2013). Partial racial segregation on wintering sites has also been reported (Burton et al., 2002). However, the segregation in feeding areas between birds from adjacent roosting sites is seldom studied, although studies have explored the linkages between roosting and feeding areas (Rogers et al., 2006a; Rogers et al., 2006b; Bakker et al., 2021). In colonial seabirds, there is evidence of partitioning of available foraging habitat into mutually exclusive territories during the breeding season (Wakefield et al., 2013). According to the same author, individual Northern gannet (*Morus bassanus*) from the same colony appeared to share information about foraging sites, which contributed to the long-term segregation. It is hypothesised that partitioning may occur in wader populations during the non-breeding season in estuaries. For example, curlew appeared to show strong fidelity to roosts (where individual-level public information transfer may occur), resulting in roost-specific home ranges. We believe this needs to be investigated across the estuary by capturing and GPS tagging curlew from various roosting sites.

Furthermore, with the development of the IBM model for the Welwick managed realignment site, there is an opportunity to examine a range of scenarios regarding habitat changes that are occurring within a realignment site (as the result of the sedimentation process). In addition to habitat change, there is an opportunity to examine the role of terrestrial habitats, in particular coastal grasslands. At temperate latitudes where coastal grasslands are utilized by waders in winter, predicting their contribution to overall bird fitness through an IBM is of value to enhance conservation measures for wader populations. This is particularly relevant for many estuaries in northwest Europe where the space to re-create tidal flats is limited, as they are surrounded by dense industrial and residential areas. Where it has not been possible to re-create intertidal flats in estuaries, these coastal grasslands could play a significant role in maintaining the fitness of over-wintering curlew in estuaries.

6.3 Study limitations

The biggest limitations in this study related to the tag attachment, the battery lifespan and the distribution of the capture sites in the outer Humber Estuary. It is now possible to attach tags using leg loop harnesses on curlew, with the attachment capable of supporting the device for up to two years. In this thesis, with the specific goal to understand within-winter movements, the tags were glue-mounted and expected to detach three months after deployment. Furthermore, the relatively short battery life of the GPS with UHF download used in this study used meant that a trade-off had to be made between the sampling regime and the tracking duration to cover the tidal rhythm and ensure representative coverage of the non-breeding season. The miniaturisation of tags means that GPS/GSM technology is now available for birds the size of curlew and therefore individuals can be tracked at a higher sampling frequency and for a more extended period e.g., over the full non-breeding season (from July to March) and beyond, and over multiple years using attachment methods such as leg loop harnesses (Schwemmer et al., 2021). In our study, we were able to GPS track individuals from September to April, but the majority of birds were captured from November onwards. A further limitation of the study is that we were only able to track individuals over a single winter because glue-mounted GPS devices detached from the birds after approximately three months. Thus, we could not examine inter-annual variability amongst individuals. Furthermore, we only sampled birds from two sites in the outer Humber Estuary where the large intertidal flats offered a longer feeding window than the upper estuary's intertidal flats, which are narrower and thus more quickly submerged. The availability of suitable habitats for curlew (e.g., wet grassland) behind the flood wall varies across the estuary, and this will affect habitat use and home range.

6.4 Concluding remarks

This thesis has contributed to knowledge both on the wintering ecology of curlew in estuaries and on the responses of waders to habitat creation schemes. To our knowledge, this is the first study to examine the home ranges and habitat selection of wintering curlew, and the results have direct value in informing an individual-based model developed to assess the impacts of estuarine habitat creation, and thus the design and effective implementation of such schemes. GPS tracking of 21 individuals in four separate winters highlighted the relatively small home range size of curlew and limited use of terrestrial habitats (beyond 1.5 km from the shoreline) by birds wintering in the outer Humber Estuary. Curlew relied on the managed realignment site for roosting and primarily used intertidal habitats, including saltmarsh and habitats created through the realignment of flood defences, for foraging, suggesting that there was limited need for curlew to use terrestrial habitats in this wintering area to fulfil their daily energy requirements. It also highlighted the value of the managed realignment site in providing nocturnal and diurnal roosting sites for curlew. When positioned close to intertidal foraging areas, these compensatory sites can reduce daily energy expenditure for curlew which commute between foraging and roosting sites across the tidal cycle. In contrast, we also showed the potential limitations of managed realignment sites for foraging benthivorous species, including curlew. It was found that numbers of foraging curlew (and other waterbirds) were limited by high elevation, increasing accretion and low prey density in a developing managed realignment site. Practitioners should take into account the effect of accretion and elevation when designing and implementing nature-based solutions such as managed realignment site. The collective understanding of the responses of waterbirds to the creation of the managed realignment site and of the space and habitat use of curlew has been crucial in informing and validating simulations from the individual-based model. Outputs from the model allow us to predict how future realignment sites might benefit and help set effective conservation measures for the species, which has a high conservation status in northwest Europe. The results highlight the value of managing terrestrial habitats adjacent to estuaries to buffer the effect of future habitat losses due to increasing sea-level rise.

