

**IMPACT OF HUMAN DISTURBANCE ON COASTAL BIRDS:
POPULATION CONSEQUENCES DERIVED FROM
BEHAVIOURAL RESPONSES**

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Declaration

I declare that the work presented in this thesis is my own work, with the following exceptions:

Chapter 2 has been published (Appendix 10) in collaboration with Richard Stillman, Angus Garbutt, Mick Yates, Ed Rispin and Tina Yates as:

Collop, C., Stillman, R. A., Garbutt, A., Yates, M. G., Rispin, E. and Yates, T. (2016). Variability in the area, energy and time costs of responding to disturbance for wintering waders. *Ibis* 158(4):711-725.

Data collection was undertaken by Angus Garbutt, Mick Yates, Ed Rispin and Tina Yates as part of an English Nature funded project. Full details are reported in chapter 3 of: Stillman et al. (2005) Estuary Special Protection Areas – Establishing Baseline Targets for Shorebirds.

In Chapter 4 data collection was designed and initiated by British Association for Shooting and Conservation (BASC): Matt Ellis and members of Dorset Wildfowlers' Association assisted with project logistics and data collection.

The individual-based model used in **Chapter 5** was based on the framework created by Stillman (2008) and further developed and parameterised for Poole Harbour by K. M. Bowgen (Bournemouth University).

Catherine H. Collop

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Abstract

Impact of human disturbance on coastal birds: population consequences derived from behavioural responses.

Catherine Collop

Disturbance of wildlife is inevitable in a world with a rapidly increasing human population. Whilst improving engagement with the natural world can have the benefit of encouraging people to help protect it, there is also the issue of increased potential for damaging effects of disturbance. A better understanding is needed of the circumstances under which disturbance would be expected to be a conservation problem, either alone or in combination with the impacts of other human activities. The aim of this thesis is therefore to address these questions: using wintering waders in estuarine habitats as the study system and taking a joint fieldwork and simulation modelling approach. Fieldwork was centred on Poole Harbour; an estuary and wetland of international importance located on the south coast of the UK. Disturbance experiments and observations showed that bird responses to disturbance are highly variable and related to factors including body mass, environmental conditions, site quality, and disturbance type. The energetic and lost-feeding-opportunity costs of responding to individual disturbance events were relatively small and therefore considered unlikely to cause major reductions in individual body condition or significantly limit overwintering population size, given observations of present-day spatial and temporal patterns of human activities. Simulation modelling using two types of individual-based model (IBM) supported this conclusion. Although high levels of disturbance can have a significant impact on wintering bird populations, current frequencies of human activities in Poole Harbour were not found to be reducing the carrying capacity of the site. Increased disturbance frequencies were predicted to be problematic, however, in combination with environmental change that reduced bird ability to meet their daily energy requirements: such as loss of foraging habitat through sea level rise, or reductions in prey availability due to over-exploitation. This has important implications for identifying the most effective conservation management methods. As well as site-specific management recommendations, this research contributes to understanding of the mechanisms by which disturbance may or may not have a significant impact on wintering wader populations; along with applications to other systems; and tools and general principles that conservation managers and decision makers can use to prioritise further investigation and action.

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List of acronyms and abbreviations used

ABM	Agent-based model
AEWA	African Eurasian Waterbirds Agreement
AFDM	Ash-free dry mass
AIC _c	Alkaike's information criterion (corrected)
Barwit	Bar-tailed godwit
BASC	British Association for Shooting and Conservation
Blackwit	Black-tailed godwit
BMR	Basal metabolic rate
BTO	British Trust for Ornithology
<u>BTO two letter codes for bird species:</u>	
AV	Avocet
BA	Bar-tailed godwit
BG	Brent goose
BW	Black-tailed godwit
CG	Canada goose
CU	Curlew
DN	Dunlin
GJ	Greylag goose
GK	Greenshank
GV	Grey plover
KN	Knot
L.	Lapwing
MA	Mallard
OC	Oystercatcher
PT	Pintail
RK	Redshank
RP	Ringed plover
SS	Sanderling
SU	Shelduck
T.	Teal
TT	Turnstone
WN	Wigeon
BU	Bournemouth University
CI	Confidence interval
CRoW Act	Countryside and Rights of Way Act
dB	Decibels
DWA	Dorset Wildfowlers' Association
EDD	Effective disturbance distance
FACE	European Federation of Associations for Hunting and Conservation
FID	Flight initiation distance
FMR	Field metabolic rate
IBM	Individual-based model
IEEM	Institute of Ecology and Environmental Management
IFCA	Inshore Fisheries and Conservation Association

IFIR	Interference-free intake rate
IUCN	International Union for Conservation of Nature
JNCC	Joint Nature Conservation Committee
LCT	Lower critical temperature
MCZ	Marine Conservation Zone
RNLI	Royal National Lifeboat Institute
RoRo	Roll-on, roll-off terminal
RSPB	Royal Society for Protection of Birds
SAC	Special Area of Conservation
SPA	Special Protection Area
SSSI	Site of Special Scientific Interest
WeBS	Wetland Bird Survey
WHT	Wildlife Habitat Trust

Chapter 1 – Introduction

1.1 Background to the topic

Disturbance of wildlife is inevitable in a world with a rapidly expanding human population and an ever-increasing demand for resources. In addition, non-material benefits – ‘cultural services’ – through having access to nature are now well recognised (Millennium Ecosystem Assessment 2005), so people are encouraged to make more use of natural open spaces for recreational purposes to improve health and wellbeing (ten Brink et al. 2016). Whilst improving engagement with the natural world can have the benefit of encouraging people to help protect it, there is also the issue of increased potential for damaging impacts of disturbance, either alone or in combination with the impacts of other human activities (housing development, economic activities, tourism etc.) and other forms of environmental change (e.g. habitat loss, climate change, pollution, spread of invasive non-native species). Nevertheless individuals, populations and ecosystems are to some extent resilient to environmental perturbations and are able to compensate for certain amounts of disturbance without being adversely affected (Holling 1973, Nattrass and Lusseau 2016). Disturbance is therefore not automatically a problem from a conservation perspective even though some people might consider any disturbance of wildlife to be ‘morally’ unacceptable.

Conservation managers often attempt to prevent disturbance from occurring by limiting particular activities or excluding people altogether from some areas (Davidson and Rothwell 1993, Livezey 2016). However such management measures risk high enforcement costs or even failure if they are not accepted by the affected users (who may give higher priority to other activities): to be successful, measures must be based on sound evidence along with effective stakeholder consultation (Holsman et al. 2010, Glover et al. 2011, Johnson 2013). Over-precautionary policies in one area may also foster general mistrust and reduced compliance for any management measures regardless of whether they are over-precautionary or not. The purpose of this research, therefore, is to (1) improve understanding of the impacts of human disturbance on wildlife and the circumstances under which it is or is not likely to be a conservation problem, and (2) develop tools to help minimise the impacts in situations where action is considered to be necessary. More-detailed aims and objectives are listed in section 1.4.

The rest of this chapter summarises current understanding and relevant research methods relating to human disturbance of wildlife (with a focus on non-breeding estuarine birds);

identifies key knowledge gaps; and introduces the study system and its suitability in this context. The chapter concludes with an overview of the structure of the rest of the thesis.

1.1.1. Human-induced disturbance of wildlife

The term 'disturbance' can mean any event that leads to an animal response that would not have taken place in the absence of that event. This might be for example due to natural occurrences such as attack by a predator or the rising and falling of the tides; or anthropogenic, where recreation or industry brings humans and wildlife into close proximity; or it could result from acoustic stimuli. This thesis uses the definition of human-induced disturbance as given by Fox and Madsen (1997) in relation to waterbirds, which can also easily be applied to any other animal taxon: *'any activity that constitutes a stimulus (equivalent to a predation threat) sufficient to disrupt normal activities and/or distribution of waterbirds relative to the situation in the absence of that activity'*.

Responses – the risk-disturbance hypothesis

Fox and Madsen's (1997) definition recognises the fact that animals respond to the perceived risk from human disturbances in the same way that they respond to predation risk (Frid and Dill 2002) i.e. by making trade-offs between avoidance of the risk and prioritising other fitness-maximising activities such as feeding, mating or parental care. Following this 'risk-disturbance hypothesis', animal responses to disturbance can therefore be expected to vary between individuals according to a variety of factors related to the perceived risk, the individual's current state, availability of alternative habitat, and the costs of responding (Gill et al. 2001a, Beale and Monaghan 2004a).

The process that animals go through when they detect a potential predator or disturbance source (stimulus), involves one or more behavioural and physiological responses according to the duration and intensity of the stimulus: i) heart rate and metabolic rate increase in preparation for fleeing; ii) animals stop what they are doing and become visibly alert; iii) they may flee or approach the stimulus; and then iv) take a certain amount of time to return to their original behaviour and physiological state (Figure 1.1).

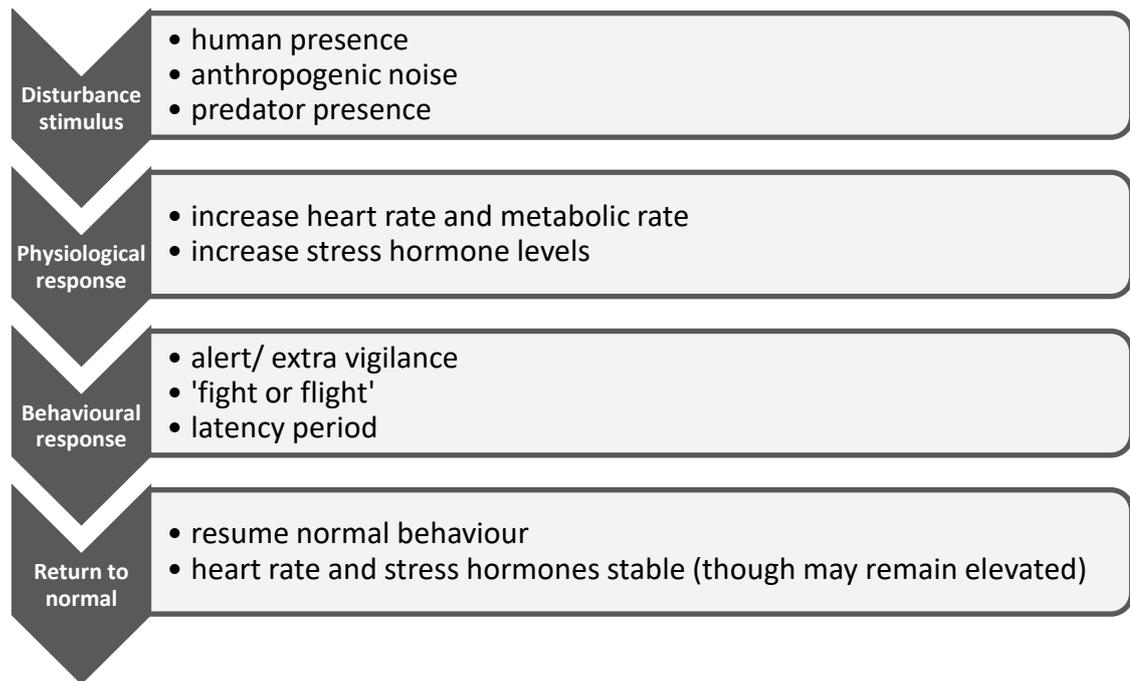


Figure 1.1. Process of animal response to a potential predator or human disturbance.

Impacts – the individual and population consequences

Responses to disturbance can have fitness consequences for the individual through reduced time and area available for feeding (Gill et al. 1996), breeding (de Jong et al. 2013) or resting (Rosa et al. 2006) and increased energy expenditure through locomotion (Houston et al. 2012) or physiological responses (Ackerman et al. 2004). One prediction of the risk-disturbance hypothesis is that long-term and intense disturbance stimuli can cause population declines through reduced body condition and therefore reduced breeding success (Frid and Dill 2002). Understanding the cumulative impacts of many relatively small-scale disturbance events, interactions with other risk factors and individual compensatory ability, however, is not straightforward (Sutherland 2007).

Animal responses to human disturbance and the associated impacts have long been a subject of interest and concern amongst behavioural ecologists, land managers and conservationists; for example early publications include investigations into the fleeing behaviour of hunted mammals (Altmann 1958, Behrend and Lubeck 1968); studies of disturbance responses of breeding birds (Stephen 1963, Mathisen 1968); proposed evidence for habituation (Walker 1972); and reports of the impacts of human activity on animal numbers (Watson 1979). Despite the fact that there have been many studies and reviews in the intervening decades (e.g. Boyle and Samson 1985, Hockin et al. 1992, Fox and Madsen 1997, Hill et al. 1997, Steven et al. 2011 and the other studies already mentioned; also see Table 1.1), as Sutherland

(2007) points out there is still much to learn when it comes to understanding disturbance-related impacts on wildlife.

Table 1.1. Selected examples of documented impacts of human disturbance.

Species studied	Details
Pink-footed goose <i>Anser brachyrhynchus</i>	Madsen (1995). Geese in undisturbed areas increased their abdominal profiles more rapidly and reproduced more successfully than those from disturbed sites.
European nightjar <i>Caprimulgus europaeus</i>	Langston et al. (2007). Nests which failed were significantly closer to paths; closer to the main points of access to heaths; in areas with higher footpath density; and in areas of notably high levels of use.
Little tern <i>Sternula albrifrons</i>	Medeiros et al. (2007). Human disturbance and predation were the main factors in explaining breeding success.
Snowy plover <i>Charadrius nivosus</i>	Webber et al. (2013). Site occupancy and colonisation was negatively associated with human disturbance and site extinction was positively associated with disturbance.
Yellow-eyed penguin <i>Megadyptes antipodes</i>	McClung et al. (2004). Tourist numbers may affect fledgling weight and therefore probability of survival.
Hoatzin <i>Opisthocomus hoazin</i>	Müllner et al. (2004). Chick survival was much lower for tourist-exposed nests than for undisturbed nests.
Wood lark <i>Lullula arborea</i>	Mallord et al. (2007). Probability of suitable habitat being colonised was lower in areas with greater disturbance, but density-dependent breeding success partially balanced the negative impacts of disturbance.

From a conservation perspective, a key issue that has only relatively recently begun to receive recognition is that the distinction needs to be made between *responses to* disturbance and *impacts of* disturbance. In the past, the visible responses of animals have been used as a measure of relative need for protection, for example by Klein et al. (1995). However, Gill et al. (2001a) showed that the magnitude of animal response is not necessarily a good indicator of the impact of that disturbance in terms of whether or not individual or population survival or fecundity are altered. This will depend on individual ability to

compensate for the short-term fitness costs of responding – for example by feeding for longer or more efficiently (Stillman and Goss-Custard 2002) – and the action of density-dependent population processes (Mallord et al. 2007). Individuals showing little or no response may in fact be those with most to lose from changing their behaviour. Beale and Monaghan (Beale and Monaghan 2004b) found that turnstones *Arenaria interpres* whose condition had been enhanced by supplementary feeding showed greater responsiveness to human disturbance; birds in good condition flew away at greater distances from the observer, scanned for predators more frequently and flew further when flushed. Future research therefore needs to move away from pure behavioural studies and consider the impacts of disturbance from a demographic and population process point of view (Gill 2007).

As Nisbet (2000) points out in relation to colonial waterbirds, demonstrating causal relationships between human disturbance and fitness measures like survival is not easy as it is also influenced by many other factors that are difficult to control for. Whilst there are a number of studies that document the impacts of disturbance on reproductive success (Table 1.1), there do not appear to be any that demonstrate impacts outside of the breeding season even though these might be expected to occur. Making predictions about the true impacts of disturbance is therefore challenging and this issue will be discussed in more detail in sections 1.2.2 and 1.3.

1.1.2. Legislation and policy relating to disturbance

The UK is signatory to four main conventions that direct its biodiversity policy, along with several key European directives that make reference to the impacts of disturbance; the obligations of which have been transposed into national law (Figure 1.2). Between them they: provide for public access to the countryside whilst ensuring wildlife interests are not damaged; outline measures for the identification, management and protection of Sites of Special Scientific Interest (SSSIs), Special Areas of Conservation (SACs), Special Protection Areas (SPAs) and Marine Conservation Zones (MCZs); and list and give extra protection to threatened species of particular conservation concern. The Countryside and Rights of Way Act (2000) makes it an offence to *'intentionally or recklessly disturb any animal'*; the Birds Directive (EC 2009) instructs Member States *'in respect of the protection areas...take appropriate steps to avoid ... any disturbances affecting the birds... in so far as these would be significant'*; and similarly, the Habitats Directive (EEC 1992) includes the obligation to *'take appropriate steps to avoid, in the special areas of conservation... disturbance of the species for which the areas have been designated, in so far as such disturbance could be significant'*.

The UK is also a signatory on the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA), in which disturbance is recognised as an issue that needs to be addressed and researched (AEWA Secretariat 2012); and Sutherland et al.'s (2006) list of 100 ecological questions of high policy relevance in the UK included three that relate to research into the impacts of human disturbance (#32: *what are the impacts of recreational activities on biodiversity?* #37: *what are the consequences for biodiversity of fragmentation by development and infrastructure?* #38: *what are the ecological impacts on semi-natural habitats and ecosystems of adjacent large developments?*). Estuarine intertidal habitats and the assemblages of wintering waders and wildfowl they support, along with their considerable importance for human recreation and economic uses, offer a useful study system for such research.

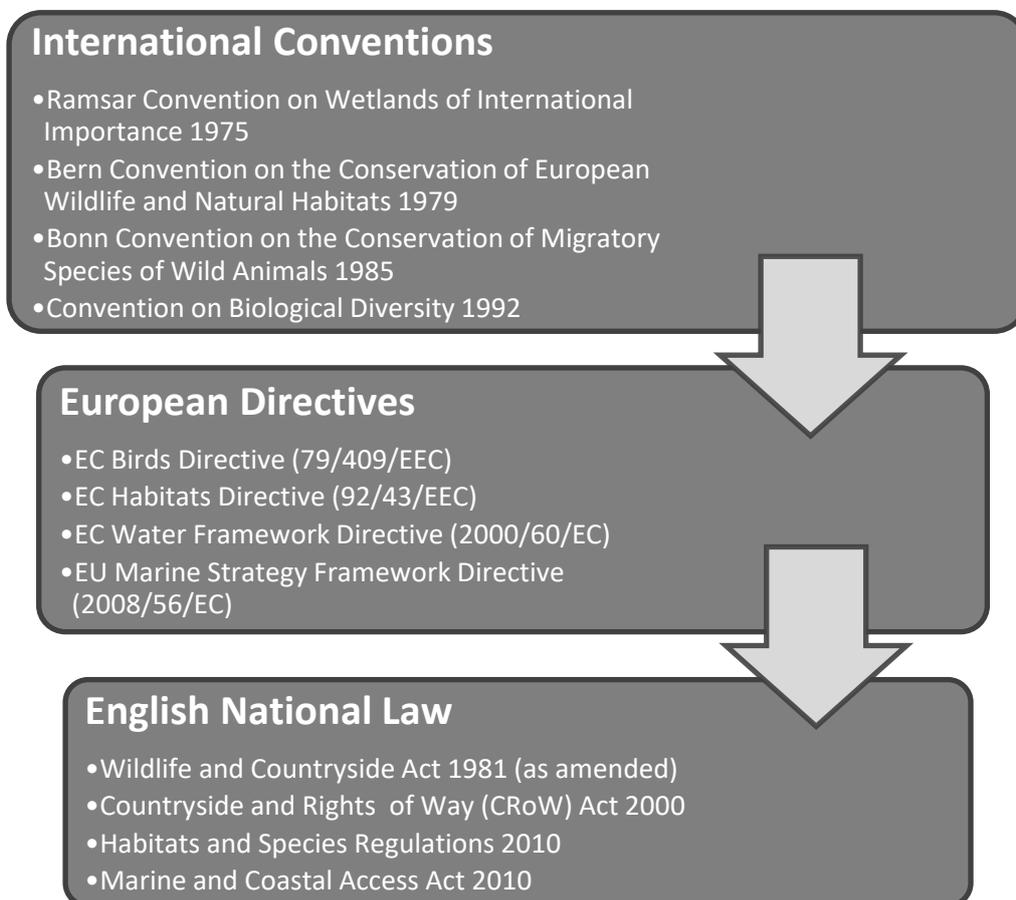


Figure 1.2. Framework of international conventions, European directives and English national law that relate to public access to the countryside and human-induced disturbance of wildlife.

1.1.3. Importance of intertidal flats

Intertidal flats are areas of the sea floor that are periodically exposed and covered by the falling and rising of the tides, and are characterised by their relative proportions of sandy and muddy sediments according to differences in water flow and availability of fine sediments

(Davies et al. 2001). They occur at the edges of shallow seas all around the world, and in the UK they make up a major component of the country's estuaries and embayments (Davies et al. 2001, van de Kam et al. 2004). The Millennium Ecosystem Assessment (2005) demonstrated that such habitats are responsible for a wide variety of ecosystem services i.e. the benefits that people obtain from ecosystems; including playing a vital role in the processing of nutrients, regulating climate and offering opportunities for many different recreation and economic activities (reviews by Barbier et al. 2011 and Foster et al. 2013). Similarly, in a review of paradigms relating to estuarine structure and functioning, Elliott and Whitfield (2011) suggest that estuaries are one of the most valuable aquatic ecosystems serving human needs.

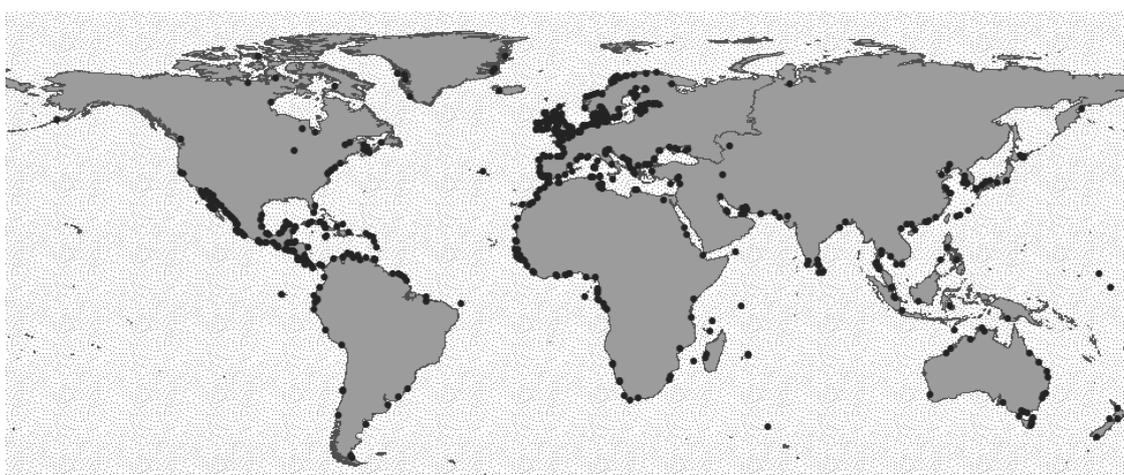


Figure 1.3. 653 (29%) Ramsar wetlands of international importance include estuarine waters; intertidal mud, sand or salt flats; or intertidal marshes. Produced using ArcGIS basemap imagery © ESRI, Inc. (2000) and data from Ramsar Sites Information Service (Ramsar 2016a).

Mudflats in particular are of considerable biodiversity value due to the rich communities of invertebrates, birds and other taxa that they support; as such many are recognised as wetlands of international importance via the Ramsar Convention (Figure 1.3) and in the European Nature Directives. Many estuarine sites around the UK receive legal protection as a result (see section 1.1.2). Soft mudflats often support high densities of oligochaete and polychaete worms and bivalve molluscs, which provide vital food for millions of waterbirds worldwide particularly during the non-breeding season and on passage (Davies et al. 2001, Austin et al. 2014). These benthic invertebrates and other associated species also represent a valuable commercial and recreational fisheries resource: for example UK commercial fishing vessels landed £7.9 million worth of cockles in 2014 (Marine Management Organisation 2015); and many fish species and crustacea feed on marine worms and bivalve larvae. In addition, mudflats provide essential nursery areas for commercial fish species such as plaice

Pleuronectes platessa, bass *Dicentrarchus labrax* and dab *Limanda limanda* (Raffaelli and Hawkins 1996, Weerts and Cyrus 2002, França et al. 2008). Nursery areas are often associated with eelgrass *Zostera* spp. beds (Costa et al. 1994, Polte and Asmus 2006, Warren et al. 2010, Bertelli and Unsworth 2014), which also provide an important food resource for herbivorous waterbirds – in particular all subspecies of brent goose *Branta bernicla* (Wilson and Atkinson 1995, Ganter 2000, Desmouts et al. 2009).

Section 1.4 gives more specific examples from two different sites of the value of estuarine habitats to both people and wildlife.

1.1.4. Threats to estuarine systems

Like most (if not all) natural habitats worldwide, estuarine systems are threatened, both directly and indirectly, by human activities; and they may have more human-induced pressures than other system (Elliott and Whitfield 2011). Given that coastal areas are a focus for development and economic activity, with further population growth predicted, the seriousness of many threats continues to increase and there is an urgent need for habitat creation and restoration, and the implementation of sustainable management practices (Thom et al. 2005). This section gives a brief description of the overarching threats and sets the topic of this thesis – disturbance – in the context of these additional pressures.

Habitat loss and degradation

Habitat removal, modification, dredging, sediment deposition and drainage due to developments for housing, tourism, ports, marinas, agriculture and aquaculture, often in combination with associated increases in pollution/nutrient enrichment have caused widespread losses in terms of quality and extent of habitat, and abundance and diversity of flora and fauna (McLusky et al. 1992, Goldberg 1995, Buchan 2000, Atkinson et al. 2001, Thrush et al. 2004, Ducrotoy and Elliott 2008, Holmes et al. 2012).

A particularly extreme example is that of the Yellow Sea where 28% of tidal flats present in the 1980s had been lost by the 2000s, and 65% were lost between the 1950s and 2000s (Murray et al. 2014). This represents approximately 728,000 ha – almost as much as the extent of intertidal flats in the whole of the Wadden Sea, and more than twice the total area of intertidal flats in the UK (Davidson et al. 1991). The Yellow Sea provides vitally important stopover habitat for migratory birds using the East Asian-Australasian Flyway (van de Kam et al. 2010), and current rates of loss put the whole flyway at risk of collapse (Yang et al. 2011, Piersma et al. 2016).

Over-exploitation

The ecological integrity of many estuarine systems is also threatened by over-exploitation, particularly in relation to fisheries activities (deFur and Rader 1995, Jackson et al. 2001, Piersma et al. 2001). Declines in bivalve stocks in the 1980s and 1990s due to suction dredging for cockles and harvest of mussels in the Wadden Sea, for example, have been implicated in the declines of oystercatcher *Haematopus ostralegus* and eider duck *Somateria mollissima* around the same time (Camphuysen et al. 2002, Ens 2006). Resource over-exploitation and coastal degradation also undermine subsistence use of coastal ecosystems, harming local communities as well as national economies (Millennium Ecosystem Assessment 2005).

Invasive non-native species

The connected nature of aquatic environments means that invasive non-native species can be even more of a problem in marine and freshwater systems than they are on land: once established they may be very difficult or prohibitively expensive to remove. Eno et al. (1997) reported that no non-native marine species has been successfully removed from British waters, and attempts to remove such species can even be unintentionally damaging (Zavaleta et al. 2001, Bergstrom et al. 2009, Zarnetske et al. 2010). Instead, Olenin et al. (2011) suggest a more appropriate post-establishment response is to focus on containment, control and mitigation.

Sea level rise

Global sea levels rose throughout the 20th century in response to climate change, and although the magnitude is uncertain, these rises will almost certainly accelerate further through the 21st century (Nicholls and Cazenave 2010). The normal response of intertidal habitats to sea level rise is to 'migrate' inland; providing that there is sufficient sediment, sea level rise is not too fast, topography allows, and their landward edges have not been reinforced with hard structures for flood prevention or modified by humans in other ways (Kirwan and Megonigal 2013, Gittman et al. 2015). If intertidal habitats are not able to migrate inland at a fast enough rate, losses are likely to occur through erosion and inundation and interactions between physical and ecological processes (Akib et al. 2012, Pontee 2013, Passeri et al. 2015). When the high water mark is fixed by a hard defence or structure and sea level rise causes the low water mark to migrate inland, the resulting habitat loss is termed 'coastal squeeze' (Pontee, 2013). This, like other forms of intertidal habitat loss and

modification, will have implications for associated flora and fauna (Short and Neckles 1999, Fujii and Raffaelli 2008, Clausen and Clausen 2014).

Disturbance

Coping with the costs of disturbance can be particularly problematic for some susceptible groups (Baillie et al. 2004), and interactions between threats can amplify the overall impacts so that in combination impacts are worse than would be expected based on analysis of single threats alone (Crain et al. 2008, Mantyka-Pringle et al. 2015). Threats to biodiversity rarely occur in isolation so disturbance, when occurring in combination with other threats, could have significant negative consequences for wildlife populations, particularly those whose fitness is already reduced through the impacts of those other stressors. Similarly there could be interactions between different types disturbance. Though conversely, there may also be situations where impacts are reduced through interactions with other threats.

When identifying threats and assessing their impacts it is important to make the distinction between the potential in combination impacts of multiple threats and/or disturbance types and the cumulative impacts of repeated occurrences of a single threat type. However, the term 'cumulative' impact is sometimes used to refer to in-combination impacts as well (International Finance Corporation 2013; RenewableUK 2013; Natural England 2014).

1.1.5. Human activities relevant to estuarine systems which may cause disturbance to non-breeding waterbirds

Since estuaries are such important resources for a wide variety of human recreational and economic activities as well as large populations of wintering waterbirds, there are many different ways that humans might cause disturbance to those birds. The responses and impacts will depend on the type of activity, its frequency of occurrence, and where and when it takes place in relation to the daily activities and movements of birds (Figure 1.4). The rest of this section describes some of the most common activities that take place in estuarine environments and the mechanisms by which they may or may not disturb wintering birds.

Walking

Walking is a popular outdoor pastime in many different types of habitat and estuarine environments are no exception. For example studies in Cork Harbour (SW Ireland) (O'Mahony et al. 2009), and in UK estuaries (Fearnley et al. 2010, 2012, Liley et al. 2011, Liley and Fearnley 2012) found walking to be the most frequently observed recreational activity. Many people keep to shoreline footpaths or beaches above the high water mark (e.g. 77% of

walker routes on the Exe estuary did not involve using intertidal areas (Liley et al. 2011)); however, others may walk on the intertidal area depending on the state of the tide and the muddiness of the sediment (Goss-Custard and Verboven 1993). Consequently, on estuaries with wide expanses of mudflats that are difficult or dangerous to walk on, birds feeding at the water's edge at low tide will encounter few, if any, walkers. Whereas on narrower and sandier intertidal areas and at times when the tide brings feeding birds close to the upper shore area, there will be a greater likelihood that walkers may disturb birds.

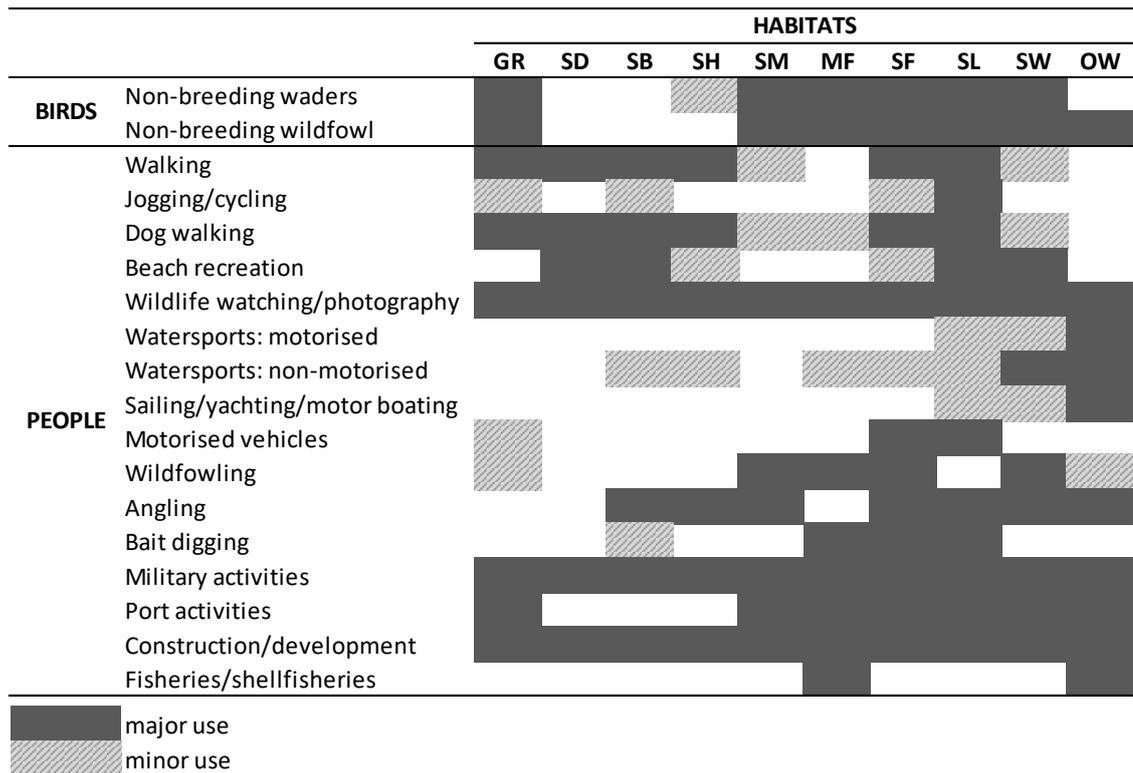


Figure 1.4. Use of estuarine habitats by birds and people during the non-breeding season (autumn/winter/spring). Habitat abbreviations are: GR grassland; SD sand dune; SB sandy beach; SH shingle beach; SM saltmarsh; MF mudflat; SF sandflat; SL shoreline; SW shallow water; OW open water. Adapted from Davidson and Rothwell (1993).

The distribution of people around an estuary and associated disturbance levels will be related to the access opportunities (Liley and Sutherland 2007, Mallord et al. 2007, Coombes et al. 2008, Wolf et al. 2012): more people are likely to be found near car parks and where there are shoreline footpaths. Conversely, intertidal areas that are backed by wide expanses of saltmarsh with tidal creeks and/or private land will experience less intense pedestrian visitor pressure. Feeding or roosting birds on fields or land with public access, such as recreation grounds, football pitches and golf courses (Liley and Hoskin 2011, Morrison 2015), will also be

at greater risk of disturbance. These relationships are likely to apply for most types of recreation, with the exception of some water-based activities.

Jogging/cycling

Some researchers have suggested that speed of approach is an important factor in determining bird responses to disturbance: for example Burger (1981) and Glover et al. (2011) both found that shorebirds were more responsive to joggers than they were to slow walkers; and Fitzpatrick and Bouchez (1998) observed increased vigilance in oystercatcher, curlew *Numenius arquata* and redshank *Tringa totanus* in the presence of faster moving human activities (jogging and cycling) versus slow (walking and stationary people). However there are other studies that have demonstrated the opposite relationship (e.g. Lafferty 2001, Rees et al. 2005), or no difference between fast and slow moving people (Lord et al. 2001). The importance of speed of approach may be confounded by or interact with other site-, species-, or situation-specific factors.

Dog walking

As well as being the most popular companion animal, domestic dogs perform valuable herding, guarding, hunting and disability-support roles, and the global owned dog population is estimated to be nearly one billion (Gompper 2014). Since dogs need daily exercise and people like to visit coastal and estuarine habitats, there is plenty of scope for dogs and wintering waders to come into conflict (in addition to the potential problems associated with free-roaming and feral dogs), with dogs representing a perceived – or sometimes real – risk of predation (Marks and Redmond 1994, Ritchie et al. 2014). The probability of dogs disturbing birds will be greater when they are not under close control or on a short lead since they may roam across the intertidal habitat and enter the water, and may also chase birds. Lafferty (2001b) found that dogs on a lead were no more likely to disturb birds than walkers without dogs, but dogs off lead were more likely to disturb birds and disturbed more birds at a time. Dogs that chased birds were even more likely to cause a disturbance, although the number of birds disturbed per event was not significantly different to dogs off lead that didn't chase birds (Lafferty 2001b).

Most research relating to the impacts of dogs on shorebirds focusses on the breeding season (Pienkowski et al. 1984b, Yalden and Yalden 1990, Lord et al. 2001, Weston and Elgar 2007), the findings of which have resulted in regulations either excluding dogs or requiring them to be kept on a lead in certain areas. Where regulation has been adhered to there have been successes (e.g. Lafferty et al. 2006); however there is evidence that regulations are often

ignored and further work is needed to find ways to improve levels of compliance (Dowling and Weston 1999, Lafferty 2001b, Williams et al. 2009, Glover et al. 2011, Stigner et al. 2016).

Angling and bait digging

In the UK there is a public right to collect intertidal fish, shellfish and other invertebrates where there is public access to the shore (not including commercial bait collection, and subject to regulation by local byelaws) (Fowler 1999). By virtue of remaining in one place for relatively long periods of time, angling, bait digging and other similar activities may be expected to cause fewer disturbances than activities that involve movement across or alongside intertidal habitats. For example Goss-Custard and Verboven (1993) noted that after the initial disturbance when anglers and mussel pickers arrived, oystercatchers soon resettled and some even fed nearby. However, in situations where there is only a small amount of intertidal habitat available, the presence of stationary humans evenly spread across the intertidal area can prevent birds from feeding or roosting (Townshend and O'Connor 1993, Navedo and Masero 2007). This will be especially true in the case of bait diggers, who favour the same areas as feeding birds i.e. those areas with high densities of specific benthic invertebrates and may cover large areas of intertidal habitat (albeit slowly).

Wildlife watching/photography

The effects of people engaged in wildlife watching and photography are likely to be similar to those of walkers, or perhaps lessened by the fact that they may be stationary for extended periods of time. They may also show a greater awareness and reluctance to disturb their subjects and employ field-craft accordingly (Weston et al. 2015); although conversely, direct approach and a desire to get as close as possible to their subject could in fact increase the likelihood of disturbance occurring (Boyle and Samson 1985, Sekercioglu 2002).

Watersports and motorised vehicles

Watersports can be divided into motorised (e.g. jet skiing, water skiing, power boating, yachting) and non-motorised activities (e.g. canoeing, paddle boarding, windsurfing, kitesurfing, sailing) and may take place in shallow water with the potential to disturb nearby feeding or roosting birds, as well as occurring further out on open water, where rafting wildfowl may be disturbed. Birds using intertidal areas may also be affected if recreationists set up on and cross this habitat in order to access the water.

Noise from nearby road or rail transport links can result in disturbance of feeding or roosting birds, or cause them to avoid otherwise suitable habitat (Reijnen et al. 1995, Hirvonen 2001).

In addition to the noise disturbance, off-road vehicles can cover large areas and have the potential to cause substantial disturbance when present on beach and intertidal areas: larger vehicles have been shown to be more disruptive than smaller ones (Schlacher et al. 2013b), though in some cases vehicles could approach birds more closely than pedestrians (McLeod et al. 2013). Aside from some studies of breeding shorebirds (Buick and Paton 1989, Borneman et al. 2016), there has been very little research into the impacts of these activities on coastal and estuarine waterbirds separate from other forms of human disturbance; although see Méndez Roldán (2013) and an observation by Fraser (1987). Similarly, the increasing popularity of drones (unmanned aerial vehicles) as survey tools and for general recreation represents a novel potential disturbance type and highlights the need for more specific research into the impacts of different activities (Allport 2016; McEvoy et al. 2016; Rümmler et al. 2016).

Whilst water-based activities may cause disturbance in similar ways to other activities simply due to the presence of people, there may be other mechanisms involved. For example, the noise from motorised watersports presents an additional, potentially disturbing, stimulus; and non-motorised watersports such as canoeing and kayaking allow people to access areas such as saltmarsh creeks and islands that may not otherwise be disturbed by other activities due to access limitations.

Wildfowling/hunting

Wildfowling – also known as waterfowl hunting – involves the shooting of ducks and geese for sport and for the plate, usually with a shotgun from the shoulder (or a large gun mounted on a boat known as a punt (Townshend and O’Connor 1993), though this is now rare).

Wildfowling takes place on estuaries and coastal marshes as well as inland freshwater habitats, and in the UK the activity dates back to 16th and 17th centuries with the increased popularity and effectiveness of the shotgun around that time (Marchington 1980, Kear 1990).

The activity is popular worldwide: in 2011 in the US 2.6 million people hunted migratory birds such as ducks, geese and doves – representing more than 1% of the adult population, and a 13% increase since 2006 (US Fish and Wildlife Service 2012). The ‘voice of European hunters’, including wildfowlers, is the European Federation of Associations for Hunting and Conservation (FACE), whose members are national hunting associations from 36 countries including all EU Member States (FACE 2016). Wildfowlers in the UK are represented by the British Association for Shooting and Conservation (BASC).

It is in the interests of hunters to maintain large populations of their target species, and in America for example conservation management and maintenance of the wildfowl resource for harvest are almost synonymous (Owen and Black 1990). Hunters and nature-lovers alike can purchase the annual 'Duck Stamp' which allows access to wetlands for hunting and free access to national wildlife refuges; 98% of the proceeds are spent on wetland conservation work (US Fish and Wildlife Service 2015). The equivalent in the UK is coordinated by the Wildlife Habitat Trust (WHT); funds raised from sale of the UK Habitats Stamp help to fund land acquisition and site management for shooting and conservation projects (WHT 2016).

Wader hunting is prohibited in most parts of the world, yet there are still some areas, particularly in the Western Hemisphere where it does occur either legally or illegally (Watts and Turrin 2016). For example professional hunters in Bangladesh and Myanmar rely on trapping waders for their family livelihood, including the critically endangered spoon-billed sandpiper *Eurynorhynchus pygmeus* (Chowdhury 2010, Zöckler et al. 2010); there is considerable hunting pressure on waders in the Caribbean (Andres 2011); and although waders are legally protected in Suriname, tens of thousands are estimated to be killed by hunters annually (Morrison et al. 2012). Aside from these and other exceptions (golden plover *Pluvialis apricaria*, snipe *Gallinago gallinago* and woodcock *Scolopax rusticola* in the UK), most species of wader that spend the winter in coastal and estuarine habitats are not legal quarry for wildfowling (BASC n.d.); nevertheless they are likely to be disturbed by the sound of a shotgun being fired nearby and the subsequent retrieval of shot quarry by a dog; and the presence of a wildfowler may exclude foraging waders from certain areas of mudflat depending on the state of the tide.

Whilst there have been a number of studies researching the effects of wildfowling disturbance on quarry species (e.g. Townshend and O'Connor 1993, Fox and Madsen 1997, Madsen 1998a, 1998b, Bregnballe et al. 2004, Casazza et al. 2012), the population-level impacts are still not well understood. Furthermore, there is a lack of research into the impacts of wildfowling on non-quarry species groups such as wintering waders; although the subject has been considered for other forms of hunting (Hofer et al. 1996, Grignolio et al. 2011).

Military activities

Many military training bases are located in estuarine and coastal habitats around the world, so birds may be subject to noise and physical disturbance both during the day and at night from aircraft and weapons training operations (Boice 1997, Ministry of Defence 2015). Whilst disturbance from such activities could be severe (Smit and Visser 1993), it may not be frequent, and birds may in fact benefit from the exclusion of other potentially disturbing activities. For example one of the largest UK grey seal colonies can be found at the RAF Donna Nook bombing range on the Lincolnshire coast, along with a rich diversity of birds, plants and other taxa (Bishop et al. 2015, Lincolnshire Wildlife Trust 2016).

Commercial activities

Given that coastal and estuarine habitats are often important centres of commercial activity for fishing, shell fishing and bait harvesting, cargo and passenger ports, construction and many other activities (see sections 1.1.3 and 1.4), the associated large numbers of people, boats and noise could be considerable sources of disturbance to wintering birds. However, with a few notable exceptions (e.g. Cutts et al. 2009, Fearnley et al. 2013), their impacts have not been studied separately from other human activities, or the focus has been on associated habitat degradation and loss as opposed to direct disturbance and the resulting fitness consequences through physiological and behavioural responses (Piersma et al. 2001, Ens 2006, Atkinson et al. 2010).

Deliberate disturbance

One aspect of this topic that this study does not attempt to address is deliberate disturbance, for example to protect vulnerable agricultural crops (Nolet et al. 2016; Simonsen et al. 2016) or through safety concerns at airports (Swaddle et al. 2016) and management of landfill sites (Cook et al. 2008). Nevertheless, an improved understanding of the factors that affect bird responses to disturbance and the associated fitness consequences could provide insights into whether disturbance will be effective in these situations and to determine the most appropriate methods to use.

1.1.6. Choice of focal activities

It was beyond the scope of this study to investigate bird responses to, and the impacts of, all types of potentially disturbing activity so two activities were chosen for fieldwork and in-depth analysis: walking and wildfowling. They were chosen because experimental disturbance by an approaching pedestrian is a commonly used and accepted method for

investigating bird responses to disturbance (see next section) so there are suitable data available for comparison with the results of this research. Walking is also the most frequent recreational activity that takes place on estuaries, so understanding its impacts can make a major contribution to understanding the impacts of recreational disturbance in general. Furthermore, there is scope to add to knowledge and improve the usage of such data to inform conservation management, which will be discussed further in Chapters 2 and 3. By comparison, although wildfowling has taken place in estuarine habitats for hundreds of years, its impacts on non-quarry species have been relatively poorly studied. The mechanisms by which birds are disturbed by this activity are quite different to the more commonly investigated pedestrian disturbance, so wildfowling provides an opportunity to take a novel approach to investigating bird responses to (and the impacts of) disturbance. This gap in knowledge will be addressed in Chapter 4.

1.2 Quantifying responses to and impacts of disturbance

1.2.1. Measuring and understanding responses to disturbance

Experimentally disturbing animals (for example by walking towards them or using a noise stimulus) and recording characteristics of their physiological or behavioural responses is a commonly used and effective method for studying disturbance, and all of the examples listed in Table 1.2 employed this method. Other researchers have taken an observational approach by recording animal responses to real-world disturbances (e.g. Yalden and Yalden 1990; Riddington et al. 1996; Schlacher et al. 2013a).

The most consistently reported measure of response is flight initiation distance (FID); also referred to as 'escape distance' or 'flush distance', it is the distance between an animal and approaching predator or disturber at which it begins to flee (Bonenfant and Kramer 1996, Blumstein et al. 2003), and may be considered as the distance beyond which an activity (potential disturbance) would not be expected to result in a costly flight response. Reported FIDs are therefore often used to inform the size of buffer zones and set-back distances for species protection by separating human activities from key areas (Glover et al. 2011; Weston et al. 2012; Chatwin et al. 2013; Schlacher et al. 2013a; Koch and Paton 2014). However, this method has its drawbacks:

- i) FID is highly variable between species and within species (as predicted by the risk-disturbance hypothesis (Frid and Dill 2002), so values recorded in one study may not be applicable to new sites or situations. For example, the studies listed in Table 1.2 identified 14 different factors that could explain variation between individuals in their FID and other responses to disturbance;
- ii) in order to prevent disturbance of all species present, the FID of the species that has been found to be least 'tolerant' must be used, which may result in unnecessarily precautionary buffers especially since larger FIDs do not indicate greater vulnerability (see section 1.1.1);
- iii) use of FID does not account for the potential costs of disturbance related to behavioural and physiological changes both before and after initiation of flight – such as the metabolic costs of elevated heart rate or lost feeding opportunities due to increased vigilance (Figure 1.1); and
- iv) it is perhaps more important to determine the frequency of disturbance that will have a negative impact on a population i.e. the threshold above which disturbance cannot be compensated for.

Despite the potential problems with relying on measured FID values, alone, experimental disturbance studies continue to be valuable tools for informing evidence-based conservation management (Livezey et al. 2016). With a better understanding of the factors that explain variation in FID and other measures of response, we will be able to determine the applicability of reported values to new sites and situations and make more accurate predictions about the impacts of disturbance at the population level.

Table 1.2. Selected examples from the literature of animal disturbance studies with recorded measures of response and explanatory variables identified.

Taxon	Response(s) measured	Factor(s) affecting response	Details
Mammals	Vigilance; Foraging time; FID	Type of disturbance; age	Li et al. (2011). When the presence of motorised vehicles and bicycles was high, yellow-bellied marmots <i>Marmota flaviventris</i> increased the proportion of time spent vigilant and decreased the time spent foraging. FID decreased with increased frequency of disturbance. Juveniles tolerated closer bicycle approaches than did adults or yearlings.
Birds	FID	Species; site	Blumstein et al. (2003). Both species and site influenced FID, but species was a relatively more important factor in explaining variation between individuals.
Birds	FID	Species; body size; starting distance; flock size; previous experience; disturbance type	Glover et al. (2011). Species with higher body masses exhibited longer FIDs. Depending on the species, FID was significantly influenced by the starting distance of the human approach, flock size, previous exposure to humans and stimulus type (walker, jogger, or walker with dog).
Birds	FID; Vigilance; Distance fled	Individual condition	Beale and Monaghan (2004b). Birds whose condition had been enhanced showed greater responsiveness to standardised human disturbance, flying away at greater distances from the observer, scanning more frequently for predators and flying further when flushed.
Birds	Proportion of flock that is feeding	Stage of season; temperature	Stillman and Goss-Custard (2002). The proportion of feeding oystercatchers increased later in the season, and was particularly high on unusually cold days.
Birds	Heart rate; FID	None tested	Ackerman et al. (2004) found that flushing behaviour is a reasonable indicator of acute changes in physiological state (heart rate) of white-fronted geese <i>Anser albifrons elgasi</i> in response to experimental disturbance.
Reptiles	Number that flee; Distance fled	Angle of approach	Cooper (2009). During indirect approaches, fewer lizards fled, and they ran shorter distances.
Fish	FID	Body size; distance to refuge; disturbance frequency	Gotanda et al. (2009). Body size, reserve protection, and distance to a refuge, had strong support in explaining parrotfish FID.
Amphibians	Time to resume original behaviour	Frequency of disturbance	Rodriguez-Prieto and Fernández-Juricic (2005). Repeated disturbance events increased frog time to resume pre-disturbance activities.