6.5 References

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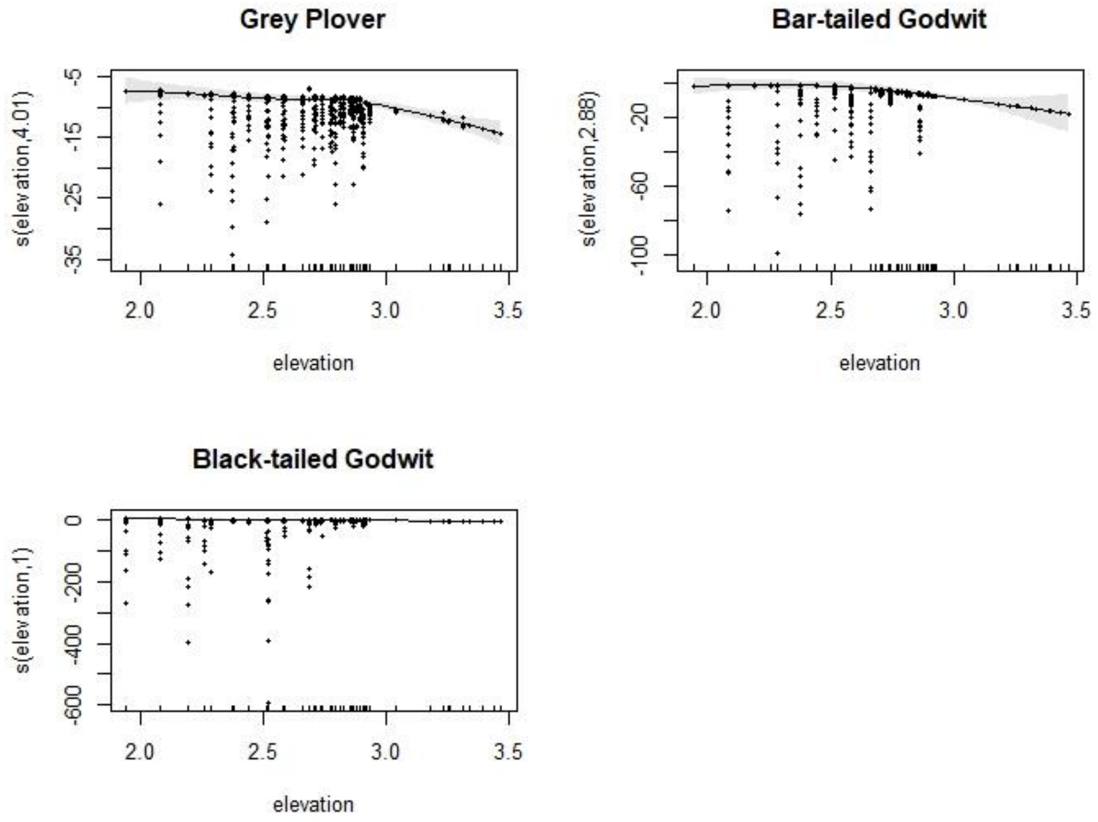
Appendix 1. Species and trophic guilds derived in the study site from winter diet in estuaries (Cramp & Simmons, 1983).

Foraging guilds	Species	Description
Herbivorous geese, swans and ducks	Mute swan (*Cygnus olor*) Pink-footed goose (*Anser brachyrhynchus*) Greylag goose (*Anser anser*) Canada goose (*Branta canadensis*) Barnacle goose (*Branta leucopsis*) Brent goose (*Branta bernicla*) Eurasian wigeon (*Anas penelope*) Gadwall (*Anas strepera*)	Geese, swans and ducks feeding on plant material.
Benthivorous ducks	Common shelduck (*Tadorna tadorna*) Northern pintail (*Anas acuta*)	Duck species feeding on epibenthic and benthic invertebrates on mudflats and sandflats.
Omnivorous ducks and rails	Eurasian teal (*Anas crecca*) Mallard (*Anas platyrhynchos*) Common moorhen (*Gallinula chloropus*) Eurasian coot (*Fulica atra*) Little grebe (*Tachybaptus ruficollis*)	Ducks and rails feeding on a range of animal and plant food.

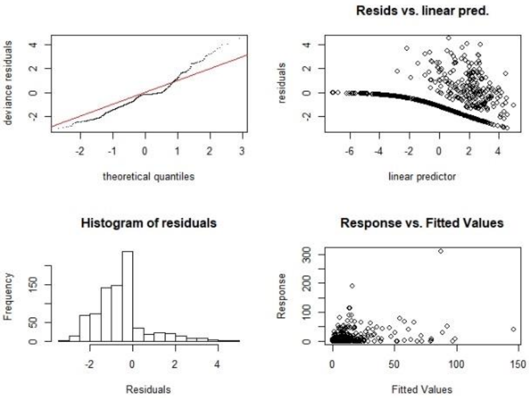
Piscivorous grebes, cormorants and herons	Great cormorant (*Phalacrocorax carbo)* Grey heron (*Ardea cinerea)* Little egret (*Egretta garzetta)*	Grebes, cormorants and herons feeding on fish.
Benthivorous waders	Eurasian oystercatcher (*Haematopus ostralegus)* Common ringed plover (*Charadrius hiaticula)* Grey plover (*Pluvialis squatarola)* Red knot (*Calidris canutus)* Sanderling (*Calidris alba)* Dunlin (*Calidris alpina*) Black-tailed godwit (*Limosa limosa*) Bar-tailed godwit (*Limosa lapponica*) Eurasian curlew (*Numenius arquata*) Common redshank (*Tringa totanus*)	Wader species feeding on epibenthic and benthic invertebrates on mudflats and sandflats.

Appendix 2. GAM smoothing temporal terms (line) fitted to centre of gravity data for other benthivorous species at Paul Holme Strays. Shaded area and points represent pointwise confidence bands and partial residuals respectively.