1.2.2. Linking individual responses to population consequences

Ability to compensate

As described earlier, it is important to distinguish between bird responses to individual disturbance events (causing short-term physiological and behavioural changes), the cumulative impacts on individual survival (e.g. through lost feeding opportunities, higher energy requirements, and increased predation risk) and the corresponding population consequences. However, such impacts cannot be predicted using data from short-term experimental or observational disturbance studies alone, since measuring responses may, at best, give an indication of whether there might be negative consequences for individuals. For example, birds that spend all or most of their available time foraging are unlikely to have much spare capacity to compensate for the costs of responding to even infrequent disturbance events (if feeding efficiency cannot be increased (Goss-Custard et al. 1977)).

Optimal foraging theory (Stephens and Krebs 1986) predicts that birds will select foraging strategies and locations in order to maximise intake rate whilst minimising energy expenditure, predation risk and disease risk (Evans 1976). Disturbance that temporarily or permanently excludes birds from optimal foraging areas may therefore force them to feed for longer in less profitable areas and/or result in density-dependent reductions in intake rate through interference competition (Goss-Custard 1980, Cayford 1993, Frid and Dill 2002). Increased levels of interference competition, however, are likely to disproportionately affect juveniles and sub-dominant adults, as well as less-efficient foragers (Goss-Custard et al. 2001) so not all individuals will be affected equally by disturbance. Furthermore by spending more time in sub-optimal habitats, some or all birds may experience greater rates of predation (Hilton et al. 1999, McGowan et al. 2002) or higher disease risk (Clark et al. 2016).

So whilst the costs of individual disturbance events may be low, the cumulative impacts of frequent disturbance events could be considerable, and the overall impact can be amplified (or reduced) due to interaction with other factors like pollution events or declines in food availability – so-called ‘in-combination impacts’ (Goss-Custard et al. 2006a, Crain et al. 2008, Halpern et al. 2008, IEEM 2010, Leighton et al. 2010, Oro et al. 2012, Weber et al. 2012). Therefore in order to make robust predictions about the impacts of disturbance on individuals and populations, detailed knowledge is needed of bird energetics, foraging behaviour, food availability, patterns of disturbance, environmental conditions, responses to disturbance, density dependent processes, and other factors that may affect bird fitness.

Defining significant impact

Before making any judgement about whether disturbance is a conservation problem, it is necessary to first define what we mean by 'significant impact'. The strictest interpretation of the term could be that any change in behaviour or physiology as a result of human activities is unacceptable. Some members of society may take this view, morally, however ecologically, such a definition is likely to be unnecessarily precautionary given that all biological systems have a certain capacity to cope with natural as well as some anthropogenic disturbances – so-called ecological resistance and resilience (Gunderson 2000, Groffman et al. 2006). In their review of ecological concepts and definitions Elliott et al. (2007) define resistance as the amount of a given pressure that can be applied to a system without a deterioration in status; and resilience as the degree of recovery once a pressure is removed, though recovery may not be complete (i.e. partial resilience).

At the other extreme, disturbance might only be considered to be a conservation issue if it causes long term, sustained population decline and eventual extinction – by which point any intervention would be too late. In the case of wintering waders, a more reasonable threshold could be the amount of disturbance that would lead to a statistically significant reduction in the number of birds that survive the winter period or do not abandon the site in favour of suitable habitat elsewhere (i.e. a reduction in the carrying capacity of a site (Goss-Custard et al. 2002)). This recognises the fact that birds are able to compensate for minor or infrequent disturbances if there is sufficient intertidal exposure time and food availability and their thermoregulatory requirements are not high (Stillman and Goss-Custard 2002). It also allows for some overwinter mortality as long as mortality is compensatory rather than additive – individuals that die as a result of the costs of disturbance may have died anyway through predation or starvation during periods of cold weather (Burnham and Anderson 1984, Sandercock et al. 2011). From a regulatory perspective this 'number of birds supported' definition fits well with the conservation objectives for sites that have been designated due to their nationally and internationally important populations of wintering birds.

In the absence of large amount of data to test for statistically significant reductions in carrying capacity under different disturbance scenarios, an alternative (though more conservative) approach could be to assess the impact of disturbance over the period of time that birds attempt to balance their energy budget – approximately 24 hours for waders (Kersten and Visser 1996a). Disturbance levels would then be considered unacceptable if they prevent birds from balancing their energy budget or achieving sufficient fat deposition rates in preparation for migration and breeding as normal, even if there is not an overall decrease

in numbers of birds supported over winter. Chapters 5 and 6 will explore how these different definitions affect predictions about 'acceptable' levels of disturbance.

Having a clear definition, along with robust evidence of the impacts of disturbance is essential for the acceptance and effective enforcement of any associated regulation or management measures: though problems can arise when stakeholders disagree on the definition or its interpretation (Dowling and Weston 1999, Lafferty 2001b, Williams et al. 2009, Glover et al. 2011, Stigner et al. 2016).

1.3 Modelling disturbance and making predictions

The studies listed in Table 1.1 all found evidence for the negative impacts of disturbance, yet what is more useful to conservation managers is the ability to predict future impacts under different environmental or management scenarios so that measures may be introduced to prevent those impacts from occurring in the first place: as the adage goes, prevention is better than cure.

The approaches taken by most studies that attempt to make predictions about the impacts of disturbance fall into one of two main categories: using numerical models (mathematical equations) or individual-based modelling (computer simulation).

1.3.1. Mathematical equations.

Many studies have taken a classical approach to modelling population dynamics and predicting disturbance impacts based on empirical (observed) data relating to demographic rates and density-dependent processes. For example, Liley and Sutherland (2007) collected data on the habitat selection and disturbance response behaviour of breeding ringed plovers *Charadrius hiaticula* to build a logistic regression model that could predict site occupancy and density-dependent breeding success, and determine equilibrium population size under different scenarios of human disturbance. Similarly, Taylor et al. (2007) used observations of the behavioural responses of stone curlews *Burhinus oedicanus* to humans to build a logistic regression model for making predictions about occupancy of 'stone curlew plots' (specifically created as part of the species recovery programme to provide suitable breeding habitat (Salisbury Plain Life Project 2003)) in relation to rates of human disturbance. Whilst they did not make predictions about actual reproductive success, the model was intended as a tool to help site managers make decisions about access and habitat management for this vulnerable species (Taylor et al. 2007).

A slightly different approach involves resource-use/depletion models such as those described by Gill et al. (1996, 2001c); for example, the proportion of remaining food not consumed at the end of the winter was used (through regression analyses) to estimate the number of pink-footed geese that could be supported by a site in the absence of disturbance.

As another example, Houston et al. (2012) go back to first principles to construct a simple mathematical model that is not restricted to any particular species or system. It is based on the principle that behavioural changes in response to disturbance have implications for animal time and energy budgets, and that for the duration of the disturbance they are unable

to feed. If disturbance is sufficiently high, animals will either run out of time or be limited by an energy constraint. They use the method to show that African wild dogs *Lycaon pictus* suffer considerable costs due to disturbance by lions *Panthera leo* and kleptoparasitism from hyenas *Crocuta crocuta*.

One benefit of using numerical models to predict the impacts of disturbance on bird is that many people will be familiar with the general approach, plus they are relatively straightforward to explain. However they may be limited in their ability to make predictions outside of the range of historical environmental conditions under which key values have been measured, since we cannot be confident that population impacts will be the same in novel situations.

1.3.2. Individual-based ecology and modelling

Individual-based models (IBMs) – known as agent-based models (ABMs) in the fields of social sciences and economics – offer an alternative approach to the deterministic, equation-based predictive methods described above. Since Huston et al.'s (1988) review, the use of IBMs has increased exponentially (Grimm 1999). They have been used to address a wide variety of issues; including understanding fish population dynamics, forest functioning, evolutionary processes, impacts of habitat loss, spread of disease, human-wildlife interactions, financial market processes, and purchasing decisions – as reviewed by Grimm (1999), DeAngelis and Mooij (2005) and Heard et al. (2015).

A form of computer simulation modelling, ecological IBMs use the individual-based ecology conceptual framework (Grimm and Railsback 2005) to model populations or systems composed of individuals, each with its own set of behavioural and physiological traits based on knowledge of the real-world system (DeAngelis and Mooij 2005, Grimm and Railsback 2005, Stillman and Goss-Custard 2010). Model individuals make fitness-maximising decisions in the same way that real animals would (even in novel situations) and simulations track their fates to predict the population-level consequences that emerge from individuals' interactions with their environment and with each other, allowing incorporation of stochastic events (Stillman et al. 2015, 2016).

The IBM approach has been used to predict the impacts of disturbance on, for example, shorebirds (West et al. 2002; Goss-Custard et al. 2006a); birds feeding in parks (Blumstein et al. 2005, Bennett et al. 2009); bats (Bennett et al. 2009); night-herons (Bennett et al. 2011); and cetaceans (Lusseau et al. 2006). West et al. (2002) showed that numerous small disturbances could be more damaging for wintering oystercatchers than fewer, larger

disturbances, especially if they occurred in late winter. Bennett et al. (2011) used their IBM for breeding black-crowned night-herons *Nycticorax nycticorax* to test recreation management scenarios and select the most effective combination of methods. And Goss-Custard et al. (2006a) found that the critical threshold of disturbance for oystercatchers in the Baie de Somme, France, was much lower when feeding conditions were poor; also with implications for shellfisheries management. Similarly, Lusseau et al. (2006) showed that whale watching can influence cetacean population dynamics and jeopardise the viability of populations that are already at risk.

By representing individuals and their local interactions in a stylised way, IBMs can achieve a level of 'structural realism' that is impossible with more aggregated mathematical models (Grimm and Berger 2016a) such as the 'state-variable' models used by Łomnicki and Ombach (1984) and Uchmanski (1985), which group individual variation into large-scale population variables and potentially ignore important mechanisms and interactions (Huston et al. 1988). However, in order for such models to be useful they must also be understood and trusted by the end-users (who may be non-scientists or unfamiliar with the modelling approach). This requires IBMs to be developed and communicated in such a way that the outputs can be used appropriately and effectively (Bart 1995, Grimm et al. 2006, Cartwright et al. 2016). If researchers follow the standardised model description methods such as those proposed by Bart (1995) and Grimm et al. (2006), along with Cartwright et al.'s (2016) communication framework, then IBMs can be expected to play a key role in future ecological modelling, particularly in tackling questions of community ecology and biodiversity research and informing environmental decision-making (McLane et al. 2011, Grimm and Berger 2016b, Stillman et al. 2016).

1.4 Scope of this thesis

1.4.1. Conceptual framework

The key literature, concepts and relationships discussed in this chapter can be distilled into a conceptual framework for understanding the impacts of disturbance on wintering waders (Figure 1.5). This framework can also serve as the basis for developing models of the system and making predictions about the impacts of disturbance under hypothetical or anticipated scenarios of environmental change. Figure 1.5 shows how this research fits into one or more of three overarching theoretical frameworks, which were used to help formulate the research objectives and hypotheses to be tested: (1) the risk-disturbance hypothesis as proposed by Frid and Dill (2002); (2) optimal foraging theory (Stephens and Krebs 1986); and (3) individual-based ecology (Grimm and Railsback 2005).

1.4.2. Aims and objectives

The major aims of this research are to understand how and when disturbance from human activities can be expected to significantly impact wintering wader populations (both in general, and specifically in Poole Harbour, UK), in order to inform effective, evidence-based conservation management. This will be achieved by addressing the following four objectives:

- i) Characterise the variability in bird responses to pedestrian disturbance, identify key explanatory factors to account for that variability and test them against the predictions of the risk-disturbance hypothesis;
- ii) Quantify bird responses to disturbance from wildfowling and make comparisons with what is known about responses to pedestrian disturbance;
- iii) Following the individual-based ecology framework and using insights from field data collection, develop a site-specific individual-based model (IBM) for Poole Harbour to determine whether current frequencies of human activities are limiting wintering wader population sizes; and
- iv) Build a generally-applicable IBM to investigate the extent to which different characteristics of estuarine sites affect the likelihood of significant disturbance from human activities.

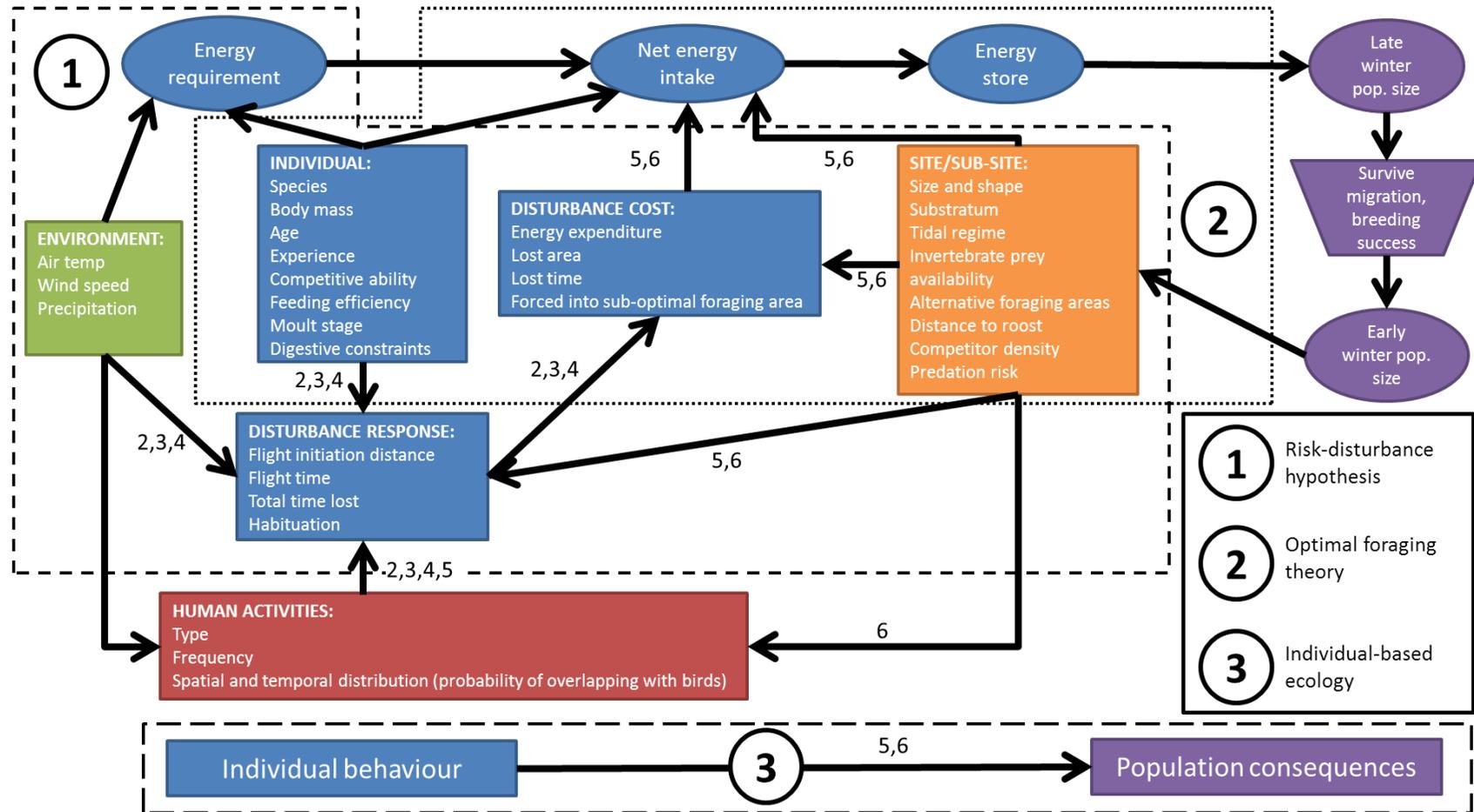


Figure 1.5. Conceptual framework for the relationships between individual wintering wader responses to disturbance and the population consequences. Arrows indicate known or potential relationships between one or more elements listed in linked boxes. Numbers alongside arrows indicate the chapters in which these relationships are investigated. Dashed lines delineate three key contributing theoretical frameworks.

1.4.3. Contribution to knowledge

In addressing the above objectives this research will contribute to knowledge of site-specific and general impacts of human disturbance on bird species of conservation importance in estuarine habitats and with applications to other human-wildlife interactions. This includes a repeatable method for incorporating the costs of responding to disturbance into other site-specific IBMs based on field observations; as well as identifying a new approach to more rapid assessment of sites for prioritising conservation action. This is also the first study to investigate in detail the impacts of hunting on non-target species in comparison with other human activities.

1.4.4. Thesis structure

In addition to the introduction and conclusions chapters, this thesis is divided into three 'data' chapters based on field data collection and two 'modelling' chapters for making general and site-specific predictions about the impacts of disturbance. Below is a brief overview of the content of the data and modelling chapters. The rest of this chapter (sections 1.5 and 1.6) introduce the study sites and species.

Chapter 2. Variability in the area, energy and time costs of responding to disturbance for wintering waders on the Wash Embayment.

Explores the results of pedestrian disturbance experiments on the Wash: identifying key explanatory variables, setting bird responses in the context of their daily energy requirements and available feeding time.

Chapter 3. The responses of wintering waders in Poole Harbour to experimental disturbance by an approaching pedestrian vary spatially, between species and with environmental conditions.

Compares the responses and key explanatory variables of bird responses to disturbance in Poole Harbour with reported results from other sites. Provides parameter values for use in Chapters 5 and 6.

Chapter 4. Factors affecting the responses of wintering waterbirds to disturbance by wildfowling and a comparison with the effects of pedestrian disturbance in Poole Harbour. *Assesses bird responses to and potential impacts of disturbance from wildfowling on non-target species through acoustic and visual stimuli; and explores the similarities and differences in impact mechanisms in comparison with pedestrian disturbance.*

Chapter 5. An individual-based model of Poole Harbour – is disturbance limiting wintering wader populations?

Describes a site-specific model for identifying the conditions under which disturbance would be expected to reduce wintering wader populations, either alone or in combination with other types of environmental change.

Chapter 6. Using individual-based modelling to investigate how site characteristics influence impacts of disturbance on non-breeding waders.

Demonstrates how knowledge of certain estuary characteristics may be useful for identifying those sites where disturbance issues could be a conservation problem; using assessment of birds' ability to balance their energy budget.

1.5 Study sites

1.5.1. The Wash

The study described in Chapter 2 took place on the Wash; a large embayment in eastern England on the North Sea coast (Figure 1.6), with a tidal range of 6.3 m on spring tides and 3.0 m during neaps. It is the largest estuarine system in the UK (JNCC 2016a) with approximately 225 km² of intertidal sand and mudflats, which support a rich benthic invertebrate fauna, and its conservation importance is recognised through several national and international designations including: SSSI, SPA, SAC and Ramsar site status (Doody and Barnett 1987). Met Office climate data for Wainfleet, near Skegness, from 1981 to 2010 (Met Office 2016) show mean monthly maximum temperatures for September to March ranged from 6.6°C (January) to 17.8°C (September), and mean monthly minima ranged from 1.2°C (February) to 10.1°C (September). Relatively mild winter temperatures such as these help make UK coastal sites so attractive to wintering migratory bird species.

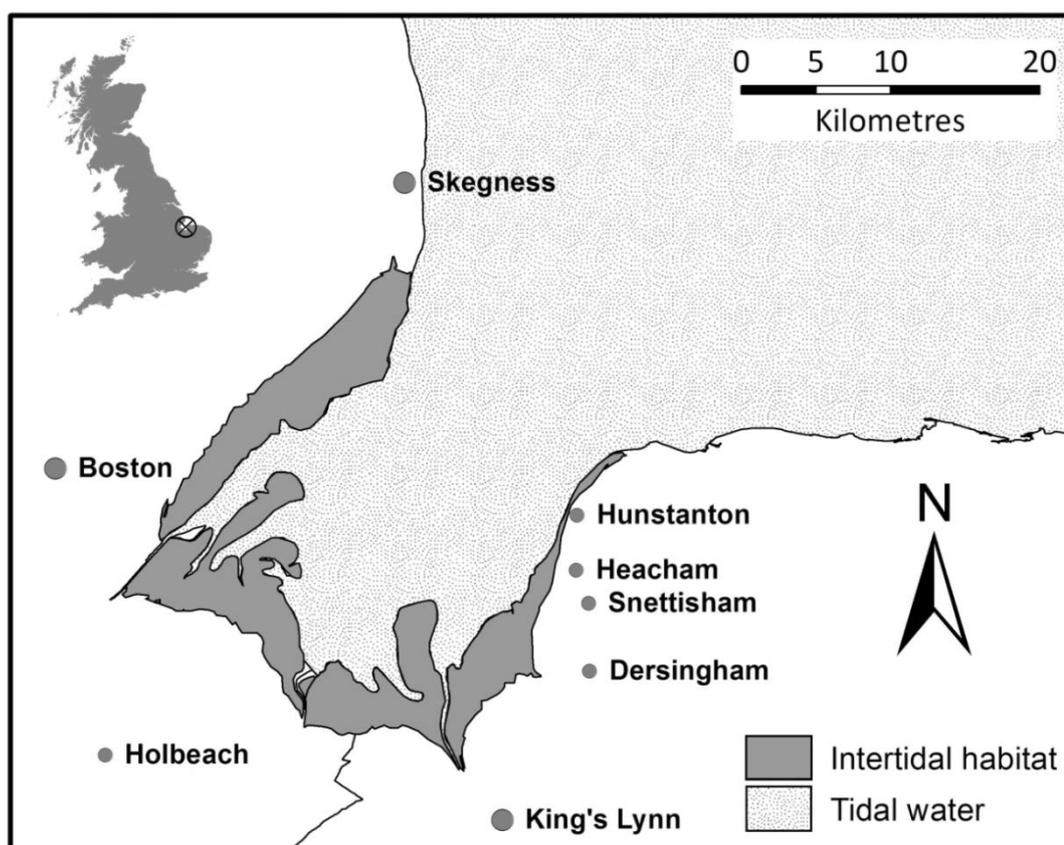


Figure 1.6. Extent of intertidal habitat of the Wash embayment (52°56'16"N, 00°17'16"E).

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As well as being of European importance for breeding birds (common tern *Sterna hirundo*, little tern and marsh harrier *Circus aeruginosus*), 'in terms of total numbers, the Wash is the key site for wintering waterbirds in the UK' (Austin et al. 2014). It supports internationally important wintering populations of avocet *Recurvirostra avosetta*, bar-tailed godwit *Limosa lapponica*, black-tailed godwit *Limosa limosa*, curlew, dark-bellied brent goose, dunlin *Calidris alpina*, golden plover, grey plover *Pluvialis squatarola*, knot *Calidris canutus*, oystercatcher, pink-footed goose, pintail *Anas acuta*, redshank, shelduck *Tadorna tadorna*, turnstone and whooper swan *Cygnus cygnus*. It is also of considerable importance during spring and autumn migration for ringed plover and sanderling *Calidris alba*, and qualifies as a wetland of international importance by regularly supporting at least 20,000 wintering waterbirds – the five year mean peak count for 1991/92 to 1995/96 was 400,273 individual birds (JNCC 2016a).

The Wash supports the largest colony of common seals *Phoca vitulina* in the UK, which is in part due to the availability of extensive intertidal flats where seals can haul out and breed. And subtidal sandbanks provide important nursery grounds for young commercial fish species, including plaice, cod *Gadus morhua* and sole *Solea solea* (JNCC 2016b) which are fished along the open coast and in the North Sea beyond the mouth of the Wash.

As is typical of many estuaries, the Wash is also of considerable importance for human activities: the port of Boston handles around 1.3 million tonnes of cargo annually (UK Ports 2016), and there is heavy fishing pressure for cockles, mussels and shrimps (Eastern IFCA 2016). The seaside resorts of Hunstanton and Heacham attract large numbers of visitors each year, as do the RSPB reserves at Frieston, Frampton and Snettisham and other sites for wildlife-related tourism (Anon. 2010); and a network of shoreline footpaths provides access for general recreation. There are four wildfowling clubs that operate around the Wash, and sailing clubs at Wainfleet, Skegness, Snettisham and Hunstanton. Watersports including windsurfing, water skiing and power boating are generally restricted to the beach areas around Hunstanton and Heacham, where zoning of water craft is managed by the local authority (JNCC 2008a). There is also a 39 km² Air-Weapons Range at RAF Holbeach for military training, with eight targets for bombing practice located on the intertidal mud and saltmarsh and a helicopter landing pad (Defence Training Estates n.d.).

1.5.2. Poole Harbour

Poole Harbour (Figure 1.7) was the study site for most of the field data collection (see Chapters 3 to 6). It is a shallow estuary on the south coast of the UK with approximately 36 km² of water at spring tide high water (Humphreys and May 2005) and nearly 20 km² of intertidal mud, sandflats and marshes between mean low water and the highest astronomical tides (Powell 2005). The estuary has a small tidal range (1.8 m during spring tides, 0.6 m on neaps). A tidal phenomenon that occurs due to the shallow waters along the coast around Poole Harbour means that it has a non-standard tidal regime and experiences ‘double high tides’ (Figure 1.8): water levels are often above mean tide level for 16 out of 24 hours (Humphreys 2005). Intertidal exposure period is therefore approximately eight hours per day, rather than the more usual twelve. Met Office climate data for Bournemouth Airport weather station (UK Meteorological Office 2015), from 1996 to 2015 show mean monthly maximum temperatures for September to March ranged from 8.7°C (January) to 19.8°C (September), and mean monthly minima ranged from 1.6°C (January) to 9.7°C (September).

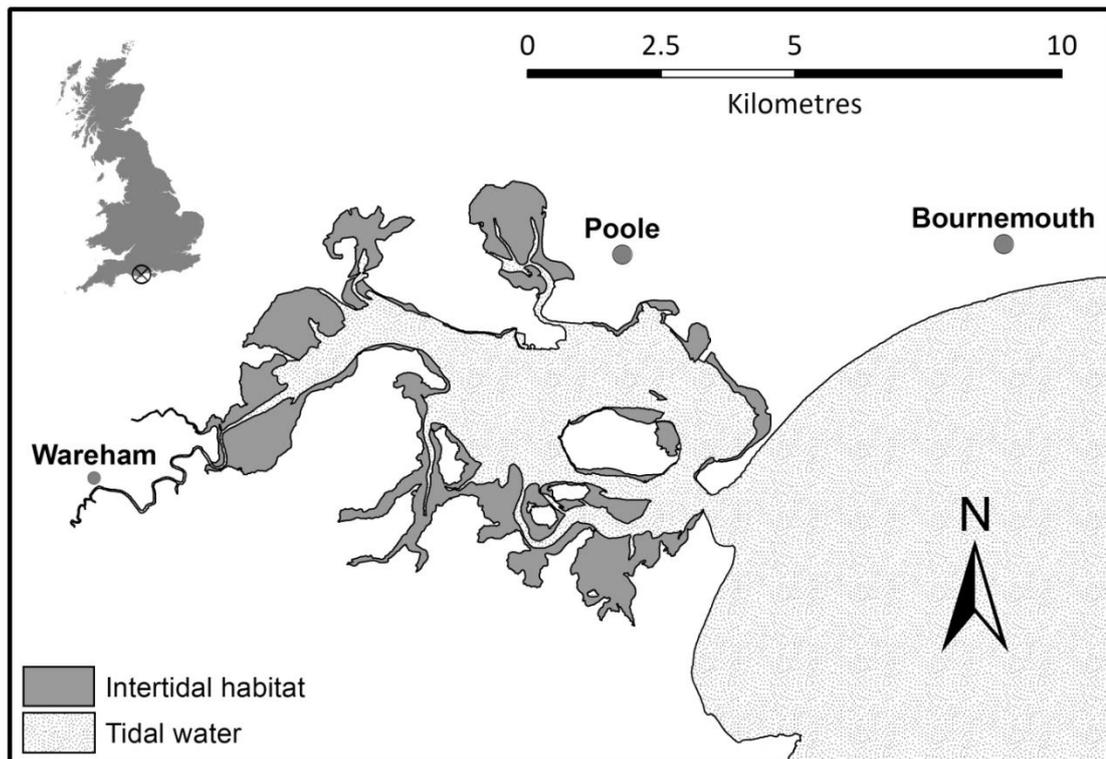


Figure 1.7. Extent of intertidal habitat in Poole Harbour (50°41'47"N, 01°59'46"W).

Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

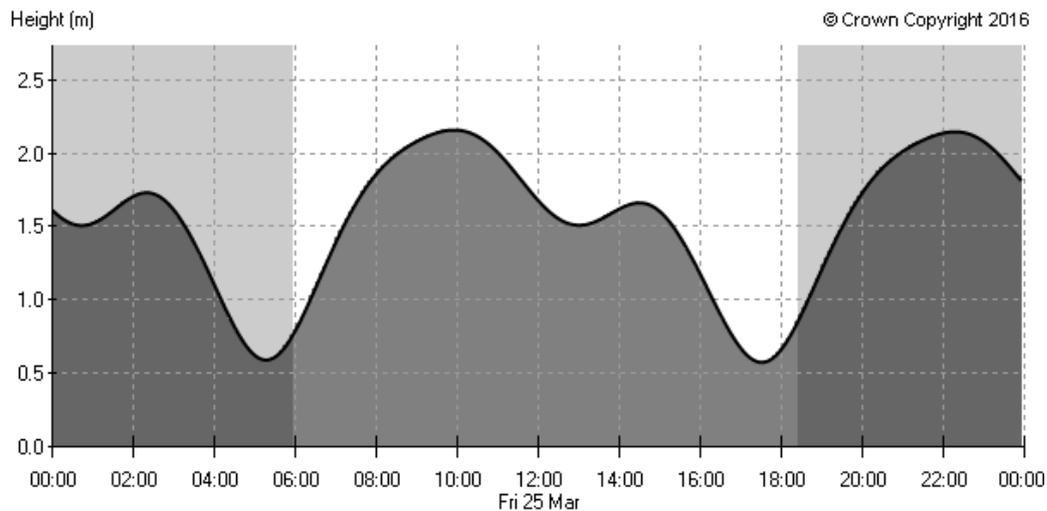


Figure 1.8. Example tidal curve in Poole Harbour showing the ‘double high tides’.

Reproduced from UK Hydrographic Office Admiralty EasyTide © Crown copyright 2016.

Like the Wash, the national and international biological importance of the habitats in Poole Harbour and the species that they support are recognised through a variety of conservation designations; SSSI, Ramsar wetland, SPA and Heritage Coast status. The site is of international importance for breeding common tern and Mediterranean gull *Larus melanocephalus*, and for aquatic warbler *Acrocephalus paludicola* and little egret *Egretta garzetta* on passage. The main ornithological interest, however, is during the winter; with internationally important numbers of avocet, little egret, black-tailed godwit and shelduck, and an overall waterbird assemblage of more than 20,000 birds (five year mean peak count for 1998/99-2002/03 was 24,709 (JNCC 2008b)). Other key species include redshank, curlew, dunlin, lapwing *Vanellus vanellus*, red-breasted merganser *Mergus serrator*, goldeneye *Bucephala clangula*, pochard *Aythya farina*, shoveler *Anas clypeata*, dark-bellied brent goose and cormorant *Phalacrocorax carbo* (JNCC 2016c).

Much of the southern and western parts of the 100 km shoreline are natural and fringed by reedbeds and saltmarsh, and public access is limited. By comparison, northern and eastern areas are much more accessible and dominated by artificial walls, embankments, marinas and moorings associated with the heavily populated areas of the Poole and Bournemouth conurbation (Humphreys and May 2005). In addition to the large human population of local residents, Poole Harbour is a popular tourist destination for coastal recreation as well an important port for commerce and travel. 600,000 passengers, more than 5000 commercial shipping movements and 2.3 million tonnes of cargo are handled annually (Poole Harbour Commissioners 2012, UK Ports 2016); luxury yachts are built here; Poole is the national headquarters for the Royal National Lifeboat Institute (RNLI); and Wytch Farm is the largest

onshore oil field in Europe (Drake and Bennett 2011). The area is popular with bird watchers and for general outdoor recreation (walking, dog walking, cycling, jogging etc.) and Dorset Wildfowlers' Association (DWA) oversees wildfowling on the intertidal areas in the south and west of the Harbour. Watersports occur all year round and management of many recreational activities is achieved through a zoning scheme (Figure 1.9), which was first introduced in 1994 with the first edition of Poole Harbour Aquatic Management Plan, and serves to minimise disturbance of environmentally sensitive areas and safely separate powered and non-powered motor craft (Drake and Bennett 2011).

Poole Harbour is an important resource for commercial and recreational fishing – monitored and regulated by the Southern Inshore Fisheries and Conservation Authority (IFCA) – in particular aquaculture for oysters and mussels, hand-picked and dredged clams and cockles, and bait dragging and digging for ragworm and lugworm (Southern IFCA 2013, 2016).

As demonstrated in Figure 1.9, Poole Harbour is a seemingly very 'crowded' estuary with many potentially conflicting activities and interests, so from a conservation management point of view there is a clear need for a good understanding of the human-wildlife interactions that occur, the situations where they are likely to be a problem, and effective methods to minimise the impacts of disturbance where necessary.

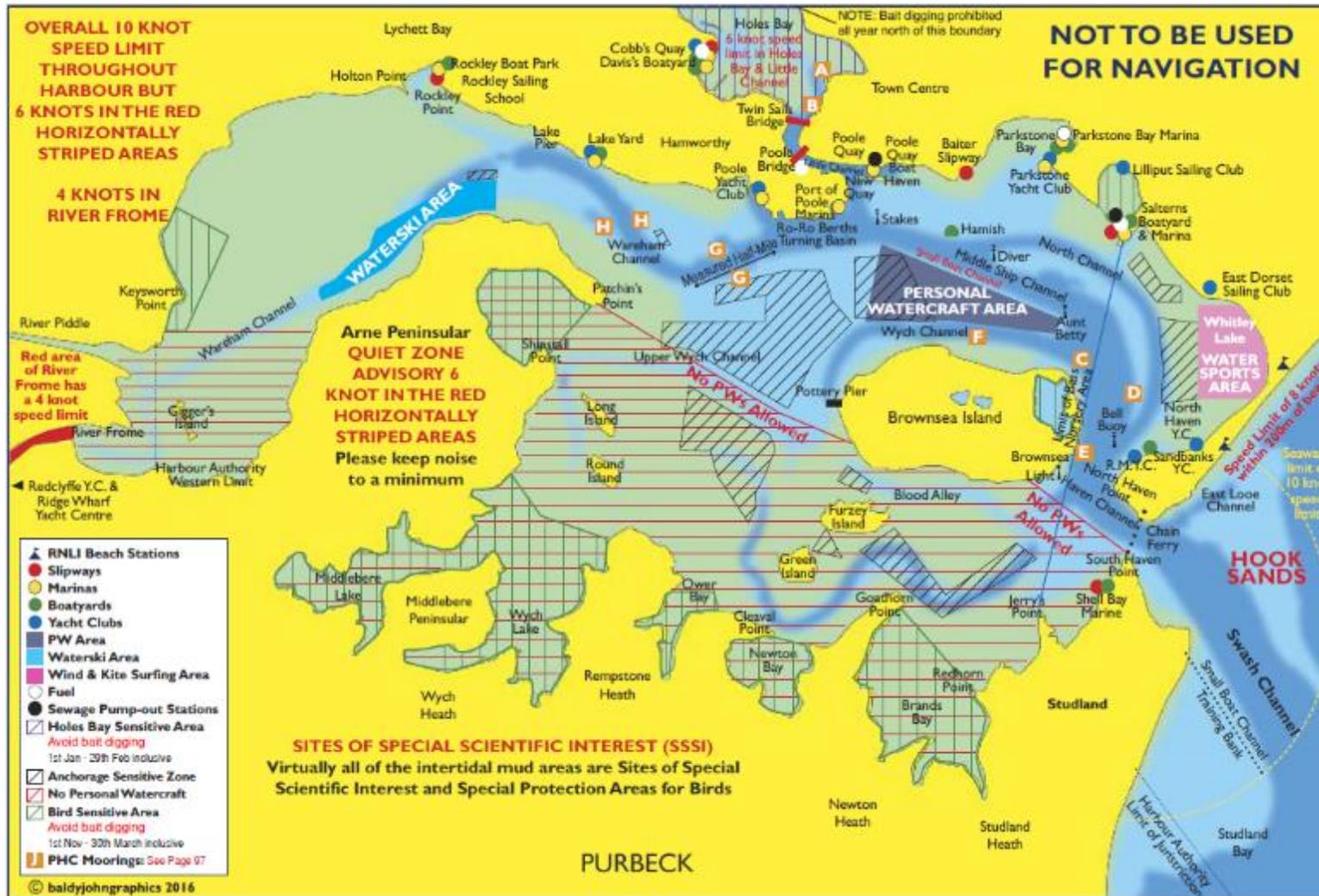


Figure 1.9. Activity zones in Poole Harbour. Reproduced from the Poole Harbour Guide (Poole Harbour Commissioners 2016).

1.6 Study species

1.6.1. Wintering waders

Life history

Waders (Order: Charadriiformes), often interchangeably referred to as shorebirds, are a highly variable group of species with differing life history strategies, yet the 217 species from 14 different families also share a number of characteristics that make them attractive subjects for scientific study (Piersma 2007). Most are migratory and outside of the breeding season they gather in large numbers in estuarine areas to take advantage of abundant food and relatively low disease-risk (van de Kam et al. 2004). Wintering waders using estuarine habitats therefore offer a useful study system for investigating the impacts of human disturbance on wildlife, with opportunities for direct application of the results to inform conservation management. As an example, Figure 1.10 illustrates how numbers of migratory waders on UK estuaries increase in autumn, remain high during the winter and then decline in spring as they depart for their breeding grounds.

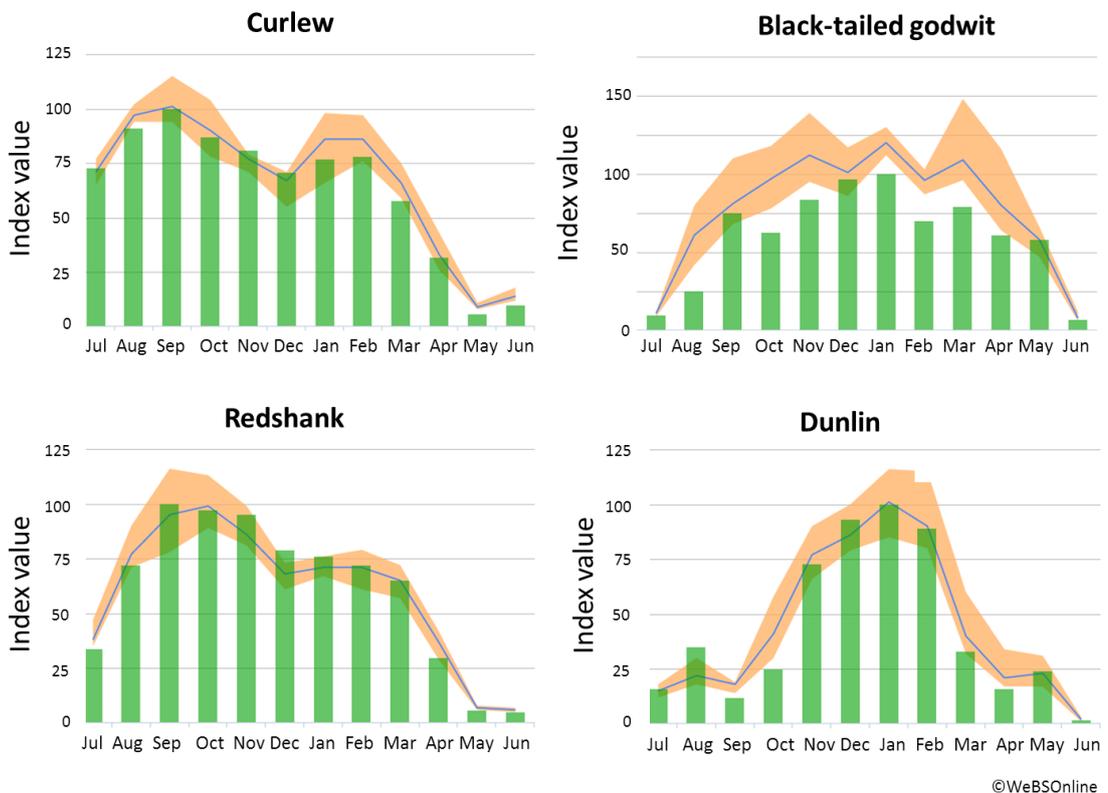


Figure 1.10. Relative monthly population estimates for four wader species using UK estuaries – reproduced from Wetland Bird Survey (WeBS) data 1975/76 to 2014/15 (Frost et al. 2016). Index (green bars); mean (blue lines); and range (orange shading). Index = 100 for the month in which each species peak count occurs.

Waders that winter in northern latitudes may experience harsh weather conditions (Camphuysen et al. 1996), and the energy demands of thermoregulation can be high (Kersten and Piersma 1987). Time and energy budgets are further restricted by the intertidal exposure period and shorter winter day lengths (although some species may feed inland (Milsom et al. 1998, Masero and Pérez-Hurtado 2001, Smart and Gill 2003, Yasué and Dearden 2009) and/or at night (Mouritsen 1994, McNeil and Rodríguez S. 1996, Dodd 1998, Hötker 1999, Lourenço et al. 2008)). Additionally, intertidal-foraging waders are reliant on the availability of safe roost sites that are not too far from their feeding grounds on which they can spend the high tide period (Luís et al. 2001, Rogers 2003, Rogers et al. 2006).

Overwinter survival is not the only challenge that migratory waders face: in order to successfully complete journeys of many thousands of kilometres, some of which are made in a single flight (Gill et al. 2009, Battley et al. 2012), waders need to store large fuel loads within their body tissues. This requires them, at specific times of the year, to assimilate energy at rates well above their daily requirement for maintaining stable body mass (Kvist and Lindström 2003, Piersma et al. 2005), and highlights the importance of high quality stopover sites for species that do not complete their journeys in one go (Baker et al. 2004, Atkinson et al. 2007). In addition, some species are reliant on pre-migratory fattening to ensure successful reproduction (or even survival) on their Arctic breeding grounds, since environmental conditions upon arrival can be unpredictable (Morrison and Hobson 2004, Meltofte et al. 2007, Morrison et al. 2007). Any factors that reduce their ability to build up fat reserves at key times could therefore have fitness consequences for individual birds.

Threats and population trends

Most of the threats to waders in the non-breeding season relate to the threats to the habitats upon which they rely during that time (section 1.1.4), as well as potential impacts of lost feeding opportunities and energetic costs associated with high frequencies of human disturbance (section 1.2.2), and direct mortality in parts of the world where hunting occurs either legally or illegally (section 1.1.5).

Large numbers of professional and volunteer wader enthusiasts contribute to monitoring programmes around the world: such as the Wetland Bird Survey (WeBS) in the UK; the International Shorebird Survey in North, Central and South America; and the Asian Waterbirds Census in the Asia-Pacific region. These data are collated by Wetlands International to produce population status and trends (Table 1.3) for as many species of waterbird as possible (Wetlands International 2016). Whilst many species currently remain

numerous, Table 1.3 shows that 22% of populations are declining, and several species are listed as critically endangered, including: St Helena plover *Charadrius sanctaehelenae*, spoon-billed sandpiper, slender-billed curlew *Numenius tenuirostris*, eskimo curlew *Numenius borealis* (possibly extinct) and sociable lapwing *Vanellus gregarius*. Worryingly, trends are not available for a further 44% of populations (Wetlands International 2016).

Table 1.3. Current population trends for waders and wildfowl derived from Wetlands International’s Waterbird Population Estimates (2016). Waders: 537 populations of 224 species. Wildfowl: 468 populations of 168 species.

Trend	Proportion of populations	
	Waders	Wildfowl
Increasing	6.7%	20.9%
Stable	23.3%	23.3%
Fluctuating	2.2%	2.4%
Declining	22.2%	29.9%
Extinct/ possibly extinct	1.3%	2.8%
Unknown	44.3%	20.7%

1.6.2. Wintering wildfowl

Whilst waders are the main focus of this research, they share some winter habitat requirements, threats and legal protection with wildfowl (Family: Anatidae). The Anatidae family consists of 168 species of ducks, geese and swans (Wetlands International 2016); and includes the target species (subject to various restrictions) of one of the focal activities – wildfowling. This section refers mainly to those wildfowl species that, like many waders, are migratory and gather in large numbers in coastal and estuarine habitats in winter or on passage.

Life history

Like wintering waders, wintering wildfowl are subject to the challenges of harsh weather (Stout and Cornwell 1976, Bergan and Smith 1993), the need to build sufficient energy stores for migration (Lindström and Piersma 1993), and the constraints of the tidal cycle (Owen and Williams 1976, Mathers and Montgomery 1996, Burton et al. 2004). Nocturnal feeding, however, is more prevalent in wildfowl and may be actively preferred by many species to avoid daytime disturbance and predation risk (McNeil et al. 1992). Additionally, intertidal habitats are less important as foraging habitat for some species, rather they are often used for resting and preening (Owen and Williams 1976, Owen et al. 1986). These differences in

the feeding habits of waders and wildfowl mean that the mechanisms for the impacts of disturbance could be slightly different: daytime disturbance of wildfowl on estuaries may therefore only have energetic costs, rather than the additional lost feeding opportunity costs experienced by many waders.

Threats and population trends

Threats to wintering wildfowl, like for waders, relate mostly to the threats to their roosting and foraging habitats, costs of disturbance, and direct mortality through hunting. Hunting pressure can be very high for some species, for example Hirschfeld and Heyd (2005) estimate that 243,885 geese and 7,443,972 ducks are shot in the EU each year; and the corresponding numbers for the US in 2014/15 were estimated to be 13,270,000 ducks and 3,338,400 geese (Raftovich et al. 2015). Though the sustainability of such harvests will depend on each species' population status and the extent to which mortality is compensatory or additive – see review by Sutherland (2001), who points out that mortality '*will generally tend towards being compensatory at high population sizes* [when mortality rates are higher due to density-dependence] *and tend towards being additive once the population* [and mortality rate] *is at a low level*' e.g. Bartmann et al. (1992).

Current population trends are shown in Table 1.3, which shows that when compared to waders, more wildfowl populations are increasing and there are fewer populations for which trends are unknown. However there are also more populations in the declining and extinct/possibly extinct categories.

Chapter 2 – Variability in the area, energy and time costs of responding to disturbance for wintering waders on the Wash Embayment.

2.1 Abstract

Bird responses to human disturbance are interesting due to the similarities with anti-predator behaviour, and understanding this behaviour has practical applications for conservation management by informing measures such as buffer zones to protect priority species. To better understand the costs of disturbance and whether it will impact population size, studies should quantify time-related responses as well as the more commonly reported flight initiation distance (FID). Using wintering waders on an estuarine area as the study system, birds on the Wash Embayment, UK, were experimentally disturbed by walking towards them and recording their responses (FID, alert time, time spent in flight, time taken to resume feeding, and total feeding time lost). Data are presented for 10 species of conservation concern: curlew *Numenius arquata*, oystercatcher *Haematopus ostralegus*, bar-tailed godwit *Limosa lapponica*, grey plover *Pluvialis squatarola*, redshank *Tringa totanus*, knot *Calidris canutus*, turnstone *Arenaria interpres*, ringed plover *Charadrius hiaticula*, sanderling *Calidris alba* and dunlin *Calidris alpina*. Larger species responded more strongly; response magnitude was greater under milder environmental conditions; and responses varied over both small and large spatial scales. The energetic costs of individual disturbance events, however, were low relative to daily requirements and unlikely to be frequent enough to seriously limit foraging time. The results suggest, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period. This is also likely to be the case at other estuarine sites with comparable access levels, visitor patterns, invertebrate food availability and environmental conditions.

2.2 Introduction

The term 'disturbance' can mean, in its broadest sense, any event that leads to a change in behaviour or physiology. This might be for example due to natural events such as attack by a predator; or anthropogenic disturbance where recreation or industry brings humans and birds into close proximity; or indirect disturbance through pollution events or noise impacts. However, for the purposes of this chapter in relation to wintering waders, the definition adopted by signatories to the African-Eurasian Waterbirds Agreement (AEWA 2015) will be used, as given by Fox and Madsen (1997): *'Any human-induced activity that constitutes a stimulus (equivalent to a predation threat) sufficient to disrupt normal activities and/or distribution of waterbirds relative to the situation in the absence of that activity.'*

As recognised in this definition and according to the widely accepted risk-disturbance hypothesis (Frid and Dill 2002, Beale and Monaghan 2004b, Blumstein et al. 2005), animals respond to the perceived risk from human disturbances in the same way that they respond to predation risk i.e. by making trade-offs between avoidance of the risk and prioritising other fitness-maximising activities such as feeding, mating or parental care (Frid and Dill 2002). Bird responses to disturbance can therefore be expected to vary between individuals according to a variety of factors related to the perceived risk, the individual's current state, and the costs of responding (Gill et al. 2001a, Beale and Monaghan 2004b). We can test the relative importance of such factors using experimentally collected field data. Estuarine sites, given their importance for both wildlife and human activities (Ramsar Convention 1971, Millennium Ecosystem Assessment 2005), offer useful study systems for such research.

Waders (Order: Charadriiformes) form a relatively long-lived group of species and many are migratory, so survival during the non-breeding period, is an important part of the annual cycle with regards to the long-term persistence and viability of populations (Recher 1966, Sæther et al. 1996, Piersma and Baker 2000, Piersma et al. 2016). For day-to-day survival, and particularly in winter, birds must optimise their daily energy intake to avoid starvation, whilst minimising the risk of predation and disease. Consequently, human activities can impact a bird's energy budget since responding to disturbance events results in both reduced time and area available for feeding (Gill et al. 1996) as well as increased energy expenditure through locomotion (Houston et al. 2012) or physiological responses (Ackerman et al. 2004). Survival will be reduced as a result if the birds are unable to compensate, for example by moving to other sites and/or increasing feeding time or efficiency (Urfi et al. 1996, Gill et al. 2001a, 2001b, Stillman et al. 2001, West et al. 2002, Navedo and Masero 2007).

Walking towards animals and recording characteristics of their response is a frequently used and effective method for studying disturbance avoidance behaviour, and the most commonly reported measure of response to disturbance is FID – flight initiation distance. Also known as ‘escape distance’ or ‘flush distance’, it measures the distance between the disturbance source and animal when it begins to flee (Bonenfant and Kramer 1996, Blumstein et al. 2003). The method has been used for a range of taxa: including mammals (Li et al. 2011); birds (van Dongen et al. 2015); reptiles (Cooper 2009); fish (Gotanda et al. 2009); and amphibians (Rodriguez-Prieto and Fernández-Juricic 2005). However, FID does not quantify the full time and potential energy costs incurred between the point that an animal detects a disturber and when it returns to its original behaviour and physiological state. Very few researchers have studied or reported these time or energy-related measures, which is a clear knowledge gap that will be addressed here.

Other studies on the variable responses of waders to experimental disturbance have identified a number of potential explanatory factors, including: species or body size (Blumstein et al. 2003, 2005, Glover et al. 2011); flock size (Ikuta and Blumstein 2003, Glover et al. 2011); habituation (Urfi et al. 1996, Ikuta and Blumstein 2003, Lin et al. 2012); whether or not birds are quarry species (Laursen et al. 2005); environmental conditions (Stillman and Goss-Custard 2002); type of disturbance (Glover et al. 2011); starting distance (Ikuta and Blumstein 2003); and individual condition (Beale and Monaghan 2004b). Whilst this shows that FID has been relatively well studied in waders, much of the research has been carried out in Australia and North America (Blumstein et al. 2003, 2005, Ikuta and Blumstein 2003, Glover et al. 2011, Koch and Paton 2014), with multi-species studies of the birds of the East Atlantic Flyway being limited to the Dutch and Danish Wadden Sea (Smit and Visser 1993, Laursen et al. 2005). By focussing this research on the Wash Embayment in eastern England, this research therefore adds new understanding to the suite of information available on bird responses to disturbance around the world.

Given that measuring physiological responses to disturbance was beyond the scope of this study and flushing behaviour is a good indicator of acute physiological changes associated with experimental disturbance (Ackerman et al. 2004), this study focuses on visible behavioural responses. Using data that were collected as part of a wider project, entitled ‘Estuary Special Protection Areas – Establishing Baseline Targets for Shorebirds’ (Stillman et al. 2005) this chapter will explore both between-species and within-species differences in responses to disturbance to identify key explanatory variables and test four hypotheses:

- H₁ All aspects of the visible response to disturbance are positively correlated with each other;
- H₂ FID, time spent in flight and total time lost differ between species, and increase with body size;
- H₃ Magnitude of response (FID, time spent in flight and total time lost) decreases under harsher weather conditions; and
- H₄ Responses (FID, time spent in flight and total time lost) vary from site to site and over time (number of days through the winter season).

The results will be discussed in the context of bird daily energetic requirements to determine whether disturbance may be limiting wintering bird populations on the Wash. A fundamental issue will also be discussed relating to the applicability of data from studies such as this to other sites and situations, and the use of reported FIDs to inform conservation measures – buffer zones – for minimising human-wildlife conflicts.

2.3 Methods

2.3.1. Study site

The study took place on the Wash ($52^{\circ}56'16''\text{N}$, $00^{\circ}17'16''\text{E}$), a large embayment in eastern England on the North Sea coast with extensive intertidal sand and mudflats. Its conservation importance is recognised through several national and international designations including: Site of Special Scientific Interest (SSSI), Special Area of Conservation (SAC), Special Protection Area (SPA), and Ramsar site status (Doody and Barnett 1987, JNCC 2014). *'In terms of total numbers, the Wash is the key site for wintering waterbirds in the UK'* (Austin et al. 2014) and supports internationally important wintering populations of all the species that were included in this study: curlew, oystercatcher, bar-tailed godwit, grey plover, redshank, knot, turnstone, ringed plover, sanderling and dunlin.

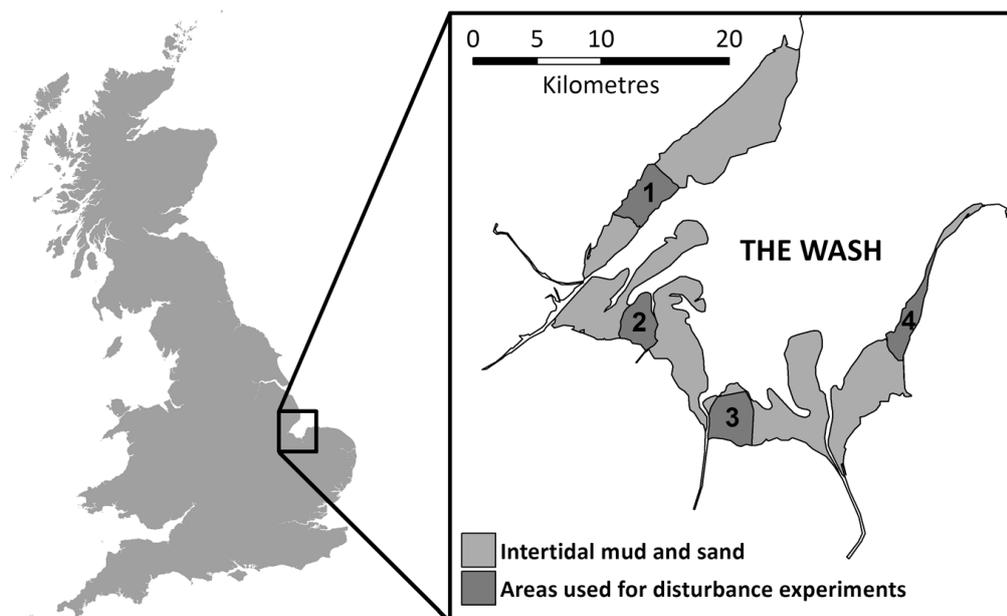


Figure 2.1. The intertidal areas of the Wash on which disturbance observations were made in winter and early spring of 2002/03, 2003/04 and 2004/05. 1-Wrangle; 2-Maretail; 3-Breast Sand; 4-Stubborn Sand. Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

The intertidal flats used for the disturbance experiments (Figure 2.1) were selected because of the wide range of wader species that were known to feed at low tide (Goss-Custard et al. 1988, Goss-Custard and Yates 1992, Yates et al. 2004) and the relatively even distribution of

the birds within them. They were also selected based on the surveyors' local knowledge of the differing distances from human populations, ease of access, and resulting frequencies of human activities (such as walkers, dog walkers, bait diggers etc.) on the intertidal area and sea wall. Sites one to three can be characterised as areas of low disturbance, with a visitor frequency in the order of around three times per week; whereas the more easily accessible site four, on the eastern side of the Wash, had a comparatively high frequency of disturbance i.e. on a daily basis (Mick Yates, pers. obs.). Together the areas encompassed all shore levels and both regularly disturbed and undisturbed parts of the Wash, and so can be considered to be representative of the whole embayment.

2.3.2. Field experiments

All experiments took place during mid-December to late March of winters 2002/03, 2003/04, and 2004/05 and within the period of minimal tidal movement two hours either side of low water on spring tides, which on the Wash occur around midday. The intention was to survey all sites in all years, though circumstances dictated that site two was not used in 2002/03 and site three was only used in 2003/04. Between them, Angus Garbutt, Mick Yates, Ed Rispin and Tina Yates completed the field data collection. Two observers worked together using binoculars or the naked eye to observe the birds and digital stopwatches were used to time the birds' behavioural responses to the nearest second.

The procedure was to mutually agree on a target bird, which remained unobscured from view for the duration of the observation, and then to walk side-by-side directly towards it at a comfortable pace on the soft sediment (approximately 2.5 km/h). The length of time for which the bird was visibly alert was noted and when the bird took flight both observers stopped walking. One timed the 'flight time' (the period from taking off to landing) and the 'latency time' (length of time between landing and the first attempt at feeding). Total time lost was calculated by summing alert time, flight time and latency time. The second observer kept their eyes on the place from which the bird had taken off and waited until the other observations had been completed before pacing out the FID. Distances were measured by counting paces which were later converted to metres after calibrating against a known distance in similar walking conditions. Isolated individuals of species that would normally be expected to feed in small groups or flocks were not selected for observation as their behaviour was considered unrepresentative of the usual behaviour of individuals of that species. Disturbance experiments took place on 38 separate survey days and the number of disturbances during each low tide survey period varied from three to 37 (median = 17.5; median for same species on same day = 3), depending on the number of birds present and

how many experiments could be completed in the time available. Care was taken to ensure that the same birds were not disturbed more than once during a single survey; by searching for each target bird in a direction at least 90 degrees from that taken by the previous target bird when it flew off and landed. The surveyors also only selected birds that were at least 200 metres further away than the anticipated FID. Daily replicates were therefore well spread out in time and space so as to avoid order effects in the data.

In addition to the behavioural response parameters listed, a variety of environmental measurements were recorded relating to factors that may affect bird responses; air temperature and wind speed (using a hand-held thermometer and anemometer), and the part of the shore at which each disturbance took place. This was assigned by dividing each site equally on a three-point scale from 'low' (1), through 'mid' (2) and 'upper' (3) shore, as an indication of the relative proximity to the saltmarsh or sea wall (most likely source of human disturbance) i.e. upper shore is closest. Shore width (distance between sea wall or marsh and the low tide mark) was approximately 2.5 km at site four and 3-4.5 km at the other three sites. The date of each survey was also converted to the continuous variable 'winter day': with winter day 1 = 1st August.

Since warm bodies lose heat to the surrounding environment at faster rates when exposed to greater wind speeds (Williamson 2003), measurements of air temperature and wind speed from each disturbance experiment were converted to a wind chill equivalent temperature index (*WCTI*) using the following equation:

$$WCTI = 13.12 + 0.6215 \times T - 11.37 \times V^{0.16} + 0.3965 \times T \times V^{0.16} \quad \text{Equation 2.1}$$

where T is the air temperature in °C, and V is the wind speed in km/h (Williamson 2003, Oscewski and Bluestein 2005). This is considered a more appropriate independent variable, in relation to thermoregulation and energy budgets of birds, than records of air temperature alone (Wiersma and Piersma 1994).

2.3.3. Energy and time costs of responding to disturbance

To set birds' time-related responses in the context of daily energy requirements energy cost per flight was calculated using the following equation from (Kvist et al. 2001):

$$Cost (kJ) = \frac{10^{0.39} \times M^{0.35} - 0.95}{1000} \times time\ spent\ in\ flight\ (s) \quad \text{Equation 2.2}$$

and Nagy et al.'s (1999) equation was used to estimate thermoneutral requirements:

$$Energy\ requirement\ (kJ) = 10.5 \times M^{0.681} \quad \text{Equation 2.3}$$

where M = body mass in grams.

The results were also used to estimate the number of disturbances that would result in a 1%, 5%, and 10% reduction in available feeding time based on the data for total time lost per disturbance (assuming that disturbance events do not overlap). Numbers are presented as a range based on the fact that birds are able to feed throughout the tidal cycle on neap tides, but not able to feed for two hours either side of high tide on spring tides (Goss-Custard et al. 1977). Data from Goss-Custard et al. (1977) on how much of the available feeding time is used by each species, serve as an indicator of their likely capacity to compensate for the costs of responding to disturbance (also presented as a range according to the spring-neap tidal cycle).

2.3.4. Model selection and data analysis

General linear models were used, alongside a multi-model inference approach (Symonds and Moussalli 2011, Pap et al. 2013) to find variables with high explanatory power for the three different response variables (FID; flight time; and total time lost). Preliminary analyses (see Appendix 1) showed no effect of winter year, so the data from all three winters were combined. When deciding on the global models to be tested for each response variable, initially all biologically plausible two-way interactions were included in addition to the potential explanatory variables as main effects. Interactions that were found to be non-significant were subsequently excluded from the candidate model set – as recommended by Schielzeth (2010). In situations where the Akaike weight of the best AIC_c-ranked model in the candidate set was considerably higher than that of the next best model, inferences were made based on that model alone (Symonds and Moussalli 2011). However, if this was not the case, model averaging was undertaken using all models with $\Delta_i < 4$ to estimate the relative importance of the predictor variables under consideration. This involves summing the Akaike weights for each model in which that variable appears (Symonds and Moussalli 2011). The larger the sum of the Akaike weights (up to a maximum value of 1), the more important the variable is relative to the others in the global model (Burnham and Anderson 2002). Burnham and Anderson (2002) suggest ranking variables according to their relative importance; so in the analyses, variables with a relative importance value greater than 0.9 were considered 'moderate'; and the term 'low explanatory power' was used for variables with relative importance less than 0.6.

The single-species models that were tested included 'site' as a fixed factor, with 'shore level', 'wind chill index' and 'winter day' as covariates. The all-species models also included 'species mass' in grams (using Wash-specific data from Johnson (1985)) as a covariate, and two yes/no

variables called 'is it an oystercatcher?' and 'is it a plover?' since these species are in different families to the others (*Haematopididae* and *Charadriidae*, respectively versus *Scolopacidae*) and have different feeding strategies from the other species (Goss-Custard et al. 2006b).

Before carrying out the analyses the input variables were centred and standardised (following Gelman (2008) and Grueber et al. (2011)) to facilitate interpretation of the relative strength of parameter estimates, particularly where interaction terms were involved. This involved subtracting the mean (centring) and then dividing by two standard deviations (standardising) for numeric variables with more than two values; binary variables were rescaled to have a mean of 0 and a difference of 1 between their two categories (Gelman and Su 2015). The three response variables were also natural-log-transformed, which helped to achieve a better distribution of the model residuals in relation to the assumptions of the statistical tests used.

To assess the relationships between the different response variables Spearman's rank correlation tests were used along with visual inspection of the bivariate scatterplots.

Visual inspection of diagnostic plots of the residuals for the statistical tests performed, as recommended by Zuur et al. (2010) showed no issues with lack of normality, heterogeneity of variance, collinearity or undue leverage; however, as is often the case with ecological studies, the assumption of independence was not met. Therefore inferences beyond the sample space are made with care, and the possibility will be discussed that this could be an indication that an important covariate was not measured (Zuur et al. 2010).

Details of preliminary data exploration and statistical tests not reported in the main text can be found in the Appendices. Analyses were carried out in R (R Core Team 2015) using functions available in 'arm' (Gelman and Su 2015) to standardise model predictors, and the multi-model inference package 'MuMIn' (Bartoń 2015) for model selection and averaging; plots were produced using 'ggplot2' (Wickham 2009) and 'PerformanceAnalytics' (Peterson and Carl 2014). Means are presented \pm one standard error.

2.4 Results

Ten different species of wader were approached a total of 677 times; and the responses to the experimental disturbances are summarised in Table 2.1. During the survey period, the wind chill index ranged from -4.74 °C up to a maximum of 14.27 °C, which is within the range of typical winter temperatures for the area after accounting for wind speed (Met Office 2016).

Following Frid and Dill (2002), all measures of response to disturbance were hypothesised to be correlated with each other, and Figure 2.2 shows that this was well supported by the data. Flight time and latency time were strongly positively correlated both with each other and with total time lost; although alert time was not significantly correlated with flight time or latency time, and was only weakly correlated with total time lost. Individuals that exhibited greater FIDs spent longer in flight and took longer to resume feeding (particularly at FIDs below 200 m), and consequently lost more time in total. However, there was no correlation between FID and alert time.

Mean FID for all species was $89.7 \text{ m} \pm 3.1$ (5–570 m, $N = 677$), but it was significantly different between species ($F_{9,667} = 122.1$, $p < 0.001$). There was also a significant difference between species in flight time ($F_{9,667} = 20.9$, $p < 0.001$) and total time lost ($F_{9,677} = 29.5$, $p < 0.001$).

Table 2.1. Mean, maximum and minimum responses to an approaching pedestrian for each species. Species are presented in order of decreasing body size. FID = flight initiation distance; FlightTime = time spent in flight; TotalTimeLost = time taken to resume feeding after becoming alert, flying and landing.

Species	Mass(g)	N	FID (m)			FlightTime (s)			TotalTimeLost (s)		
			mean	s.e.	range	mean	s.e.	range	mean	s.e.	range
Curlew (CU)	751	39	340.33	18.23	88-570	34.20	2.35	12-78	75.27	4.8	28-163
Oystercatcher (OC)	500	147	97.28	2.97	30-228	21.17	0.94	6-61	59.86	2.0	21-136
Bar-tailed godwit (BA)	297	92	84.36	3.93	32-225	20.07	1.20	5-53	47.03	2.4	14-118
Grey plover (GV)	215	55	132.27	6.81	35-251	22.82	1.65	6-56	58.22	3.4	19-154
Redshank (RK)	143	53	79.83	5.95	28-187	17.44	1.67	4-58	45.16	3.4	11-120
Knot (KN)	134	78	71.83	3.92	20-240	19.58	1.26	6-59	43.71	2.6	15-125
Turnstone (TT)	105	40	31.50	3.00	5-75	12.84	1.49	2-41	32.79	2.8	7-85
Ringed plover (RP)	64	30	41.07	2.55	20-74	12.35	1.16	4-32	36.15	2.7	11-72
Sanderling (SS)	54	26	25.00	2.65	9-51	10.08	1.27	3-34	26.69	2.6	10-72
Dunlin (DN)	48	117	43.93	2.68	9-197	13.61	0.69	3-41	32.05	1.4	8-85

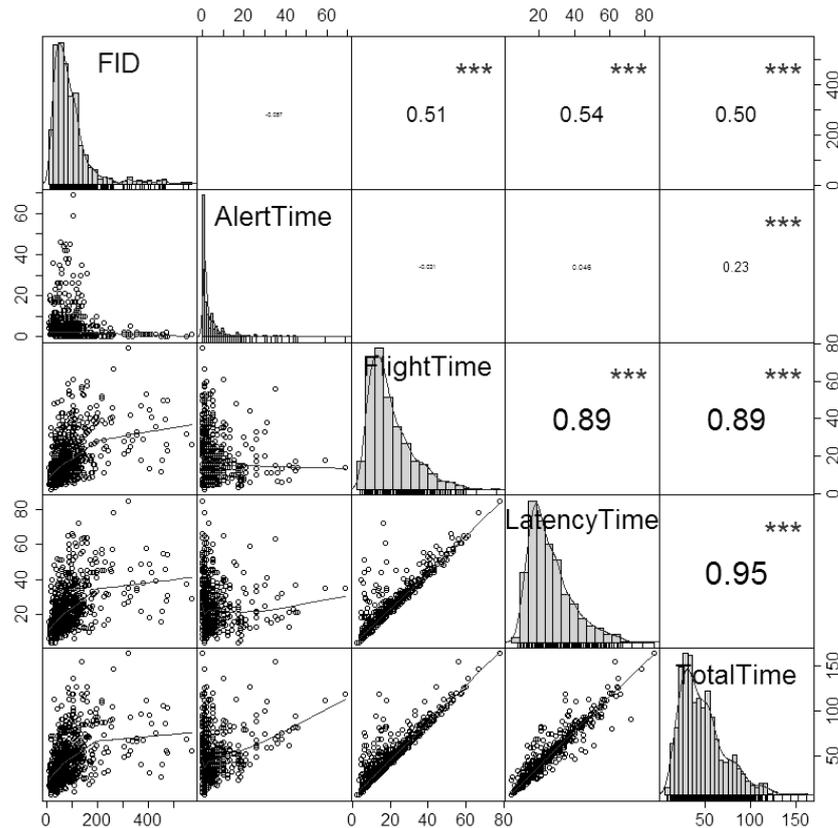


Figure 2.2. Correlation matrix chart for all recorded measures of bird responses to experimental disturbance. Bivariate scatterplots are presented with a fitted line, and Spearman’s coefficients, along with stars to indicate significance level. Significance codes: ‘***’ <0.001 ‘**’ <0.01 ‘*’ <0.05.

Model selection and ranking by AIC_c (Table 2.2) revealed clear support for the top model, with all potential predictors included, when explaining both FID and time spent in flight (each with a model weight (ω_i) > 0.8). Whereas in the case of total time lost, the top model only had a model weight of 0.727; though the cumulative model weight of the top two models ($\text{acc } \omega_i$) = 0.993, setting them well apart from the lower ranked models in the candidate set. Standardised and model averaged parameter estimates are shown in Table 2.3, and with all the coefficients being positive for ‘species mass’ and ‘wind chill’, these results support hypotheses 2 and 3 that FID, time spent in flight and total time lost increase with body size (Figure 2.3), and that response magnitude decreases under harsher environmental conditions (i.e. lower values of wind chill equivalent temperature, Figure 2.4). There is also support for Hypothesis 4 (that responses vary both between sites and over time); a mixture of positive and negative coefficients indicates differences in bird responses between sub-sites (Figure 2.5); and negative coefficients for the relationships with ‘winter day’ indicate that response magnitude decreases as the season progresses (although the 95% confidence interval for FID

includes zero). In addition to the between-site differences in response, there were within-site differences; with the negative coefficients for 'shore level' indicating a trend for greater response magnitudes when birds were feeding closer to the low water mark.

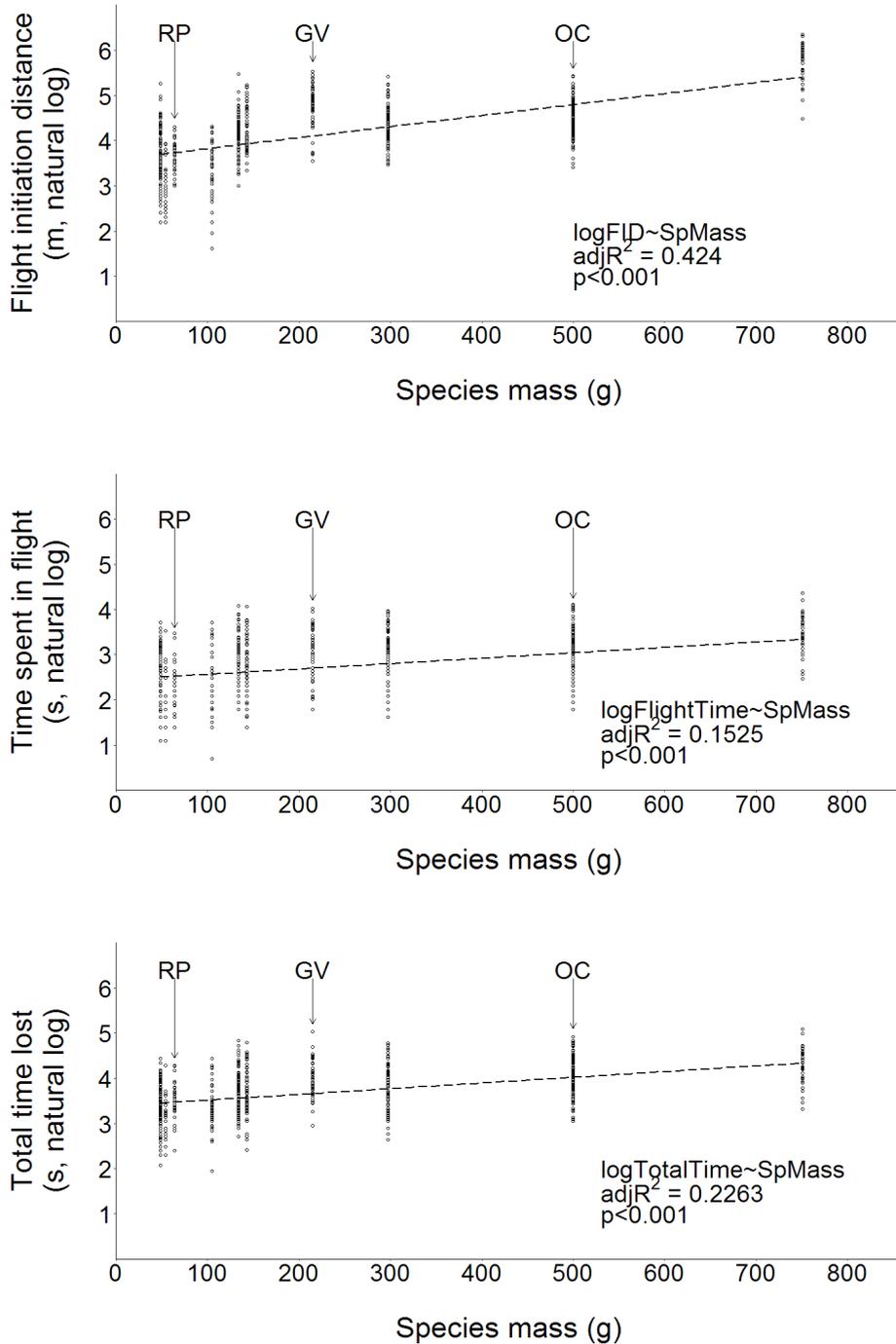


Figure 2.3. Relationship between species mass and three measures of responses to disturbance. Dependent variables have been natural log-transformed. RP=ringed plover; GV=grey plover; OC=oystercatcher.

Table 2.2. Model selection tables – top five AIC_c-ranked models in each candidate set. Δ_i = difference in AIC_c between model and top model. ω_i = Aikaike model weight. acc ω_i = cumulative model weight. SpMass = species mass (g); WindChill = wind chill equivalent temperature (°C); IsItOC = is it an oystercatcher?; IsItPlover = is it a plover? See text for more-detailed parameter descriptions.

a) Global model = $\log(\text{FID}) \sim \text{SpMass} + \text{Site} + \text{ShoreLevel} + \text{WindChill} + \text{WinterDay} + \text{IsItOC} + \text{IsItPlover} + \text{Site:WinterDay}$

	Candidate models	adjR ²	AIC _c	Δ_i	ω_i	acc ω_i
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.66561	971.232	0	0.916	0.916
2	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.66083	976.398	5.166	0.069	0.985
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.65683	980.328	9.096	0.010	0.995
4	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover	0.65371	982.901	11.669	0.003	0.997
5	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.65325	983.581	12.348	0.0019	0.999

b) Global model = $\log(\text{FlightTime}) \sim \text{SpMass} + \text{Site} + \text{ShoreLevel} + \text{WindChill} + \text{WinterDay} + \text{IsItOC} + \text{IsItPlover} + \text{Site:WinterDay}$

	Candidate models	adjR ²	AIC _c	Δ_i	ω_i	acc ω_i
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.29671	1107.022	0	0.892	0.892
2	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.28098	1112.770	5.749	0.050	0.943
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.28106	1114.778	7.757	0.018	0.961
4	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.28326	1115.192	8.170	0.015	0.976
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+Site:WinterDay	0.28268	1115.627	8.605	0.012	0.988

c) Global model = $\log(\text{TotalTimeLost}) \sim \text{SpMass} + \text{Site} + \text{ShoreLevel} + \text{WindChill} + \text{WinterDay} + \text{IsItOC} + \text{IsItPlover} + \text{Site:WinterDay}$

	Candidate models	adjR ²	AIC _c	Δ_i	ω_i	acc ω_i
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.39716	860.499	0	0.727	0.727
2	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.39724	862.515	2.016	0.265	0.993
3	SpMass+Site+ShoreLevel+WindChill+IsItPlover	0.37560	871.248	10.749	0.003	0.996
4	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.37590	873.077	12.578	0.001	0.998
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover	0.37566	873.266	12.767	0.001	0.999

Inclusion of the two dummy variables 'is it an oystercatcher?' and 'is it a plover?' demonstrated additional between-species differences over and above the species mass relationship described. With positive and negative coefficients respectively, plovers had larger magnitude responses than expected for their size; and oystercatchers were relatively more 'tolerant' i.e. exhibiting shorter FIDs and spending less time in flight, though any relationship was poorly supported for total time lost (Table 2.3: relative importance = 0.267, and the 95% confidence interval includes zero).

Given the support for the two species-related dummy variables, the data for each species were also analysed separately (Table 2.4) to explore in more detail the mechanisms behind the inter- and intra-specific variation in bird responses to disturbance. As with the all-species analysis, there was strong support for the influence of 'site', 'winter day', 'wind chill' and 'shore level' on FID for some (but not all) species, though not all relationships were in the same direction (see Appendix 2 for parameter estimates). The degree of support for different predictor variables in relation to time spent in flight and total time lost also varied widely between species, and in the case of curlew, there was no candidate predictor variable that stood out with strong or even medium support.

Table 2.3. Standardised parameter estimates and confidence intervals for eight potential predictors of wader responses to disturbance. Dependent variables have been natural log transformed. See Tables 2.1 and 2.2 for parameter abbreviations.

Predictor	logFID ^a				logFlightTime ^a				Relative importance	logTotalTimeLost ^b			
	Estimate	s.e.	95% confidence interval		Estimate	s.e.	95% confidence interval			Estimate	s.e.	95% confidence interval	
			Lower limit	Upper limit			Lower limit	Upper limit				Lower limit	Upper limit
Intercept	4.430	0.035	4.361	4.499	2.915	0.039	2.839	2.991		3.796	0.032	3.732	3.859
1 SpMass	1.263	0.050	1.165	1.361	0.564	0.055	0.456	0.673	1	0.512	0.039	0.435	0.589
2 WindChill	0.109	0.041	0.029	0.189	0.163	0.045	0.075	0.252	1	0.163	0.038	0.089	0.237
3 ShoreLevel	-0.165	0.040	-0.244	-0.086	-0.164	0.044	-0.251	-0.077	1	-0.154	0.037	-0.226	-0.081
4 Site ^c									1				
Site2-Maretail	-0.093	0.210	-0.506	0.320	-0.245	0.232	-0.702	0.211	-	-0.111	0.194	-0.492	0.270
Site3-Breast Sand	0.098	0.126	-0.150	0.345	0.208	0.140	-0.066	0.482	-	0.237	0.116	0.009	0.464
Site4-Stubborn Sand	-0.361	0.042	-0.445	-0.278	-0.257	0.047	-0.350	-0.165	-	-0.137	0.039	-0.214	-0.061
5 WinterDay	-0.101	0.073	-0.244	0.042	-0.229	0.080	-0.386	-0.071	1	-0.222	0.067	-0.354	-0.091
6 IsItOC ^d	-0.533	0.060	-0.651	-0.416	-0.211	0.066	-0.340	-0.081	0.267	0.004	0.029	-0.054	0.061
7 IsItPlover ^d	0.487	0.061	0.367	0.606	0.219	0.067	0.087	0.351	1	0.330	0.056	0.220	0.440
8 Site:WinterDay ^e									1				
Site2-Maretail:WinterDay	-0.228	0.333	-0.882	0.426	-0.072	0.368	-0.795	0.652	-	-0.099	0.308	-0.703	0.504
Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	-	0	0	0	0
Site4-Stubborn Sand:WinterDay	0.298	0.087	0.127	0.469	0.324	0.096	0.135	0.514	-	0.321	0.080	0.163	0.479

^a Based on top model only.

^b Results of model averaging top two models.

^c Reference category is 'Site1-Wrangle Flats'.

^d Reference category is 'No'.

^e Reference category is 'Site1-Wrangle Flats:WinterDay'.

Table 2.4. Species-specific model averaging results – relative importance of potential predictors. Values ≥ 0.6 (high and medium support) highlighted in bold. See Table 2.1 for species codes.

a) logFID

Predictor	Species									
	CU	OC	BA	GV	RK	KN	TT	RP	SS	DN
Site	1	1	0.817	1	1	0.406	0.538	-	0.218	-
WinterDay	0.694	0.313	0.591	0.743	0.189	1	0.379	0.186	0.262	0.822
WindChill	0.498	1	1	0.410	0.630	0.243	0.917	0.829	0.172	0.464
ShoreLevel	0.163	0.971	1	1	0.238	0.977	1	0.153	0.188	0.334
Site:WinterDay	-	-	-	0.706	-	-	-	-	-	-

b) logFlightTime

Predictor	Species									
	CU	OC	BA	GV	RK	KN	TT	RP	SS	DN
Site	0.044	0.397	0.328	1	1	0.582	0.864	-	0.466	0.920
WinterDay	0.230	0.262	0.236	0.319	0.388	0.713	0.242	0.205	0.422	0.232
WindChill	0.236	1	0.971	0.282	0.210	0.202	0.466	0.616	0.688	0.542
ShoreLevel	0.308	0.618	0.845	0.326	0.271	0.205	0.595	0.173	0.409	0.381
Site:WinterDay	-	-	-	-	-	0.420	-	-	-	-

c) logTotalTimeLost

Predictor	Species									
	CU	OC	BA	GV	RK	KN	TT	RP	SS	DN
Site	0.052	0.213	0.291	0.945	0.587	0.690	0.738	-	0.573	0.699
WinterDay	0.246	0.204	0.273	0.393	0.311	0.803	0.297	0.367	0.345	0.229
WindChill	0.234	1	0.939	0.266	0.340	0.215	0.197	0.934	0.253	0.486
ShoreLevel	0.323	0.682	0.704	0.254	0.206	0.225	0.732	0.254	0.968	0.764
Site:WinterDay	-	0.040	-	-	-	0.593	-	-	-	-

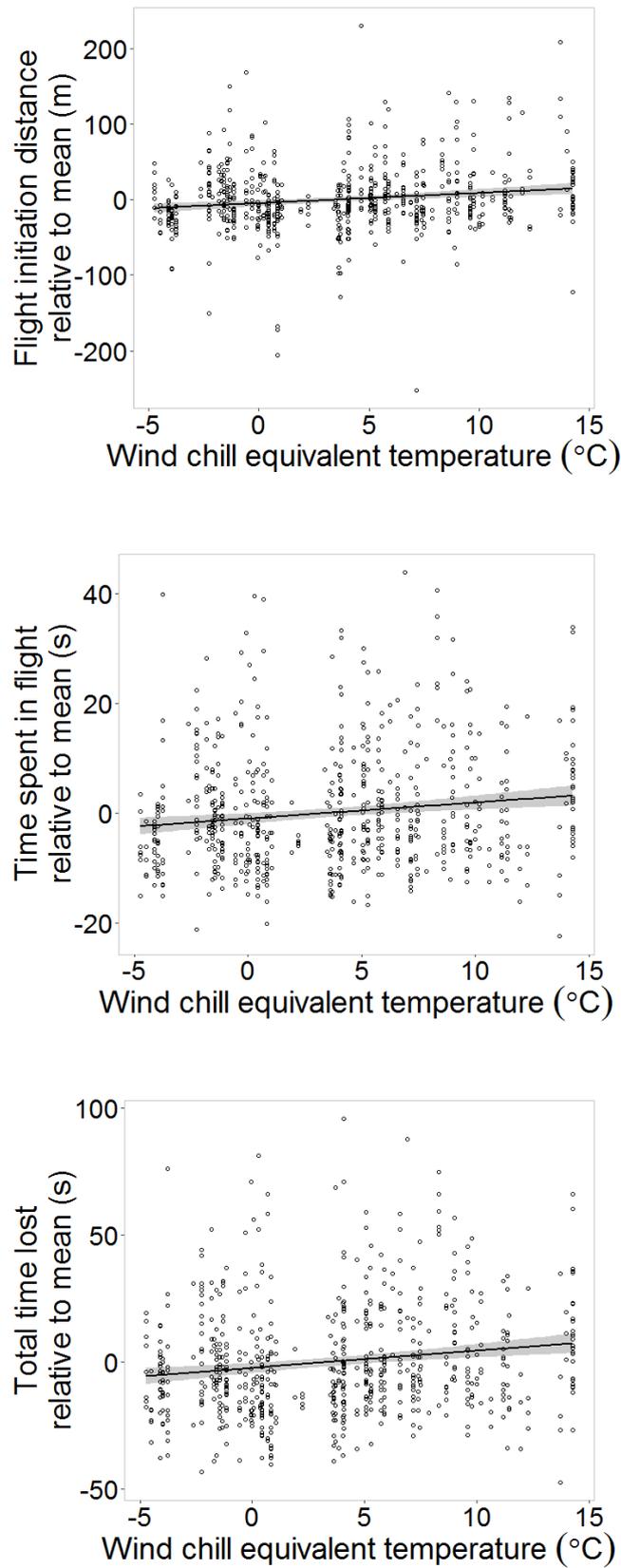


Figure 2.4. Relationships between wind chill equivalent temperature and measures of response to disturbance, adjusted relative to the mean response of each species. Regression lines with 95% confidence intervals.

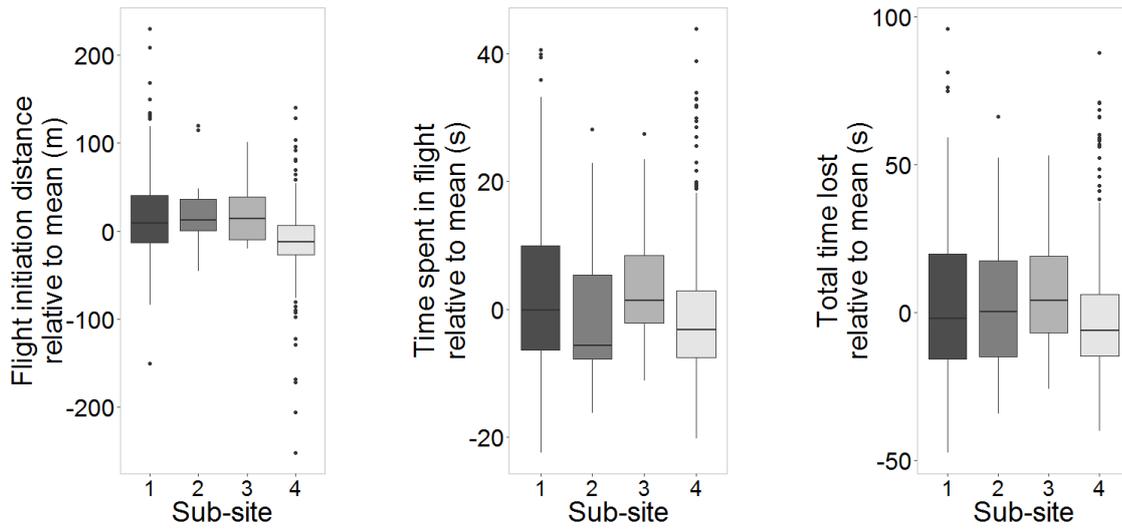


Figure 2.5. Variation between sub-sites in bird responses to disturbance, adjusted relative to the mean response of each species. Sub-site codes: 1 = Wrangle; 2 = Maretail; 3 = Breast Sand; 4 = Stubborn Sand.

Table 2.5. An assessment of the time and energy costs incurred by waders per disturbance response, and the number of disturbances that would be expected to reduce available feeding time by 1%, 5% and 10%. See text for a description of the calculations involved. Data reproduced from Goss-Custard et al. (1977) give an indication of birds' likely capacity to compensate by extending their feeding time.

Species	Cost per flight response (kJ) ^a	Thermoneutral daily energy requirement (kJ) ^b	Cost per flight as % of daily intake requirement	Number of disturbances that would reduce available feeding time (day and night) by:			% available daylight time spent feeding ^c
				1%	5%	10%	
Curlew	0.820	953.89	0.086	8-11	38-57	77-115	50-80
Oystercatcher	0.437	723.08	0.060	10-14	48-72	96-144	50-70
Bar-tailed godwit	0.342	507.15	0.068	12-18	61-92	122-184	70-85
Grey plover	0.345	406.99	0.085	10-15	49-74	99-148	70-80
Redshank	0.227	308.30	0.074	13-19	64-96	128-191	90-100
Knot	0.248	294.95	0.084	13-20	66-99	132-198	97-100
Turnstone	0.148	249.82	0.059	18-26	88-132	176-263	not recorded
Ringed plover	0.118	178.32	0.066	16-24	80-120	159-239	not recorded
Sanderling	0.090	158.84	0.057	22-32	108-162	216-324	not recorded
Dunlin	0.117	146.59	0.080	18-27	90-135	180-270	95-100

^a using cost per second of flight from Kvist et al. (2001)

^b using Nagy et al.'s (1999) allometric equation

^c as observed by Goss-Custard et al. (1977)

The data on mean flight time and mean total time lost were used to look in more detail at the energetic consequences and the lost feeding opportunity costs of responding to disturbance for each species (Table 2.5). A 5% reduction in daily available feeding time would be expected to result from responding to between 38 and 162 separate disturbance events (depending on species and tidal stage). The mean cost per individual flight response represented less than a tenth of a percent of each species' daily energy requirements: Figure 2.6 shows there was no significant relationship between body mass and energetic cost of responding to a single disturbance when expressed in this way ($F_{1,675} = 0.565, P = 0.45$).

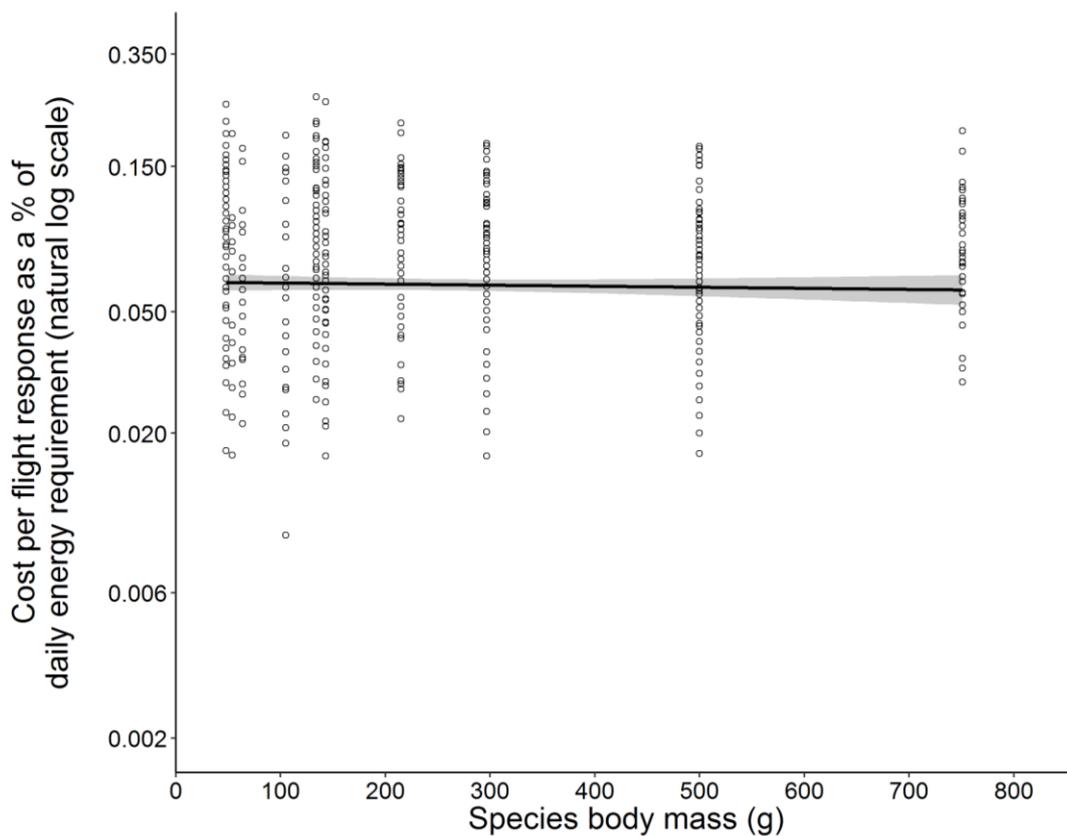


Figure 2.6. Relationship between species body mass and energetic costs of flight in response to disturbance. y-axis presented on a natural log scale.

2.5 Discussion

This study provides data for 10 species of wader on FID, flight time and total time lost, along with associated energy costs, when birds flee an approaching pedestrian during the non-breeding season. In line with the findings of other studies worldwide (Urfi et al. 1996, Stillman and Goss-Custard 2002, Blumstein et al. 2003, 2005, Ikuta and Blumstein 2003, Glover et al. 2011, Lin et al. 2012), all four hypotheses about how bird responses to disturbance vary were supported by the results. Waders showed a great deal of variation in their responses, and much of that variation can be explained by species, body mass, environmental conditions, and site differences on both small and larger spatial scales.

Below, potential reasons and alternative explanations for this variability are discussed. The results are interesting for behavioural ecology as well as having applied relevance: so the chapter concludes with a discussion of their use by conservation managers wanting to minimise the impacts of disturbance on wintering waders, bearing in mind the context-specific nature of responses.

2.5.1. Relationships between response measures

With the exception of alert time, all of the time- and distance-related measures of response that were recorded were correlated with each other. This supports the hypothesis that disturbance avoidance behaviour depends on the relative costs of fleeing and remaining (Frid and Dill 2002): when starvation risk is lower, birds fly from further away (FID), flee further (longer flight time) and spend more time being vigilant (alert and latency time). The lack of a strong relationship between alert time and the other variables could be due to the fact that this was more difficult to record accurately, especially at greater distances. Or perhaps alert time is simply not a useful measure of response to disturbance in this case, since it is likely to be related to speed of approach, which was approximately constant in these experiments.

2.5.2. Between-species differences

Larger species had greater FIDs, spent more time in flight, and lost more feeding time overall than did smaller species. Møller et al. (2013) suggest that longer FIDs in larger species are due to the aerodynamic cost of large body size: this explanation may work for FID, but does not explain the additional body mass relationships with flight time and total time lost. Another explanation could be that since smaller birds generally spend a greater proportion of the available time feeding (Goss-Custard et al. 1977) and have proportionally lower body fat reserves upon which they can rely if they are unable to meet their daily intake requirements

(Piersma and Van Brederode 1990), they have less capacity to compensate for the costs of responding to disturbance. Indeed, the trade-off becomes apparent when the energetic cost per flight response is expressed as a percentage of the daily requirements of that species, and the body mass relationship disappears (Figure 2.6).

2.5.3. Effect of environmental conditions

One prediction of the risk-disturbance hypothesis is that '*fleeing probability and FID increase when... environmental conditions are mild*' (Frid and Dill 2002) because when birds are able to meet their daily energetic requirements easily, the balance in the trade-off between avoidance of starvation and predation shifts towards greater FIDs. This was also found to be the case on the Wash: birds also spent significantly longer in flight and lost more time overall when conditions were milder (i.e. higher wind chill equivalent temperatures).

2.5.4. Within- and between-site differences

The magnitude of all three measures of response varied on both small and larger spatial scales; birds responded less strongly to disturbance when feeding further from the low water mark and at site four (negative parameter estimates in Table 2.3 and the confidence intervals do not include zero). Site four was the site with easiest access, closest proximity to residential areas, and highest frequency of potential disturbers, so this result could be attributed to habituation. However, it is not possible to rule out alternative explanations without detailed knowledge of the differences between sites and individual birds, which unfortunately are not available. For example, if birds feeding on high disturbance sites are in poorer condition they will prioritise feeding more than higher quality birds feeding on low disturbance sites. Or with differences between sites in food availability and competitive ability of birds, birds feeding at lower quality sites would be expected to be more tolerant of disturbance because of a lack of alternatives (Frid and Dill 2002). Similar arguments and explanations relating to habitat quality and individual differences could also apply to the observed relationship with shore level.

Whilst it was also beyond the scope of the study to collect detailed information on types and frequencies of human activities, future studies should consider using an objective measure of disturbance (such as number of visitors per day) which lends itself better to comparisons between sites and shore levels.