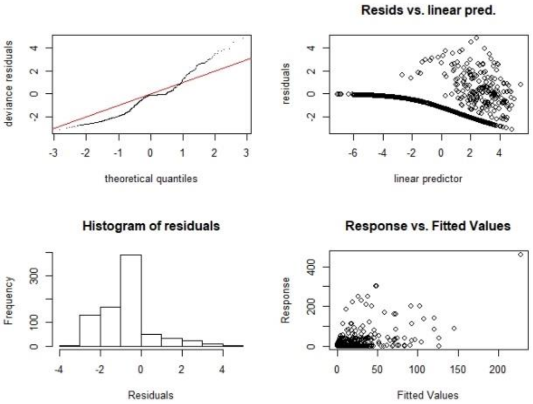


Appendix 3. Diagnostic for the fitted GAM model using gam.check

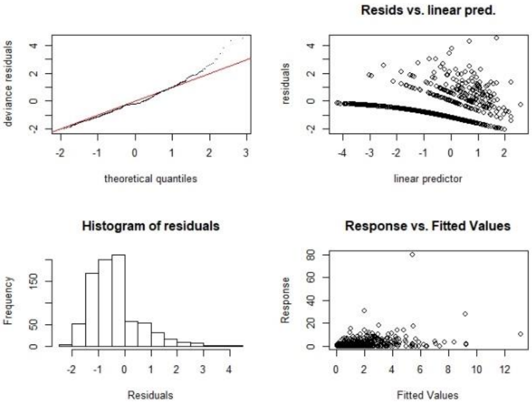
Common shelduck



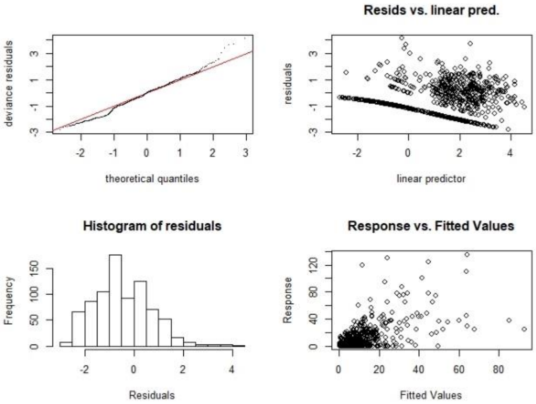
Dunlin



Eurasian curlew



Common redshank



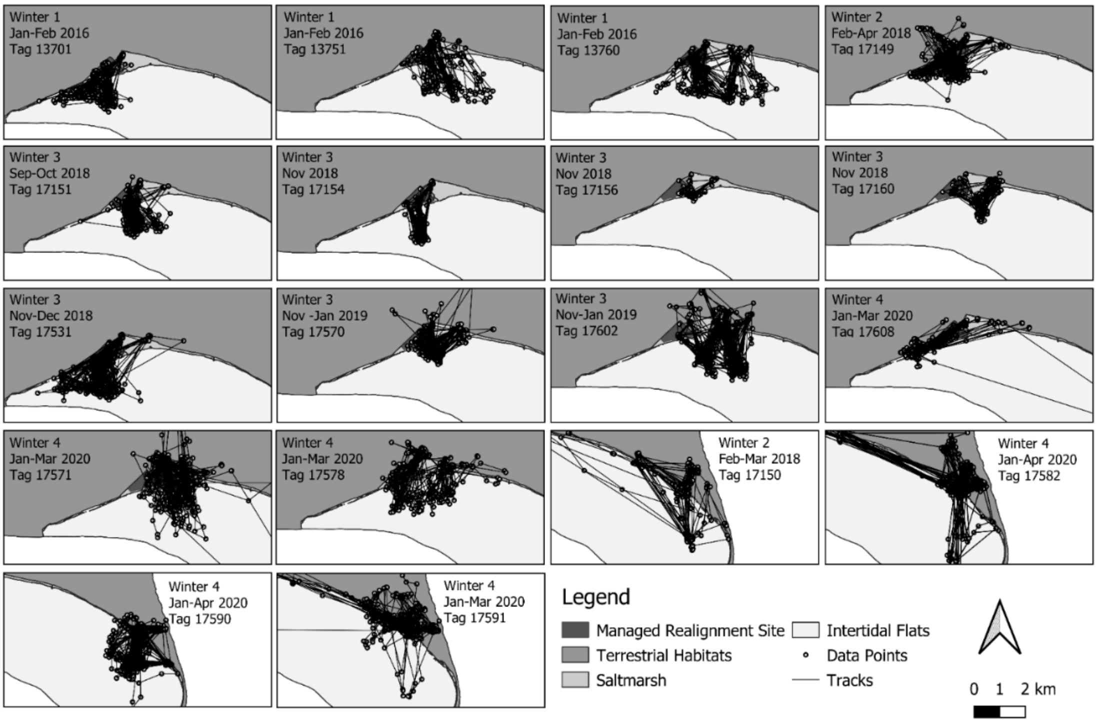
Appendix 4. Number of curlew (by age and sex) caught per site and date of capture.

	Welwick				Long Bank Marsh				
Date	Adult Male	Adult Female	Adult Unassigned	First Winter	Adult Male	Adult Female	Adult Unassigned	First Winter	Total
24 Jan 2016		1	2						3
03 Feb 2018			1						1
17 Feb 2018								1	1
26 Sep 2018	1		1						2
25 Oct 2018	1								1
06 Nov 2018	1	5		1					7
26 Nov 2019		1							1
25 Jan 2020		1		1					2
27 Jan 2020			1		2			1	4
Total	3	8	5	2	2	0	0	2	22

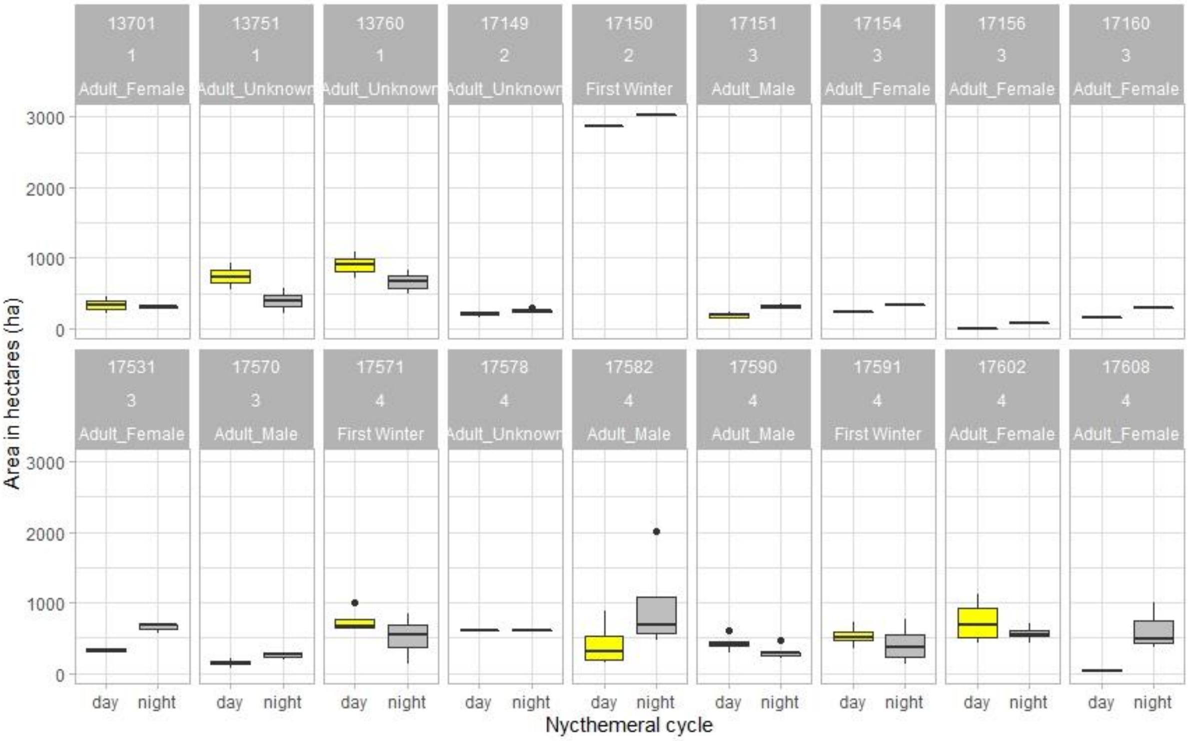
Appendix 5. Estimated core (50%) and total (90%) home range sizes of wintering curlew (ha) based on Kernel Density Estimators (KDEs) with href.

Site	Individual	no. of fixes	KDE (50%)	KDE (90%)
Welwick Saltmarsh	13701	537	90.0	325.2
	13751	522	78.1	504.9
	13760	627	185.8	699.9
	17149	960	64.8	282.3
	17151	549	57.7	248.7
	17154	340	74.4	278.6
	17156	260	8.9	59.5
	17160	316	67.9	254.6
	17531	821	147.3	532.3
	17570	941	52.4	199.3
	17602	1027	177.9	666.6
	17608	645	67.6	368.0
	17571	887	143.6	639.6
	17578	521	289.0	802.3
Long Bank Marsh	17150	347	720.2	2632.7
	17582	1043	123.1	689.9
	17590	1115	68.7	327.6
	17591	979	104.8	486.5
Mean		691	76.1	555.5

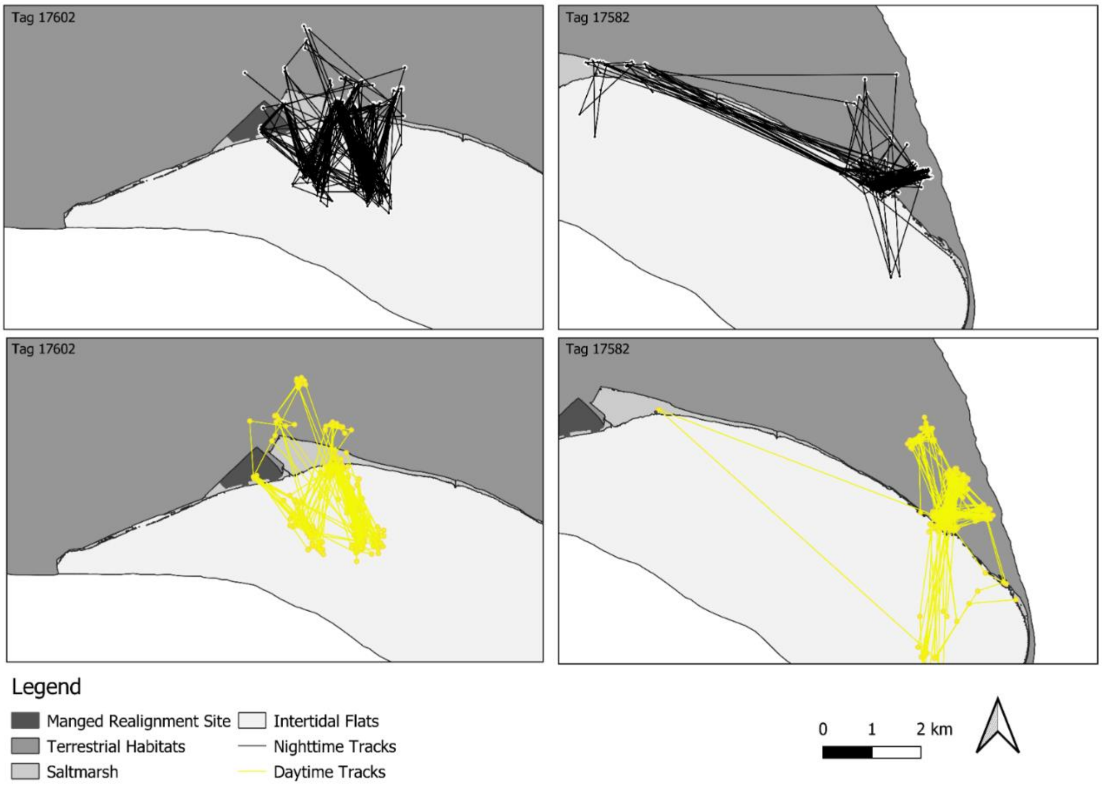
Appendix 6. Map showing movements of individual wintering curlew captured and tagged at Welwick Saltmarsh (Tag 13701, 13751, 13760, 17149, 17151, 17154, 17156, 17160, 17531, 17570, 17602, 17608, 17571, 17578) and Long Bank Marsh (Tag 17150, 17582, 17590, 17591).