2.5.5. Within-species differences

Separate analysis of the data for each species showed that the important explanatory variables relating to responses to disturbance may not be the same for all species. For example, there was strong support for variation between sites in the FIDs of curlew, oystercatcher, bar-tailed godwit, grey plover, and redshank, but not for knot, turnstone, ringed plover, sanderling or dunlin. Similarly, there was variation between species in the level of support for winter day, wind chill and shore level when explaining FID and in relation to flight time and total time lost. Though this could be attributed to low statistical power for the species with fewer observations, it also highlights the fact that these analyses did not include any measure of variation between individuals (c.f. species mass in the all-species analyses), such as individual body condition, age, sex, territoriality or experience. This is a limitation of the field observations approach and highlights the usefulness of a combined approach including studies on marked populations or with captive birds; such as Urfi et al. (1996), Beale and Monaghan (2004b), and Liley and Sutherland (2007).

2.5.6. Costs of responding to disturbance

In addition to the energetic costs of flight, responding to disturbance reduces available feeding time. Feeding intensity data (Goss-Custard et al. 1977) show that most birds on the Wash are likely to be able to cope with at least a 5% reduction, which were estimated in this study to be caused by between 38 and 162 separate disturbance events per day, depending on species and tidal stage. Curlew, oystercatcher, bar-tailed godwit and grey plover may even be able to cope with a more serious reduction of 10% (caused by between 77 and 184 daily disturbance events). While objective data on visitor frequencies and distribution across the intertidal habitat in this study area are lacking, current levels on most parts of the embayment are likely to be well below these values (Mick Yates, pers. obs.), especially at lower shore levels (in the order of around three visitors per week); though perhaps with the exception of the more easily accessible eastern area around site four on busier weekend days. As an example, the popular RSPB Titchwell Marsh Nature Reserve (7 km east of site four) receives on average 217 visitors per day (Visit England 2015), and as few as 10% of visitors might cause disturbance events (Liley and Fearnley 2012). This suggests, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period.

Further work to quantify disturbance of high tide roosts would complement this study and allow a more confident assessment of the overall impacts of disturbance (or lack thereof) on

wintering waders on the Wash. As well as requiring high tide refuges upon which to rest and preen, some species are known to rely on supratidal habitats for foraging when they are not able to meet their energy requirements during the intertidal exposure period; for example due to increased requirements during extreme cold weather or reduced intertidal exposure during storm events (Goss-Custard 1969, Milsom et al. 1998, Smart and Gill 2003). In such situations, the time and energy costs associated with responding to disturbance could be particularly problematic, especially if birds are forced to fly long distances to an alternative roost site (Rehfishch et al. 1996).

Of course, the data presented here do not take account of the potential additional energetic costs of physiological responses (increased heart rate, stress hormones etc.) that may be incurred even when birds do not flee, and which can last longer than visible response behaviours (Ackerman et al. 2004, Elliott et al. 2015). More research is needed in this area; however Ackerman et al. (2004) found that the largest increase in heart rate occurs during a the period immediately before and after initiation of flight, so the contribution made by physiological changes not associated with flight is expected to be small compared to that due to the costs of flight and lost feeding time.

2.5.7. Applications and conclusions

An obvious application of an improved understanding of animal responses to disturbance is to inform measures such as buffer zones or set-back distances for minimising the impacts of disturbance on sites of conservation importance (Blumstein et al. 2003, Holmes et al. 2005, Burger et al. 2010, Glover et al. 2011, Malo et al. 2011, Andersen et al. 2012, Weston et al. 2012, Koch and Paton 2014). The size of such buffer zones has tended to be based on the largest FID value recorded for the species of interest, or even larger to incorporate alert distances (Livezey et al. 2016). However, use of FID in this way does not distinguish between 'response' and 'population impact' (Gill et al. 2001a), and effectively ignores the fact that birds exhibiting the largest FID could actually be at least risk of reduced fitness. Nor does this approach take account of visitor frequencies, the likelihood of visitors and birds interacting, or whether any redistribution of birds will cause reductions in bird intake rates (Goss-Custard et al. 2001, Duijns and Piersma 2014). On expansive sites like the Wash (~300 km²), which are relatively inaccessible (for humans), where the width of the shore tends to be much greater than the largest observed FID (though less-so at site four), and where potentially disturbing activities are largely restricted to the upper shore, buffer zones are unlikely to be necessary. In effect the site is already implementing its own buffer zone.

Nevertheless, setting buffer zones on the basis of observed response distances could be appropriate when birds are constrained to a particular location: at breeding sites (Burger and Gochfeld 1983, Holmes et al. 2005), on established territories (Immitzer et al. 2014), or where feeding (Kirsch et al. 2008, Velando and Munilla 2011) or roosting (Rogers et al. 2006) opportunities are limited. In such situations birds will be much less able to compensate for the consequences of fleeing the disturbance (Ydenberg and Dill 1986, Gill et al. 2001a, Frid and Dill 2002) and buffer zones based on observed responses in these cases are unlikely to be over-precautionary.

The few published studies with comparable data to this study show that there can be considerable between-estuary variation in responses (Smit and Visser 1993, Urfi et al. 1996, Fitzpatrick and Bouchez 1998, Laursen et al. 2005), as well as the within-estuary variation observed on the Wash. This makes it difficult to make inferences about behaviour at other sites. Similarly, given the influence of environmental conditions, it is important to note the temperature range over which experiments take place – for example, during an abnormally cold winter FIDs would be lower than those exhibited under more commonly experienced conditions. This study on the Wash adds to the suite of available data from a range of sites, providing more options for informed comparisons with new sites.

Finally, greater emphasis is needed on recording time-related measures of responses to disturbance – to better understand the constraints on bird time and energy budgets – rather than simply reporting FID. Doing so would also add value by providing the information necessary for parameterising simulation models for understanding population-level impacts of different levels of disturbance and to predict the effectiveness of proposed management options (e.g. Blumstein et al. 2005, Stillman et al. 2007).

Chapter 3 – The responses of wintering waders in Poole Harbour to experimental disturbance by an approaching pedestrian vary spatially, between species and with environmental conditions.

3.1 Abstract

Understanding bird responses to human disturbance has applications for assessing and managing population impacts on estuarine sites that are designated for their national and international importance for wintering waders. In this study wintering waders in Poole Harbour were experimentally disturbed so that aspects of their behavioural responses to pedestrian disturbance could be recorded. Data were analysed using an information-theoretic approach (multi-model inference) to identify key explanatory variables and test predictions of the risk-disturbance hypothesis. The results provide new information for eleven species of wader: adding to the relatively small number of sites for which comparable data are available. Responses were highly variable across both large and small spatial scales, as well as between species and according to environmental conditions. When expressed as a proportion of total energy requirements or spare time available for feeding, the costs of individual disturbance events were small. Consequently present day patterns of human activities in Poole Harbour are unlikely to have a significant impact on wintering bird populations. However, more detailed simulation modelling is required to test this statement.

3.2 Introduction

Interactions between threats to biodiversity can amplify their impacts (Mantyka-Pringle et al. 2015). Disturbance from human activities could therefore be ‘the straw that breaks the camel’s back’ when combined with the considerable threats of habitat loss and fragmentation (Ford et al. 2009, Sodhi et al. 2010), agricultural intensification (Donald et al. 2001), over-exploitation of resources (Mullon et al. 2005, Darimont et al. 2015), spread of invasive non-native species (Simberloff 2005, Nogales and Marrero 2006), and climate change (Maclean and Wilson 2011). Disturbance can also be a significant driver of population change on its own (Rodriguez-Prieto and Fernández-Juricic 2005, Liley and Sutherland 2007, Mallord et al. 2007). In a global assessment of the IUCN Red List of Threatened Species™, Baillie et al. (2004) noted that while human disturbance has had less impact than other threats in terms of total number of species affected, it can be particularly serious for some susceptible groups.

At the international level, the EU Nature Directives (EEC 1992, EC 2009) highlight disturbance as something that Member States should take appropriate steps to avoid (in relation to key species and in special protection areas), and in the Agreement on the Conservation of African-Eurasian Migratory Waterbirds it is recognised as an issue that needs to be addressed and researched (AEWA Secretariat 2012). Similarly, a list of 100 ecological questions of relevance to UK policy (Sutherland et al. 2006) included three references to disturbance from recreational activities and urban development (Sutherland 2007). So despite a large body of past work relating to disturbance, there is still a clear need from a conservation and a regulatory perspective for an improved understanding of the mechanisms behind animal responses to disturbance and, importantly, the resulting population consequences. Estuaries and the assemblages of waders that they support during the non-breeding season offer a useful study system for such research.

In estuarine habitats, the tidal cycle limits the time available to waders for foraging and they must optimise their intake rate in order to ensure that they meet their daily energy requirements to avoid starvation and achieve suitable body condition for migration and reproduction. One way to assess the ease/difficulty with which birds are able to meet their daily energy intake requirements is to measure the proportion of their total daily time budget devoted to feeding (Urfi et al. 1996, Hötker 1999). The proportion of birds feeding at any one time has been shown to be relatively constant throughout the intertidal exposure period (Goss-Custard 1969, Baker 1981, Burton et al. 2004), whereas the proportion of exposure

time that birds spend away from their roost varies seasonally and according to changing energetic demands (Goss-Custard 1969, Hutchinson and O'Halloran 1994, Burton et al. 2004).

Given that animal responses to disturbance are similar to anti-predator behaviour (with increased vigilance and avoidance according to perceived risk (Frid and Dill 2002)), anthropogenic disturbance can affect bird energy intake in three main ways:

- i) Site avoidance and fleeing from disturbers results in a reduction in the extent of available foraging habitat – which may force birds into less favourable areas and/or increase competition between individuals;
- ii) Increased vigilance and time lost while fleeing reduces the time available for foraging;
- iii) Extra energy expenditure through locomotion and due to stress-related physiological responses increases individual daily energy requirements.

If birds are unable to compensate for these costs, fitness will be reduced and the number of birds that can be supported by a particular site (carrying capacity) may be lower than would otherwise be possible in the absence of disturbance – one way of measuring whether disturbance is having a 'significant' impact. Though as Gill et al. (2001b) demonstrate, the presence of humans does not always result in significant changes in habitat use or the numbers of birds supported. It is therefore important to understand the circumstances under which disturbance may or may not cause a conservation problem; this requires an understanding of the factors that determine how birds respond to disturbance events, as well as a clear definition of what is considered 'significant impact' (see section 1.2.2).

As described in the previous chapter, a commonly used method to measure and understand animal responses to disturbance is to experimentally disturb them and record their behaviour (Blumstein et al. 2005, Laursen et al. 2005, Cooper 2009, Li et al. 2011, van Dongen et al. 2015). Flight initiation distance (FID), also known as 'escape distance' (Laursen et al. 2005, Bregnballe et al. 2009) or 'flush(ing) distance' (Holmes et al. 1993, Burger et al. 1995, Meillère et al. 2015), is the most frequently and consistently reported measure since it has applications for the setting of conservation buffer zones or set-back distances to prevent disturbance from occurring on protected sites (Blumstein et al. 2003, Burger et al. 2010, Glover et al. 2011, Koch and Paton 2014, Livezey et al. 2016). However, in the context of foraging waders, caution is needed when using FID values for this purpose without knowledge of the conditions under which the data were collected or of relevant site characteristics that may affect the applicability of the data to new locations. It is also important to remember that magnitude of response does not necessarily reflect the

population consequences of disturbance as birds exhibiting larger FIDs could in fact be at lower risk of suffering negative consequences than those that allow humans to approach more closely i.e. birds that are in poorer condition are likely to give higher priority to avoiding starvation compared to anti-predator/disturbance avoidance behaviour (Gill et al. 2001a, Frid and Dill 2002). Nevertheless, disturbance response data together with accompanying site- and survey-specific information, offer a useful starting point for understanding the significance of disturbance to populations of conservation concern and for determining appropriate management methods (Thomas et al. 2002, Stillman et al. 2012).

The risk-disturbance hypothesis (Frid and Dill 2002) predicts that bird responses to disturbance will be stronger when perceived risk is greater. It follows, therefore, that all measures of response by a bird during a single disturbance event would be expected to be positively correlated. For example, larger FIDs should be accompanied by longer flight times, more time spent latent, and therefore also larger values for total feeding time lost. Also following Frid and Dill (2002) and in line with the findings described in the previous chapter and other studies (e.g. Blumstein et al. 2003, 2005, Glover et al. 2011 and see Table 1.2), species body size and wind chill equivalent temperature are expected to be important predictors of bird responses to disturbance. Larger birds are predicted to exhibit greater FIDs, spend more time in flight and lose more feeding time overall; whereas responses are expected to be lower for lower wind chill equivalent temperatures. Several authors have pointed out that responses measured in one place may not apply to other areas (e.g. Laursen et al. 2005, Weston et al. 2012, and see Chapter 2); bird responses would be expected to vary spatially if there are differences between and/or within sites that affect perceived risk. Blumstein et al. (2003) and Glover et al. (2011) show that important factors might include visitor frequency (i.e. habituation to benign disturbances could lead to reduced responses), or estuary size (which could influence disturber starting distance and the availability of alternative feeding areas).

In this chapter field data from disturbance experiments in Poole Harbour (UK), the results presented in the previous chapter, and reported responses from other European estuaries will be analysed and compared to test the following three hypotheses:

- H₁ All measures of individual bird responses to disturbance are positively correlated with each other;
- H₂ Species body size and wind chill equivalent temperature are important predictors of responses to disturbance – showing positive and negative relationships, respectively, with FID, time spent in flight, and total feeding time lost; and
- H₃ Bird responses to disturbance vary on both small- (between sub-sites of the same estuary) and large- (between estuaries) spatial scales due to differences in visitor frequency and estuary size. Responses are expected to be greater on larger estuaries and when visitor frequency is lower.

3.3 Methods

3.3.1. Study area

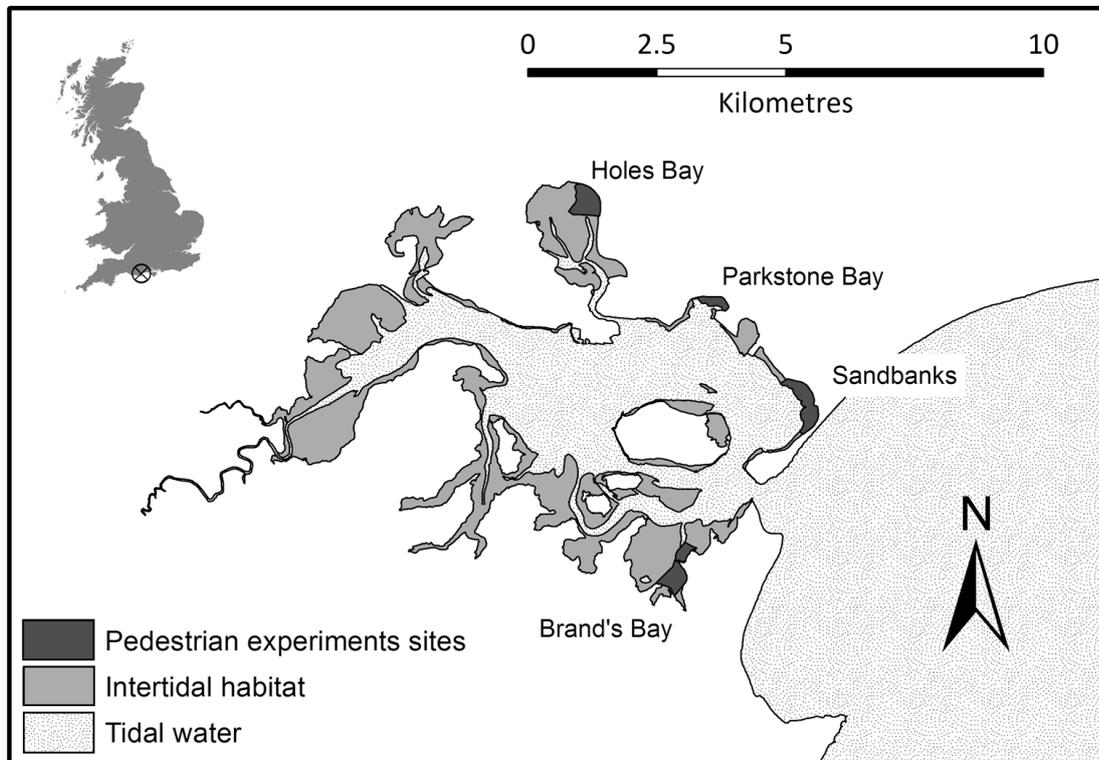


Figure 3.1. Poole Harbour, UK (50°41'47"N, 01°59'46"W) – extent of intertidal habitats and pedestrian disturbance experiment locations. Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

Poole Harbour is a shallow estuary on the south coast of the UK with approximately 36 km² of water at high water spring tide (Humphreys and May 2005) and nearly 20 km² of intertidal mud, sandflats and marshes between mean low water and highest astronomical tides (Powell 2005). The national and international biological importance of these habitats and the species that they support are recognised through a variety of conservation designations; including Heritage Coast status, Site of Special Scientific Interest (SSSI), Ramsar wetland and Special Protection Area (SPA). SPA features of particular relevance to this study are the internationally important numbers of wintering black-tailed godwit *Limosa limosa* and an overall wintering waterbird assemblage of over 20,000 birds; including dunlin *Calidris alpina*, curlew *Numenius arquata* and redshank *Tringa totanus* in nationally important numbers (English Nature 1999).

Much of the southern and western parts of Poole Harbour's 100 km shoreline are natural; fringed by reedbeds and saltmarsh, but the northern and eastern areas are dominated by

artificial walls, embankments and marinas associated with the heavily populated areas of the Poole and Bournemouth conurbation (Humphreys and May 2005). In addition to the large human population of local residents, Poole Harbour is a popular tourist destination for coastal recreation as well as an important port for commerce and travel, with more than 5000 commercial shipping movements annually (Poole Harbour Commissioners 2012). There are therefore many potential opportunities for human activities to conflict with the conservation importance of Poole Harbour, across a gradient of intensity of use, making it an ideal study site for investigating the mechanisms behind the varying responses of birds to such activities.

Figure 3.1 shows the locations of the four sub-sites selected for field data collection. The intertidal habitat at Sandbanks, as its name suggests, is dominated by sandy sediments; at the top of the shore there are remnants of saltmarsh and a narrow beach. The sea wall separates it from the adjacent footpath and road. The area is popular for watersports including kite surfing and wind surfing, as well as being used by walkers, dog walkers and bait diggers, and for general beach recreation. Intertidal areas at Parkstone Bay are muddier than at Sandbanks so fewer people leave the shoreline footpath; though bait diggers and dog walkers may be found here, as well as activities associated with the adjacent marina. Large numbers of people make use of the recreation ground and cycle/footpath that run along the perimeter of the site and continue west towards Poole Quay. Holes Bay also has a cycle path along much of the shoreline as well as the busy A350 dual carriageway; however, the muddy sediment here means that very few people walk onto the intertidal area, and most visitors remain on the path. In contrast to the other three sites, Brand's Bay is further from human habitation and therefore experiences relatively few visitors, many of whom only use the bird hide that overlooks the site. It is also very muddy so few visitors leave the narrow beach at the top of the shore and the likelihood of them interacting with birds feeding at the low water mark is low. Bait digging is not permitted at Brands Bay (November to March inclusive) or Holes Bay (all year round) – see Figure 1.8.

These sub-sites were selected because they are known to support a wide variety of wading birds (Pickess 2008), which would allow for between-species comparisons in the analyses. They were also chosen based on the expected differences in visitor frequencies due to the varying levels of access described above. These differences were later confirmed by field observations: instantaneous scan sampling (Altmann 1974) was used to determine the frequency of recreational activities at each sub-site; based on surveys conducted on 82 separate occasions (Table 3.1). See Chapter 5 for a more detailed description of the fieldwork methods and results relating to visitor patterns in Poole Harbour.

Table 3.1. Observed frequency of recreational activities and estimated number of disturbance events at each sub-site. Site rank is shown in brackets.

Poole Harbour sub-site	Extent of intertidal habitat (km²)	Length of shoreline (km)	Frequency of potential disturbers on intertidal (N/km²/scan)	Frequency of potential disturbers on the shoreline (N/km/scan)	Estimated number of disturbances per day (Equation 3.1)
Brand's Bay	0.1939	0.6430	3.15 (3)	1.44 (4)	2 (4)
Holes Bay	0.2698	1.1363	0.41 (4)	2.03 (3)	3 (3)
Parkstone Bay	0.0963	0.5577	10.48 (1)	46.09 (1)	28 (1)
Sandbanks	0.3055	1.6416	7.70 (2)	3.59 (2)	9 (2)

Each hour-long survey took place within an hour of low tide and consisted of scans every ten minutes, during which the number and type were noted of all activities occurring on the intertidal area, and adjacent shallow water, beach and shoreline footpaths. With the exception of some western areas of the estuary with little or no public access, the four sub-sites are representative of the range of visitor access levels across the whole estuary. The final column in Table 3.1 gives a value for the estimated number of potential disturbance events that result in birds flying away (using Equation 3.1, though not necessarily all experienced by the same individual birds). This value is based on the frequencies of activities that were observed during daylight hours; an average of ten hours daylight per day between September and March; information from Stillman et al. (2012) who noted that 6% of coastal visits in autumn/winter occur during darkness; and Liley et al.'s (2012) observation that 10% of potential disturbers result in one or more birds flying away.

$$\text{Day visitors } (V_{day}) = ((V_{inter} \times A_{inter}) + (V_{shore} \times L_{shore})) \times 10 \quad \text{Equation 3.1a}$$

$$\text{Night visitors } (V_{night}) = \frac{V_{day}}{0.94} \times 0.06 \quad \text{3.1b}$$

$$\text{Disturbances per day} = (V_{day} + V_{night}) \times 0.1 \quad \text{3.1c}$$

3.3.2. Field data collection – pedestrian experiments

Disturbance experiments took place over the course of three wading bird non-breeding seasons: January to March 2013; September 2013 to March 2014; and October 2014 to March 2015. In order to allow comparison with other studies, data collection followed a similar method to that as described in the previous chapter to record bird behavioural responses to an approaching pedestrian. The procedure was to identify a target bird (either feeding alone or as part of a flock), note how far away it was, and then to walk directly towards it at a comfortable constant pace on the soft sediment (approximately 2.5 km/h). In some cases it was necessary to approach on a tangent if the muddy sediment was not solid enough to walk directly towards the bird safely alone. The type of approach was noted in case it affected how the birds responded. All aspects of the target bird's response were recorded into a dictaphone (Sony ICD-PX312M digital voice recorder) – noting when the bird became alert, fled, landed and resumed feeding. A laser range finder (Longridge Pin Point GADFL1 6x magnification) was used to measure the distances in metres at which the bird became alert, fled and landed. By playing back the recordings, it was then also possible to determine the length of time (to the nearest second) that birds spent in each stage of

response, and the total time disturbed. In addition, a variety of variables that were considered to be potential predictors or confounding factors of the birds' responses to experimental disturbance were recorded or looked up at a later date: including flock size, whether the first response was to walk or fly away, and environmental conditions. Air temperature (°C) and wind speed (km/h) records were taken from the nearest weather station at Bournemouth Airport, 11 km away (UK Meteorological Office 2015). Since warm bodies lose heat to the surrounding environment at faster rates when exposed to greater wind speeds (Williamson 2003), the measurements of air temperature and wind speed for each disturbance experiment were converted to a wind chill equivalent temperature (T_w) using the following equation:

$$T_w = 13.12 + 0.6215 \times T - 11.37 \times V^{0.16} + 0.3965 \times T \times V^{0.16} \quad \text{Equation 3.2}$$

where T is the air temperature in °C and V is the wind speed in km/h (Williamson 2003, Osczevski and Bluestein 2005). This is considered to be a more appropriate independent variable than records of air temperature alone in relation to thermoregulation and energy budgets of birds (Wiersma and Piersma 1994).

Data were collected from the four sub-sites on 91 separate occasions, and the number of disturbances during each survey varied from 1 to 17 (median = 6; median for same species = 2) depending on the number of birds present and how many experiments could be completed in the time available. When selecting a target bird for each experiment, care was taken not to disturb the same bird or group of birds more than once per survey, and the experiments were spread out in time and space in order to avoid pseudoreplication and non-independence in the data (as far as was possible). All species of wader that were encountered on survey visits were included in the experiments.

In the same way as described in the previous chapter, mean observed flight time and mean total time lost were used to determine the energetic consequences and lost feeding time opportunity costs of responding to disturbance using the following equations (Nagy et al. 1999, Kvist et al. 2001), where M = body mass in grams:

$$\text{Cost (kJ)} = \frac{10^{0.39} \times M^{0.35} - 0.95}{1000} \times \text{time spent in flight (s)} \quad \text{Equation 3.3}$$

$$\text{Energy requirement (kJ)} = 10.5 \times M^{0.681} \quad \text{Equation 3.4}$$

3.3.3. Field data collection – proportion of time that birds spent feeding

The overall proportion of available time spent feeding can be derived from the product of the proportion of birds feeding at any one time and the proportion of exposure time that birds spend away from the roost (Goss-Custard et al. 1977). This was achieved using scan sampling (Altmann 1974) with multiple one-hour surveys throughout the winter (n = 60). During each one hour survey, every ten minutes, counts were made of the number of birds of each species that were feeding and the total number present to find the proportion of birds feeding. The mean proportion of birds feeding was taken for each survey and the results were averaged across all surveys and sites to derive a single value per species for the whole of Poole Harbour. These could then be combined with information from surveys that were carried out over the full intertidal exposure period. During the full tidal exposure surveys counts were made of the number of birds present and the proportion feeding. A scan was completed every twenty minutes, beginning shortly before the time that the intertidal area was expected to be exposed by the falling tide. Each survey ended when the tide covered the area again and/or all birds had departed the study area. The length of time for which at least 50% of the total number of each species was present on the intertidal area was taken as the length of time that an average bird of that species spent away from the roost. Time constraints dictated, however, that these full exposure surveys could only take place during the early stages of the non-breeding season; so they may not reflect bird arrival and departure times at all stages of the season.

3.3.4. Model selection and data analysis

As in the previous chapter, data analysis followed Burnham and Anderson's (2002) information theoretic approach to model selection, which balances model complexity against goodness of fit (Garamszegi 2011). Multi-model inference and model averaging (Johnson and Omland 2004, Symonds and Moussalli 2011) were used to understand the strength and direction of the relationships between the measured response behaviours and potential predictor variables. Preliminary data exploration showed no difference in responses whether a bird's first response was to walk or to fly (except perhaps for black-tailed godwit – see Appendix 3) so the data were combined, and the FID values presented here refer to the distance between the bird and disturber when the bird first started to move away. Preliminary results also suggested that it was appropriate to combine data from all three winter years without needing to include this as a potential predictor variable (Appendix 4).

Although eight separate measures of response were recorded (alert distance, FID, landing distance, alert time, walking time, flight time, latency time and total time lost – see Figure 3.2), just three were chosen for in-depth investigation: FID (because this is the most commonly reported variable in other studies); flight time (which relates to the majority of the additional energy costs of responding to disturbance); and total disturbance time (which relates to the full lost-feeding-time cost of each disturbance event). As described in the previous chapter, it is important to record and report time-related measures of response as well as FID in order to achieve a better understanding of the full impacts of disturbance. When deciding on the global models to be tested for each response variable, initially all of the independent variables listed in Table 3.2 (except ‘response 1’ and ‘winter year’) were included along with all biologically plausible two-way interactions. Some interactions were found to be non-significant, however, so these were subsequently excluded from the candidate model set – as recommended by Schielzeth (2010). Two dummy variables called ‘is it an oystercatcher?’ and ‘is it a plover?’ were also included since oystercatcher *Haematopus ostralegus*, ringed plover *Charadrius hiaticula* and grey plover *Pluvialis squatarola* are in different families to the other eight species (*Haematopidae* and *Charadriidae* versus *Scolopacidae*) and have different feeding behaviours from the rest (Goss-Custard et al. 2006b), which might affect how they perceive and avoid disturbance risk. Model averaging was performed on the 95% confidence model set after centring (subtracting the mean) and standardising (dividing by two standard deviations) the input variables – to facilitate interpretation of the relative strength of parameter estimates (following Gelman 2008 and Grueber et al. 2011). The three response variables were also natural-log-transformed before carrying out the analyses, which helped to achieve a better distribution of the model residuals in relation to the assumptions of the statistical tests used, which were checked by visual inspection of diagnostic plots as recommended by Zuur et al. (2010).

Table 3.2. Measured response variables and potential predictor variables.

Name	Details	Units
Response variables		
FID	Flight initiation distance – the distance between bird and disturber when the bird first starts to move away.	metres
FlightTime	The length of time a bird spends in flight in response to disturbance.	seconds
TotalLost	The total feeding time lost in response to a disturbance – from becoming alert to resuming feeding.	seconds
Potential predictor variables		
Approach	Whether the disturber approached a bird directly or on a tangent. (0=Direct, 1=Tangent).	-
FlockSize	Number of conspecifics feeding with the target bird.	-
Response1*	Whether a birds' initial response was to walk or fly away.	walk/flight
IsItOC	Dummy variable – “is it an oystercatcher?” (0=No, 1=Yes).	yes/No
IsItPlover	Dummy variable – “is it a plover?” (0=No, 1=Yes).	yes/No
SpMass	Mean mass of target species (using values reported by BTO, British Trust for Ornithology (2015)).	grams
StartDist	Distance between the bird and observer before starting to approach.	metres
VisitFreq	Mean frequency of potential disturbers on the intertidal area at each sub-site. See Table 3.1.	number per km ² per scan
WindChill	Wind chill equivalent temperature using data from the nearest weather station (Bournemouth Airport, UK Meteorological Office (2015)). See Equation 3.2.	°C
WinterDay	A measure of the number of days through the non-breeding season. Winter day 1 = 1 August.	-
WinterYear*	Factor indicating in which season the observation took place.	-

* [Preliminary data exploration indicated that the variable could be excluded from final analyses].

R was used for all analyses (R Core Team 2015), with functions available in ‘arm’ (Gelman and Su 2015) to standardise model predictors, and the multi-model inference package ‘MuMIn’ (Bartoń 2015) for model selection and averaging: plots were produced using ‘ggplot2’ (Wickham 2009) and ‘PerformanceAnalytics’ (Peterson and Carl 2014). Means are presented \pm one standard error.

3.3.5. Literature search

Response distances measured in one place may not apply to other areas (e.g. Laursen et al. (2005), Weston et al. (2012) and see Chapter 2). This statement was tested by searching the available literature for suitable studies for comparison with the data presented here for Poole Harbour i.e. those that report responses to disturbance for multiple species of wader that spend the non-breeding season on the estuaries of Western Europe. The search revealed six studies that reported wader FID values in response to experimental disturbance at different European sites. FID was the only measure of response that was consistently reported by all six studies; other measures such as alert distance or total time disturbed were only reported by some of the studies, and were therefore not included. The results are not intended to be an exhaustive list, although there appear to be no other published, multi-species studies of this kind for this group of species – such studies seem to mainly be restricted to Australian and American species.

3.4 Results

Waders from 11 species were experimentally disturbed on a total of 597 occasions across the three non-breeding seasons between January 2013 and March 2015, during which the wind chill equivalent temperature of each survey ranged from a minimum of -7.2°C up to 17.9°C (mean = 5.24 ± 0.20). Bird responses are summarised in Table 3.3 and Figure 3.3. Note that ringed plover and greenshank *Tringa nebularia* have been excluded from some tests and graphical representations in this section due to the low numbers of observations.

3.4.1. Relationship between measures of response

Most pairs of measured response variable were significantly positively correlated with each other (Figure 3.2), with particularly strong positive associations between alert distance and FID, and between landing distance and flight time. However, there were also some pairs of response measures that were significantly *negatively* correlated with each other; for example, birds that spent longer walking away had shorter flight times and latency times.

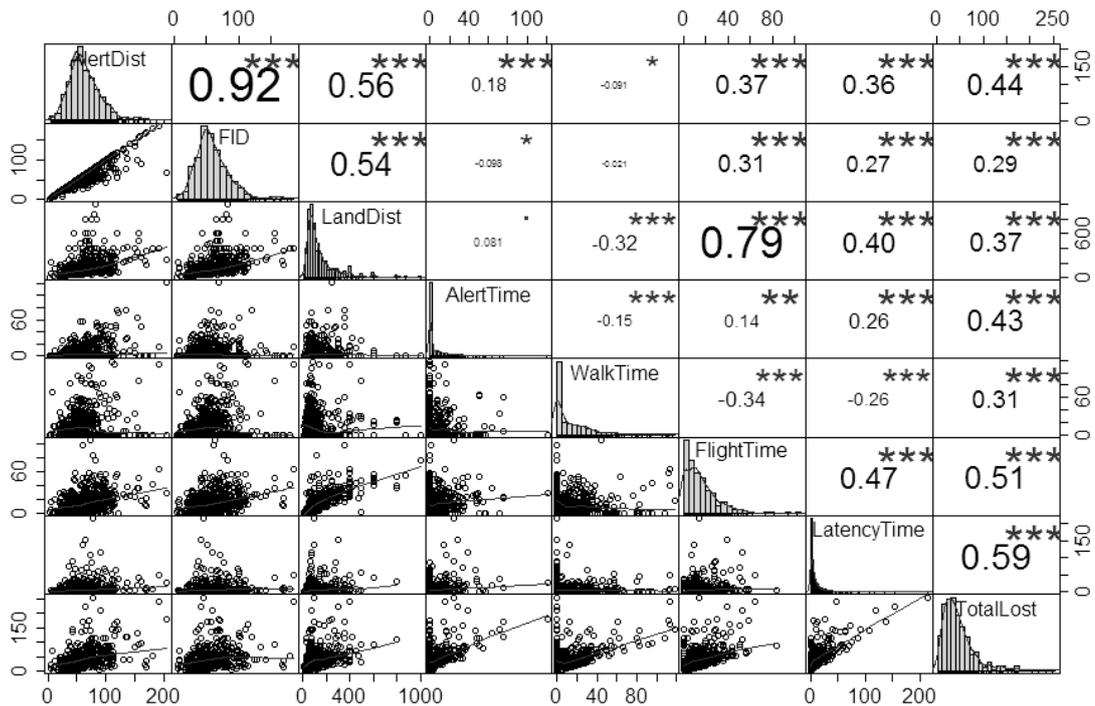


Figure 3.2. Correlation matrix chart for all measured responses to disturbance, with Spearman rank correlation coefficients (font size relates to effect size) and stars to indicate significance level (‘***’ <0.001; ‘**’ <0.01; ‘*’ <0.05).

Table 3.3. Summary of responses to disturbance by an approaching pedestrian during the non-breeding season for eleven species of wader. Flight initiation distance (FID); time spent in flight (FlightTime); and total time for which birds are prevented from feeding (TotalLost). Species are presented in order of decreasing body size.

Species	Body mass (g)	FID (m)					FlightTime (s)					TotalLost (s)				
		N	Median	Mean	s.e.	Range	N	Median	Mean	s.e.	Range	N	Median	Mean	s.e.	Range
Curlew (CU)	782	93	84	88.25	3.45	33-186	66	23	25.61	1.9	3-84	66	51	63.02	5.41	10-241
Oystercatcher (OC)	546	281	56	58.19	1.06	24-170	169	13	16.64	0.9	1-59	169	44	52.78	2.94	8-254
Bar-tailed godwit (BA)	306	66	43	44.97	1.66	25-83	44	15	17.05	1.7	3-58	44	33.5	36.57	2.45	6-71
Black-tailed godwit (BW)	299	22	50	53.5	4.93	26-105	11	18	18.36	3.3	4-36	11	30	49.55	12.7	6-143
Grey plover (GV)	243	16	64.5	63.75	4.61	31-85	9	15	14.44	1.9	7-23	9	56	69.78	14.1	28-172
Greenshank (GK)	199	2	70.5	70.5	13.5	57-84	2	8	8	1	7-9	2	48	48	24	24-72
Redshank (RK)	153	56	52	59.09	3.4	21-115	28	12	13.89	1.8	4-43	28	36	39.89	4.79	8-120
Turnstone (TT)	108	13	24	25.46	6.3	3-87	11	12	12.55	1.7	4-22	11	34	33.45	4.52	13-58
Ringed plover (RP)	68	1	46	46	-	46-46	0	-	-	-	-	0	-	-	-	-
Sanderling (SS)	58	27	22	22.33	1.86	6-52	15	7	9.73	2.1	1-30	15	20	24.67	3.96	2-49
Dunlin (DN)	50	20	27.5	33.4	4.05	15-96	11	10	11.73	1.9	4-24	11	19	22.55	5.44	4-57

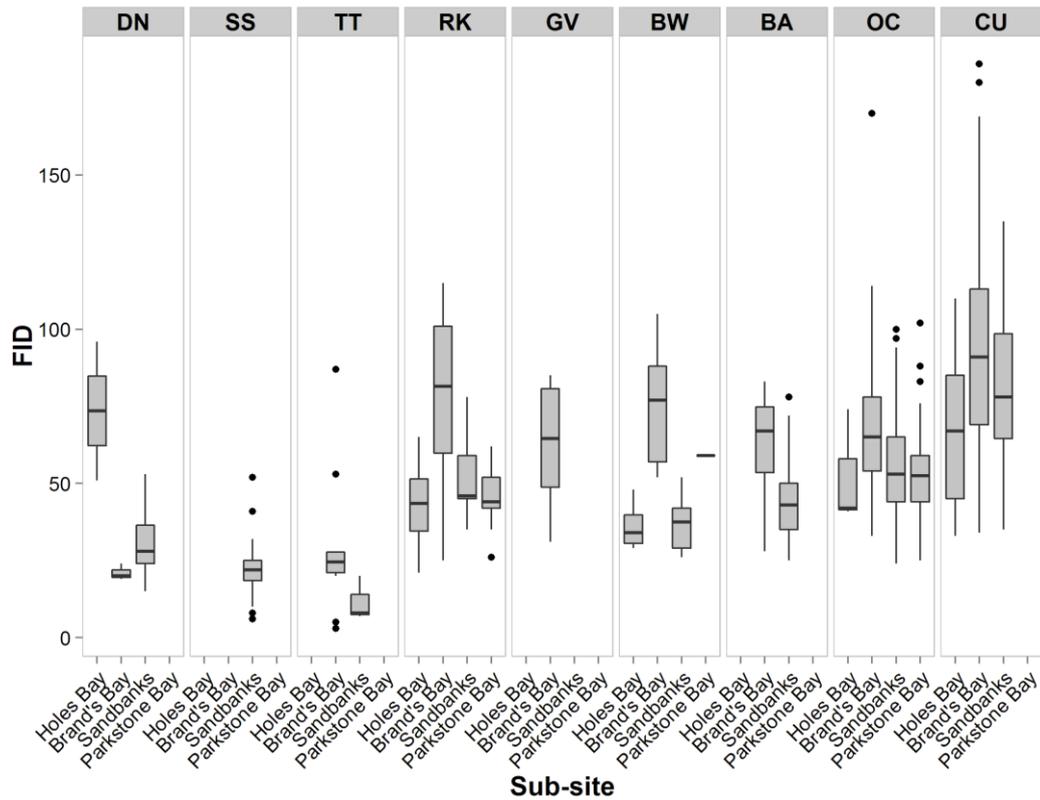


Figure 3.3. Variation in flight initiation distance (FID) between species and sub-sites. Sites are ordered from left to right by increasing frequency of activities observed on the intertidal. CU=curlew; OC=oystercatcher; BA=bar-tailed godwit; BW=black-tailed godwit; GV=grey plover; RK=redshank; TT=turnstone; SS=sanderling; DN=dunlin.

3.4.2. Factors affecting responses to disturbance

There was a significant difference between species in all three measures of disturbance: $\log(\text{FID})$ ($F_{10,586} = 51.85, p < 0.001$); $\log(\text{FlightTime})$ ($F_{9,356} = 6.108, p < 0.001$); $\log(\text{TotalLost})$ ($F_{9,356} = 7.31, p < 0.001$). In support of Hypothesis 2, linear regressions showed that this difference between species is significantly positively related to body size (Figure 3.4); with larger species exhibiting longer FIDs, spending more time fleeing, and losing more feeding time overall as a result of responding to disturbance. However, within-species responses were highly variable – for example across the range of wind chill equivalent temperatures – and the respective adjusted R^2 values were low, indicating that only a small proportion of the variability in behavioural responses to disturbance can be explained by species body mass. Other factors must also play a role; for example site-related differences in FID can be seen for several species in Figure 3.3.

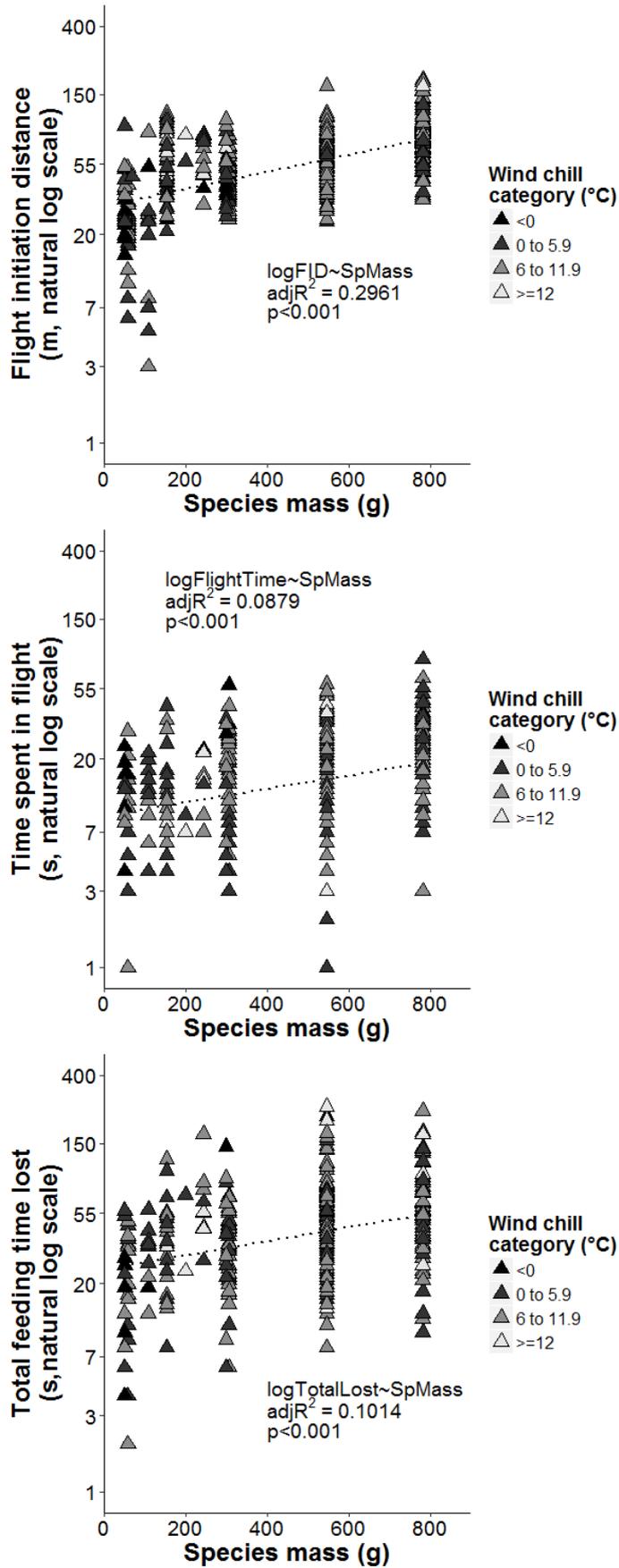


Figure 3.4. Relationship between species mass and responses to disturbance, with influence of wind chill equivalent temperature.

When candidate models were ranked by AIC_c no single model stood out with much higher support than the others, and model weights were generally low (Appendix 5) so model averaging was used on the 95% confidence set to find parameter estimates and measures of relative importance for each predictor variable (Table 3.4). This revealed both similarities and differences in the most important predictors of bird responses to disturbance between the three measures of response. In all three cases, species mass had a relative importance of 1 – indicating that it was present in all models in each of the three 95% confidence sets. Similarly, start distance and visit frequency were well supported (relative importance > 0.75) for the three response measures. Wind chill equivalent temperature was well supported for FID, but less-so for the time-related measures of response; and conversely, flock size was poorly supported in relation to FID, yet well supported for flight time and total time lost. The dummy variable ‘is it a plover’ was well supported for FID, and ‘is it an oystercatcher’ in relation to flight time. ‘Approach type’, however, was consistently poorly supported in relation to all three measures of response to disturbance; i.e. there was no difference in response whether the disturber approached directly or on a tangent.

The directions of the coefficients indicate that magnitude of response was greater in larger birds, at sites with lower visit frequencies, and on occasions when the disturber began to approach from further away. Plovers had greater FIDs and lost more feeding time overall than predicted by their size, and oystercatchers spent more time in flight for their size. Birds in larger flocks spent more time in flight and lost more feeding time overall than birds feeding singly or in small groups. However, there is uncertainty in the precision of the estimates for the less well supported predictor variables since the 95% confidence intervals include zero (Table 3.4).

Table 3.4. Relative importance and model averaged centred and standardised coefficients (across the 95% confidence set) of predictors for bird responses to disturbance; based on linear models with natural-log-transformed dependent variables. Predictors were centred and standardised following Gelman (2008) and Grueber et al. (2011) to allow direct comparison of their magnitudes. Estimates whose 95% confidence interval does not include zero have been highlighted in bold. See Table 3.2 for parameter abbreviations.

a) logFID

Predictor	N containing models	Relative importance	Estimate	s.e.	95% CI	
					Lower limit	Upper limit
Intercept	-	-	3.958	0.015	3.929	3.987
SpMass	42	1	0.447	0.037	0.376	0.519
StartDist	42	1	0.372	0.034	0.306	0.438
VisitFreq	42	1	-0.111	0.035	-0.180	-0.041
SpMass:VisitFreq	42	1	0.220	0.061	0.099	0.340
IsItPlover	28	0.87	0.185	0.113	-0.036	0.406
WindChill	29	0.83	0.065	0.047	-0.026	0.156
WinterDay	18	0.48	0.026	0.039	-0.050	0.103
IsItOC	21	0.43	-0.018	0.031	-0.080	0.043
Approach	19	0.42	0.027	0.046	-0.063	0.117
FlockSize	17	0.26	-0.004	0.017	-0.037	0.030

b) logFlightTime

Predictor	N containing models	Relative importance	Estimate	s.e.	95% CI	
					Lower limit	Upper limit
Intercept	-	-	2.650	0.056	2.541	2.759
SpMass	395	1	0.470	0.099	0.276	0.664
VisitFreq	262	0.81	-0.145	0.102	-0.345	0.056
StartDist	251	0.76	0.130	0.103	-0.071	0.332
IsItOC	262	0.74	-0.122	0.101	-0.319	0.076
FlockSize	243	0.71	0.210	0.213	-0.208	0.627
FlockSize:SpMass	165	0.62	0.562	0.532	-0.481	1.605
WinterDay	219	0.55	0.073	0.103	-0.129	0.274
WindChill	217	0.52	-0.003	0.072	-0.143	0.137
Approach	262	0.49	0.054	0.112	-0.166	0.273
WindChill:WinterDay	93	0.31	-0.108	0.182	-0.466	0.249
IsItPlover	147	0.24	-0.001	0.120	-0.235	0.234
Approach:SpMass	123	0.21	0.051	0.132	-0.207	0.309

c) logTotalLost

Predictor	N containing models	Relative importance	Estimate	s.e.	95% CI	
					Lower limit	Upper limit
Intercept	-	-	3.726	0.048	3.632	3.820
SpMass	121	1	0.433	0.091	0.256	0.611
VisitFreq	114	0.99	-0.195	0.082	-0.356	-0.034
StartDist	95	0.95	0.195	0.090	0.019	0.372
FlockSize	91	0.88	0.310	0.199	-0.079	0.700
IsItPlover	92	0.87	0.473	0.281	-0.078	1.024
FlockSize:SpMass	76	0.84	0.848	0.495	-0.122	1.818
WinterDay	85	0.83	-0.082	0.083	-0.245	0.080
VisitFreq:WinterDay	48	0.66	-0.207	0.188	-0.574	0.161
IsItOC	59	0.48	0.052	0.077	-0.098	0.202
WindChill	58	0.41	0.039	0.072	-0.103	0.181
Approach	47	0.36	-0.045	0.095	-0.231	0.142

Separate single-species analyses (Table 3.5) showed support for some predictor variables in relation to the FIDs of some species, though with the exception of 'start distance' there are no clear patterns. For all species except turnstone *Arenaria interpres*, FID was greater when starting distance was greater. Most predictor variables had poor explanatory power in relation to fleeing time and total time lost, and most of the 95% confidence intervals for the parameter estimates include zero (Table 3.6), so there is a great deal of uncertainty and noise in these results and it is likely that there is at least one important explanatory variable that was not measured (as was also the case on the Wash as described in the previous chapter).