Appendix 7. Boxplots showing estimated diurnal and nocturnal total (90% KDE) home range sizes (ha) of individual wintering curlew. Legends show the tag ID, the winter of tracking (1-4) and age/sex of individuals. Home range size was computed for between one and up to five 14-day periods (spring tide to spring tide) per individual within the given winter.



Appendix 8. Examples of maps showing daytime (in yellow) and nighttime (in black) movements of individual wintering curlew captured and tagged at Welwick Saltmarsh (Tag 17602 and 17578) and Long Bank Marsh (Tag 17582 and 17590).



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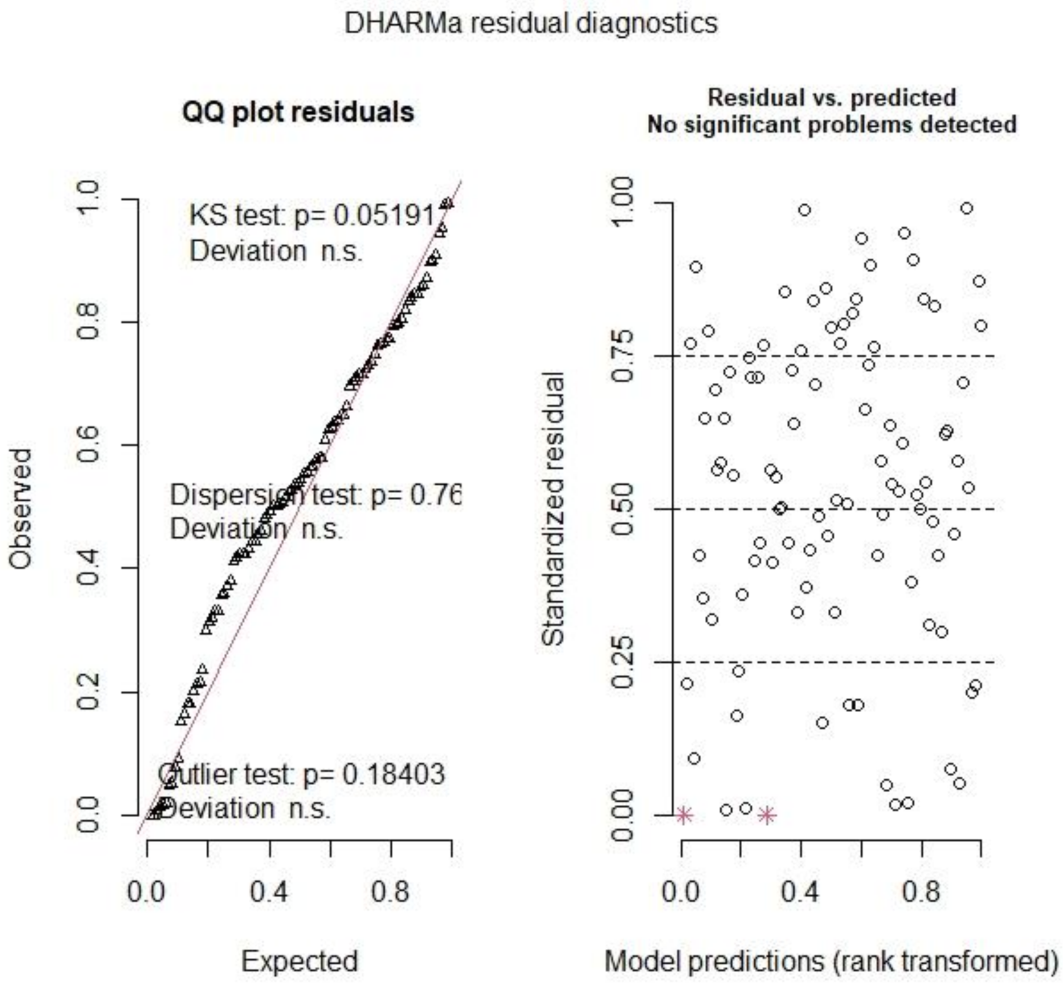
Appendix 9. DHARMa residuals diagnostics of full model.