Table 3.5. Species-specific model averaging results – relative importance of potential predictors. Values ≥ 0.6 (high and medium support) highlighted in bold. See Table 3.2 for parameter abbreviations.

a) logFID

Predictor	Species								
	CU	OC	BA	BW	GV	RK	TT	SS	DN
StartDist	1	1	1	0.887	0.819	1	0.361	0.831	0.990
WinterDay	0.798	0.274	0.320	0.973	0.115	0.312	0.128	0.182	0.834
FlockSize	0.685	0.368	0.229	0.157	0.103	0.212	0.087	0.537	0.087
WindChill	0.289	0.630	0.344	1	0.163	0.677	0.142	0.304	0.394
VisitFreq	0.247	0.975	0.365	0.109	-	0.922	0.255	-	0.469
Approach	0.233	0.905	0.655	0.265	0.146	0.859	0.171	-	0.654
Approach:VisitFreq	-	0.780	-	-	-	0.814	-	-	-
VisitFreq:WinterDay	-	-	0.097	-	-	-	-	-	-

b) logFlightTime

Predictor	Species								
	CU	OC	BA	BW	GV	RK	TT	SS	DN
StartDist	1	0.245	0.200	0.117	0.113	0.166	0.132	0.130	0.095
FlockSize	0.462	0.239	0.194	0.076	-	0.609	0.085	0.380	0.153
WinterDay	0.285	0.485	0.852	0.099	0.064	0.156	0.089	0.121	0.433
WindChill	0.246	0.470	0.879	0.079	0.097	0.223	0.074	0.086	0.065
VisitFreq	0.226	0.926	0.436	0.083	-	0.848	0.123	-	0.084
Approach	0.220	0.447	-	0.097	0.077	0.827	0.089	-	0.073
WindChill:WinterDay	-	0.299	0.833	-	-	-	-	-	-
VisitFreq:WinterDay	-	-	-	-	-	-	0.012	-	-
Approach:VisitFreq	-	-	-	-	-	0.765	-	-	-

c) logTotalLost

Predictor	Species								
	CU	OC	BA	BW	GV	RK	TT	SS	DN
StartDist	0.965	0.612	0.504	0.152	0.051	0.212	0.067	0.117	0.296
VisitFreq	0.924	0.471	0.213	0.077	-	0.207	0.037	-	0.053
Approach	0.772	0.674	-	0.084	0.215	0.403	0.097	-	0.039
WindChill	0.261	0.589	0.237	0.079	0.049	0.206	0.429	0.140	0.047
WinterDay	0.228	0.367	0.304	0.076	0.094	0.316	0.060	0.129	1
FlockSize	0.221	0.388	0.310	0.106	0.086	0.360	0.970	0.245	0.047
Approach:FlockSize	-	0.222	-	-	-	-	-	-	-

CU=curlew; OC=oystercatcher; BA=bar-tailed godwit; BW=black-tailed godwit; GV=grey plover; RK=redshank; TT=turnstone; SS=sanderling; DN=dunlin.

Table 3.6. Standardised parameter estimates and confidence intervals for six potential predictors of wader responses to disturbance (with interactions). Dependent variables have been natural-log-transformed. Estimates whose 95% confidence interval does not include zero have been highlighted in bold. See Table 3.2 for parameter abbreviations.

a) logFID

Predictor	Species								
	Curlew			Oystercatcher			Bar-tailed godwit		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	
Intercept	4.411	4.35	4.47	4.067	4.00	4.14	3.767	3.70	3.84
1 FlockSize	-0.087	-0.25	0.07	-0.012	-0.06	0.04	-0.005	-0.07	0.06
2 StartDist	0.450	0.32	0.58	0.180	0.11	0.25	0.214	0.07	0.35
3 WinterDay	0.119	-0.05	0.29	-0.002	-0.05	0.04	-0.004	-0.10	0.09
4 WindChill	0.015	-0.09	0.12	0.038	-0.04	0.12	-0.026	-0.14	0.09
5 VisitFreq	0.008	-0.07	0.09	-0.022	-0.13	0.08	-0.006	-0.06	0.05
6 Approach	0.008	-0.08	0.10	0.540	-0.12	1.20	0.350	-0.55	1.25
7 Approach:VisitFreq	-	-	-	0.595	-0.23	1.42	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-0.028	-0.22	0.17
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Predictor	Species								
	Black-tailed godwit			Grey plover			Redshank		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	
Intercept	3.895	3.79	3.99	4.111	3.96	4.26	4.135	3.93	4.34
1 FlockSize	-0.016	-0.14	0.11	-0.002	-0.13	0.13	-0.008	-0.12	0.10
2 StartDist	0.277	-0.02	0.58	0.298	-0.09	0.69	0.441	0.22	0.66
3 WinterDay	0.310	0.07	0.55	-0.002	-0.12	0.11	0.037	-0.15	0.22
4 WindChill	0.537	0.26	0.81	0.018	-0.14	0.18	0.134	-0.12	0.39
5 VisitFreq	0.001	-0.08	0.08	-	-	-	0.117	-0.29	0.52
6 Approach	-0.067	-0.37	0.24	0.015	-0.14	0.17	0.280	-0.24	0.80
7 Approach:VisitFreq	-	-	-	-	-	-	1.088	-0.25	2.43
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Predictor	Species								
	Turnstone			Sanderling			Dunlin		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
	Lower	Upper	Lower	Upper	Lower	Upper	Lower	Upper	
Intercept	2.874	2.31	3.43	3.009	2.84	3.18	3.408	3.27	3.55
1 FlockSize	-0.010	-0.44	0.42	0.157	-0.23	0.54	0.001	-0.11	0.11
2 StartDist	0.328	-0.78	1.44	0.324	-0.11	0.76	0.680	0.24	1.12
3 WinterDay	-0.055	-0.59	0.48	0.018	-0.19	0.23	0.349	-0.09	0.78
4 WindChill	-0.078	-0.72	0.56	0.065	-0.23	0.36	0.118	-0.25	0.48
5 VisitFreq	-0.048	-0.27	0.17	-	-	-	-0.169	-0.62	0.28
6 Approach	0.210	-1.16	1.58	-	-	-	-0.395	-1.13	0.33
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

b) logFlightTime

Predictor	Species								
	Curlew			Oystercatcher			Bar-tailed godwit		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	3.064	2.92	3.21	2.574	2.44	2.71	2.422	2.13	2.71
1 FlockSize	0.098	-0.19	0.39	0.003	-0.10	0.11	0.0005	-0.18	0.18
2 StartDist	0.553	0.25	0.86	-0.007	-0.12	0.11	-0.012	-0.19	0.17
3 WinterDay	0.038	-0.17	0.24	0.085	-0.20	0.37	0.448	-0.19	1.09
4 WindChill	-0.024	-0.20	0.15	0.064	-0.18	0.31	0.220	-0.35	0.78
5 VisitFreq	0.010	-0.15	0.17	-0.285	-0.56	-0.01	0.105	-0.23	0.44
6 Approach	0.012	-0.19	0.21	0.125	-0.27	0.52	-	-	-
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-0.153	-0.67	0.37	-1.371	-2.87	0.13
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Predictor	Species								
	Black-tailed godwit			Grey plover			Redshank		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	2.690	2.16	3.22	2.599	2.28	2.92	2.789	2.28	3.29
1 FlockSize	-0.007	-0.35	0.33	-	-	-	0.325	-0.35	1.00
2 StartDist	-0.038	-0.48	0.41	0.034	-0.26	0.33	0.003	-0.25	0.26
3 WinterDay	-0.028	-0.43	0.37	0.007	-0.18	0.20	-0.018	-0.22	0.19
4 WindChill	0.011	-0.32	0.35	-0.026	-0.29	0.24	0.046	-0.23	0.32
5 VisitFreq	0.016	-0.33	0.36	-	-	-	0.275	-0.59	1.14
6 Approach	0.036	-0.62	0.70	-0.014	-0.22	0.20	0.483	-0.71	1.68
7 Approach:VisitFreq	-	-	-	-	-	-	2.482	-0.88	5.84
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Predictor	Species								
	Turnstone			Sanderling			Dunlin		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	2.425	2.07	2.78	1.827	1.21	2.44	2.321	1.94	2.70
1 FlockSize	-0.009	-0.24	0.23	-0.342	-1.49	0.80	-0.063	-0.50	0.37
2 StartDist	-0.034	-0.37	0.30	-0.030	-0.53	0.47	-0.013	-0.39	0.36
3 WinterDay	-0.011	-0.41	0.39	0.013	-0.45	0.48	-0.294	-1.15	0.56
4 WindChill	0.004	-0.21	0.22	-0.025	-0.45	0.40	-0.009	-0.23	0.22
5 VisitFreq	-0.004	-0.10	0.09	-	-	-	-0.020	-0.31	0.27
6 Approach	-0.022	-0.43	0.39	-	-	-	0.019	-0.29	0.33
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-0.023	-0.46	0.41	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

c) logTotalTime

Predictor	Species								
	Curlew			Oystercatcher			Bar-tailed godwit		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	3.933	3.78	4.08	3.769	3.67	3.87	3.488	3.33	3.64
1 FlockSize	0.007	-0.16	0.17	0.024	-0.13	0.18	0.049	-0.18	0.28
2 StartDist	0.511	0.08	0.94	0.115	-0.13	0.36	0.121	-0.21	0.45
3 WinterDay	0.013	-0.16	0.19	-0.041	-0.22	0.14	-0.051	-0.30	0.20
4 WindChill	0.029	-0.18	0.23	0.107	-0.13	0.35	-0.022	-0.22	0.18
5 VisitFreq	-0.456	-0.91	0.00	-0.074	-0.29	0.14	-0.014	-0.13	0.11
6 Approach	-0.426	-1.06	0.20	0.271	-0.26	0.81	-	-	-
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	0.312	-1.04	1.66	-	-	-

Predictor	Species								
	Black-tailed godwit			Grey plover			Redshank		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	3.532	2.86	4.20	4.120	3.73	4.51	3.506	3.27	3.75
1 FlockSize	-0.047	-0.60	0.51	-0.036	-0.40	0.33	-0.123	-0.59	0.34
2 StartDist	-0.087	-0.78	0.61	0.008	-0.20	0.22	-0.036	-0.33	0.25
3 WinterDay	-0.004	-0.41	0.41	0.037	-0.30	0.38	-0.095	-0.51	0.32
4 WindChill	-0.015	-0.44	0.41	0.006	-0.20	0.21	-0.026	-0.33	0.27
5 VisitFreq	-0.010	-0.42	0.40	-	-	-	-0.033	-0.35	0.28
6 Approach	-0.009	-0.76	0.75	0.112	-0.43	0.65	-0.165	-0.72	0.39
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Predictor	Species								
	Turnstone			Sanderling			Dunlin		
	Estimate	95% CI		Estimate	95% CI		Estimate	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Intercept	3.415	3.20	3.63	2.914	2.39	3.44	2.804	2.481	3.127
1 FlockSize	-0.793	-1.40	-0.19	-0.125	-0.82	0.57	-0.009	-0.193	0.175
2 StartDist	-0.012	-0.17	0.14	0.002	-0.38	0.38	-0.216	-1.026	0.594
3 WinterDay	-0.005	-0.17	0.16	-0.027	-0.45	0.39	-1.621	-2.514	-0.729
4 WindChill	-0.199	-0.76	0.36	0.040	-0.42	0.50	0.009	-0.169	0.186
5 VisitFreq	0.000	-0.03	0.03	-	-	-	0.013	-0.202	0.228
6 Approach	0.053	-0.47	0.58	-	-	-	-0.003	-0.185	0.180
7 Approach:VisitFreq	-	-	-	-	-	-	-	-	-
8 VisitFreq:WinterDay	-	-	-	-	-	-	-	-	-
9 WindChill:WinterDay	-	-	-	-	-	-	-	-	-
10 Approach:FlockSize	-	-	-	-	-	-	-	-	-

Table 3.7. An assessment of the time and energy costs incurred by waders in Poole Harbour per disturbance response, the number of disturbances that would be expected to reduce available feeding time by 1%, 5% and 10%, and observations of proportion of time spent feeding.

Species	Cost per flight response (kJ) ^a	Thermoneutral daily energy requirement (kJ) ^b	Energy cost per flight as % of daily intake requirement	Time cost per flight as a % of available feeding time (8hrs of exposure per 24hrs)	Number of disturbances to reduce available feeding time (based on 8hrs of exposure per 24hrs) by:			Proportion of available time spent feeding ^c
					1%	5%	10%	
Curlew	0.623	980.53	0.064	0.219	5	23	46	0.61
Oystercatcher	0.355	767.75	0.046	0.183	5	27	55	0.59
Bar-tailed godwit	0.294	517.57	0.057	0.127	8	39	79	0.53
Black-tailed godwit	0.314	509.47	0.062	0.172	6	29	58	0.47
Grey plover	0.229	442.37	0.052	0.242	4	21	41	0.29
Greenshank	0.118	386.11	0.030	0.167	6	30	60	-
Redshank	0.185	322.82	0.057	0.139	7	36	72	0.49
Turnstone	0.147	254.65	0.058	0.116	9	43	86	0.30
Ringed plover	0.095	185.84	0.051	0.086	12	58	117	-
Sanderling	0.090	166.76	0.054	0.086	12	58	117	0.31
Dunlin	0.102	150.73	0.068	0.078	13	64	128	0.41

^a using cost per second of flight from Kvist et al. (2001)

^b using Nagy et al.'s (1999) allometric equation

^c observations made in this study

3.4.3. Costs of responding to disturbance

For all species the energetic cost of flight in response to a single disturbance event was less than 0.1% of daily energy requirement (Table 3.7). The time cost per individual response was similarly low (less than 0.3%) so a large number of disturbance events that would have to occur to cause even a moderate reduction in available feeding time; for example a 5% reduction in available feeding time was predicted to result from between 21 and 64 response flights. Estimates of the proportion of available intertidal feeding time used by each species ranged from 29% (grey plover) to 61% (curlew).

Differences in flight time between species meant that there was no significant relationship between species mass and the energetic cost of flight per disturbance response when expressed as a percentage of daily requirement (Figure 3.5; $F_{1,364} = 0.00046$, $p = 0.98$).

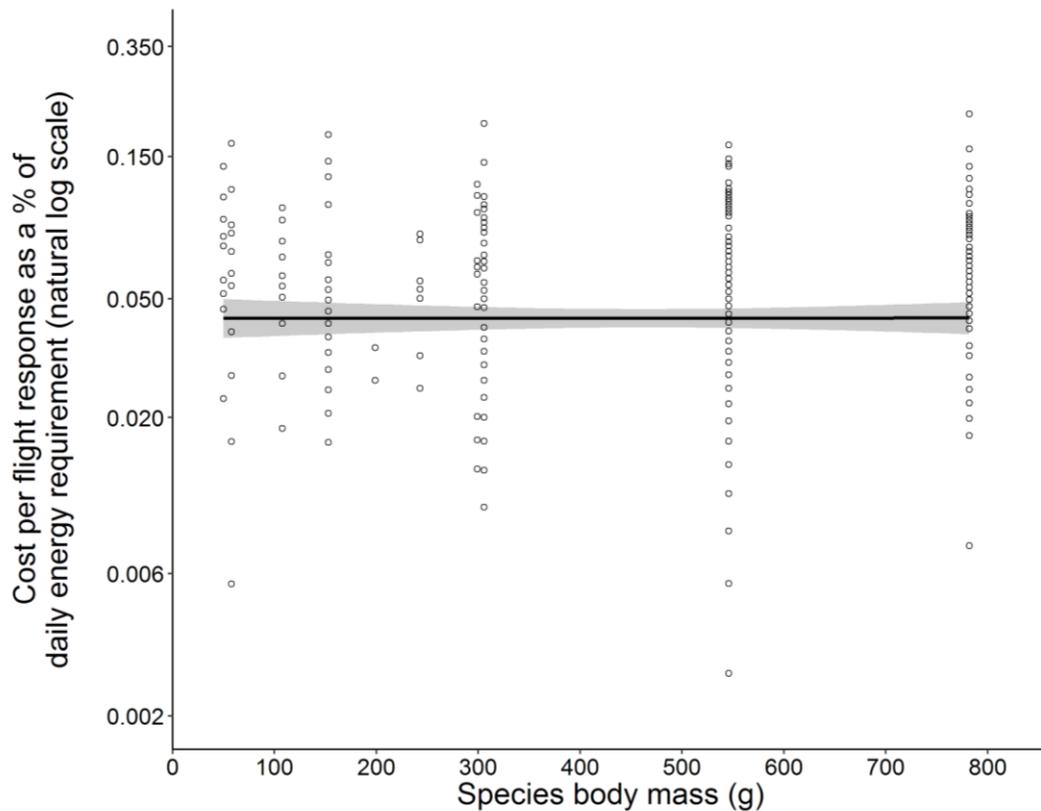


Figure 3.5. Relationship between species body mass and energetic costs of flight in response to disturbance. y-axis presented on a natural log scale.

3.4.4. Comparisons with other sites

The literature search for comparable response data from other sites (Figure 3.6) showed considerable variation both within and between sites – more so than the within site variation observed in this study in Poole Harbour. It is apparent that both the mean and range of FIDs exhibited by birds in Poole Harbour were lower than those reported from the other sites (except Belfast Lough), and the difference was particularly marked for the larger species (curlew, oystercatcher, bar-tailed godwit *Limosa lapponica* and grey plover).

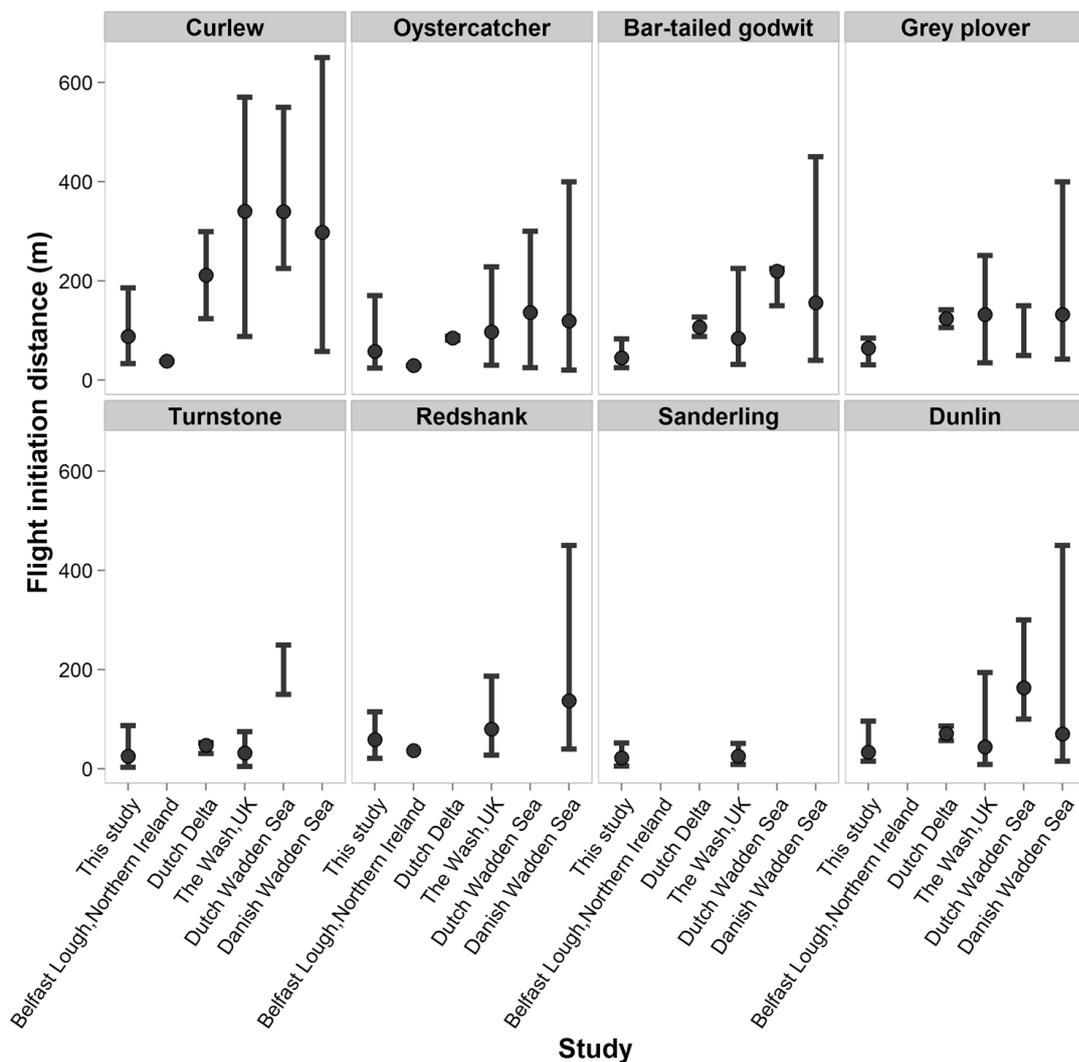


Figure 3.6. A comparison of published FID values (dots = mean; bars = range): Poole Harbour (this study); Belfast Lough (Fitzpatrick and Bouchez 1998); Dutch Delta (summarised by Smit and Visser (1993)); The Wash (Chapter 2); Dutch Wadden Sea (summarised by Smit and Visser (1993)); Danish Wadden Sea (Laursen et al. 2005). N.B. Laursen et al. (2005) collected data during the autumn and spring staging periods as opposed to throughout the winter season.

3.5 Discussion

This pedestrian disturbance study in Poole Harbour provides new data on the disturbance responses of wintering waders, adding to the relatively small number of sites for which comparable data are available. The results offer insights into the mechanisms behind the observed variability in bird responses, as well as allowing further comparisons between sites to judge the applicability of individual studies to new sites and situations. Hypothesis 1 that all measures of response would be positively correlated was well supported; this was the case for most pairs of the eight measures of response that were recorded. This shows that the major stages of the anti-predator/disturbance-avoidance response are related to the relative costs of fleeing or remaining (as predicted by Frid and Dill's (2002) risk-disturbance hypothesis). However, within that process there appear to be trade-offs; for example, birds that walked away for longer tended not to fly as far or for as long. The broad patterns observed in data the results of disturbance experiments on the Wash (Chapter 2), which were the basis for Hypothesis 2, were also apparent in this study: larger species exhibited greater responses (longer FIDs; more time in flight; greater total time lost) and FID was lower at lower temperatures. But although there are similarities in the broad patterns between sites, there are also clear differences in responses at both large- (between sites) and smaller- (within site) spatial scales (supporting Hypothesis 3). This was demonstrated in Figure 3.6 with differences in mean and range of FID values reported by different studies; and by the fact that the visitor frequency (VisitFreq) was a well-supported candidate predictor for FID, flight time and total time lost in Poole Harbour.

3.5.1. Understanding factors affecting response

Aside from the importance of between-species differences and the effect of temperature (adjusted for wind chill), two main variables were well supported in relation to all three measures of response: distance between the disturber and the target bird when starting to approach (StartDist) and visitor frequency at each sub-site (VisitFreq). Each will be discussed in turn.

Blumstein (2003), too, found a significant positive relationship between starting distance and FID, as well as a significant interaction with species (i.e. the relationship between starting distance and FID was different for different species). He also points out that species living in open habitats, like estuarine systems, have greater opportunities to detect and respond to disturbances at greater distances, resulting in larger and more variable FIDs. Both these points could help to explain the between-estuary differences shown in Figure

3.6, and the fact that the differences are more pronounced for some species. The Wash and the Wadden Sea, for example, are expansive sites, and Poole Harbour by comparison has fewer areas where greater starting distances can occur.

The negative relationship between visitor frequency and magnitude of response offers some evidence for habituation occurring at more frequently disturbed sites. However, as is often the case in such studies (as it was in the previous chapter), it is impossible to rule out alternative explanations without precise knowledge of the body condition and past experiences of individual birds, and without detailed analysis of invertebrate food availability in relation to the different diets consumed by each species (Higham and Shelton 2011). As Bejder et al. (2009) point out, confirmation of habituation occurring requires long-term sequential measurements of responses by known individuals to controlled stimuli. Habituation may be occurring to some extent in Poole Harbour, but these results suggest that other factors are more important (Table 3.4) and therefore mask the effects or limit the extent to which birds can modify their responses through habituation. Indeed, if habituation were a key factor in explaining variation in bird responses, winter day might be also expected to be important as birds 'get used to' the presence of humans throughout the winter, yet this was not found to be the case in the all-species analyses. The only significant relationships that were found in relation to winter day were a decrease in total time lost for dunlin, and an *increase* in FID for black-tailed godwit.

In fact the single-species analyses were relatively inconclusive in general: some variables were well supported for some species, though almost all of the 95% confidence intervals for the parameter estimates included zero. Like with the single-species analyses of the Wash data in the previous chapter, it appears that the important predictor variables may be different for different species, and it is likely that other mechanisms are involved that were beyond the scope of this study to measure – such as variations in individual body condition (Beale and Monaghan 2004b), age and sex (Durell and Atkinson 2004), territoriality (Turpie 1995, Colwell and Mathis 2001) or experience (Laursen et al. 2005, Lin et al. 2012).

It was surprising that the all-species analyses did not show much support for the effect of type of approach (relative importance <0.5 for all three measures of response), given that anecdotally it is easier to approach waders when walking on a tangent, and has been shown in for example American robins (Eason et al. 2006) and iguanas (Burger et al. 1992). In the few single-species analyses for which approach type was well supported (oystercatcher and redshank) FID was actually higher when birds were approached on a tangent – though again, the 95% confidence intervals for the parameter estimates include zero. Since this

research was not specifically designed to test for the effects of approach type (the majority of approaches were direct) and it was not evenly spread across sub-sites (no tangential approaches at Sandbanks or Parkstone Bay), if there is an effect of approach type it could have been confounded by site and/or other factors.

Laursen et al. (2005) found that flock size is an important predictor of FID, with larger flocks responding at greater distances, however, this was not found to be the case in Poole Harbour. Flock size was the least well supported candidate predictor variable in relation to FID (Table 3.4a), though there was some support for birds spending more time in flight and losing more time overall when they were feeding as part of larger flocks (Table 3.4b&c). The analyses could have been limited by the small range of flock sizes that were encountered during the disturbance experiments (range = 1-200; median = 2) and it could be the case that a relationship only exists at larger flock sizes (Glover et al. 2011).

3.5.2. Applications

Information on bird responses to disturbance, particularly FID, can and has been used to inform conservation management measures such as buffer zones or to determine likely disturbance levels from new or existing activities (Blumstein et al. 2003, Glover et al. 2011, Weston et al. 2012, Koch and Paton 2014, Livezey et al. 2016). However, in order for data from one study to be usefully applied elsewhere, knowledge is needed of the conditions under which the data were collected – particularly the variables described above: temperature, food availability, visitor frequency and starting distance. Even so, the variability and relative unpredictability relating to individual responses to disturbance force FID-related conservation measures to be very precautionary, and therefore risk being challenged or ignored. A key element of Sutinen and Kuperan's (1999) framework for explaining regulatory compliance is 'perceived legitimacy', whereby compliance is more likely when regulations are considered to be efficient, effective and fair. For example, Holsman et al. (2010) describe how deer hunters rejected a regional disease-management plan in part due to uncertainties in the plan's efficacy and perceived lack of credibility in the agency. Further examples are given by Sant (1996), Viteri and Chávez (2007) and Thomassin et al. (2010). It would be useful and effective, therefore, to have an alternative approach to determining where and when conservation measures are needed by identifying 'acceptable' levels of disturbance rather than attempting to prevent disturbance from occurring at all.

One option is to use data on time-related measures of response, together with knowledge of the ease/difficulty with which birds are achieving their daily energy requirements. This study has shown how they can be used to estimate the number of responses that is likely to cause a problem and compare that with known visitor frequencies and the resulting number of disturbances per day. For all eleven species the energetic cost per flight response was smaller than the relative reduction in feeding time so the time cost of responding to disturbance is likely to be the more important factor in terms of whether birds are able to compensate (though this may not be the case at sites where the exposure period is not so limited as in Poole Harbour). Observations of the proportion of available time spent feeding suggest that birds in Poole Harbour have enough spare time to compensate for considerable amounts of disturbance (at least a 39% time reduction). However, since data could only be collected during the early winter period, these values may underestimate the proportion of time allocated to feeding during prolonged periods of cold weather or harsher-than-average winters. Nevertheless estimates for a 5% reduction in available feeding time (c.f. Chapter 2) equated to between 41 and 128 disturbances, which is well above the estimated number of daily disturbance at all four study sites (see Table 3.1). Even using the more conservative 5% threshold, Parkstone Bay is still the only one of the study sites where disturbance might be expected to cause a problem for some species (28 disturbances per day is greater than the estimated threshold value for curlew, oystercatcher and grey plover – Table 3.7). This could explain why relatively low numbers of birds use this area (Caldow et al. 2005, Herbert et al. 2010, Liley and Fearnley 2012). Parkstone Bay, however, is an extreme case and less than 3% of the intertidal habitat in Poole Harbour is likely to experience visitor frequencies as high as that seen at Parkstone Bay. Using this simple method, it would appear that disturbance is not a major issue in Poole Harbour, at least not for an average bird at current population numbers and current visitor frequencies. However, Bejder et al. (2006) caution against assuming that short-term behavioural responses are sufficient indicators of the impacts of human disturbance, and this assertion needs to be investigated using other methods.

3.5.3. Further work

There is a clear need for a better understanding of the degree to which individual-specific factors (such as body condition, age and past experience) influence responses to disturbance, which is only possible through studies of captive birds or tagged individuals with known life histories. Tagging studies could also be used to more accurately determine the proportion of time that birds spend feeding, by recording roost departure and arrival

times, which allows calculation of the time spent on the intertidal area relative to the exposure period. Similarly, a better understanding is needed of visitor patterns; what factors affect the likelihood of potential disturbances actually resulting in a disturbance response, and the numbers/species of birds affected. These questions will be addressed in Chapter 6.

In order for the rapid assessment method (using flight costs or total feeding time lost to identify threshold disturbance frequencies) to be useful, confidence is needed in the assumptions upon which it is based. These could be tested using simulation modelling using the response data collected as part of this study to parameterise an individual-based model (Stillman 2008) to track the progress of model birds throughout a winter season and make predictions about survival, site use and final energy stores under different scenarios of environmental change and visitor pressure. Chapter 5 will explore this approach further.

Lastly, most experimental studies of bird responses to disturbance tend to focus on the effect of an approaching pedestrian, yet there are many other activities that also take place on and adjacent to intertidal areas. It is important to understand how responses vary according to type of disturbance. The next chapter investigates bird responses to wildfowling in Poole Harbour and makes comparisons with what we have learnt about pedestrian disturbance here.

Chapter 4 – Factors affecting the responses of wintering waterbirds to disturbance by wildfowling and a comparison with the effects of pedestrian disturbance in Poole Harbour.

4.1 Abstract

Most studies of bird responses to disturbance involve an approaching pedestrian as the disturbance stimulus. However, there is also a need for better understanding of responses in relation to other activities. Wildfowling – hunting ducks and geese – in estuarine environments offers a useful activity for investigating the mechanisms behind bird responses to impulsive noise as well as for comparing the relative costs of responding to different forms of human recreation. In this study experimental disturbance of birds in Poole Harbour by mimicking wildfowling activities showed that the magnitude of response (time and area disturbed) is greater per individual wildfowler than for a single pedestrian. The two activities, however, occur at very different frequencies, such that the cumulative effect of pedestrians across the whole of the winter season is likely to be considerably higher than for the currently consented number of wildfowling visits per season. This is the first study to investigate the responses of non-quarry species (i.e. waders) to disturbance from wildfowling. Larger birds were less likely to respond to the sound of the shotgun at any given distance, which is the opposite of the species mass relationship with pedestrian disturbance observed in other studies, where larger species exhibited larger flight initiation distances (FID). The data collected here also provide values for parameterisation of models to test the conclusion that neither wildfowling nor pedestrian disturbance is currently significantly reducing the carrying capacity of Poole Harbour for wintering waders.

4.2 Introduction

Given that estuaries like Poole Harbour provide vital foraging and roosting habitats for internationally important numbers of wintering migratory waders and wildfowl, whilst also being of considerable importance for a wide variety of human activities, management measures often need to be put in place to minimise conflict between competing interests (Ferreira et al. 2007; European Commission 2014). As well as interventions to maintain the quality and extent of habitat, management to ensure that the site continues to support the numbers of birds for which it was designated may involve restrictions to limit the amount of disturbance and direct mortality from hunting and other human activities (e.g. Drake et al. 2011). Such management should be based on an understanding of the ways in which different types of activity may disturb birds and the circumstances under which they would be expected to become a conservation problem.

Most researchers that have taken an experimental approach to investigating animal responses to disturbance have used an approaching pedestrian as the disturbance stimulus (Laursen et al. 2005, Rodriguez-Prieto and Fernández-Juricic 2005, Bregnballe et al. 2009, Cooper 2009, Gotanda et al. 2009, Glover et al. 2011, Li et al. 2011, Weston et al. 2012, van Dongen et al. 2015). Some authors do report bird responses to other types of stimulus; for example shooting (Dooley et al. 2010), motor vehicles (McLeod et al. 2013; Schlacher et al. 2013b) and bicycles (McLeod et al. 2013), however such studies are far less numerous (Livezey et al. 2016). Whilst studying pedestrian disturbance can offer important insights into the behavioural ecology of disturbance response, humans on foot are certainly not the only type of disturbance that birds are likely to experience, given the variety of recreational and economic activities that take place on estuaries around the world. This chapter therefore will investigate bird responses to a second focal activity (see section 1.1.6) – wildfowling – which presents an acoustic disturbance stimulus as well as visual.

4.2.1. Noise disturbance

In addition to the visual disturbance stimulus of the presence of a person, sudden and/or loud, as well as chronic, noise can also alter birds' actual or perceived risk and lead to changes in behaviour. For example, traffic noise has been found to reduce densities of birds using otherwise suitable habitat (Reijnen et al. 1995, Hirvonen 2001) and increase FID in house sparrows *Passer domesticus* (Meillère et al. 2015); Quinn et al. (2006) showed that chaffinches *Fringilla coelebs* increased vigilance and decreased foraging rates in the presence of increased background noise; and Randler (2006) found that coots *Fulica atra*

significantly increased their vigilance in response to the sound of a dog barking. There is also potential for considerable time and energetic costs of flight in response to novel sounds, for example from fireworks displays or military activities (Riddington et al. 1996, Shamoun-Baranes et al. 2011).

Noise disturbance can come from a wide range of sources in addition to those mentioned above; including motorised watersports, wildfowling, construction, and port or industrial activities – some of which may be subject to regulations or restrictions, particularly on sites of nature conservation importance. With the exception of research into bird responses to military training activities (Conomy et al. 1998, Küsters and Raden 1998, Goudie 2006, Delaney et al. 2011), the effects of sudden or impulsive noise disturbance have not been well studied (except see Wright et al. 2010). To date regulation has therefore generally relied on a precautionary approach based on unpublished observations (Cutts et al. 2013). A better understanding of bird responses to noise stimuli is therefore needed for a more complete picture of potential disturbance impacts of human activities on estuarine birds to inform management and planning decisions.

4.2.2. Wildfowling

Background

The practice of wildfowling in Poole Harbour provides a good opportunity to study bird responses to impulsive noise (i.e. that of the wildfowler's shotgun) as well as offering a useful comparison activity with the more commonly studied pedestrian disturbance. Wildfowling, also known as waterfowl hunting, involves shooting wild ducks and geese for food and recreation on estuaries and coastal marshes or inland wetland habitats. The pastime is popular worldwide, involving for example more than 1% of the adult population in the USA (US Fish and Wildlife Service 2012); and membership of the European Federation of Associations for Hunting and Conservation (FACE) includes national hunting organisations from 36 countries (FACE 2016). In the UK it has a long history, which dates back to the 16th and 17th centuries with the increased popularity and effectiveness of the shotgun around that time (Marchington 1980, Kear 1990). Quarry species and open seasons vary from country to country and state to state, along with restrictions on capture methods, bag limits, harvest quotas and points systems to control the numbers and types of birds that are shot. Restrictions in some countries may be set in law, whilst others take an adaptive management approach to regulating wildfowling, using an iterative process of monitoring, assessments and decision-making based on annual population estimates,

habitat assessments and past modelling accuracy (Kanstrup 2006, Schmidt 2006, Nichols et al. 2007).

This study will focus on coastal wildfowling practices in the UK, where individuals generally need to be a member of a wildfowling club in order to have access to land where wildfowling is permitted. In 2012 there were 8,237 people registered with one or more wildfowling clubs around the UK (Ellis 2014a). The coastal wildfowling season is limited to the period between 1st September and 20th February (31st January in Northern Ireland), designed to avoid the late winter/early spring period when many birds are preparing for migration. There are also provisions through the Wildlife and Countryside Act (1981, as amended) for temporary suspension of wildfowling during periods of prolonged cold weather (Stroud et al. 2006, Ellis 2012).

Table 4.1. Summary of wildfowling returns for Poole Harbour 2001/02 to 2012/13 (adapted from Dorset Wildfowlers' Association (2013)). Wetland Birds Survey (WeBS) mean peak counts over the same period (Frost et al. 2016) given for comparison.

Species	Mean (\pm s.e.) number of birds shot per year	WeBS mean winter peak count
Teal <i>Anas crecca</i>	298.0 \pm 42.19	2008
Wigeon <i>A. penelope</i>	221.3 \pm 25.68	2003
Mallard <i>A. platyrhynchos</i>	79.6 \pm 10.25	346
Pintail <i>A. acuta</i>	41.9 \pm 6.72	200
Canada goose <i>Branta canadensis</i>	33.7 \pm 5.84	400
Gadwall <i>A. strepera</i>	14.3 \pm 5.74	86
Shoveler <i>A. clypeata</i>	7.0 \pm 2.06	120
Snipe <i>Gallinago gallinago</i>	0.8 \pm 0.3	43
Tufted duck <i>Aythya fuligula</i>	0.6 \pm 0.29	86
Greylag goose <i>Anser anser</i>	0.5 \pm 0.42	23
Pochard <i>Aythya ferina</i>	0.4 \pm 0.34	240
Goldeneye <i>Bucephala clangula</i>	0.1 \pm 0.08	117
Total visits (mean \pm s.e.)	131.3 \pm 10.34	
Individual wildfowlers (mean \pm s.e.)	20.0 \pm 2.23	
Birds per visit (mean \pm s.e.)	5.3 \pm 0.54	

Coastal wildfowling is generally a solitary pursuit, with wildfowlers concealing themselves on the intertidal habitat; sometimes using decoys or duck and goose calls to attract birds closer to their hide (Ellis 2014b). Visits are timed to coincide with the natural movements of ducks and geese as they move between feeding and roosting sites at dawn and dusk and with the changing tides. Table 4.1 gives a summary of wildfowling activities in Poole Harbour between 2001/02 and 2012/13; showing that the majority of birds shot are teal and wigeon, and the mean number of visits was well below the maximum consented value of 183 per season (Dorset Wildfowlers' Association 2013).

Although the wader species studied here are not quarry species, they are still likely to be disturbed by the sound of a shotgun being fired nearby, and the presence of a wildfowler may exclude waders from certain areas of foraging habitat or roost sites depending on how well concealed they are and the state of the tide.

Shooting noise

When investigating the impacts of noise disturbance on wildlife it is important to be aware of the factors that affect how sound travels from source to receiver. In theory, a sound-wave front travels outwards from a point source in a spherical manner, resulting in a reduction in intensity of 6 dB per doubling of distance (Forrest 1994). At short distances, therefore, a small difference in the distance from source can result in a considerable difference in the sound level experienced (Pater et al. 2009). However, source direction, atmospheric conditions (including air pressure), terrain and wind speed and direction all influence sound attenuation and propagation (Forrest 1994, Sutherland and Daigle 1998, Pater et al. 2009).

Source direction and wind speed/direction are perhaps most important in relation to wildfowling (Figure 4.1). A study by Bentley (2010) found that sound dispersal from a shotgun has an 'egg shaped' pattern: most sound dispersed to the front up to an angle of 45 degrees; and at 90 degrees the dispersion was considerably less. In the absence of wind effects, noise to the rear of the gun was estimated to be 12-15 dB lower than for the same distance in front of the gun. The shape of the contours in Figure 4.1 also shows the influence of the wind.

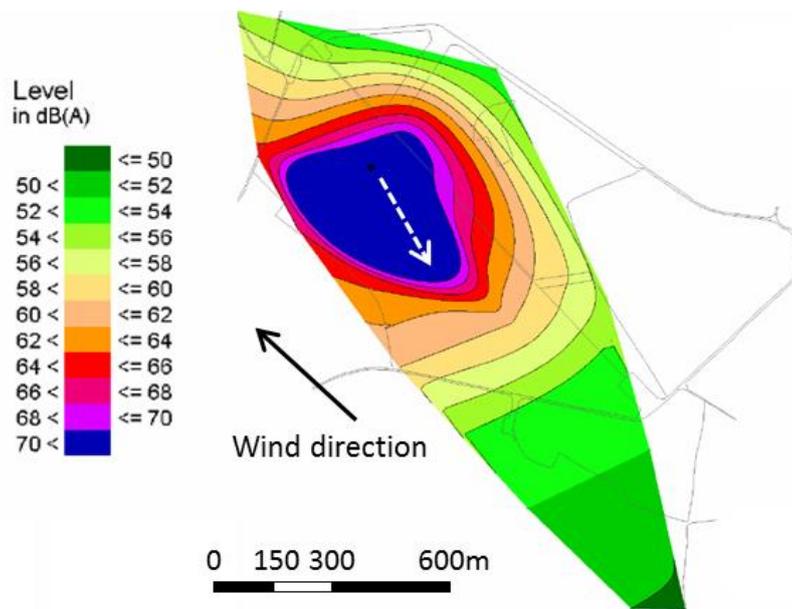


Figure 4.1. Noise contour plot for the sound of a shotgun fired from the black dot in the direction of the white dashed line. Reproduced from Bentley (2010).

If sound intensity or noise above a threshold dB level is associated with greater perceived risk (Frid and Dill 2002), and since dB level decreases with distance from the source, birds at greater distances from a wildfowler are expected to be less likely to respond when the shotgun is fired. Similarly, magnitude of response (e.g. flight response versus only becoming alert) is expected to decrease with distance. Wright et al. (2010) found both to be the case for roosting waders that they experimentally disturbed with an air horn. They also found interspecific differences in bird responses. Following the risk-disturbance hypothesis (Frid and Dill 2002) and based on the results from Chapters 2 and 3, responses are also likely to vary according to environmental conditions; with lower response magnitudes expected at lower wind chill equivalent temperatures.

4.2.3. Addressing a knowledge gap

Recreationists may underestimate their effects on wildlife and often hold members of other user groups responsible for negative impacts on wildlife rather than themselves (Taylor and Knight 2003). Indeed, Fearnley et al. (2012) noted that some user groups wanted to see evidence that their activity caused disturbance, with particular recommendation for further study relating to angling and wildfowling.

The fact that the sound of a shotgun being fired results in a visible behavioural response from nearby birds demonstrates that wildfowling constitutes a disturbance greater than the physical presence of a human. Additionally, wildfowling visits can last several hours with

repeated shotgun discharges so the effect of a single wildfowling visit is likely to be greater than that of a single pedestrian visitor. However, unlike for wildfowling, pedestrians are not restricted in terms of numbers or the times of year when they can visit. The cumulative effect of all pedestrian visitors during the course of the non-breeding season may therefore be much greater than the effects of relatively infrequent activities such as wildfowling. None of these assumptions have previously been formally tested and reported, and despite the strict consenting processes for wildfowling on protected sites (Wildlife and Countryside Act 1981 (as amended); Countryside and Rights of Way Act 2000), the impacts on wildlife (particularly non-quarry species) are relatively poorly understood. The aim of this chapter is to address these gaps by testing the following hypotheses.

- H₁ Responses to the sound of the shotgun are negatively correlated with distance from the wildfowler, and vary between species and according to environmental conditions;
- H₂ The effect (area disturbed and total feeding time lost) of disturbance from a single wildfowler is greater than that of a single pedestrian; and
- H₃ The cumulative effect of wildfowling is less than that of pedestrian disturbance due to the differences in frequency of activities.

4.3 Methods

4.3.1. Study area – wildfowling in Poole Harbour

Figure 4.2 shows the areas of Poole Harbour where wildfowling can take place, and the locations of the experiments. Dorset Wildfowlers' Association (DWA) has exclusive rights to shooting here; they lease the sporting rights for the intertidal foreshore from the Crown Estate, although not all areas are shot over (i.e. wildfowling does not take place in refuge areas). Shooting levels are controlled via a permit scheme. Areas where shooting can occur cover 7.4 km², which is approximately half of the total intertidal area in Poole Harbour. Access to these areas for wildfowling is only permitted by boat so wildfowlers cannot walk on the saltmarsh with their gun (Dorset Wildfowlers' Association 2013) – this is a restriction that is specific to Poole as most other wildfowling clubs around the country have access on foot (Matt Ellis – BASC, pers. comm.).

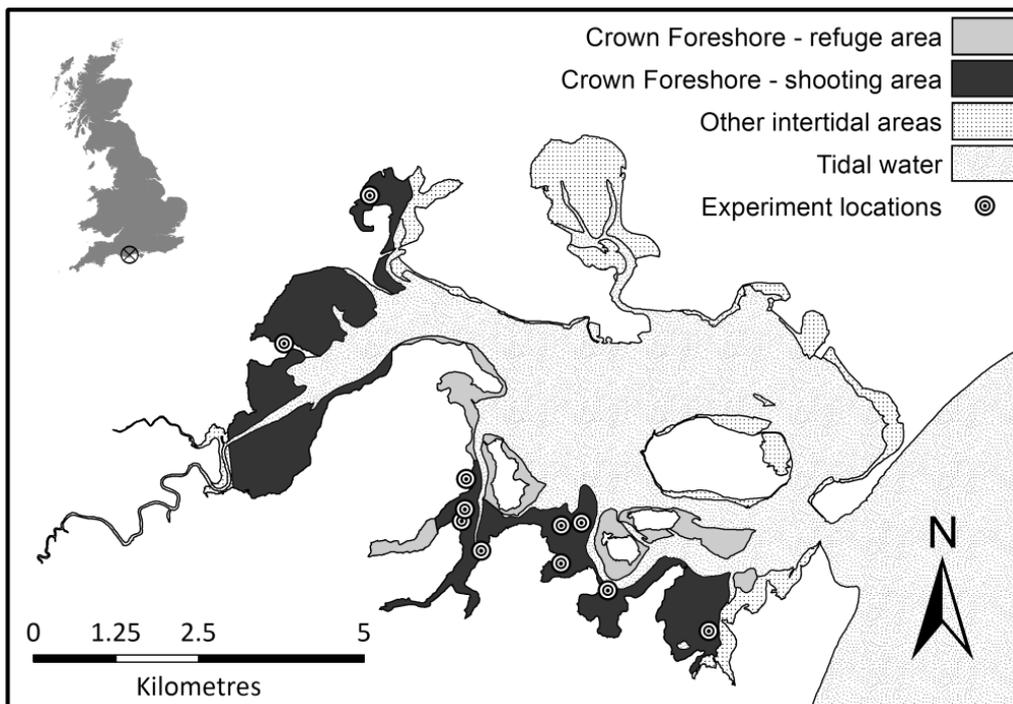


Figure 4.2. Poole Harbour, UK (50°41'47"N, 01°59'46"W) – extent of intertidal habitats, wildfowling areas, refuge areas and disturbance experiment locations. Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

A tidal phenomenon that occurs due to the shallow waters along the coast around Poole Harbour means that it has a non-standard tidal regime and experiences 'double high tides'. This means that the main low water is followed by a main flood tide, a subsidiary low water

and then a second high water which precedes the next main low water (Humphreys 2005). The optimal time for wildfowling is often during the 3-4 hours between these double high tides (Dorset Wildfowlers' Association 2013 and see Figure 1.8).

4.3.2. Field data collection – wildfowling experiments

The experiments to measure feeding wader responses to wildfowling activities took place with assistance from BASC (British Association for Shooting and Conservation) and Dorset Wildfowlers' Association over the course of three wildfowling seasons (i.e. between 1 September and 20 February) during the winters of 2011/12, 2012/13 and 2013/14. On each survey day a location was selected within Poole Harbour and accessed by boat on a falling tide, usually in the period between the double high tides. As the water level dropped the boat was positioned (without using the engine) as inconspicuously as possible whilst maintaining a clear view of the area where waders and wildfowl were expected to subsequently settle and feed: camouflage netting was then set up (Figure 4.3).



Figure 4.3. Preparing to undertake some wildfowling disturbance experiments.

As the intertidal area became exposed and birds began to feed on the mud and in the shallow water, a number of focal birds within 1000m of the boat were selected to be monitored. The cut-off of 1000m was chosen because more distant birds were not expected to respond, and would be harder to confidently identify and observe through the

course of each experiment. The species, flock size and distance from the boat were noted before firing a shotgun in the direction of the focal birds (but to miss). Details of the responses were then recorded as follows:

1. Response type in one of four categories – none (0); alert but no flight (1); flight and landing nearby (2); and flight with abandonment of the visible area (3).
2. Time taken to resume feeding (if still visible).

Distances were measured in metres using a laser range finder (Longridge Pin Point GADFL1 6x magnification), and times were recorded in seconds as accurately as possible whilst monitoring several birds at once. Environmental variables were looked up later – air temperature (°C) and wind speed (km/h) data from the weather station at Bournemouth Airport (UK Meteorological Office 2015) – and converted to a wind chill equivalent temperature, (see Equation 3.2). Body mass values were taken from BTO Ringing Scheme data (British Trust for Ornithology 2015). Table 4.2 gives an overview of all measured response variables and potential predictor variables.

Once the birds had re-settled and resumed feeding, and if tidal conditions allowed, the process was repeated (without repositioning the boat) with a new set of focal birds. In order to minimise pseudo-replication in the data, if the only birds feeding within 1000m of the boat were thought to be birds for which responses had already been recorded, then no further experiments were undertaken during that survey visit unless new birds arrived. The survey ended when the tide rose sufficiently to re-float the boat. Data were collected on 27 separate occasions, with the number of shots per visit ranging between one and six (median = 1).

In reality, wildfowlers would not wait until a large amount of mud is exposed with large numbers of feeding and roosting waterbirds, however, this experimental protocol was adopted as a trade-off between mimicking wildfowling activities in Poole Harbour as closely as possible, whilst maximising the amount of data that could be collected per visit. The gun used was a 12 bore shotgun with 32g steel cartridges (shot size 4), and the boat was a 12 ft Dell Quay Dory; typical of the type of boat used by wildfowlers in Poole Harbour.

Table 4.2. Measured response variables and potential predictor variables.

Name	Details	Units
Response variables		
Response	How the focal bird responded to the sound of the shotgun – selected from four categories: none (0); alert but no flight (1); flight and landing nearby (2); and flight with abandonment of the visible area (3)	-
TotalLost	The length of time between when the shotgun was fired and the focal bird resumed feeding. See text for treatment of birds that flew out of sight.	seconds
Potential predictor variables		
Distance	Distance between focal bird and the boat before the shotgun was fired.	metres
IsItOC	Dummy variable – “is it an oystercatcher?” (0=No, 1=Yes).	Yes/No
IsItPlover	Dummy variable – “is it a plover?” (0=No, 1=Yes).	Yes/No
SpMass	Mean mass of each focal species (using values reported by British Trust for Ornithology (2015)).	grams
WindChill	Wind chill equivalent temperature (Osczevski and Bluestein 2005) using data from the nearest weather station (Bournemouth Airport, UK Meteorological Office (2015)).	°C
FlockSize	Number of conspecifics feeding with the focal bird.	-
WinterDay	A measure of the number of days through the non-breeding season. Winter day 1 = 1 August.	-

4.3.3. Data analysis

Flight response

Given that bird responses to the sound of the shotgun were measured on an ordinal scale, the intention was to use ordinal logistic regression to determine the most important factors that affect the magnitude of response. However, graphical checking of the data, by plotting the means of all potential predictors against each ordinal class of the response (Figure 4.4), showed that in all cases the key assumptions of ordinality (consistent relationship between predictor variable and response levels) and proportional odds (constant change in log odds between response levels) were not met. In such situations Harrell et al. (1998) and Guisan and Harrell (2000) suggest combining some of the response categories, however, this did not improve the situation. Instead, separate binary logistic regression models (Hosmer and Lemeshow 2000) were used for three selected response categories (any response/flight/flight with abandonment).

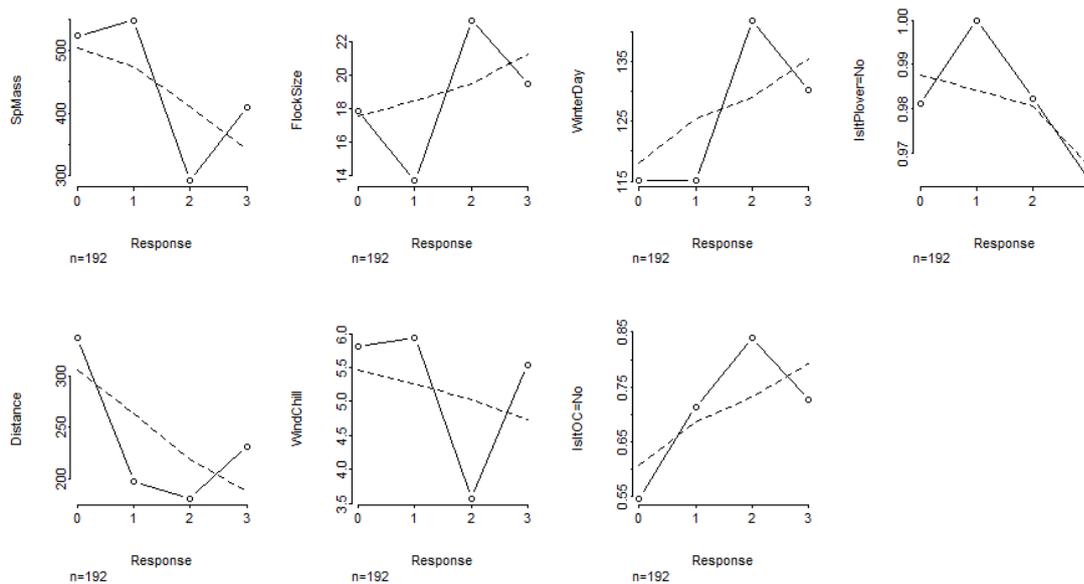


Figure 4.4. Diagnostic plots for the waders data set showed that the assumptions of logistic regression models were not met – inconsistent slope of solid line (\neq ordinality); dotted line does not match solid line (\neq proportional odds).

Taking an information theoretic approach (Burnham and Anderson 2002), the relative importance was tested of potential predictors for the probability of three (non-mutually exclusive) response categories (any response, flight response, and flight with abandonment of the immediate area), and model averaging (Symonds and Moussalli 2011) was used to derive parameter estimates for each predictor variable, along with confidence intervals for those estimates. Before performing the analyses the input variables were centred and standardised (following Gelman 2008, Grueber et al. 2011) to facilitate interpretation of the relative strength of parameter estimates. This involved subtracting the mean (centring) and then dividing by two standard deviations (standardising) for numeric variables with more than two values; binary variables were rescaled to have a mean of 0 and a difference of 1 between their two categories (Gelman and Su 2015).

Data for waders and wildfowl were analysed separately in case there are differences between the two groups in the mechanisms that govern their responses to a sudden noise. Since sample sizes were relatively low (192 responses recorded for waders and 107 for wildfowl) and for ease of interpretation, potential predictors were included as main effects only without any interaction parameters in the models. The goodness of fit of the fitted models was assessed by testing their predictive ability against the original data (Rana et al. 2010).

In addition to testing the responses of all species combined in one dataset, the same analyses were performed, with appropriate potential predictor variables, on the three most commonly observed wader species (curlew *Numenius arquata*, oystercatcher *Haematopus ostralegus* and redshank *Tringa totanus*) to identify interspecific similarities or differences in the response patterns.

Total time lost

The total time lost data collected here are directly comparable to the data that were collected in the pedestrian experiments described in Chapter 3. However there were many occasions when birds flew out of sight (Table 4.3), and it was therefore not possible to record a value for the total time lost for these individuals. Excluding these birds from the analyses could mean ignoring an important component of bird responses to impulsive noise. Since it is likely that these birds took longer to resume feeding than the birds that remained in the vicinity of the boat, excluding the birds that flew out of sight would underestimate lost feeding time when responding to the sound of the shotgun. A slightly different approach was therefore needed compared to that used in Chapter 3. The data for waders and wildfowl were still analysed separately using AIC model selection and model averaging on the 95% confidence set (Johnson and Omland 2004, Symonds and Moussalli 2011) to understand the strength and direction of the relationships. However, instead of general linear models, survival analysis was used (proportional hazards regression (Cox 1972)) to explore potential predictor variables for the time that birds took to resume feeding after being disturbed by the sound of the shotgun. This approach allows for the fact that some of the data are 'right censored' i.e. the birds had not yet resumed feeding after an observed amount of time (Kaplan and Meier 1958, Klein and Moeschberger 1997). For all the right-censored birds (i.e. those that flew out of sight), the time value used was equal to the maximum observed for that species during the same survey, or if no such data were available, the maximum observed for the same species group was used (waders or wildfowl). A probability curve could then be produced, using all of the available data, for the proportion of birds that would be expected to have resumed feeding at a given time after the shotgun was fired. In this way, total time lost would not be underestimated. Following Grambsch and Therneau (1994) graphical diagnostics were used: visual inspection of the Schoenfeld residuals for each predictor variable plotted against time showed no clear relationship and therefore no reason to doubt assumption of proportional hazards. i.e. the difference in probability of resuming feeding for two different levels of each covariate was proportional for all values of time since disturbance.

Table 4.3. Observed numbers of flights (with percentage in brackets) that resulted in birds remaining or abandoning the visible area.

Disturbance and species group	Response = fly&stay	Response = fly&leave
Pedestrian – waders	452 (92.8%)	35 (7.2%)
Wildfowling – waders	56 (50.5%)	55 (49.5%)
Wildfowling – wildfowl	27 (45%)	33 (55%)

Comparison with responses to pedestrian disturbance

The results of the binary logistic regression analysis described above were used to estimate an effective disturbance distance (EDD) for each species (Stillman et al. 2012) to derive FID-like values for each species response to the sound of the shotgun. This involves calculating the probability of response for each species for each one metre interval up to the maximum recorded distance, and then summing the predicted probabilities across all intervals to find the EDD (see Appendix 6 for a worked example). EDD is therefore the distance from the wildfowler within which all birds of that species are expected to respond to the noise disturbance – so it can be considered as an equivalent measure to bird FIDs as recorded during the pedestrian disturbance experiments, thus enabling comparison between the two activities. An FID-like value was also estimated for the exclusion effect of a wildfowler’s boat by taking the minimum recorded distance between the boat and an individual of each species for each survey, and calculating the mean value across all surveys.

Following van der Meer (1985) as presented by Smit and Visser (1993) it is possible to calculate the theoretical area of intertidal habitat from which birds are excluded by a pedestrian walking across it (Figure 4.5a) – by using information on their alert distances and FIDs, recovery times for each zone and walking speed of the average pedestrian. Similarly, an equivalent conceptual diagram for the exclusion effect of a wildfowler is shown in Figure 4.5b, though this is precautionary since in reality the disturbed area will be smaller and more ‘egg-shaped’ due to the way that sound travels (see section 4.1.3). By adding a duration element for each activity, the ‘space-time’ that is disturbed by a single pedestrian and a single wildfowler could be calculated (Equations 4.1 & 4.2) and compared for each species across a range of activity frequencies. Values used included: the disturbance responses described in this chapter (wildfowling experiments) and in Chapter 3 (pedestrian experiments), along with a pedestrian walking speed of 2.5 km/h; a pedestrian visit length of one hour; a wildfowling visit length of three hours; and an average of four shots fired per hour (Mark Greenhough – BASC, pers. comm.).

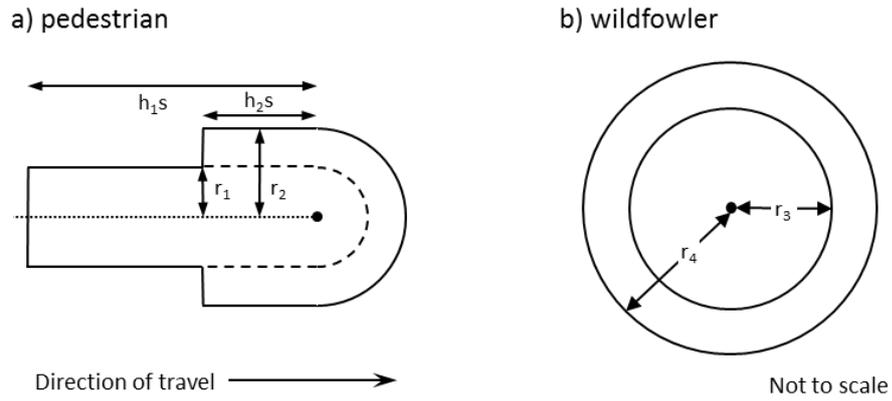


Figure 4.5. Conceptual diagram of the area influenced by a) pedestrian* and b) wildfowling disturbance. r_1 =FID; r_2 =alert distance; h_1 =recovery time after flight due to pedestrian; h_2 =recovery time after alert due to pedestrian; s =pedestrian walking speed; r_3 =boat disturbance distance; r_4 =EDD (gunshot); h_3 =recovery time after shot; n =number of shots per wildfowling visit; t =duration of stay by disturber.

* reproduced from van der Meer (1985) in Smit and Visser (1993).

$$Space-time (pedestrian) = \left(\frac{\pi r_2^2}{2} + 2r_1 \cdot h_1 \cdot s + 2(r_2 - r_1) \cdot h_2 \cdot s \right) \cdot t \quad \text{Equation 4.1}$$

$$Space-time (wildfowler) = \pi r_3^2 \cdot t + \pi(r_4^2 - r_3^2) \cdot h_3 \cdot n \quad \text{Equation 4.2}$$

All statistical analyses were carried out in R (R Core Team 2015) using functions available in 'arm' (Gelman and Su 2015) to standardise model predictors; 'survival' (Therneau 2015) for the time-related analyses; and the multi-model inference package 'MuMIn' (Bartoń 2015) for model selection and averaging; plots were produced using 'ggplot2' (Wickham 2009).

4.4 Results

Ten species of wader and eight species of wildfowl were experimentally disturbed on 27 occasions across the three wildfowling seasons, and response data were recorded for 299 individual birds (Table 4.4 and Figure 4.6). Species with low numbers of data points have been excluded from some of the figures to improve ease of interpretation, however all data were included in the analyses. Visual inspection of diagnostic plots for the statistical tests performed (see methods) did not give cause for concern about the violation of test assumptions.

4.4.1. Factors affecting probability of response

Wader flight responses

Figure 4.6 shows birds' distance from the boat when each shot was fired, divided according to species and response type. There is considerable variation in the distance at which birds responded, with a lot of overlap between the different categories of response, but visual inspection suggests that birds with a response category of 0 (no response) tended to be further away from the boat compared to when they did exhibit a response (this is particularly clear for dunlin, redshank and curlew). This relationship was confirmed for waders by the binary logistic regression and model averaging results (Table 4.5a and Appendix 7); with strong support for 'distance' (relative importance = 1) as well as showing high relative importance for the variables 'is it an oystercatcher?' and 'species mass'. More distant and larger birds were less likely to respond to the sound of the shotgun, particularly if they were an oystercatcher. Aside from this, there was limited support for the other potential predictor variables that were tested and the 95% confidence intervals for their estimated odds ratios include 1 so there is some uncertainty in the accuracy of these parameter estimates (Hosmer and Lemeshow 2000). Yet the predictive ability of the fitted model (after model averaging) was reasonably good, with a prediction error of 23.4%.

'Species mass' and 'distance' were also well supported in relation to probability of flight, in addition to high relative importance for both 'wind chill' and 'winter day'. Larger and more distant birds were less likely to fly, but probability of flight was higher in warmer conditions and later in the season. However the goodness of fit for this model was relatively poor – prediction error = 30.7% – as demonstrated by the wide confidence interval for probability of flight in Figure 4.7.

The model goodness of fit was also relatively poor for predicting whether a wader will abandon the immediate area (prediction error = 28.6%); none of the potential predictor variables that were tested were well supported, and all of the 95% confidence intervals for the odds ratios include 1 (Table 4.5a). In fact, the best supported model in the candidate set was the intercept-only model (Appendix 7).

Table 4.4. Summary of bird responses to the sound of the shotgun.

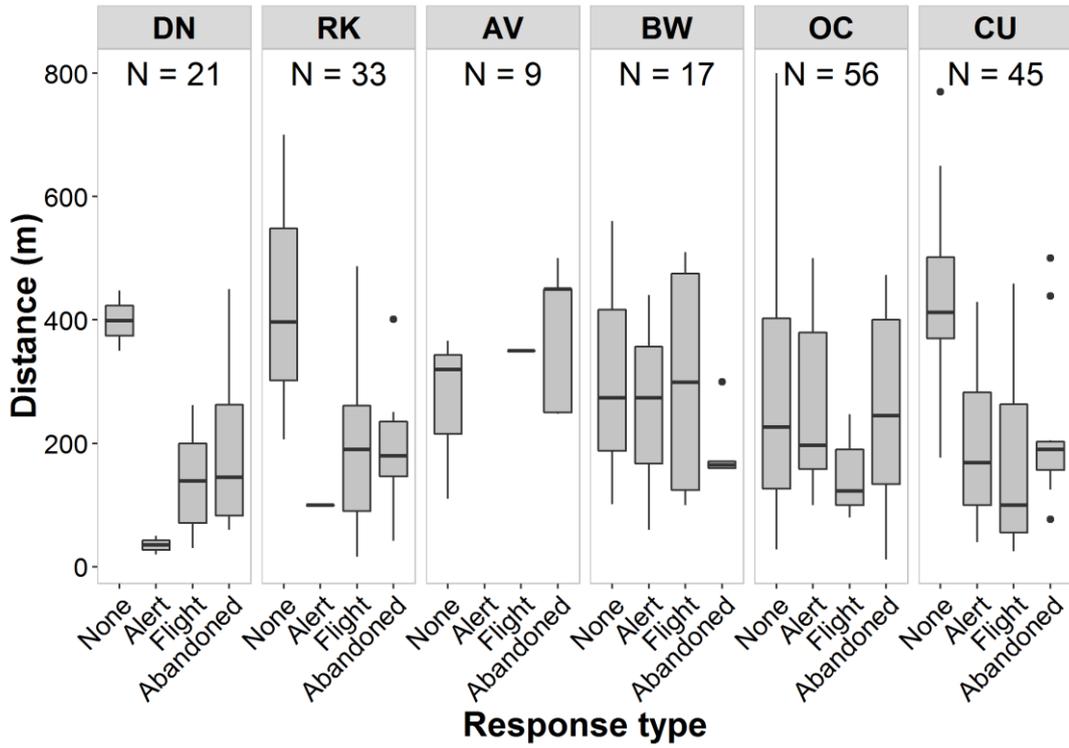
a) Waders:

Species	Body mass (g)	Frequency of response types				Response distance (m) [responses 2&3]				Total time lost (s) [responses 1&2]			
		0-None	1-Alert	2-Flight	3-Abandon	Median	Mean	s.e.	Range	Median	Mean	s.e.	Range
Curlew (CU)	782	15	12	7	11	180	203.00	34.70	25-500	30	44.21	10.72	10-180
Oystercatcher (OC)	546	24	8	9	15	160.5	215.13	27.10	12-473	20	31.44	6.71	3-100
Black-tailed godwit (BW)	299	3	3	6	5	171	251.18	45.99	100-510	40	41.25	12.56	5-105
Avocet (AV)	280	3	0	1	5	400	374.67	44.44	248-500	30	30	-	30-30
Lapwing (L.)	250	0	1	1	1	175	175.00	125.00	50-300	10	10	0	10-10
Grey plover (GV)	243	1	0	1	2	103	127.33	31.06	90-189	15	15	-	15-15
Greenshank (GK)	199	1	1	0	0	-	-	-	-	120	120	-	120-120
Redshank (RK)	153	3	1	17	12	180	196.52	21.87	16-487	30	43.06	13.30	5-250
Knot (KN)	138	1	0	1	0	20	20.00	-	20-20	10	10	-	10-10
Dunlin (DN)	50	2	2	13	4	139	153.82	25.57	30-450	30	44.87	15.76	5-240

b) Wildfowl:

Species	Body mass (g)	Frequency of response types				Response distance (m) [responses 2&3]				Total time lost (s) [responses 1&2]			
		0-None	1-Alert	2-Flight	3-Abandon	Median	Mean	s.e.	Range	Median	Mean	s.e.	Range
Canada goose (CG)	3960	0	1	2	0	130	130.00	50.00	80-180	150	170	36.06	120-240
Greylag goose (GJ)	3340	1	0	0	0	-	-	-	-	-	-	-	-
Brent goose (BG)	1250	4	2	4	6	312.5	316.50	52.57	90-641	135	261.67	108.21	40-600
Shelduck (SU)	1250	13	6	8	13	248	259.57	30.97	40-470	60	82.14	19.83	5-200
Mallard (MA)	1210	4	0	1	0	700	700.00	-	700-700	10	10.00	-	10-10
Pintail (PT)	936	0	2	0	3	410	370.00	61.10	250-450	302.5	302.50	297.5	5-600
Wigeon (WN)	749	5	0	5	7	240	247.00	48.05	65-540	80	115.00	48.43	15-240
Teal (T.)	323	7	2	7	4	261	284.91	53.19	25-600	30	73.11	23.35	8-200

a) Waders:



b) Wildfowl:

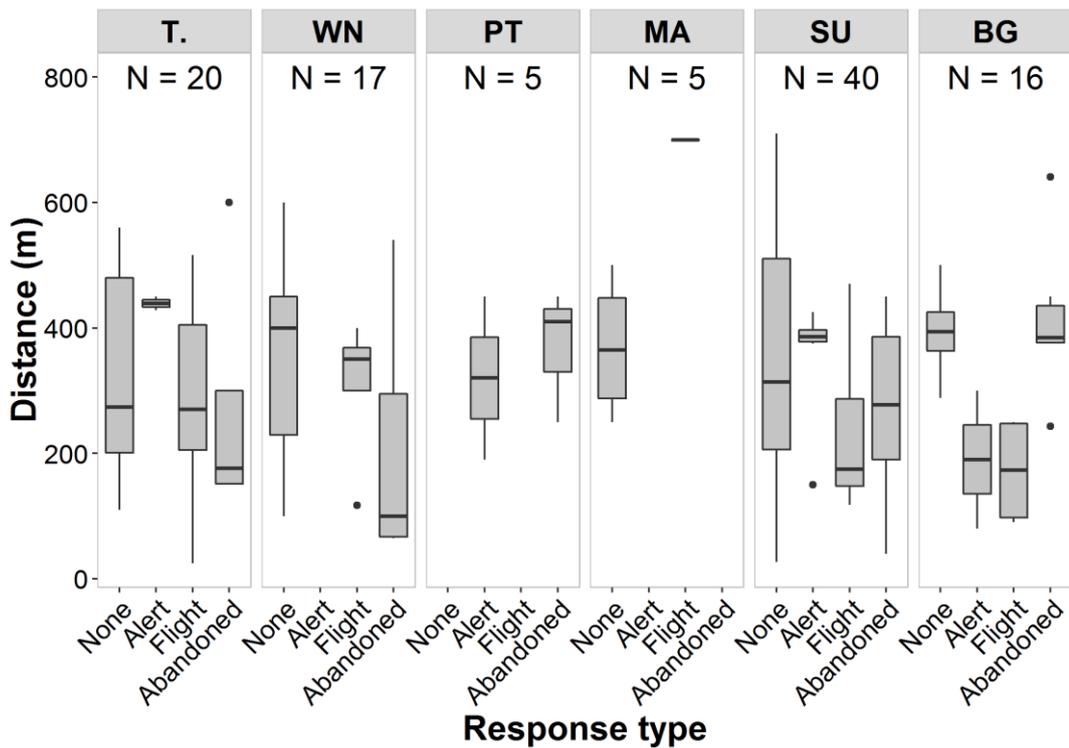


Figure 4.6. Response distances of waders and wildfowl to the sound of the shotgun (only species with at least 5 data points are presented). DN=dunlin; RK=redshank; AV=avocet; BW=black-tailed godwit; OC=oystercatcher; CU=curlew; T.=teal; WN=wigeon; PT=pintail; MA=mallard; SU=shelduck; BG=brent goose.

Table 4.5. Model averaging results: binary logistic regression odds ratios and relative importance of seven potential predictor variables for probability of three categories of response. Odds ratios for which the 95% confidence interval (CI) does not include 1 are highlighted in bold. Predictor variables were initially centred and standardised.

a) Waders:

Response	Predictor variable	Relative importance	Odds ratio	95% CI		Prediction error after model averaging
				Lower	Upper	
P(AnyResponse)	Intercept	-	10.875	1.027	115.098	0.234
	Distance	1.00	0.995	0.992	0.997	
	IsItOC	0.96	0.358	0.166	0.773	
	SpMass	0.72	0.998	0.997	1.000	
	WindChill	0.59	1.080	0.974	1.198	
	WinterDay	0.48	1.010	0.995	1.025	
	FlockSize	0.34	1.005	0.994	1.016	
	IsItPlover	0.25	1.518	0.044	51.861	
P(Flight)	Intercept	-	0.597	0.060	5.924	0.307
	SpMass	1.00	0.997	0.996	0.999	
	WinterDay	0.98	1.018	1.005	1.032	
	WindChill	0.93	1.119	1.027	1.218	
	Distance	0.88	0.997	0.995	1.000	
	IsItOC	0.46	0.619	0.305	1.258	
	IsItPlover	0.29	2.588	0.155	43.331	
	FlockSize	0.26	1.001	0.991	1.011	
P(Abandon)	Intercept	-	0.294	0.062	1.395	0.286
	WindChill	0.41	1.044	0.964	1.130	
	WinterDay	0.39	1.006	0.994	1.018	
	IsItPlover	0.34	2.672	0.351	20.314	
	SpMass	0.28	1.000	0.998	1.001	
	Distance	0.26	1.000	0.998	1.002	
	IsItOC	0.24	0.905	0.441	1.858	
	FlockSize	0.23	1.000	0.992	1.009	

b) Wildfowl:

Response	Predictor variable	Relative importance	Odds ratio	95% CI		Prediction error after model averaging
				Lower	Upper	
P(AnyResponse)	Intercept	-	1.109	0.076	16.085	0.318
	WinterDay	0.63	1.011	0.997	1.025	
	Distance	0.57	0.998	0.995	1.001	
	WindChill	0.41	1.073	0.945	1.218	
	FlockSize	0.28	1.004	0.991	1.017	
	SpMass	0.24	1.000	0.999	1.001	
	QuarryUK	0.24	0.835	0.351	1.987	
P(Flight)	Intercept	-	1.155	0.130	10.270	0.383
	Distance	0.68	0.998	0.995	1.000	
	WinterDay	0.54	1.008	0.997	1.019	
	FlockSize	0.30	1.004	0.993	1.015	
	WindChill	0.30	1.035	0.927	1.156	
	SpMass	0.25	1.000	0.999	1.000	
	QuarryUK	0.23	1.003	0.443	2.267	
P(Abandon)	Intercept	-	0.015	0.001	0.430	0.234
	WinterDay	1.00	1.024	1.005	1.043	
	FlockSize	0.90	0.979	0.955	1.004	
	WindChill	0.71	1.124	0.991	1.275	
	QuarryUK	0.28	0.733	0.260	2.065	
	Distance	0.26	1.001	0.998	1.004	
	SpMass	0.24	1.000	0.999	1.001	

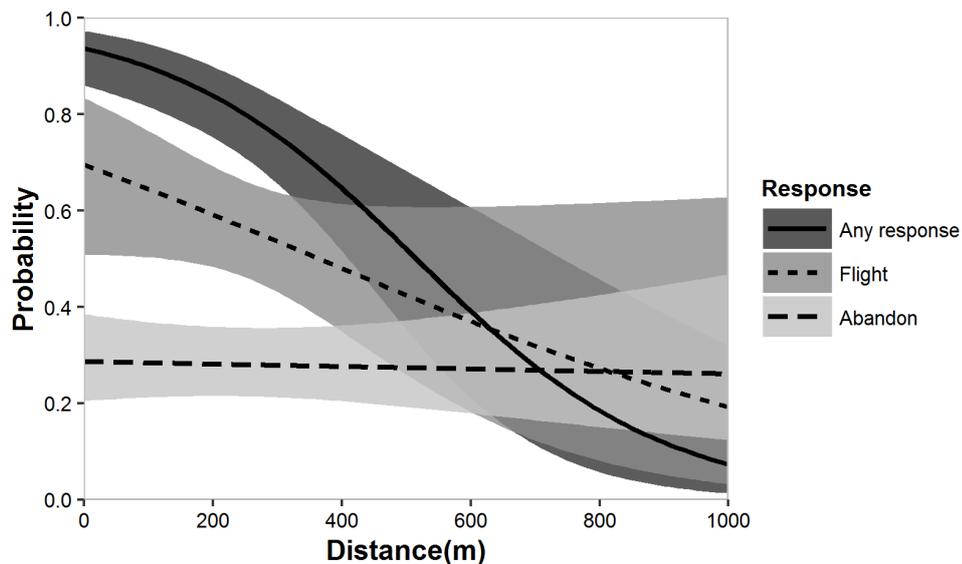


Figure 4.7. Model averaged predictions with 95% confidence intervals: probability of three categories of response for a wader of average mass [426g] that is not an oystercatcher or plover, average flock size[19], with a wind chill equivalent temperature of 5.1°C and mid-way through the wildfowling season [winter day 117 = 25 November].

Wildfowl flight responses

Analysis of the wildfowl response data showed poor predictive ability of the models and variables tested (Table 4.5b). There was strong support for winter day in relation to the probability that wildfowl would abandon the visible area (more likely later in the season), however for all other variables and response categories tested the 95% confidence intervals for the odds ratios included 1. This is exemplified in the wide confidence intervals in Figure 4.8.

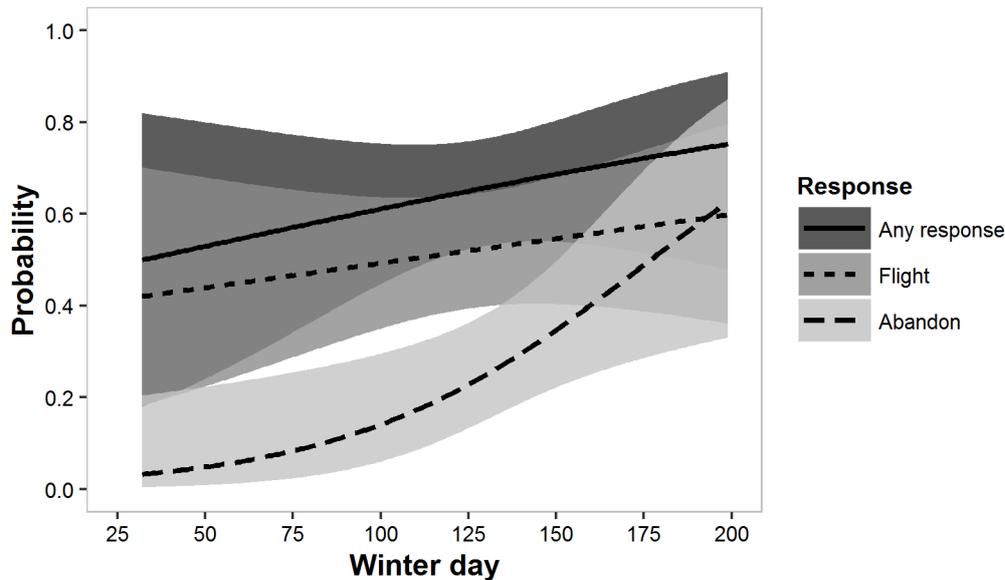


Figure 4.8. Model averaged predictions with 95% confidence intervals: probability of three categories of response for a quarry species of wildfowl of average mass [1076g], with average flock size [20], a wind chill equivalent temperature of 5.8°C and at 400m from the boat. NOTE that the x axis is different from Figure 4.7.

Flight responses – single-species analyses

Single-species analyses (Table 4.6 and Appendix 8) for the three most frequently observed wader species also showed generally low support for the potential predictors tested, particularly in relation to the probability of birds abandoning the area: and in most cases the 95% confidence intervals for the odds ratios include 1. Nevertheless the prediction error for some models was relatively low, and there was strong support for 'distance' and 'winter day' in relation to curlew probability of response and probability of flight respectively.

Table 4.6. Model averaged species-specific results for curlew, oystercatcher and redshank (relative importance and odds ratios for four candidate predictor variables). Odds ratios for which the 95% confidence interval (CI) does not include 1 are highlighted in bold.

a) P(AnyResponse):

Species	Predictor variable	Relative importance	Odds ratio	95% CI		Prediction error after model averaging
				Lower	Upper	
Curlew	Intercept	-	17.067	0.572	509.495	0.222
	Distance	1.00	0.990	0.984	0.997	
	FlockSize	0.41	1.026	0.987	1.066	
	WinterDay	0.34	1.015	0.987	1.044	
	WindChill	0.29	1.089	0.881	1.346	
Oystercatcher	Intercept	-	0.252	0.002	32.641	0.222
	WindChill	0.64	1.165	0.949	1.429	
	WinterDay	0.48	1.022	0.992	1.053	
	Distance	0.32	0.998	0.994	1.002	
	FlockSize	0.22	0.996	0.963	1.030	
Redshank	Intercept	-	9.946	0.0002	473315	0.061
	Distance	0.62	0.991	0.978	1.004	
	WinterDay	0.45	1.052	0.973	1.136	
	WindChill	0.38	0.752	0.406	1.395	
	FlockSize	0.28	1.038	0.838	1.287	

b) P(Flight)

Species	Predictor variable	Relative importance	Odds ratio	95% CI		Prediction error after model averaging
				Lower	Upper	
Curlew	Intercept	-	0.005	0.00002	1.070	0.339
	WinterDay	1.00	1.038	1.005	1.073	
	WindChill	0.73	1.209	0.983	1.488	
	Distance	0.50	0.996	0.990	1.002	
	FlockSize	0.22	1.006	0.956	1.058	
Oystercatcher	Intercept	-	0.215	0.002	19.964	0.411
	WindChill	0.67	1.151	0.948	1.397	
	Distance	0.41	0.998	0.993	1.002	
	WinterDay	0.40	1.020	0.989	1.052	
	FlockSize	0.26	0.991	0.954	1.029	
Redshank	Intercept	-	16.809	0.334	845.131	0.121
	Distance	0.52	0.994	0.986	1.002	
	WindChill	0.24	0.938	0.741	1.187	
	FlockSize	0.24	0.976	0.882	1.080	
	WinterDay	0.22	1.005	0.963	1.050	

c) P(Abandon)

Species	Predictor variable	Relative importance	Odds ratio	95% CI		Prediction error after model averaging
				Lower	Upper	
Curlew	Intercept	-	0.074	0.002	2.484	0.200
	Distance	0.29	0.998	0.992	1.003	
	FlockSize	0.27	1.012	0.974	1.053	
	WinterDay	0.71	1.018	0.998	1.039	
	WindChill	0.22	1.031	0.864	1.231	
Oystercatcher	Intercept	-	0.080	0.0002	29.619	0.268
	WindChill	0.66	1.205	0.943	1.540	
	WinterDay	0.44	1.025	0.982	1.069	
	Distance	0.27	1.002	0.997	1.006	
	FlockSize	0.97	0.905	0.814	1.006	
Redshank	Intercept	-	2.849	0.024	344.260	0.364
	Distance	0.26	0.998	0.990	1.006	
	WinterDay	0.46	0.976	0.946	1.008	
	WindChill	0.43	1.144	0.947	1.383	
	FlockSize	0.68	0.909	0.799	1.035	

4.4.2. Effective disturbance distance (EDD)

Table 4.7 shows EDDs for all of the species observed in this study, following Stillman et al.'s (2012) method and using the model averaging results in relation to the probability of observing any type of response when a shotgun is fired. Each value is calculated for the mid-point in the wildfowling season (winter day = 117), based on the mean flock size observed for that species, and using the mean wind chill equivalent temperature for the study period (5.3°C). The final two columns in Table 4.7 show the estimated mean and standard error of the minimum distance from the boat at which each species was observed feeding. The values from this table will be used later when calculating and comparing the effects of wildfowling versus pedestrian disturbance (Table 4.9).

Table 4.7. Disturbance distances for waders and wildfowl; gunshot and boat. Effective Disturbance Distances (EDD) based on probability of any type of response, using the model averaged parameter estimates from Table 4.5. See Appendix 6 for a worked example of the EDD calculation).

Species	EDD [gunshot] (m)			Boat disturbance distance (m)	
	Estimate	95% Confidence interval		Mean	s.e.
		Lower limit	Upper limit		
WADERS					
Curlew	431.36	354.44	513.70	209.85	33.69
Oystercatcher	324.43	266.97	391.42	167.63	29.94
Black-tailed godwit	525.43	464.63	589.15	265.89	62.87
Avocet	539.33	472.55	606.53	332	70.17
Lapwing	531.85	467.51	598.80	143.33	78.81
Grey plover	542.50	395.18	674.64	376.33	238.55
Greenshank	535.19	463.85	608.87	35	15
Redshank	544.38	469.70	620.31	170.31	42.52
Knot	571.05	488.53	648.97	101.5	81.5
Dunlin	567.61	485.23	647.74	139.73	43.98
WILDFOWL					
Canada goose	563.62	412.69	685.96	185.33	62.41
Greylag goose	541.50	412.89	653.18	210	0
Brent goose	538.77	448.74	620.88	266.5	82.49
Shelduck	537.44	447.14	619.91	178.6	28.38
Mallard	530.77	439.73	614.50	420	100.75
Pintail	526.88	435.36	611.37	300	110
Wigeon	537.31	440.32	625.04	272.64	55.77
Teal	524.57	429.44	612.16	296.92	46.75

4.4.3. Total time lost

Figure 4.9 shows that, for the waders that remained in the visible area, total feeding time lost was relatively low and did not vary much either within or between species. By contrast wildfowl were more variable in the length of time that individuals took to resume feeding after a flight response. However this presents only half of the story as it does not account for the birds that abandoned the immediate area and flew out of sight (Table 4.3).

The model averaging results for all birds – including those that flew out of sight – (Table 4.8) showed good support for the predictive power of ‘distance’, with waders that were disturbed at greater distances taking longer to resume feeding. However, there was little support for any of the other potential predictor variables tested in relation to waders and all of the remaining 95% confidence intervals included 1. Conversely, in the case of wildfowl (mirroring the results of the analyses of probability of response, above), there was little support for ‘distance’ but some support for ‘winter day’. Wildfowl took longer to resume feeding later in the season, though again the 95% confidence interval for this, and all other variables tested, included 1.

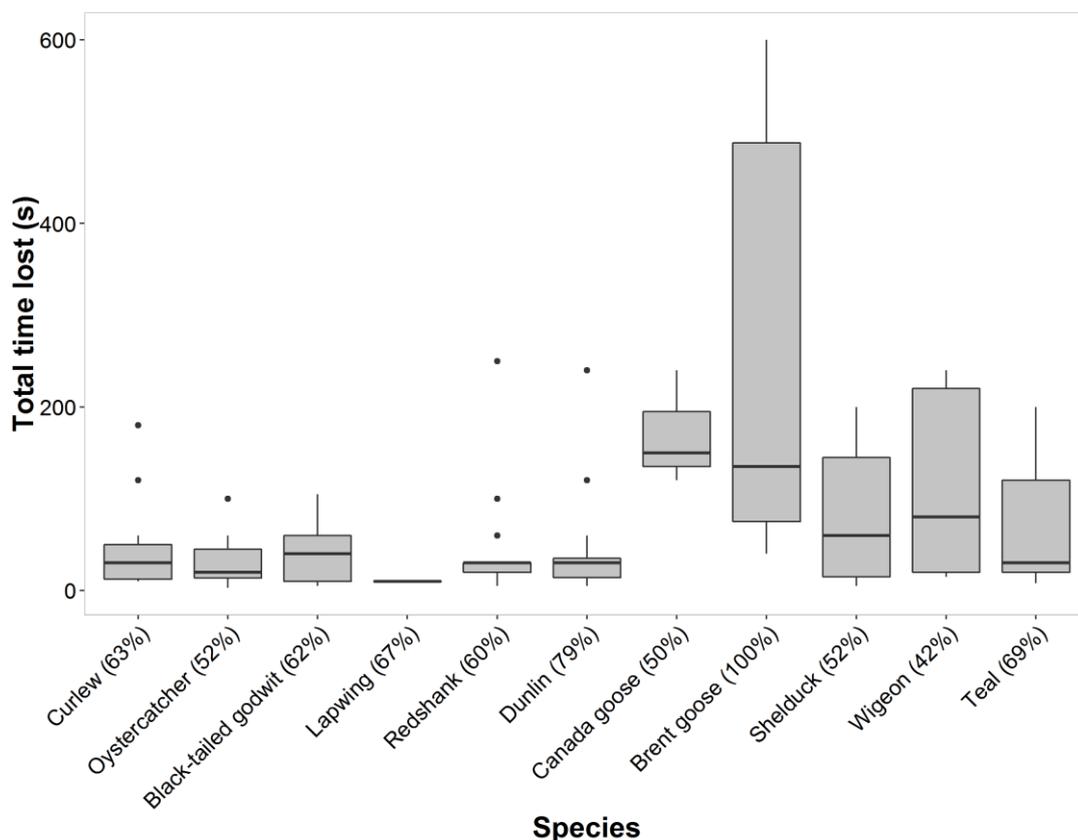


Figure 4.9. Total time lost comparison between species for birds that did not fly out of sight (percentages shown in brackets).

Table 4.8. Model averaging results: relative importance for each potential predictor variable with respect to total time lost, with hazard ratio estimates and 95% confidence intervals. Hazard ratios for which the 95% confidence interval does not include 1 are highlighted in bold.

a) Waders				
Predictor variable	Relative importance	Hazard ratio	95% confidence interval	
			Lower limit	Upper limit
Distance	0.80	0.998	0.996	1.000
FlockSize	0.35	1.003	0.997	1.010
WinterDay	0.30	1.002	0.996	1.008
WindChill	0.29	0.985	0.938	1.035
IsItOC	0.25	0.968	0.544	1.722
IsItPlover	0.24	0.905	0.124	6.594
SpMass	0.24	1.000	0.999	1.001

b) Wildfowl				
Predictor variable	Relative importance	Hazard ratio	95% confidence interval	
			Lower limit	Upper limit
WinterDay	0.64	0.991	0.982	1.001
WindChill	0.54	1.066	0.981	1.158
FlockSize	0.33	1.003	0.997	1.009
Distance	0.30	1.000	0.999	1.000
SpMass	0.26	0.999	0.997	1.001
QuarryUK	0.24	1.130	0.588	2.171

4.4.4. Comparison of wader responses to wildfowling noise and pedestrian disturbance

Although the distance data recorded for waders in the pedestrian and wildfowling experiments do not measure precisely the same thing, we can compare the effects of the two disturbance types by considering EDD for the sound of a shotgun versus alert distance when approached by a pedestrian. Figure 4.10 shows a clear difference between the two activities in the distance at which birds were disturbed; with all species responding to the sound of a shotgun at a much greater distance than when approached by a pedestrian. The Cox proportional hazards model (Figure 4.11) showed that there is also a significant effect of disturbance type on total time lost (after controlling for the two best supported variables, species mass and distance); birds lost more time when responding to the sound of the

shotgun compared to when disturbed by an approaching pedestrian (hazard ratio = 0.715, $p = 0.044$). However as Figure 4.12 shows, the relationship might not be the same for all species; for example, the relationship appears to be reversed in the case of curlew.

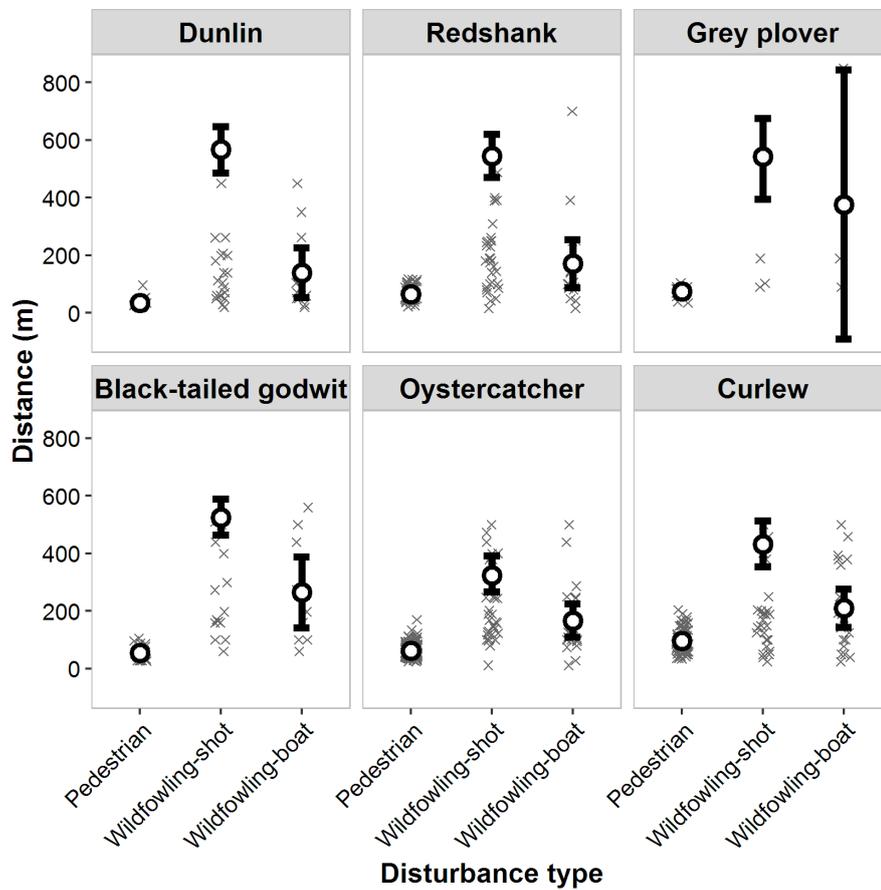


Figure 4.10. Alert distances (pedestrian disturbance), EDDs (gunshot) and the exclusion effect of the boat (minimum recorded distance) for each species. Mean (hollow circle) with 95% confidence interval (bars), and original data (crosses, displaced horizontally for clarity).

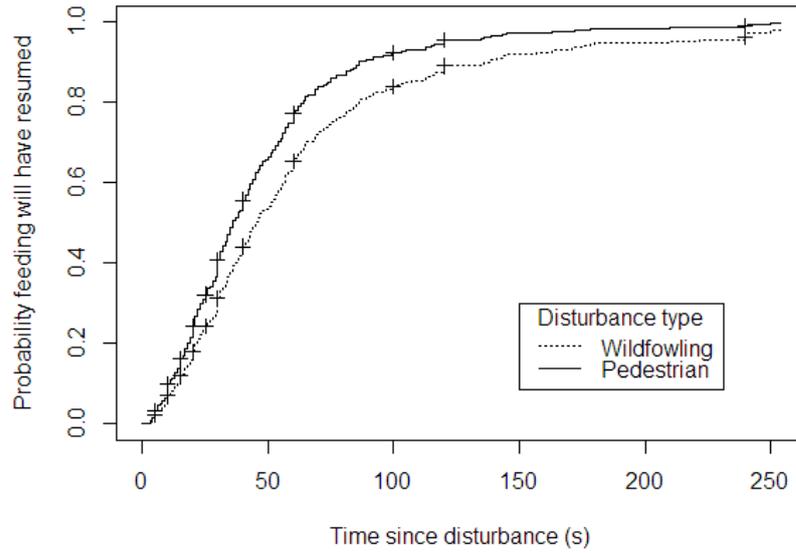


Figure 4.11. Cox proportional hazards model probability plot: the effect of disturbance type on total time lost (after for controlling for species mass and distance) – fitted model for a wader of average mass [430g] at an average distance [93m].

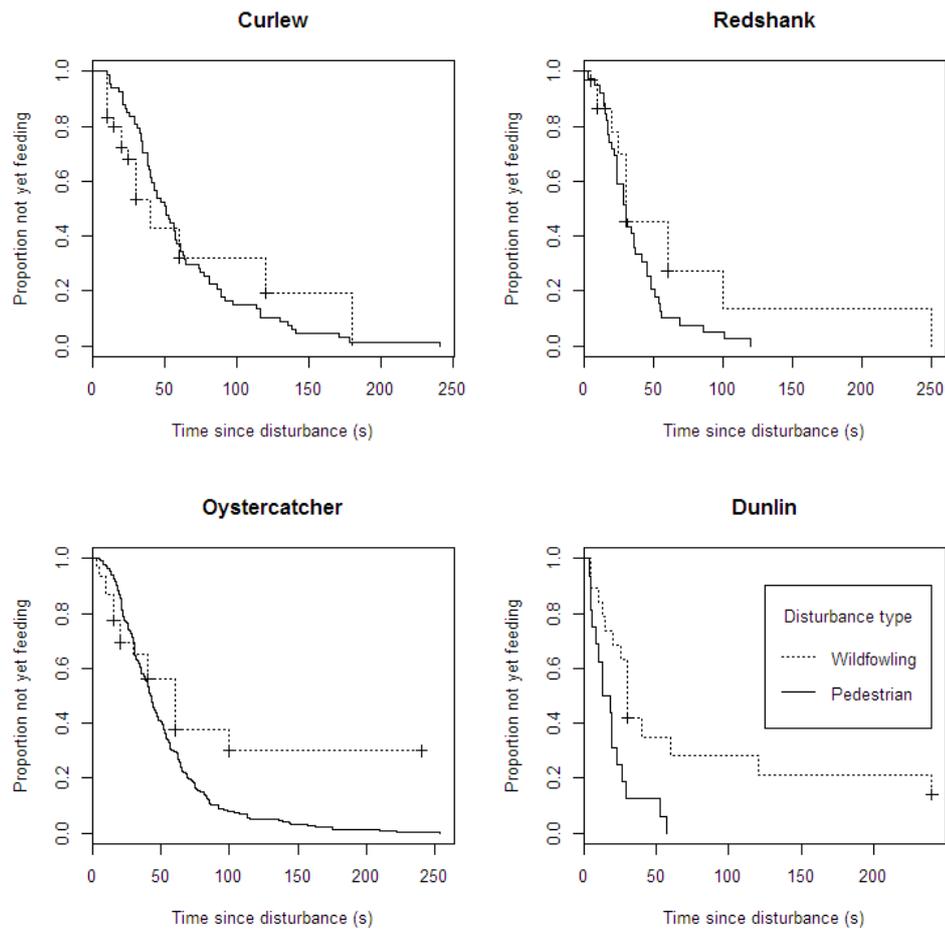


Figure 4.12. Kaplan-Meier plots showing the effect of disturbance type on total time lost for four species of wader.