Appendix 10. Supplementary information for parameterisation of IBM

Model patches parameters

The model comprised of a total of 29 patches. The terrestrial habitat was treated as one patch whilst the rest of the patches (i.e., 27 patches) were located on the intertidal habitats. We included a roost patch on the Welwick Saltmarsh which was known to be used by most waders when they were not feeding on the mudflats and sandflats. Whilst intertidal habitats were only available to the birds while they were exposed by the tide, the roost was always available. The terrestrial habitat (fields) were available during the hours of daylight as GPS tracking showed that curlew only feed on the terrestrial fields in daytime. Using digital terrain models (DTMs) collected via light detection and ranging (LiDAR) from environment.data.gov.uk, we categorised the intertidal flats into four areas according to tidal elevation (very low, low, mid or high). The tidal exposure of patches was predicted from the shore elevation of the patch and the height of the tide at Immingham. We determined the tidal height of each time step using the observed tide height (recorded at 15 min interval) from Immingham Port on the Humber Estuary (sourced from the British Oceanographic Data Centre (BODC) https://www.bodc.ac.uk). A patch was assumed to be exposed by the tide if the tidal height was less than the shore elevation of the patch.

Food resource parameters

Prey energy content at the start/end of the model period

Average ash-free dry mass (AFDM) per individual of each resource group was calculated for each feeding patch and was used as a proxy for the energy content of the individual prey items. As all invertebrate species energy had been measured in AFDM we used a conversion multiplier of 22 kJ g-1 (Zwarts & Wanink, 1993). Estimates of AFDM in grams calculated from invertebrate length are available via several sources (Thomas et al., 2004; Herbert et al., 2010). For the resource group ‘other molluscs’, we used the AFDM equation for *Scrobicularia plana* given that the assemblage of bivalves best matched this species. For crustaceans, the AFDM equation for *Gammarus* was used for predictions. For earthworms, the AFDM equation come from surveys of Poole Harbour (Durell et al., 2006). To account for the reduction in flesh size of hard shelled invertebrates of *Cerastoderma*, other molluscs, and *Peringia* throughout the winter, we applied a percentage loss figure of 28%, based on surveys of *Scrobicularia plana*, *Cerastoderma* and *Peringia* by Zwarts and Wanink (1993) between May/June and November.

Resource dynamic (density at the start and end of the model)

To account for the change in resource densities through the winter due to predation by the birds and losses due to other causes, we applied a percentage reduction in resource densities over the winter. Rather than using the value from the site-specific surveys, we used the average 'over-winter mortality' used by Bowgen (2016) in the previous model developed for the Humber Estuary, which is derived from a range of studies (Stillman et al., 2005; Durell et al., 2006; Durell et al., 2007; Durell et al., 2008; Stillman et al., 2012).

Bird parameters

Foragers

We included 11 wader species in our model to account for indirect interspecific competition through loss of resources: dunlin, sanderling, common ringed plover, ruddy turnstone, red Knot, common Redshank, grey plover, black-tailed godwit, bar-tailed godwit, Eurasian Oystercatcher and Eurasian curlew. Population size derived from the mean count (undertaken 2 hrs either side of low water) and adjusted for model calibration is shown in Table 1. Maximum peak count recorded through the half tidal cycle is also shown for information. Each of the 11 species had specific physiological and behavioural parameters that remained constant (Table 2). To expedite the running time of the models, we use 'super-individuals' of 2, 20 and 50 individuals.

Table 1. Population size used in the model

Species	Maximum peak count	Mean count (2 hrs either side of low water	Adjusted mean count (x3.4) used to calibrate model
Dunlin	1530	224	700
Sanderling	11	0	0
Common ringed plover	0	0	0
Rudy turnstone	2	0	0
Red knot	3800	517	1700
Common redshank	466	40	140

Grey plover	355	52	170
Black-tailed godwit	75	0	30
Bar-tailed godwit	119	0	0
Eurasian oystercatcher	649	7	30
Eurasian curlew	704	132	440

Table 2. Constant parameters adding individual variation for each forager.

Constant	Description
Arrival and Departure Day	All birds are present at the beginning of the model (Arrival Day = 1) and birds remain in the model until the final (Departure) day.
Arrival, Target and Departure Energy Store	The Arrival Energy Store in kJ (using conversion value from Kersten and Piersma (1987)) is used as the Target Energy Store. The value is derived from the difference in bird mass less a starvation mass per species. Bird masses were taken from the BTO's 'BirdFacts' (Robinson, 2005) whilst the starvation mass of species was derived by Bowgen (2016). This author used a linear relationship based on dead birds in the field (from unpublished work) and masses from (Robinson, 2005) to work out values for species.
Day and Night Efficiency	Following work done by Stillman et al. (2000), we added individual variation for day efficiency using a random value around a mean of 1 with a standard deviation of 0.125. Night-time foraging efficiency was sourced from the literature (Sitters, 2000; Lourenço et al., 2008). We used the night-time efficiency – calculated as the proportion of day-time energy consumption obtained during the night – from Lourenço et al. (2008) for four species: ringed plover (49%), redshank (95%), grey plover (100%) and black-tailed godwit (87%). For oystercatcher, we used an average of night-time efficiency (81%) of both individuals opening prey with the stabbing (100%) and the hammering method (62%) calculated by Sitters (2000). When night efficiency was unknown, we used an average of 82% for the rest of the modelled species. However, we assumed that bar-tailed godwit had a similar feeding efficiency to that of black-tailed godwit (81%).
Dominance	Individual variation in the sensitivity of foraging efficiency to other competitors was derived from a uniform distribution (Stillman et al., 2000).
Temperature	There are additional energy costs to birds when the temperature drops below a temperature threshold, known as the Lower Critical Temperature (LCT in °C). We used the values derived from the work by Bowgen (2016) which used a linear relationship of LCT for wading birds found in the literature against body mass (weight in grams) in order to predict the LCT for the modelled species.