Using the conceptual diagram shown in Figure 4.5 and the accompanying equations the effect of a single wildfowler and a single pedestrian can be directly compared (Table 4.9). For all species the effect of a single pedestrian was lower than that of a single wildfowler. However, Figure 4.13 shows that when the frequency of each activity was taken into account, the potential cumulative effect of all pedestrians using the intertidal habitat throughout the winter period was considerably higher than the currently consented frequency of wildfowling (183 visits per season).

Table 4.9. Space-time ($\text{km}^2\text{-hrs}$) disturbed by a single pedestrian compared with that disturbed by a single wildfowler.

Species	Space-time disturbed ($\text{km}^2\text{-hrs}$)	
	Per wildfowler	Per pedestrian
Curlew	0.683	0.023
Oystercatcher	0.346	0.011
Black-tailed godwit	0.795	0.009
Grey plover	1.383	0.015
Redshank	0.441	0.010
Knot	0.130	0.012
Dunlin	0.279	0.003

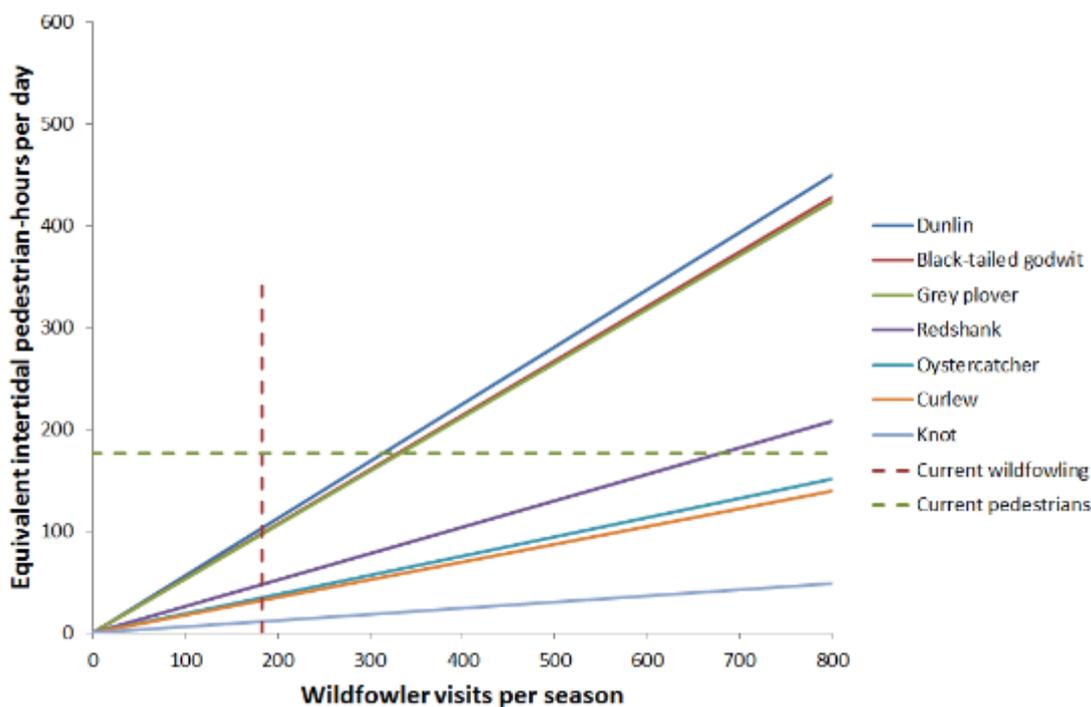


Figure 4.13. Space-time influence comparison between wildfowling and pedestrians on the intertidal over the course of a wildfowling season (173 days). See text for details of calculations.

4.5 Discussion

The aim of this study was to investigate the effects of an understudied potential source of disturbance in estuarine habitats – wildfowling – with respect to both the visual and acoustic disturbance stimuli. Comparisons can therefore be made with pedestrian disturbance, which is more commonly studied and occurs more frequently. New data are provided for ten species of wader and eight species of wildfowl on their responses to the presence of a wildfowler in a boat and the sound of the shotgun. Fox and Madsen (1997) give an overview of research into the responses to wildfowling of ducks and geese, however this is the first study to investigate the responses of non-quarry species (i.e. waders); although see Wright et al. (2010), who experimentally disturbed roosting curlew, golden plover *Pluvialis apricaria* and lapwing *Vanellus vanellus* with an air horn.

4.5.1. Probability of response

Waders and wildfowl both showed a great deal of variability in probability of response within- and, to a lesser extent, between- species. Some of this variation was explained for waders by species mass, distance from the boat when the shot was fired and environmental conditions (support for Hypothesis 1). Larger and more distant waders were less likely to respond in some way (becoming alert or fleeing). The importance of distance is not surprising, given that sound pressure level (in decibels, dB) decreases with distance from the source. Wright et al. (2010) estimated for roosting birds that a behavioural response of some kind (e.g. cease feeding, become alert, take flight) is more likely than no response at sound levels above 65.5 dB, which is broadly consistent with the patterns of shotgun sound propagation as measured by Bentley (2010, Figure 4.1) and the range of EDDs that were estimated here. However, several other factors can influence received sound levels – including source direction, atmospheric attenuation, terrain, wind speed and direction, and air pressure (Pater et al. 2009). This may account for some of the remaining unexplained variation in bird responses, since distance will not always be a precise measure of the sound levels that birds experience.

The observed negative correlation between species mass and probability of response seems contrary to the fact that larger birds exhibit greater FIDs when approached by a pedestrian, but Wright et al. (2010) also found this result for roosting waterbirds so perhaps waders perceive risk differently when the disturbance stimulus is acoustic rather than visual. A difference in risk perception may also explain the fact that when waders responded to the sound of the shotgun by taking flight, they abandoned the visible area on 49.5% of occasions compared to just 7.2% for pedestrian disturbance. When faced with the visual stimulus of an

approaching pedestrian, birds have time to assess the risk and respond accordingly; whereas response to the sudden stimulus of the sound of the shotgun may be more of an automatic reflex – allowing no time to accurately assess risk. Nevertheless none of the measured potential predictor variables could explain variation in this behaviour within the wildfowling experiments dataset, which could instead be related to availability of alternative habitat and/or differences between individual birds in body condition or experience. Further investigation is needed to understand this aspect of bird behaviour in response to sudden noise.

In contrast to the results for waders, there was no species mass relationship for wildfowl responses (even though the species involved represent a wide range of body masses), which may also suggest that waders and wildfowl assess risk from acoustic stimuli differently from each other. However, with the exceptions of winter day and flock size in relation to probability of abandoning the visible area, all of the predictor variables for each wildfowl response category were poorly supported. This could be because the sample size was too small and/or there is at least one important variable that has not been tested, for example relating to differences in individual body condition (Beale and Monaghan 2004b) or past experience (Higham and Shelton 2011).

It was somewhat surprising that whether or not a bird was a quarry species was so poorly supported, since quarry species might be expected to be more likely to respond to the sound of a shotgun because of the potentially lethal consequences of lesser responses. Laursen et al. (2005), for example, found that quarry species had greater FIDs than non-quarry species in response to pedestrian disturbance. The hunting pressure experienced by birds in Poole Harbour (Table 4.1) may not be great enough to significantly alter responses in this way. Or perhaps a significant difference would have been apparent if this study had a larger or more balanced dataset, with equal numbers of quarry and non-quarry species represented in the experiments.

4.5.2. Total time lost

The only potential predictor variable that was well supported in the wildfowling experiments dataset with respect to wader total time lost was ‘distance’ (relative importance = 1); and there was some support (relative importance = 0.64) for ‘winter day’ for wildfowl. There was very little support however for ‘species mass’ even for waders, which is surprising given its importance in relation to probability of response and in the pedestrian disturbance experiments (Chapter 3). It appears that much of the variation in total time lost is explained

by one or more factors that have not been tested here (and likely related to factors determining whether birds remain or abandon the immediate area, as discussed above). Since the sound of a shotgun is such a short stimulus, perhaps birds resume normal behaviour as soon as the stimulus is removed simply according to individual differences in body condition, energetic requirements or knowledge of alternative foraging areas. Given the assumption that total time lost is greater for birds that abandon the visible area, a better understanding is needed of the mechanisms that determine whether birds leave or remain.

4.5.3. Effect of disturbance type

Hypothesis 2 was supported in relation to both area disturbed (Figure 4.10) and total time lost (Figure 4.11); and the total space-time disturbed by a single pedestrian was more than an order of magnitude lower than that of a single wildfowler (Table 4.9). However, due to the large differences in the frequency of the two activities, Hypothesis 3 was supported: the potential cumulative effect of all pedestrians using the intertidal habitat throughout the winter period was considerably higher than the currently consented frequency of wildfowling (183 visits per season). This was particularly apparent in relation to knot, curlew, oystercatcher and redshank. In this way the potential effects of different activities can be objectively compared.

4.5.4. Recommendations for further study

Noise

Distance from source appears to be an important, but imperfect, predictor of bird responses to acoustic disturbance – specifically impulsive noise. However, for a fuller understanding and in order to more confidently predict when birds will take flight, a larger data set will be needed, which involves the use of sound meters to accurately measure received sound pressure levels at known distances from the source and/or accurate measurements of temperature, pressure, and wind speed and direction in relation to the direction of shooting, which would allow accurate estimates to be made of the received sound pressure levels (similar to the methods employed by Wright et al. (2010)). Also, given the between-site variability in responses to pedestrian disturbance, further wildfowling (or other impulsive noise) studies are needed at a variety of sites to test the degree to which there is between-site variability in response to acoustic stimuli.

Activity patterns

Estimating the amount of space-time that different activities are likely to disturb offers one way to make comparisons between disturbance types, however, the actual number of birds affected will depend on how many are (or would be) feeding in the vicinity of each type of potential disturber. This is related to the spatial and temporal patterns of occurrence of each activity and of bird distributions: for example, due to the soft, muddy nature of most of the intertidal habitat in Poole Harbour, most pedestrians are likely to remain close to top of the shore, which reduces the likelihood of birds being disturbed if preferred feeding areas are at or close to the low tide mark (Granadeiro et al. 2006). Similarly, since the most profitable time for wildfowling is often between one hour before and one hour after high tide, when relatively little intertidal habitat is exposed, again the chances of human disturbers and feeding birds overlapping in time and space is low. However, by the same logic, birds that are feeding during times of minimal intertidal exposure are likely to be those individuals that are most hard pressed and struggling to meet their energy requirements (Goss-Custard et al. 1977). So disturbance to these birds in these circumstances is more likely to have negative consequences. The timing of wildfowling visits with respect to the tide could also result in disturbance to roosting birds, if roosts and favoured wildfowling locations are in close proximity with each other. A more general recognition, therefore, of the importance of the subtleties of patterns of occurrence of potentially disturbing activities will lead to a better understanding of the scenarios under which disturbance may be considered a conservation problem.

In addition to understanding the patterns of occurrence of different activities, good knowledge is needed of the mechanisms by which each activity causes disturbance. For example, in the case of wildfowling, disturbance may occur when: (1) wildfowlers access/depart their chosen location; (2) wildfowlers are in position on the intertidal habitat; (3) the shotgun is fired; and (4) a dog is sent to retrieve shot quarry. So far this study has only investigated and discussed aspects 2 and 3. With regards to wildfowlers accessing and departing their chosen location, this is unlikely to result in considerable additional disturbance, at least in Poole Harbour. Here access only takes place by boat, which necessarily requires a certain depth of water and, for the most-part, precludes disturbance of birds on the intertidal habitat. However, any further research at other sites will need to take this into consideration, especially if access routes take wildfowlers in the vicinity of high tide roosts, or when boats travelling along channels at low water bring them in close proximity to feeding or roosting birds.

For a more complete picture of the effects of wildfowling, further work should also incorporate the disturbance element of using a dog to retrieve shot quarry. Retrieval has the potential to cause an additional disturbance if birds remain in the area after the gun is fired. However, quarry tend to be shot at close range, so if the dog is sent to retrieve immediately, any additional disturbance caused by the presence of the dog is likely to be minimal since birds will have already vacated the immediate area due to the gunshot (Mark Greenhough – BASC, pers. comm.). In addition, not all shots will be successful so it is not necessary to send the dog out on every occasion. The extra (albeit short) stimulus of the presence of a dog could lengthen recovery time before birds land and resume feeding, or result in more birds abandoning the visible area rather than resettling nearby. Nevertheless, this would not considerably increase estimates for the space-time disturbed per wildfowler since the major contributor to this value is the presence of the wildfowler on the intertidal and the exclusion area around the boat (cf. relatively infrequent gunshots and retrievals).

Individual variation

Much of the unexplained variability in bird responses that were observed in relation to impulsive noise is likely to be due to between-individual differences in experience and body condition, so any research that can measure this alongside controlled experimental disturbance would make an important contribution to knowledge. Such field studies can however be logistically difficult and financially expensive, and the results may not easily be applied to other sites and situations. An alternative approach is to use simulation modelling (Stillman 2008, Bennett et al. 2009, McLane et al. 2011) to try to answer the question “*at what level of disturbance is there likely to be a population impact?*” This approach will be investigated in the next chapter using insights from the fieldwork in Poole Harbour.

Chapter 5 – An individual-based model of Poole Harbour – is disturbance limiting wintering wader populations?

5.1 Abstract

Individual-based models (IBMs) are increasingly being used to answer different types of question in ecology and animal behaviour since they are able to make predictions outside of the range of environmental conditions under which key parameters were measured. They use knowledge of how individuals interact with each other and their environments to predict population-level responses to novel scenarios. This chapter describes how results and insights from the preceding chapters were incorporated into a site-specific IBM for Poole Harbour using the established Morph IBM framework. The aim was to use the model to determine whether current patterns of human activities are limiting the carrying capacity of the site for wintering waders. It was also used to investigate the impacts of increased levels of disturbance in combination with other forms of environmental change (habitat loss and invertebrate prey availability). This is the first study that has combined detailed field observations (patterns of both human activities and bird behaviour) with simulation modelling to quantify and compare the impacts of different types of anthropogenic disturbance in terms of the number of birds that can be supported by a site and the end-of-season body condition of surviving birds. Most birds in Poole Harbour do not appear to be negatively impacted by disturbance from current patterns of human activities, and they are likely to be able to cope with relatively large increases in visitor numbers if all other factors remain constant. However, extra disturbance from increased visitor numbers would be expected to reduce the number of birds that can be supported if this occurs in combination with other changes that reduce the quality of the site; such as reduced extent of intertidal habitat due to sea level rise or reduced availability of invertebrate prey. Results suggest that it may be more important to focus on maintaining and improving the extent and quality of key habitats rather than direct action to reduce the amount of disturbance to below current levels.

5.2 Introduction

5.2.1. Disturbance in estuarine habitats

The conservation importance of many estuarine sites is recognised through designation as Special Areas of Conservation (SACs), Special Protection Areas (SPAs) and Ramsar wetlands of international importance, which afford legal protection to the key habitats and species that they support. This also includes a specific responsibility to take appropriate steps to avoid the negative impacts of disturbance on waterbird assemblages (EEC 1992, EC 2009), with a clear need to be able to predict where and under what circumstances disturbance is likely to be a problem and identify the most effective methods to prevent or minimise the level of impact on priority species.

Estuaries are also important and popular areas for human recreation, tourism, and economic activities, which can affect wildlife populations in many ways; such as through habitat loss and modification, over-exploitation and pollution, as well as direct disturbance (Millennium Ecosystem Assessment 2005). So the potential for disturbance to cause a problem, either in isolation or in combination with other factors, can be high. However, Chapters 2 to 4 have shown that bird responses to disturbance are highly spatially and temporally variable, and short-term studies of individual behavioural responses cannot quantify impacts at the population level during the course of a winter or over longer timescales (Bejder et al. 2006). Site-specific simulation modelling, for example using Individual-based models (IBMs), therefore is an essential tool for conservation managers and policy makers to investigate novel scenarios that would be impossible or undesirable to test in the real world (Stillman et al. 2016).

5.2.2. The individual-based modelling approach

IBMs are increasingly being used to answer many different types of question in ecology and animal behaviour, as well as in genetics, the social sciences, business and finance (see reviews by Grimm 1999, DeAngelis and Mooij 2005). In ecology they are used to model populations or systems composed of individuals, each with its own set of behavioural and physiological traits based on knowledge of the real-world system (DeAngelis and Mooij 2005, Grimm and Railsback 2005, Stillman and Goss-Custard 2010). Following the individual-based ecology theoretical framework (Grimm and Railsback 2005), model individuals make fitness-maximising decisions in the same way that real animals would. Simulations track their fates to predict the population-level consequences that emerge from individual interactions with

their environment and with each other (Stillman et al. 2015, 2016). The IBM approach has the advantage over other forms of predictive methods (such as using mathematical equations based on measured demographic rates) that they are able to make predictions outside of the range of historical environmental conditions under which key values have been measured since the underlying mechanisms behind individual decisions are expected to be the same even in novel situations (Norris and Stillman 2002).

IBMs have successfully been used to predict the impacts of disturbance and compare management options in, for example, waders and wildfowl (reviewed by Stillman et al. (2007)); birds feeding in park situations (Blumstein et al. 2005, Bennett et al. 2009); bats (Bennett et al. 2009); night-herons (Bennett et al. 2011); and cetaceans (Lusseau et al. 2006).

Morph

Morph is an IBM platform designed to predict the effects of environmental change on foraging animal populations (Stillman 2008). It has been developed and tested over a period of more than 15 years, and while the focus has been on coastal waterbirds (see examples given by Wood et al. (2015)), its flexible design means it can be applied to a wide range of species and situations (Stillman 2008). Durell et al. (2006) parameterised a version of Morph for Poole Harbour to assess the site's quality for overwintering waders and make predictions about the effects of habitat loss and sea level rise, and changes in food supply and mean daily temperature. The model follows a number of key principles (described in more detail in Stillman (2008)):

- Time progresses in discrete, fixed duration time steps;
- Space is divided into patches with fixed location and area;
- Patches contain resources that can be consumed by foragers;
- Foragers remain on the same patch for the duration of a time step, and can move to a new patch at the start of each time step; and
- Foragers choose patches according to where they can maximise their perceived fitness based on full knowledge of the patches (e.g. density of competitors, invertebrate prey abundance, whether exposed or covered by the tide etc.).

The model platform has since been considerably updated by K. M. Bowgen (BU, unpublished data) with more accurate patch bathymetry and tidal regime, more realistic bird population sizes and foraging rules, standardised energetics, and to reflect improved knowledge of the distribution and abundance of intertidal invertebrates throughout the site (Herbert et al. 2010). However the model has not been used to investigate the impacts of disturbance in

Poole Harbour so this research involved adding in new parameters relating to the types, distribution and frequencies of occurrence of human activities throughout Poole Harbour, as well as adding time, area and energetic costs for birds as a result of responding to disturbance. Stillman et al. (2012) developed a similar model for the Solent to predict the impacts of planned future housing developments and the associated increases in visitor numbers: the similarities and differences in the model predictions for the two sites will be discussed later (Section 5.5).

5.2.3. Predicting the impacts of disturbance in Poole Harbour

The worldwide human population is growing and people are increasingly being encouraged to make use of natural open spaces to improve their health and wellbeing (Maller et al. 2006, Pretty et al. 2007, Yerrell 2008, Depledge and Bird 2009). The number of daily visitors in Poole Harbour is therefore likely to increase in future. The aim of this chapter is to determine whether disturbance from current patterns of human activities in Poole Harbour is reducing the carrying capacity of the site in terms of the internationally important assemblage of wintering waders that it supports; and to make predictions about the potential impacts of increased numbers of visitors. Site managers need to know whether/when action is or will be necessary to mitigate the impacts of disturbance to maintain favourable conservation status.

Given the findings described in Chapters 2 to 4 – that the time and energetic costs of responding to disturbance events are low and unlikely to be incurred frequently enough to significantly reduce birds' ability to meet their daily energy requirements – model predictions are not expected to show a reduction in carrying capacity under current conditions cf. in the absence of disturbance. However, birds might be expected to show an increase in the proportion of time spent feeding or be in poorer body condition at the end of the winter period. Large amounts of disturbance of either foraging (Madsen 1988, Gill et al. 1996) or roosting (Rehfishch et al. 1996, Rogers et al. 2006) birds could, however, be expected to reduce the carrying capacity of the site if birds are excluded from favoured areas or are disturbed frequently enough. This would be especially likely under circumstances where bird intake rates are also limited by low food availability (intertidal or supratidal) and/or short intertidal exposure times (Evans 1976, Lindström 1991); and when intake requirements for thermoregulation increase during periods of extreme cold weather (Kelly et al. 2002).

The expected relationships described above will be tested in this Chapter using field data collection to determine the distribution and frequency of different human activities, and by parameterising the Morph model to incorporate the resulting time, area and energetic costs

experienced by birds. The model will also be used to compare the impacts of the two focal activities of this research – walking and wildfowling. Results in Chapter 4 suggested that although the cost of disturbance from a single wildfowling visit is likely to be greater than that for a single pedestrian visitor, cumulative impact over the course of a winter is expected to be lower due to considerable differences between the two activities in frequency of occurrence. The model will be used to test this.

The outputs of model simulations with different parameter combinations will be used to address the following questions and test the assumptions/expectations described above:

- i) What are the predicted impacts on survival, proportion of time spent feeding and bird body condition of varying frequencies and distributions of human activities during the intertidal period?
- ii) How do predictions about the impacts of disturbance vary in combination with different frequencies of disturbance to roosting birds?
- iii) How do predictions about the impacts of disturbance vary in combination with other forms of environmental change (sea level rise and invertebrate prey availability)?
- iv) How does the impact of wildfowling compare with other forms of disturbance in Poole Harbour?

5.3 Methods

5.3.1. Study site and field data collection

Instantaneous scan sampling (Altmann 1974) was used to determine the frequency and distribution of activities at each of five intertidal sub-sites in Poole Harbour (Fig. 5.1): collecting data on a total of 95 separate occasions across the three survey seasons 2012/13, 2013/14 and 2014/15. Each hour-long survey took place within an hour either side of low tide and consisted of one scan every ten minutes, during which the number and type of all activities were recorded if occurring on the intertidal area, adjacent shallow water, beach or shoreline footpaths. Aircraft and trains were not consistently recorded so they were not included in the final analyses. Free-running dogs were counted separately from their owners, but dogs on leads and their accompanying human were counted as a single threat since a human with a dog on the lead has been shown to be no more likely to disturb birds than a lone pedestrian (Lafferty 2001b).

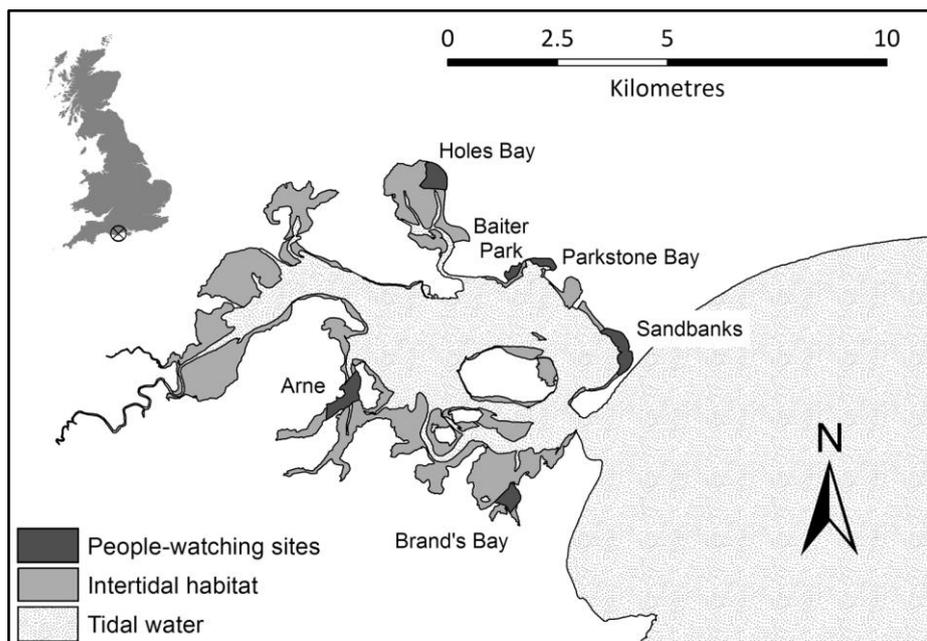


Figure 5.1. Survey sites in Poole Harbour used for observations of frequency and distribution of human activities. They are the same sites as those used for the pedestrian experiments, with the addition of Arne (saltmarsh and intertidal mud) and Baiter Park (flooded grassland), and reduction in the extent of the Brand's Bay sub-site. Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

For each sub-site the counts were converted into mean number of visitors present per km² of intertidal habitat and mean number per km of shoreline, depending on where they occurred. Activities were categorised as being on the shoreline if they were not using the intertidal

habitat but were still sufficiently close to potentially disturb feeding birds i.e. those activities that were on the beach, sea wall, footpath or saltmarsh. Activities occurring in the shallow water were combined with the intertidal counts since birds feeding at the water's edge or in the water could be disturbed by these activities.

The five intertidal sub-sites are considered to be representative of the range of visitor access levels across the whole estuary so the remaining areas of Poole Harbour were divided and each was assigned an estimate of visitor frequencies according to the most appropriate sub-site (Figure 5.2).

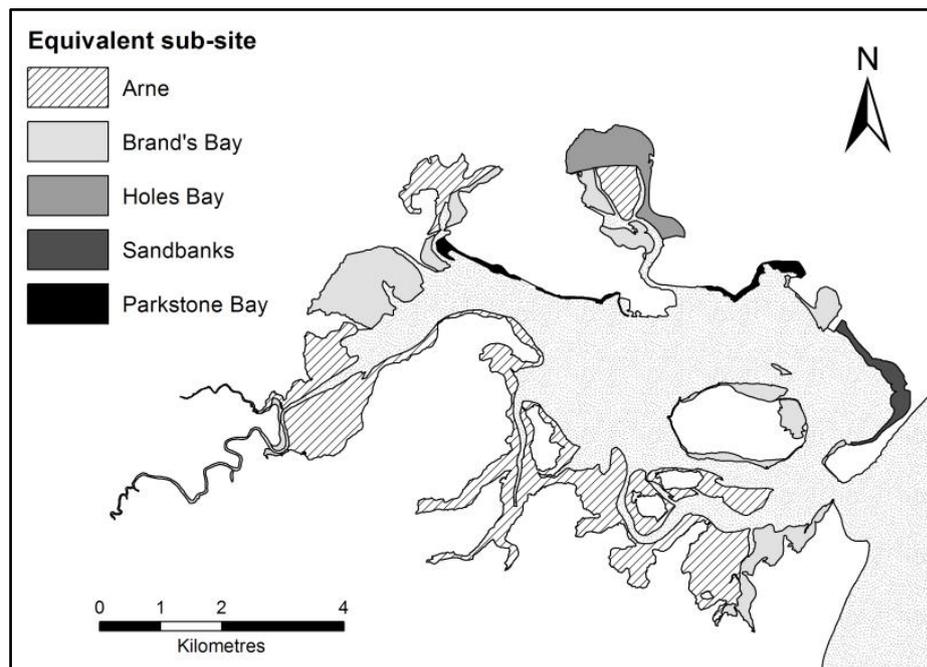


Figure 5.2. Assignment of intertidal sub-sites to the areas of Poole Harbour that they best represent. Reproduced from Ordnance Survey map data ©Crown Copyright and Database Right (2016) Ordnance Survey (Digimap Licence).

Baiter Park is a public open space on the eastern edge of Poole, separated from the intertidal habitat of Poole Harbour by the sea wall and a footpath/cycle path. The grassland floods with rainwater in winter and it is used as a high tide roost and supplementary feeding habitat mainly by brent geese *Branta bernicla* and oystercatchers *Haematopus ostralegus* (Morrison 2015). The site experiences high frequencies of human activities and birds are relatively tolerant of disturbance, either due to habituation or because they have no choice (Stillman et al. 2005). Here data collection involved six, hour-long, high tide surveys spread across the 2014/15 winter season to complement the observations of intertidal and shoreline activities. During each visit continuous recording (Martin and Bateson 1993) was used to count the number of activities per hour that occurred either on the grass or on the path around the

perimeter of the site. The number of times that a potential disturber resulted in a response from the birds was also noted, and whether the response was to walk or fly away. The other roost sites used by waders around Poole Harbour are unlikely to experience such high levels of human activity as at Baiter Park (Morrison 2015) so these results give an estimate of the maximum level of disturbance likely to be experienced by roosting birds in Poole Harbour.

5.3.2. An IBM of Poole Harbour

Working from the updated model for Poole Harbour (K. M. Bowgen, BU, unpublished data), extra parameters were added to allow the effects of disturbance to be incorporated into the model predictions. The results of the field observations described above, along with the results of the pedestrian experiments (Table 3.3) and wildfowling experiments (Table 4.7) were used to inform the parameter values. A screen shot of the model interface is shown in Figure 5.3.

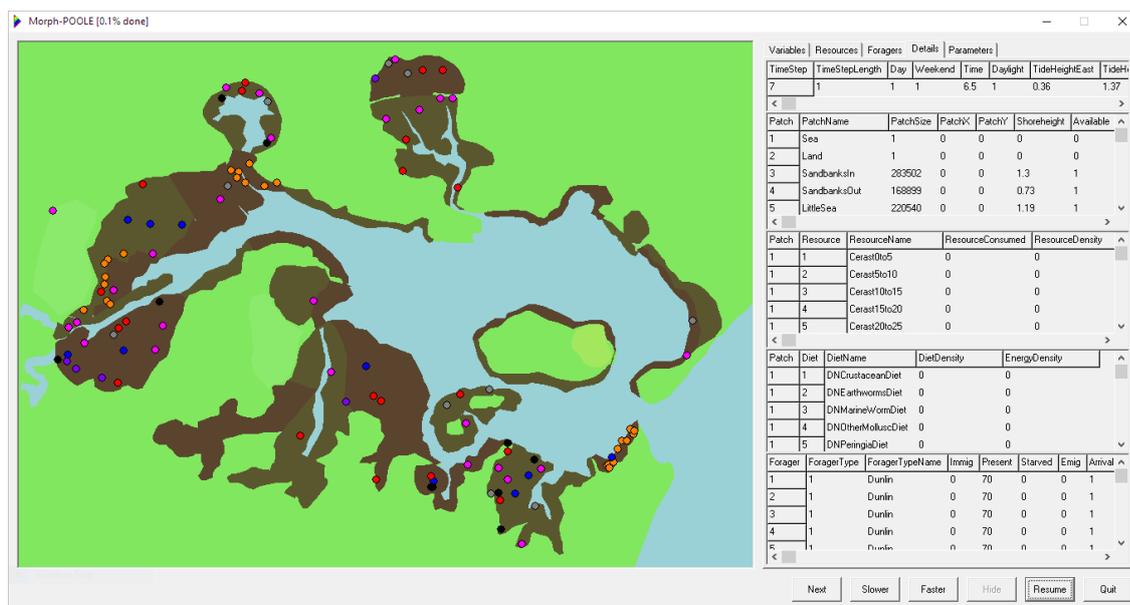


Figure 5.3. Screen shot of the Poole Harbour Morph IBM model interface.

5.3.3. Global parameters

Model time steps

Simulations were run for 212 days from 00:00 on 1 September to 23:59 on 31 March, and each day was split into 24 discrete, hour-long time steps during which environmental conditions and the presence/absence of potential disturbers remains the same. Time was included so that different human activities could be limited to different times of the day or night.

Environmental conditions

Equation 5.1 was used to estimate mean daily temperature T , where Day is the number of days since the start of the simulation, and based on records for 2011/12 from the nearest weather station at Bournemouth Airport, 11 km away (UK Meteorological Office 2015). Tide heights for each time step were taken from the 2011/12 records for the Pottery Pier and RoRo Terminal hydrographic stations using Tide Wizard software (Smartcom Software 2006). Whether or not it was daylight during each time step was calculated from times of sunrise and sunset obtained from the US Naval Observatory (2015).

$$T (^{\circ}C) = 0.000579 \times Day^2 - 0.1687 \times Day + 17.65 \quad \text{Equation 5.1}$$

Global disturbance parameters

Given that data collection was focussed on disturbance in intertidal areas, in the base model human disturbance only occurs on the intertidal patches and not on the roost or while birds are feeding in fields (see patch parameters, below). However a global variable called 'roost disturbance frequency' was also included to allow testing of the sensitivity of model predictions to additional disturbance in fields and at the roost.

5.3.4. Patch parameters

Spatial extent and patch availability

The intertidal areas of Poole Harbour were split into 31 foraging patches, including a single inland foraging patch called 'fields', plus a 'roost' patch where birds could rest at high tide but not feed. Each intertidal patch was given a shore height using tidal modelling software developed by HR Wallingford (Benson 2016), which when compared with the tide height during the time step determined whether or not it was exposed and therefore available to the birds for foraging. Fields were available at all states of the tide, but only during daylight; and the roost was always available.

Prey type, abundance, size and energy content

The distribution and abundance (density) of benthic invertebrates across the 30 intertidal patches was based on the sampling carried out by Herbert et al. (2010), and earthworm densities for the fields patch were obtained from data on surrounding wet grassland (Durell et al., 1998). Species were grouped together into eight resource types: cockles, mussels, winkles, other molluscs, crustaceans, peringia, marine worms and earthworms, which were each further sub-divided into size classes relevant to the sizes consumed by different bird species (Goss-Custard et al. 2006b). Each species size class was then given a value for energy

content based on species-specific relationships identified by Thomas et al. (2004) between body size (total length, L) and mg of ash-free dry mass ($AFDM$) (Equation 5.2), and using an energy density of 22 kJ/gAFDM (Zwarts and Wanink 1993).

$$\ln(AFDM) = Coef_1 \times (\ln(L) - Coef_2) \quad \text{Equation 5.2}$$

Wildfowler presence

Wildfowling in Poole Harbour can take place between 1 September and 20 February, inclusive, on Crown Foreshore that is not designated as a refuge area (see previous chapter for more details), and it generally takes place between dawn and dusk so it was limited to between 6am and 6pm in model simulations. Patches were given a probability of a wildfowler being present based on the following equation:

$$P(\text{wildfowler present}) = V \div D \div A \div H \times M \times Patch_{area} \times Patch_{shot} \quad \text{Equation 5.3}$$

where V is the number of visits in a season, D is the number of days in a season, A is the total area where wildfowling can occur, H is the hours of occurrence per day, M is the mean duration per visit, $Patch_{area}$ is the size of the patch, and $Patch_{shot}$ is the proportion of the patch over which shooting can occur. This probability value was used to determine for each patch and time step whether a wildfowler was present (by comparing it with a randomly selected number between zero and one). In this way, patches could not have more than one wildfowler present at a time, which is usually the case in reality (Matt Ellis – BASC, pers. comm.).

Other potential disturbers

The number of potential disturbers on the path and on the intertidal habitat was determined for each patch using the results of the field observations and according to the patch area and length of shoreline. Potential disturbers could be present in the model between 6am and 10pm, though with lower visitor frequencies between 6pm and 10pm according to the findings by Stillman et al. (2012) that 6% of coastal visits occur during darkness and by Liley et al. (2008) that most visits after dark in Poole Harbour occur before 10pm.

Table 5.1. Forager constants used in the model – see text for explanation of how the values were obtained and used. LCT = Lower critical temperature. BMR = basal metabolic rate.

Species	Initial population size (nearest 50)	Target energy store (kJ)	Daily metabolic rate 2.1 x BMR (kJ)	LCT (°C)	Thermostatic costs (kJ/day/°C)	Forager coefficient	Night foraging efficiency	Interference threshold density (birds/m ²)
Curlew	850	10115.07	768.4530	5.0	52	-1.034	0.82	0.01
Oystercatcher	850	6729.660	590.5137	10.1	31.7	-1.123*	0.81	0.01
Bar-tailed godwit	100	4079.985	385.6419	15.3	14.2	-1.266	0.87	0.01
Black-tailed godwit	1300	4716.250	380.1336	15.4	13.8	-1.271	0.87	0.01
Grey plover	100	3992.520	327.5874	16.6	10.4	-1.321	1	0.01
Redshank	750	2154.040	233.8623	18.6	5.5	-1.434	0.95	0.01
Dunlin	1400	377.643	103.3515	20.8	1.2	-1.708	0.82	0.01

* forager coefficient = -1.350 for oystercatchers when feeding on mussels.

5.3.5. Forager parameters

Species and population sizes

Model simulations included the seven most abundant wader species in Poole Harbour – curlew *Numenius arquata*, oystercatcher, bar-tailed godwit *Limosa lapponica*, black-tailed godwit *Limosa limosa*, grey plover *Pluvialis squatarola*, redshank *Tringa totanus* and dunlin *Calidris alpina* – all of which have average winter monthly Wetland Bird Survey (WeBS) counts of 100 or more individuals and contribute to the wintering waterbird assemblage that qualifies the site as a wetland of international importance (Holt et al. 2015, JNCC 2016c). Black-tailed godwit numbers are also of international importance in their own right (JNCC 2016c). Initial population sizes at the start of each simulation were based on the WeBS five year average for September to March 2009/10 – 2013/14 (Holt et al. 2015) and rounded to the nearest 50. All of the species-specific forager constants used in the model are shown in Table 5.1 and an overview of the new disturbance-related parameters is given in Table 5.2.

Body mass and energy stores

Arrival body mass values (g) for each species were set at target body mass values, obtained from the BTO Bird Facts database (British Trust for Ornithology 2015), and multiplied by the energy density of fat 34.3kJ/g (Kersten and Piersma 1987) after subtracting starvation mass to determine each species' arrival energy store (K. M. Bowgen, BU, unpublished literature review). Model birds therefore attempted to maintain that energy store throughout the winter, and they starved if their energy store dropped to zero.

$$\text{Target energy store (kJ)} = (M_{\text{arrival}} - M_{\text{starve}}) \times 34.3 \quad \text{Equation 5.4}$$

Metabolic rate and thermoregulation

Field metabolic rate (FMR) i.e. daily thermoneutral energy requirement was set at 2.1 times the basal metabolic rate (BMR) following Kersten and Piersma (1987):

$$\text{FMR (kJ per day)} = 2.1 \times 437 \times \text{Mass(kg)}^{0.729} \quad \text{Equation 5.5}$$

And thermoregulatory costs below a lower critical temperature (LCT) were calculated using the following equations:

$$\text{LCT (}^{\circ}\text{C)} = 0.0216 \times \text{Mass(g)} + 21.896 \quad \text{Equation 5.6}$$

$$\text{Cost (kJ per day per }^{\circ}\text{C below LCT)} = 0.0055 \times \text{Mass(g)}^{1.3737} \quad \text{Equation 5.7}$$

The coefficients for these two equations were estimated by plotting the relationship between actual body mass and measured thermoregulatory costs for several wader species presented in the literature (K. M. Bowgen, BU, unpublished data). Hourly metabolic costs (combined FMR and thermoregulatory costs) were deducted from the birds' energy stores at the end of each time step.

Foraging decisions and intake rates

The foraging rate of birds in the model was determined by the abundance and ease of assimilation of the energy content of invertebrate prey, the strength of interference through competition with other individuals, and whether it was day or night. Interference-free intake rate (IFIR) i.e. in the absence of density-dependent competition, was calculated using Equations 5.8 and 5.9:

$$IFIR \text{ (mg per s)} = f \frac{IFIR_{max} B}{B_{50} + B} \quad \text{Equation 5.8}$$

$$\log_e(IFIR_{max}) = C_{forager} + 0.365 \log_e(1.05 \times M_{prey}) \quad \text{Equation 5.9}$$

where f is foraging efficiency, B is patch biomass density of prey within the size range consumed (mg/m^2), $IFIR_{max}$ is the maximum intake rate when prey are superabundant, and B_{50} is the prey biomass density at which intake rate is 50% of its maximum. $C_{forager}$ is a species-specific forager coefficient related to body mass, and M_{prey} is the mean AFDM (mg) of prey within the size range consumed. Values for $C_{forager}$ and B_{50} were obtained from Goss-Custard et al. (2006b), who undertook a literature review and multiple regression analysis of the correlates of \log_e intake rates in waders. M_{prey} values for each species and size class were those measured by from Thomas et al. (2004) in a benthic core sampling survey of Poole Harbour. The foraging efficiency (f) of each individual within a population was selected from a normal distribution with mean = 1 and standard deviation = 0.125 (Goss-Custard et al. 1995), which introduced an element of stochasticity between model runs. This was adjusted by a given proportion for each species when foraging at night (Sitters (2000) and Lourenço et al. (2008) as interpreted by Stillman et al. (2012)). Assimilation efficiency was assumed to be 0.75 for most birds consuming most diets, and 0.85 for birds consuming crustaceans and oystercatchers consuming molluscs (Goss-Custard et al. 2006b). Interference effects through prey stealing by conspecifics and/or escape by mobile prey were incorporated for each species when the density of competitors on a patch exceeded the threshold density of 0.01 birds/ m^2 (Goss-Custard and Stillman 2008, K. M. Bowgen [BU] unpublished data).

At the start of each time step birds chose a patch and diet with which they could achieve the greatest final energy store by the end of that time step, up to a maximum of their target energy store. When birds reached their target they rested for the remainder of the time step. If there was more than one patch on which they could achieve their target, a patch was selected at random.

Free area

The model calculated the area of each patch available to foragers after accounting for the presence of human activities based on the species-specific responses to disturbance described in Chapters 3 and 4. Shoreline activities only disturbed the upshore area (see patch parameters) but intertidal activities could be present throughout the full extent of intertidal patches. Activities occurred randomly in space and time with the exception of wildfowling, which was assumed to take place separately from other activities. The proportion of patch disturbed was calculated with the formula given by Stillman et al. (2012) following binomial probability theory and based on the assumption that birds and potential disturbers are independently distributed in time and space:

$$\textit{Proportion disturbed} = 1 - (1 - p_1)^{n_1} \quad \textbf{Equation 5.10}$$

where p_1 is the proportion disturbed by a single activity and assumed to be the weighted mean of the proportion of a patch disturbed by stationary and moving activities respectively (based on areas calculated in Equations 5.11a-d; Figure 5.4) and n_1 is the total number of potential disturbers present.

$$\textit{Area disturbed} = \frac{\pi r_2^2}{2} + 2r_1 \cdot h_1 \cdot s + 2(r_2 - r_1) \cdot h_2 \cdot s \quad \textbf{Equation 5.11a}$$

$$\textit{Area disturbed} = \pi \cdot r_2^2 \quad \textbf{5.11b}$$

$$\textit{Area disturbed} = \frac{\frac{\pi r_2^2}{2} + 2r_1 \cdot h_1 \cdot s + 2(r_2 - r_1) \cdot h_2 \cdot s}{2} \quad \textbf{5.11c}$$

$$\textit{Area disturbed} = \frac{\pi \cdot r_2^2}{2} \quad \textbf{5.11d}$$

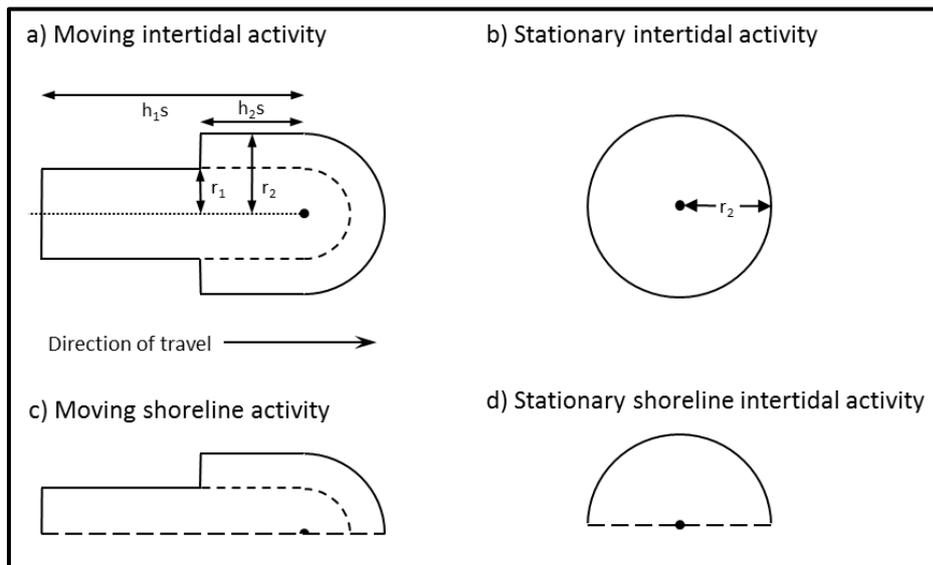


Figure 5.4. Conceptual diagram of the area disturbed by stationary and moving activities. r_1 =FID; r_2 =alert distance; h_1 =recovery time after flight; h_2 =recovery time after alert; s =speed. Adapted from van der Meer (1985) in Smit and Visser (1993).

A value of 2.5 km/h was used for s , and r_1 , r_2 and h_2 were set according to the results of the field experiments already described (Tables 3.3 and 4.7). Recovery time after flight (h_1) is likely to vary between disturbance types and depending on whether or not the redistribution of birds after a disturbance causes density dependent reductions in bird intake rates through interference competition. In the absence of site-specific field data for this, a value of 30 minutes was used for non-wildfowling disturbances – the mean recovery time for oystercatchers as reported by Stillman and Goss-Custard (2002). When a wildfowler was present in a patch, birds in the model were excluded from the area disturbed by the sound of a shotgun for the whole duration of that time step, which is consistent with observations during the wildfowling experiments (Chapter 4) whereby birds rarely fully returned to their original distribution before the end of a wildfowling visit.

The proportion of upshore area and remaining intertidal area disturbed by non-wildfowling were calculated separately and then combined with the proportion disturbed by wildfowling to give a single value of free area for each species on each patch.

Number of flight responses

Given that the size of each patch is large relative to the area disturbed by a single activity, not all birds on a patch will be disturbed by every activity present so the mean number of disturbances per bird was estimated for each patch. Following binomial probability theory, the mean number of flight responses is expected to be equal to the number of potential

disturbances multiplied by the probability of a single activity disturbing all of the birds present i.e. the proportion of the patch disturbed per activity. All birds on a patch therefore experienced the same number of disturbances.

$$\text{Number of flights per bird} = n_2 \times p_2 \quad \text{Equation 5.12}$$

Stationary activities (such as bait digging and angling) were assumed not to result in bird flight responses so n_2 is the number of moving activities only and p_2 is the probability of a single moving activity resulting in a flight response from all birds. The probability of birds being disturbed by the sound of the shotgun was calculated using equation 5.13.

$$P(\text{Flight}) = \frac{\text{Area}_{\text{shot}} - \text{Area}_{\text{boat}}}{\text{Area}_{\text{patch}} - \text{Area}_{\text{boat}}} \quad \text{Equation 5.13}$$

$\text{Area}_{\text{shot}}$ is the area disturbed by a shot, $\text{Area}_{\text{boat}}$ is the area from which birds are excluded due to the presence of the boat, and $\text{Area}_{\text{patch}}$ is the total area of the patch. Since birds were assumed not to return to the disturbed area before the end of that time step, they could only be disturbed by the first shot fired as it was assumed that no birds would be close enough to be disturbed by any subsequent shots.

Free time

Free time available to birds for foraging during each time step was calculated from the recorded species- and activity-specific values for total feeding time lost per disturbance response and the total number of disturbances experienced by each bird due to each activity type.

Energy costs of disturbance

The energetic costs of flight per disturbance were calculated from the observations of time spent in flight for each type of activity and using Equation 5.14 (Kvist et al. 2001). The cumulative energetic costs of all disturbance responses were added to the birds' hourly metabolic rate and deducted from their energy stores at the end of each time step.

$$\text{Cost (kJ per s)} = \frac{10^{0.39} \times \text{Mass(g)}^{0.35} - 0.95}{1000} \quad \text{Equation 5.14}$$

Individual variation

In addition to the variation in foraging efficiency described above, birds varied in their relative dominance (selected from a uniform distribution between 0 and 1), which influenced their susceptibility to interference from competitors and added another element of stochasticity between model runs.

Table 5.2. An overview of the disturbance-related parameters added to the model. Detailed descriptions can be found in the main text.

a) Global parameters

Parameter	Base value	Units	Details*
Recovery time [pedestrian]	0.5	hours	Time taken for birds to return to their original distribution after being disturbed by an approaching pedestrian.
Recovery time [wildfowling]	1	hours	Time taken for birds to return to their original distribution after being disturbed by the sound of the shotgun.
Roost disturbance frequency	0	per hour	Maximum value tested was based on results of observations at Baiter Park.

b) Patch parameters

Parameter	Base value	Units	Details*
Shore length	0-7	km	Length of shoreline for patches, calculated using the mean high water mark in ArcGIS 10.3.
Number of visitors on path	Calculated in model	per km	Results of the people-watching fieldwork.
Number of visitors on intertidal area	Calculated in model	per km ²	Results of the people-watching fieldwork.
Wildfowler present	0/1	-	See text.
Proportion of intertidal activities that are stationary	0-100	%	Results of the people-watching fieldwork.
Proportion of path activities that are stationary	0-100	%	Results of the people-watching fieldwork.

c) *Forager parameters*

Parameter	Base value	Units	Details*
Maximum upshore area	Calculated in model	m ²	The species-specific maximum area that can be disturbed by visitors at the top of the shore.
Proportion of patch disturbed by non-wildfowling activities	0-100	%	Used to calculate free area available for feeding.
Proportion of patch disturbed by wildfowler's boat	0-100	%	Used to calculate free area available for feeding.
Proportion of patch disturbed by sound of shotgun	0-100	%	Used to calculate free area available for feeding.
Time cost	Calculated in model	%	Proportion of time step lost due to responding to disturbance.
Energy cost	Calculated in model	kJ	Additional costs of flight due to responding to disturbance.