Foragers diet

Resource and prey size preferences of forager species selected in the model (Tables 3 and 4) were based on the Humber Estuary model previously developed by Bowgen (2016), which is itself built on a range of literature sources/previous model describing the range of prey preference and size ranges for nine species (Goss-Custard et al., 2006), sanderling (Masero, 2003; Reneerkens et al., 2009) and ruddy turnstone (Jones, 1975; Stillman et al., 2012).

Table 3. Invertebrates recorded during the survey represented in each resource in the IBM (Durell et al., 2006). The species recorded are ordered taxonomically in accordance with Howson and Picton (1997).

Resource group	Latin name of invertebrate prey species included in each resource (all scientific names correct according to WoRMS Editorial Board (2022))	Size class (mm)
Marine worms (Marine polychaeta, Oligochaeta and Nemertea)	**POLYCHAETA**	0-4.99
	Eteone longa	5-14.99
	Phyllodoce mucosa	15-29.99
	Hediste diversicolor	30-44.99
	Nephtys sp	45-59.99
	Nephtys hombergii	60-74.99
	Scoloplos armiger	75-89.99
	Polydora cornuta	90-104.99
	Pygospio elegans	and 105+
	Streblospio shrubsolii	
	Tharyx (Type 'A')	
	Mediomastus fragilis	
	Ampharete cf. acutifrons	
	Manayunkia aestuarina	
	OLIGOCHAETA	
	Paranais litoralis	
	Tubificoides benedii	
	Enchytraeidae	
Cerastoderma	*Cerastoderma edule*	0-4.99
		5-9.99

		10-14.99
		15-19.99
		20-24.99
Other molluscs	**GASTROPODA-Heterobranchia**	0-4.99
	Retusa obtusa	5-9.99
	Alderia modesta	10-14.99
	BIVALVIA	15-19.99
	Cardiidae (Family)	20-24.99
	Tellinoidea (Superfamily)	25-29.99
	Limecola balthica	30-34.99
	Abra tenuis	35-39.99
	Scrobicularia plana	40-44.99
		45-49.99
		50-59.99
Peringia	**GASTROPODA-Caenogastropoda**	0-5
	Peringia ulvae	5-10
Earthworms	**OLIGOCHAETA-Terrestrial**	5-14.99
		15-29.99
		30-44.99
		45-59.99
		60-79.99
		80-89.99
		90-104.99
Crustacea	**COPEPODA**	0-2.99
	AMPHIPODA	3-9.99
	Bathyporeia	10-19.99
	Bathyporeia sarsi	20-39.99
	Corophium arenarium	40 +
	Corophium volutator	
	ISOPODA	
	Cyathura carinata	
	TANAIDACEA	

	Tanaissus lilljeborgi	
	CUMACEA	
	Cumopsis goodsir	
	DECAPODA	
	Crangon crangon	
	Carcinus maenas	

Table 4. Species specific dietary choices in relation to available resources per size class used in the model. DN: dunlin; SS: sanderling; RP: comon ringed lover; TT: ruddy turnstone; KN: red knot; RK: common redshank; GP: European golden plover; BW: black-tailed godwit; BA: bar-tailed godwit; OC: Eurasian oystercatcher; CU: Eurasian curlew.

Resource name	mm	DN	SS	RP	TT	KN	RK	GP	BW	BA	OC	CU
Cerastoderma	0-4.99											
Cerastoderma	5-9.99					x						x
Cerastoderma	10-14.99					x						x
Cerastoderma	15-19.99										x	x
Cerastoderma	20-24.99										x	
Cerastoderma	25-29.99										x	
Cerastoderma	30-34.99										x	
Cerastoderma	35-39.99										x	
Cerastoderma	40-44.99										x	
Other molluscs	0-4.99	x	x									
Other molluscs	5-9.99	x	x		x	x	x	x	x	x		x
Other molluscs	10-14.99				x	x	x	x	x	x	x	x
Other molluscs	15-19.99					x		x	x	x	x	x
Other molluscs	20-24.99					x					x	x
Other molluscs	25-29.99										x	x
Other molluscs	30-34.99										x	x
Other molluscs	35-39.99										x	x

Other molluscs	40-44.99										x	x
Other molluscs	45-49.99										x	x
Other molluscs	50-54.99										x	x
Crustacea	0-2.99				x							
Crustacea	3-9.99	x	x	x	x		x		x			
Crustacea	10-19.99				x		x		x		x	x
Crustacea	20-39.99				x		x		x		x	x
Crustacea	40+						x		x		x	
Peringia	0-4.99	x		x	x	x	x	x				
Peringia	5-10	x			x							
Marine worms	0-4.99											
Marine worms	5-14.99	x	x	x	x	x						
Marine worms	15-29.99	x	x	x	x	x	x	x	x	x		
Marine worms	30-44.99	x	x	x	x	x	x	x	x	x		
Marine worms	45-59.99	x	x	x	x	x	x	x	x	x	x	x
Marine worms	60-74.99		x				x	x	x	x	x	x
Marine worms	75-89.99		x				x	x	x	x	x	x
Marine worms	90-104.99							x	x	x	x	x
Marine worms	105+							x	x	x	x	x
Earthworms	5-14.99	x					x					

Earthworms	15-29.99	x	x				
Earthworms	30-44.99		x	x	x		
Earthworms	45-59.99		x	x	x	x	x
Earthworms	60-74.99			x	x	x	x
Earthworms	75-89.99			x	x	x	x
Earthworms	90-104.99			x	x	x	x
Earthworms	105+			x	x	x	x

Forager feeding parameters

A number of forager-related parameters are defined in the model: Free Area and Free Time, Susceptibility To Interference (STI) and Feeding Efficiency (Table 5). Species' rates of consumption and behavioural rules can be parameterised in the MORPH model following the definition of forager-related parameters and previous constants defined above.

Table 5. Forager variables

Variables	Description
Free Area and Free Time	To aid determining patch availability and rate of consuming diets, these two variables are defined as Patch Size and Time Step Length respectively.
Susceptibility to Interference (STI)	Interference is assumed to reduce intake rate when the number of birds is above the pre-defined threshold of 100 birds per ha (0.01) (Stillman et al., 2002). We defined three types of STI for birds feeding on specific diets based on the Humber model parameterised by Bowgen (2016): 'MobilePreySTI' (for Crustacean diet with prey that can move away from foraging birds), 'WeakKlepSTI' (for relatively stationary prey) and 'largeMollKlepSTI' (for diets with large mollusc e.g., Eurasian oystercatcher and Eurasian curlew).

Rate of consumption

The intake rate of modelled birds is determined by the density of food in a patch and conspecific disturbance. Interference free intake rate (IFIR) is calculated from the functional responses utilised in the model and based on body mass, using the equation of Goss-Custard et al. (2006):

$$IFIR = f\frac{IFIR_{max}B}{B_{50}+B}$$

Where IFIR = Interference-free intake rate (mg s−1), f = foraging efficiency of the individual, B = patch biomass density of prey within the size range consumed (mg.m−2), B50 is the prey biomass density at which intake rate is 50%, Maximum, IFIRmax = maximum of the intake rate when prey are superabundant. B, f and B50 were taken from Goss-Custard et al. (2006) whilst IFIRmax which is related to the prey mass and the shorebird body mass with the following equation derived by Durell et al. (2006); Goss-Custard et al. (2006):

$$\log(IFIR_{max}) = -2.082 + 0.245log_e(M_{spec}) + 0.365log_e(rM_{prey}) + (0.5 * 0.270)$$

Mspec is the body mass (g) of a wading bird at the start of the model period, Mprey is the mean ash-free dry weigh (mg) of prey within the size consumed, r is the ratio of the size range to size in patch and 0.270 is the error mean squares.

Maximum rate of consumption

This equation used is the same as in previous models (Durell et al., 2006; Durell et al., 2007). The maximum rate of consumption per hour being set to 1000 is divided by the energy density of each diet.

Diet assimilation efficiency

The proportion of energy that is assimilated into the bird's body differed with the prey consumed. Whilst we assumed this to be 0.75 for all resources for each bird (Kersten & Piersma, 1987; Goss-Custard et al., 2006), we set a slightly higher efficiency (0.85) for crustaceans and for Eurasian oystercatcher feeding on cockles and other molluscs (Van de Kam et al., 2004).

Feeding, resting and moving metabolic rates

The metabolic rate is the amount of energy expended per time-step per bird. The BMR is calculated per species from equations set by Kersten and Piersma (1987):

$$BMR = 437*(mass\ in\ kg)^{0.729}$$

To emulate feeding and roosting, BMR is multiplied by 2.1 for feeding and by 2.0 for resting birds plus an additional 10% (Zwarts et al. 1996) to account for cost of flight. No moving BMR was incorporated given the size of the study area.

Thermoregulatory cost

The thermoregulatory cost below a lower critical temperature (LCT) was calculated using the following equation derived by Bowgen (2016). The thermoregulatory cost is calculated using measurements of energy consumption per day (Kersten and Piersma 1987) and a linear relationship against body mass (weight in grams) to predict the LCT for all modelled species.

$$\mathit{Thermostatic\ cost\ in\ kJ} = 0.0055*(\mathit{body\ mass\ in\ g})^{1.3737}$$

Emigration fitness measure, movement time

Formula can be used to calculate the probability that a forager will emigrate from the model system. We assumed that there were no emigration or movement the model. As such, the emigration fitness measure and movement time have both been set to 0.

Patch location rule

Rule for whether a patch can be located by each forager type. We assumed in our model that each forager can locate a patch as long as it is exposed by the tide (Available = 1) and that Patch Size is above >1 m$^{2.}$

Fitness component

The fitness components are used to calculate fitness measures where foragers either survive or die. In our model, we followed the “satisficing” method which allows birds to choose patches that are adequate for the birds to survive (Stillman et al., 2005). Bowgen (2016) developed the equation included in the model

$$\begin{gathered} \mathit{if((EnergyInitialStore}<(0.95*\mathit{EnergyTargetStore}))\ \mathit{or}\ (\mathit{EnergyAssimRate}>\mathit{EnergyPastAssimRate}), \\ (\mathit{if((EnergyInitialStore}<(0.95*\mathit{EnergyTargetStore})),1000+\mathit{EnergyAssimRate}, \\ 1000+(\mathit{EnergyAssimRate}>\mathit{EnergyMetabRate}))), \\ \mathit{if((Roost}=1),10,0)) \end{gathered}$$

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