* See text for calculations.

5.3.6. Model outputs and validation

At the end of each simulation the model reports the mean proportion of time spent feeding, final energy stores and ultimately survival of foragers, which was used to compare the effects and impacts of different disturbance regimes. Given that the model is a closed system (i.e. foragers only leave the simulation if they starve), the term 'predicted survival' should be considered as a measure of the number of birds that Poole Harbour is predicted to be able to support (site carrying capacity), since in real life birds that are having difficulty meeting their energy requirements may move elsewhere before their energy stores reach zero (Davidson and Evans 1982, Camphuysen et al. 1996).

The predictions of the base model were validated by comparing them with observed data on the distribution of birds around the estuary (Holt et al. 2015) and on the proportion of time that birds spent feeding (Goss-Custard and Stillman 2008 and this study; see Chapter 3). Observed and predicted values corresponded well (K. M. Bowgen, BU, unpublished data) so we can have confidence in the model predictions for different frequencies of disturbance and under different scenarios of environmental change.

5.3.7. Sensitivity analysis

Model predictions of bird overwinter survival were tested for sensitivity to variations in three disturbance-related parameters (Table 5.3) that were not included in the disturbance scenarios described in the next section. For each of the analyses the other disturbance related parameters were fixed at the levels used in the base model.

Chapters 3 and 4 demonstrated that as well as varying between species, bird responses to disturbance differ depending on environmental conditions, disturbance type and individual characteristics; however in the interests of model parsimony this level of complexity was not included in the base model and responses were fixed for each species using the mean of wildfowling-specific responses and the mean results of the pedestrian disturbance experiments (Chapter 3) for all other potential disturbance types. The effect of this simplification on model predictions was therefore tested by varying the fixed values for the magnitude of bird responses to determine the importance of detailed field experiments to inform these parameter values.

Sensitivity of model predictions was also tested in relation to variations in bird recovery time (time taken for birds to return to their original distribution after a disturbance) separately from the other response parameters since the factors that affect recovery time are likely to be different from those affecting FID, flight time, boat exclusion area etc. Most of the variation in bird FID, flight time and total time lost can be explained by species, body mass, environmental conditions and site differences, whereas recovery time is more likely to be governed by the density of birds. If the resulting density of birds after a disturbance is such that intake rate is reduced due to increased interference or kleptoparasitism, then birds would be expected to redistribute across the patch more quickly than if intake rates were unaffected at the new density of birds.

The assumption in the base model that birds disturbed by the sound of the shotgun do not return to the area until after the wildfowler has left means that birds would only be disturbed once per hour regardless of the number of shots fired. If birds returned sooner they could be disturbed by subsequent shots so sensitivity of model predictions was also tested in relation to the number of shots per hour that result in a flight response.

Table 5.3. Parameters and values included in the sensitivity analysis.

Parameter	Units	Range of values tested
Recovery time (pedestrian disturbance)	minutes	10 to 60 (base model = 30)
Magnitude of response*	% change	-50% to +50% (base model = 0)
Number of shots that disturb birds	Number per hour	1 to 6 (base model = 1)

* alert distance, FID, alert time, flight time, latency time, total time lost, boat exclusion distance, and effective disturbance distance (EDD); all adjusted by the same proportion at the same time.

5.3.8. Disturbance scenarios

The main reason for developing this model of Poole Harbour was to investigate the impacts of disturbance on wintering waders; to determine whether over-winter populations are limited by current frequencies of human activities; and to explore the contribution of wildfowling to the combined impacts of disturbance from all activities. Once calibration, validation and sensitivity analysis were complete, the model was used to test the impacts of different disturbance scenarios on the survival, body condition (final energy store as a proportion of target energy store) and proportion of time spent feeding for each species at the end of each simulation. Each tick in Table 5.5 represents one scenario with the combination of parameters indicated; and the mean outputs were calculated from ten model runs of each scenario.

Disturbance scenarios included different values for each of four parameters: disturbance index, distribution of activities, number of roost disturbance, and number of wildfowling visits. Each is described below.

The 'disturbance index' value is the relative number of potential disturbers (both wildfowling and other activities) i.e. disturbance index = 1 for the current frequency of human activities.

Activities are currently concentrated in specific areas of Poole Harbour, so increased disturbance frequency scenarios were tested both with observed distributions of activities and with an even spread across all patches. In this way the potential impact could be assessed of increased frequencies of human activities in areas of the Harbour that are currently relatively undisturbed.

The impacts of increased intensities of wildfowling were also tested in combination with different frequencies of other human activities.

Aside from the observations at Baiter Park, it was beyond the scope of this study to undertake detailed observations of disturbance to roosting birds; however this could be an important source of additional daily energetic costs (e.g. Lilleyman et al. 2016) so the model was used to test the impacts of different numbers of disturbances per hour when birds are feeding in fields or resting on the roost. This was tested in combination with different scenarios of increasing frequencies of activities on the intertidal patches.

5.3.9. Environmental change scenarios

In addition to the disturbance scenarios listed above, the predicted impacts of disturbance were also tested in combination with sea level rise and changes in the availability of invertebrate prey at the start of the model. Sea level scenarios were based on the range of estimates for 2020-2060 (Table 5.4) using UK Climate Projections data (Jenkins et al. 2009). All disturbance and environmental change scenario parameter combinations are shown in Table 5.5. Again, the model was run ten times for each scenario and mean predicted survival, body condition and proportion of time spent feeding were calculated for each species.

Table 5.4. Central estimates for each decade of relative sea level rise (London) with respect to 2010 levels (tide heights used in the model were for 2011/12). Adapted from UK Climate Projections data (Jenkins et al. 2009).

Year	Relative sea level rise (cm)		
	High emissions	Medium emissions	Low emissions
2020	4.2	3.5	2.9
2030	8.7	7.3	6.1
2040	13.5	11.3	9.5
2050	18.5	15.6	13.1
2060	24.1	20.1	16.9

Table 5.5. Parameter combinations and values used for the disturbance- and environmental change scenarios that were selected to be tested for Poole Harbour.

Index*	Distribution of activities		Distribution of activities = observed																				
			Roost disturbances per hr						Wildfowling visits per season						Sea level rise (cm)				Relative prey density				
	Observed	Even	0	2	4	6	8	10	0	100	200	300	400	500	0	5	10	20	1.1	1	0.9	0.8	0.7
0	✓	✓													✓	✓	✓	✓	✓	✓	✓	✓	✓
1	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
5	✓	✓													✓	✓	✓	✓	✓	✓	✓	✓	✓
10	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
15	✓	✓													✓	✓	✓	✓	✓	✓	✓	✓	✓
20	✓	✓													✓	✓	✓	✓	✓	✓	✓	✓	✓
25	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓

* Index = relative number of potential disturbers (both wildfowling and other activities).

Current frequency of human activities: disturbance index = 1.

5.4 Results

5.4.1. Field observations

Activities affecting the intertidal area

562 scans across the five intertidal sub-sites resulted in a total of 4501 observations of potential disturbance events, 66% of which were walkers (with or without a dog). Activities were not evenly distributed across sites (Figure 5.5) or shore levels (Figure 5.6) and the resulting values used to parameterise the model (after accounting for differences in area and length of shoreline between sub-sites) are shown in Table 5.6.

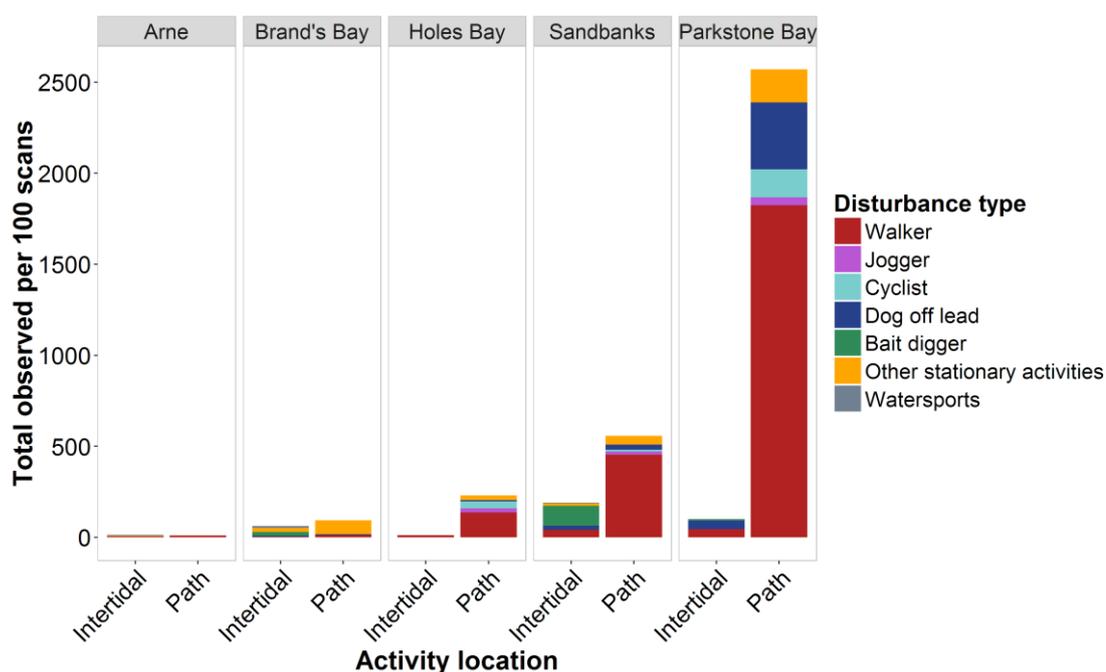


Figure 5.5. Activity types observed at each sub-site. ‘Walker’ includes dog walkers. ‘Other stationary activities’ includes people sitting on benches, birdwatchers, photographers and anglers. Total number of scans: Arne = 77; Brand’s Bay = 126; Holes Bay = 108; Parkstone Bay = 112; Sandbanks = 139.

Two types of activity that were not observed during the survey visits, but which are known to occur in Poole Harbour, are bait dragging and pump scoop dredging (Liley and Fearnley 2012, Southern IFCA 2016). Discussion of model predictions will include the potential of these activities to disturb feeding and roosting birds and alter the invertebrate prey availability. Despite two of the sub-sites being permitted wildfowling areas (Brand’s Bay and Arne), no instances of wildfowling were recorded throughout the course of these surveys, so the model used values published by Dorset Wildfowling Association, as described below.

Table 5.6. Observed values used to parameterise the model to calculate area disturbed by human activities (excluding wildfowling). The total number of scans at each site is shown in brackets.

Sub-site	Number of potential disturbers present at the same time		Proportion of activities that are stationary	
	On intertidal (per km ²)	Along shoreline (per km)	Intertidal	Shoreline
Arne (77)	0.374	0.052	0.3	0
Brand's Bay (126)	3.152	1.444	0.71	0.83
Holes Bay (108)	0.412	2.029	0	0.12
Parkstone Bay (112)	10.477	46.092	0.06	0.07
Sandbanks (139)	7.701	3.589	0.52	0.08

The contribution that wildfowling makes to the total daily occurrences of human activities was estimated based on the numbers of visits reported by Dorset Wildfowlers' Association (2013). The mean number of visits per season for the period 2001/02 to 2012/13 was 131, which equals 0.76 visits per day of the wildfowling season (Dorset Wildfowlers' Association 2013). By scaling up the results for the whole of Poole Harbour according to the proportions shown in Figure 5.2, the daily number of occurrences of human activities is estimated to be 2023, or 142 per km²; 0.038% of which is represented by wildfowling.

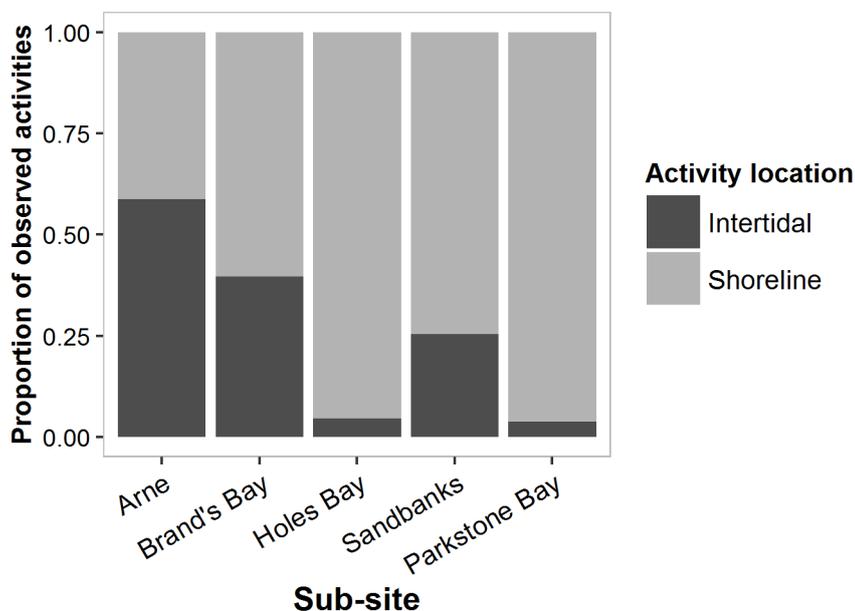


Figure 5.6. Observed distribution of activities across shore levels at each sub-site.

Roost disturbance

A total of 1194 potential disturbers were observed during the six hours of surveys at the Baiter Park high tide roost (Figure 5.7), 4% of which resulted in a disturbance response (walk or flight) from one or more birds. 88% of flight responses were caused by dogs; 10% by walkers; and 1% by stationary activities (a photographer). The mean number of disturbance responses per hour was $8.17 \pm \text{s.e. } 3.3$.

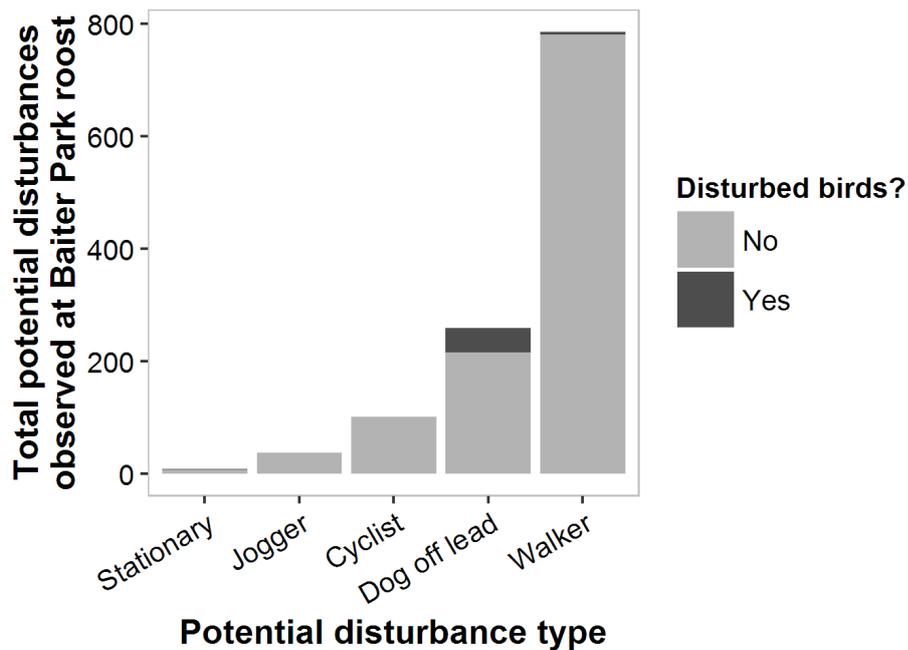


Figure 5.7. Total number of activities and disturbances observed during six hour-long surveys at the Baiter Park high tide roost.

5.4.2. Model predictions – disturbance scenarios

Visitor numbers and distribution of activities

Model outputs showed that increased frequencies of human activities in Poole Harbour (current situation: disturbance index = 1) can reduce both the predicted survival (Figure 5.8a) and body condition of surviving birds (Figure 5.8c). This was apparent for all species except oystercatcher and curlew, whose survival remained close to or at 100% across the range of visitor frequencies tested. The impact was more pronounced, particularly for bar-tailed- and black-tailed godwits, when human activities were evenly spread around the site rather than occurring more frequently in specific areas according to the distribution that were observed in the field. With the exception of bar-tailed godwit, disturbance at current visitor frequencies and distributions does not appear to be reducing the number of birds that can be supported overwinter or bird final body condition. Species that are not godwits were also

predicted to be able to cope with at least a ten-fold increase in visitor numbers before body condition was affected; and a fifteen-fold increase before showing a decline in survival. Birds were able to compensate for the costs associated with increased frequencies of disturbance by increasing their proportion of time spent feeding (Figure 5.8b).

Effect of wildfowling

Figure 5.9 shows that the model predicted no relationship between the number of wildfowling visits in a season and a) bird survival or c) final body condition. This was also the case when tested in combination with 10 and 25 times the current frequency of other human activities. In addition, increased wildfowling intensities were not predicted to affect the proportion of time that birds spent feeding (Figure 5.9b), though time spent feeding was predicted to increase at higher frequencies of other types of disturbance.

Roost and field disturbances per hour

At current levels of intertidal disturbance the model outputs showed no relationship between frequency of roost/field disturbance and bird survival (Figure 5.10a) or body condition (Figure 5.10c). Birds were predicted to increase the proportion of time spent feeding (Figure 5.10b) and could therefore cope with the range of roost disturbance frequencies tested. This was also the case with a disturbance index of ten; however, with a disturbance index of 25, increased roost and field disturbance was predicted to reduce the survival and body condition of grey plover, black-tailed godwit and bar-tailed godwit even though they increased their proportion of time spent feeding.

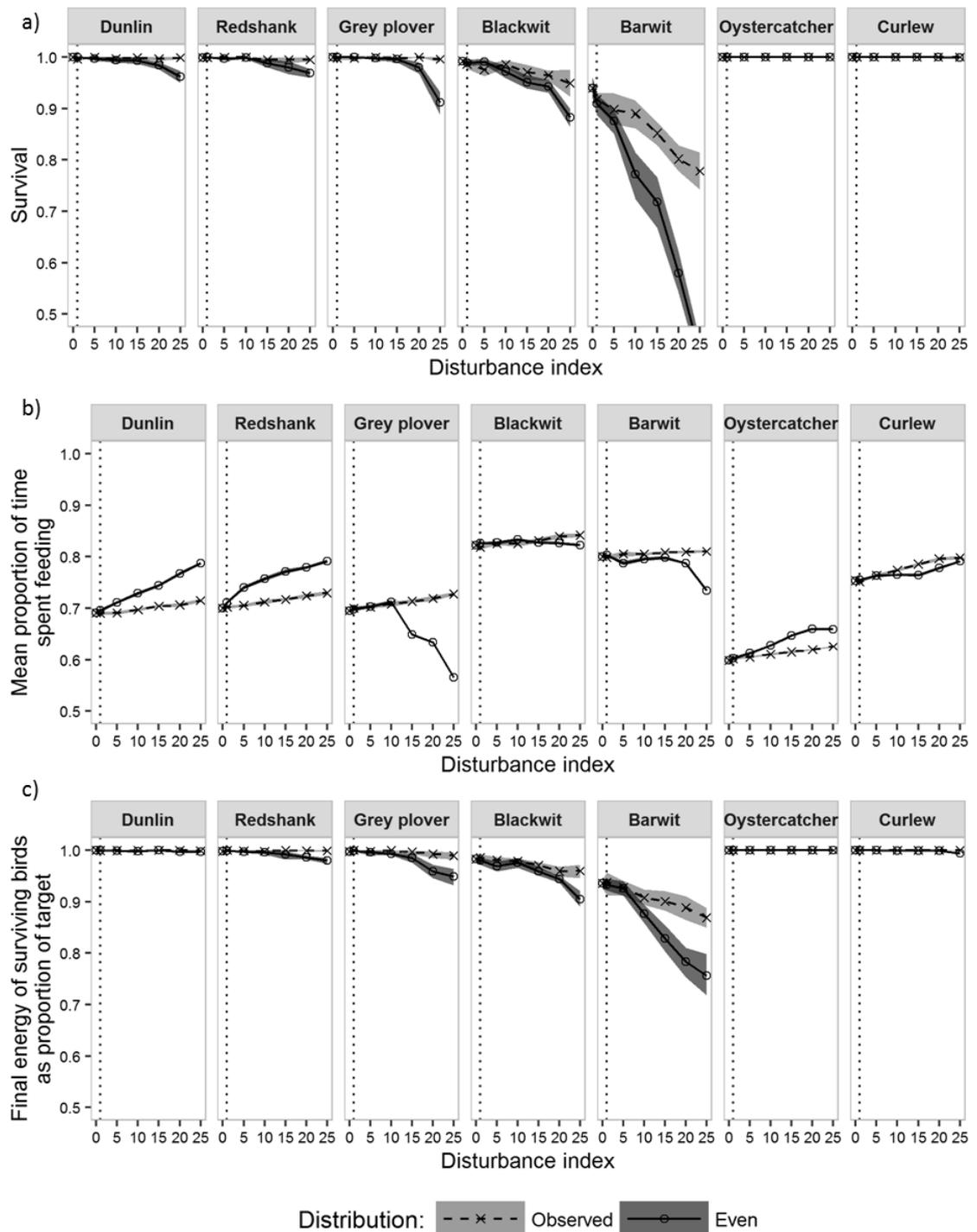


Figure 5.8. The predicted impacts of increased numbers of human visitors and the distribution of activities around Poole Harbour on a) survival; b) proportion of time spent feeding; and c) body condition of birds. The vertical dotted line marks the current situation at disturbance index = 1. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit. Shading indicates the 95% confidence interval around the mean, derived by bootstrapping.

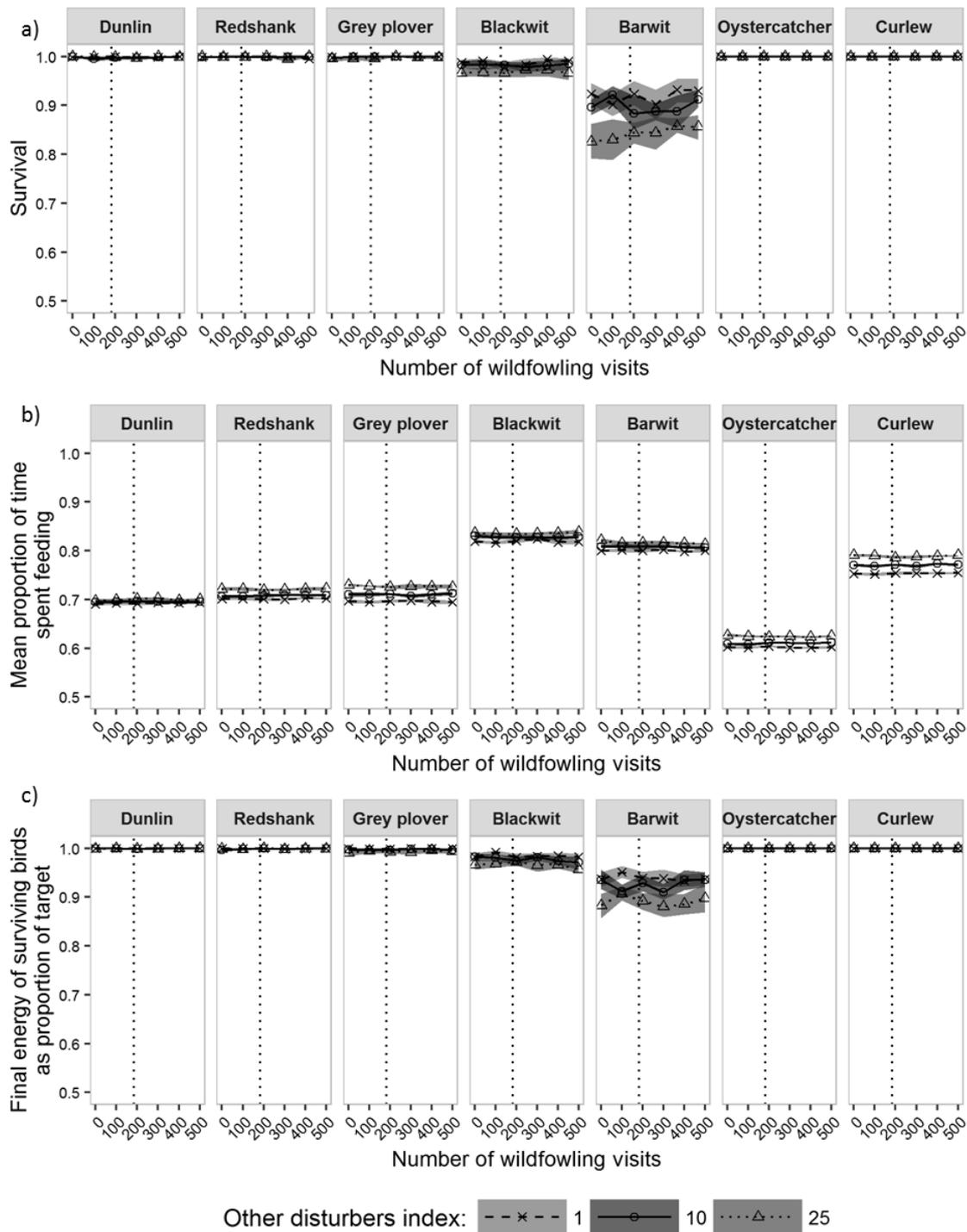


Figure 5.9. The predicted impacts of increased intensities of wildfowling in combination with other human activities in Poole Harbour on a) survival; b) proportion of time spent feeding; and c) body condition of birds. The vertical dotted line marks the maximum number of visits currently permitted (183). ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit. Shading indicates the 95% confidence interval around the mean, derived by bootstrapping.

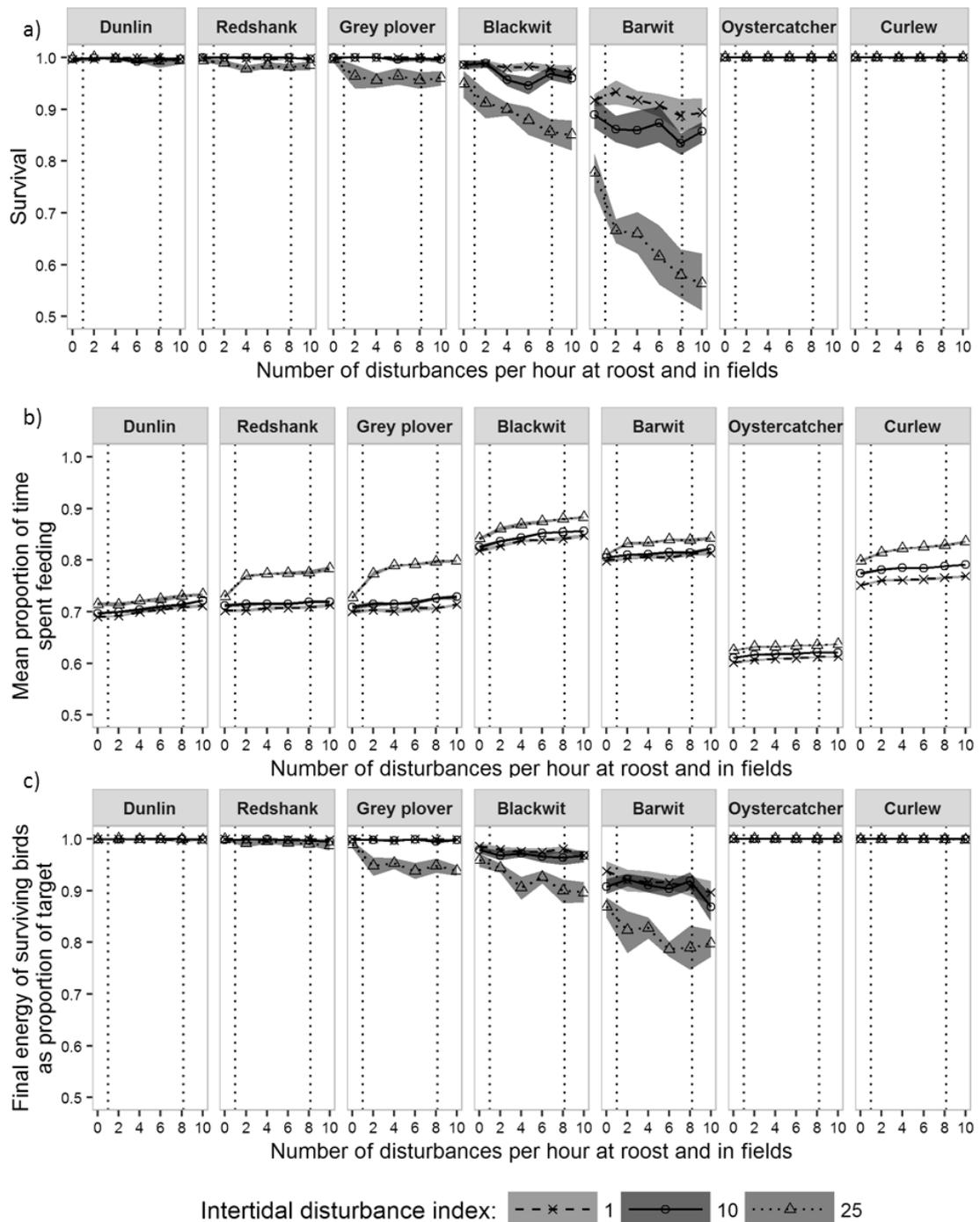


Figure 5.10. The predicted impacts of roost disturbance in combination with disturbance of foraging birds during the intertidal exposure period on a) survival; b) proportion of time spent feeding; and c) body condition of birds. The vertical dotted lines mark the roost disturbance frequency used in the base model (zero disturbances per hour) and the frequency observed at Baiter Park (8.17/hr). ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit. Shading indicates the 95% confidence interval around the mean, derived by bootstrapping.

5.4.3. Model predictions – impacts of disturbance in combination with environmental change

Sea level rise

With the exception of oystercatcher, one or more of the sea level rise scenarios that were tested with the model were predicted to result in reduced survival (Figure 5.11a) and body condition (Figure 5.11c) of birds despite increasing the proportion of time spent feeding (Figure 5.11b). This impact was greater in combination with increased numbers of human visitors; particularly with visitor numbers more than ten times current numbers. However, the interaction between disturbance index and sea level rise was less strong in relation to predicted final energy stores (Figure 5.11b; dunlin and redshank).

At current disturbance frequencies dunlin, redshank, grey plover oystercatcher and curlew are likely to be able to cope with a 5 cm increase in sea level without their survival or body condition at the end of the winter being affected. However, even under a low emissions scenario, sea level is predicted to rise beyond this by 2030 – see Table 5.4 (Jenkins et al. 2009). Additionally increases in disturbance frequencies between now and 2060 would be expected to exacerbate the impacts of sea level rise on all species except oystercatcher.

Relative prey density

Figure 5.12 shows that dunlin, redshank, oystercatcher and curlew survival and body condition were predicted to remain at or close to 100% for all scenarios of varying invertebrate prey abundance. Predicted survival and body condition of the two godwit species (and to a lesser extent grey plover), however, declined and improved respectively with decreased and increased prey availability. These species did not show an obvious increase in proportion of time spent feeding (Figure 5.12b) and the impact of reduced prey availability was amplified by increasing disturbance frequencies.

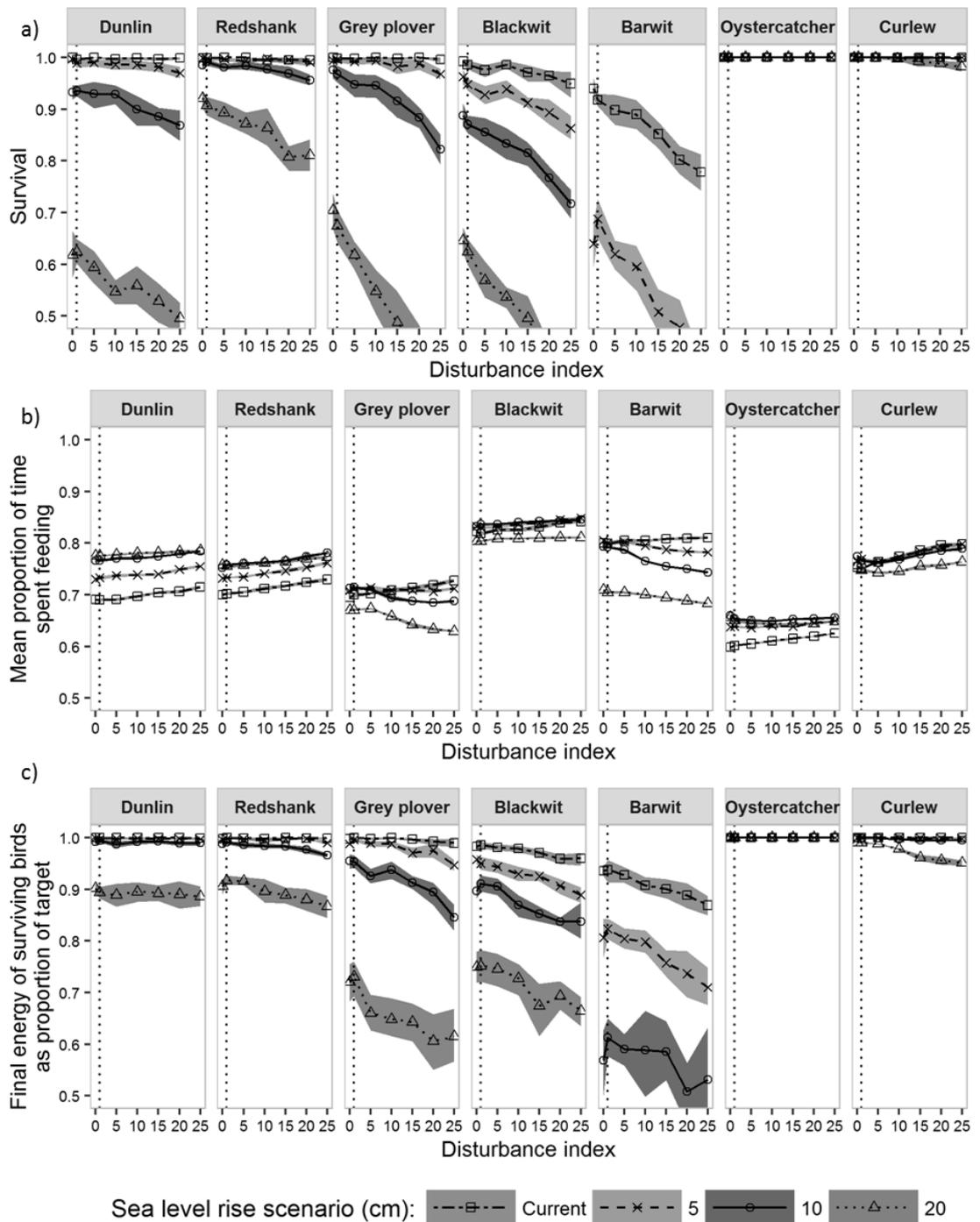


Figure 5.11. The predicted impacts of increased numbers of human visitors in combination with three sea level rise scenarios (5 cm; 10 cm; and 20 cm) on a) survival; b) proportion of time spent feeding; and c) body condition of birds. The vertical dotted line marks current visitor frequencies at disturbance index = 1. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit. Shading indicates the 95% confidence interval around the mean, derived by bootstrapping.

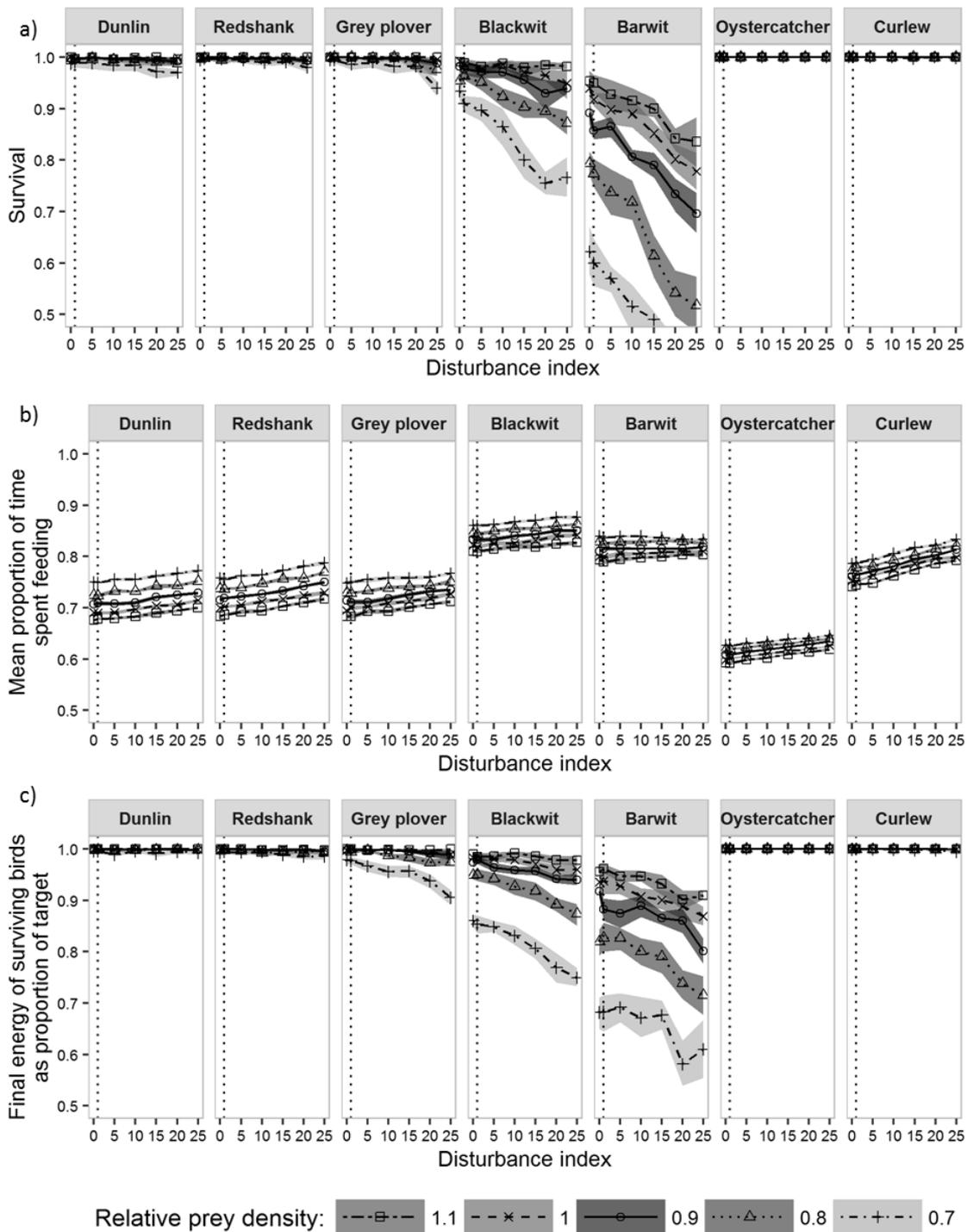


Figure 5.12. The predicted impacts of increased numbers of human visitors in combination with different scenarios of relative prey density at the start of the winter on a) survival; b) proportion of time spent feeding; and c) body condition of birds. The vertical dotted line marks current visitor frequencies at disturbance index = 1. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit. Shading indicates the 95% confidence interval around the mean, derived by bootstrapping.

5.4.4. Model sensitivity analysis

Relative change in magnitude of response

Figure 5.13 shows that with all other parameters fixed at base model values, model predictions were robust to even a 40% increase or decrease in bird magnitude of response.

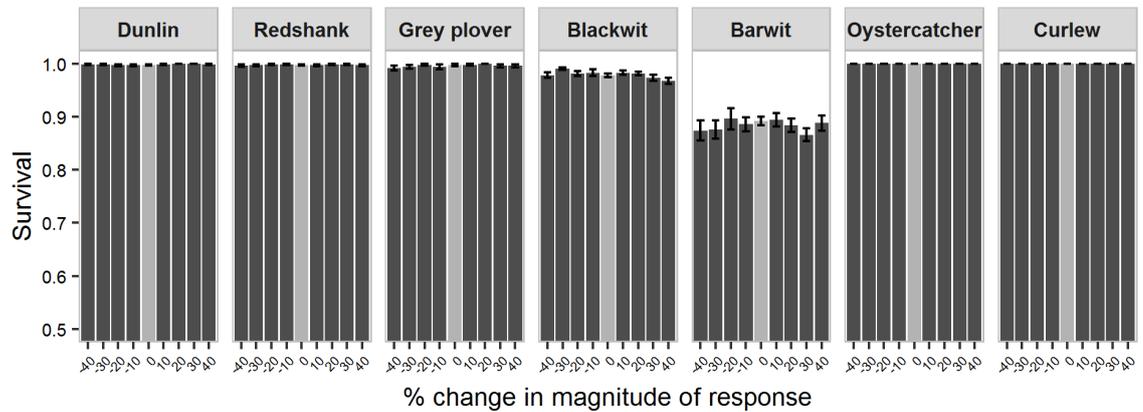


Figure 5.13. Sensitivity of model predictions of mean survival to variations in the magnitude of bird responses to disturbance (alert distance, FID, alert time, flight time, latency time, total time lost, boat exclusion distance, and effective disturbance distance). Pale grey bar indicates the parameter value used in the base model. Error bars show \pm s.e. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit.

Recovery time (pedestrian and wildfowling disturbance)

With perhaps the exception of bar-tailed godwit, when all other parameters were fixed at base model values, model predictions were robust to variations in bird recovery time following a pedestrian disturbance (Figure 5.14). This was also the case for the number of shots fired by a wildfowler per hour that cause birds to take flight (Figure 5.15).

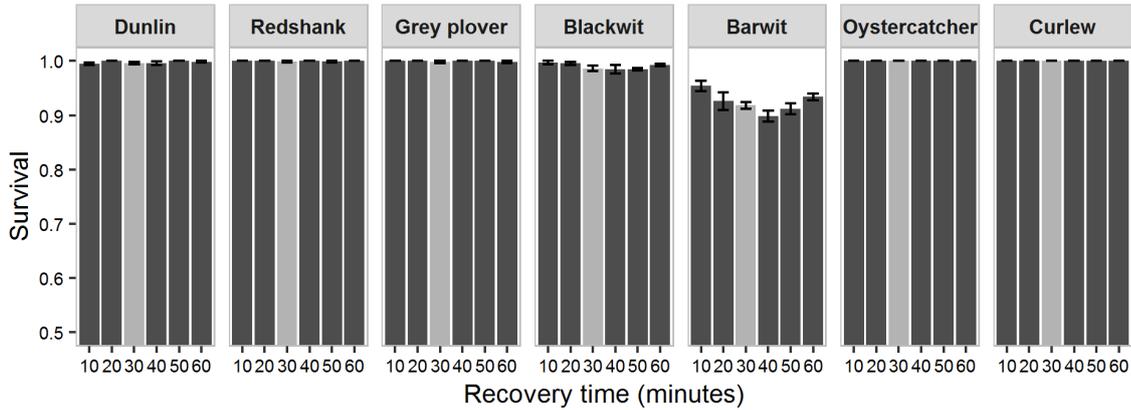


Figure 5.14. Sensitivity of model predictions of mean survival to variations in bird recovery time (time to return to original distribution after disturbance). Pale grey bar indicates the parameter value used in the base model. Error bars show \pm s.e. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit.

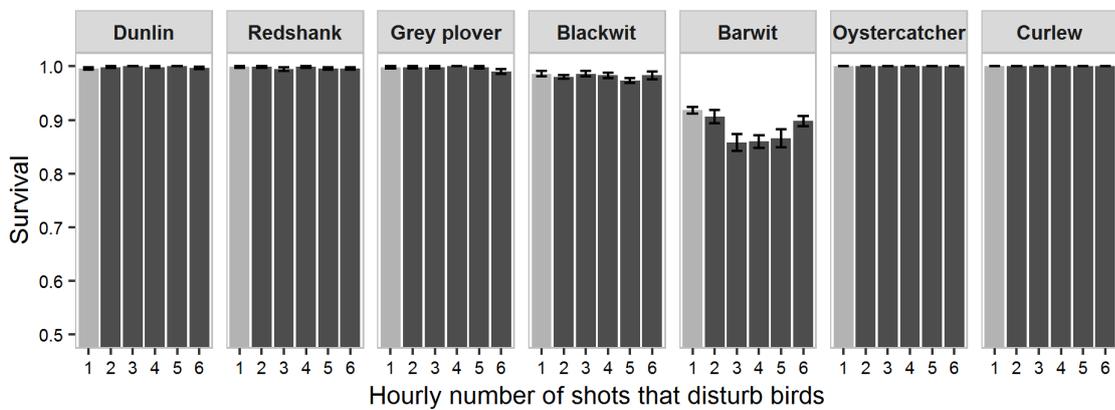


Figure 5.15. Sensitivity of model predictions of mean survival to variations in the number of wildfowler shots per hour that cause birds to take flight. Pale grey bar indicates the parameter value used in the base model. Error bars show \pm s.e. ‘Blackwit’ = black-tailed godwit and ‘Barwit’ = bar-tailed godwit.

5.5 Discussion

When assessing the condition of designated sites of international conservation importance, one key indicator is whether or not species for which the site is designated are significantly impacted by disturbance from human activities (either alone or in combination with other threats). With this knowledge conservation managers and regulators can determine where and when intervention may be necessary to maintain or restore favourable condition. This study has therefore combined detailed field observations (patterns of both human activities and bird behaviour) with simulation modelling to quantify and compare the impacts of different types of anthropogenic disturbance in Poole Harbour. Parameters relating to disturbance were incorporated into a 'Morph' IBM (Stillman 2008) for the site, which was then used to test the impacts of present-day patterns of human activities and to make predictions about different scenarios of increased visitor numbers and environmental change. The potential impacts of disturbance were quantified in three ways: estimates of the number of birds that can be supported by the site (carrying capacity); time budget measurements (proportion of time spent feeding); and the end-of-season body condition of surviving birds.

Using a similar model for the Solent, UK, Stillman et al. (2012) found that disturbance at current levels may be reducing the survival of four of the eight species tested; and increases in visitor numbers due to future housing scenarios were predicted to further reduce survival for two species. By contrast, results of this study for Poole Harbour suggest that current visitor levels are not reducing the site carrying capacity (with the exception of bar-tailed godwit). Estimates of mean daily visitor densities for the Solent (estimated using household responses to a questionnaire), however, were considerably higher than observed in Poole Harbour (49.99 people per hectare compared to 1.42 in Poole). Whilst this may be due to differences in the methods used to estimate visitor numbers, it highlights the fact that the impacts of disturbance may vary considerably between sites; in the same way that bird responses to disturbance vary, as demonstrated in previous chapters.

5.5.1. Impacts of disturbance alone and in combination with two types of environmental change

As was expected based on the results of previous chapters, most birds in Poole Harbour do not appear to be negatively impacted by disturbance from current patterns of human activities, and they are likely to be able to cope with relatively large increases in visitor numbers if all other factors remain constant. However, model predictions showed that extra disturbance from increased visitor numbers would be expected to reduce the carrying

capacity of Poole Harbour if this occurs in combination with other changes that reduce the quality of the site. This was found to be the case for reduced extent of intertidal habitat due to sea level rise over 5 cm or (to a lesser extent) reduced availability of invertebrate prey due, for example, to over-exploitation from clam dredging or baitworm dragging, or pollution events. Using an earlier version of the Morph modelling framework, Goss-Custard et al. (2006a) found that the threshold frequency of disturbance above which oystercatcher fitness was reduced was predicted to be lower in the baie de Somme, France, when feeding conditions were poor. Percival et al. (1998) used a different type of model (spatial depletion model) and reached a similar conclusion in relation to wigeon *Anas penelope* and brent geese: they found that the reduction in the number of birds that could be supported at Lindisfarne National Nature Reserve in north-eastern England was predicted to be greatest when habitat loss occurred at the top of the shore where the impacts of disturbance were expected to be greatest.

As well as the energetic and lost feeding opportunity costs of disturbance during the intertidal exposure period, disturbance to roosting birds can increase daily energetic requirements further (Lilleyman et al. 2016). The additional energy costs can be considerable if the number of suitable roost sites is low or if disturbed birds are forced to fly long distances to find alternative sites (Rehfishch et al. 1996). Morrison (2015) visited 91 occupied and previously occupied roost sites around Poole Harbour, 40 of which were identified as potentially threatened by human disturbance (though frequencies were not quantified). Nevertheless roost disturbance in Poole Harbour across the range of frequencies that were tested with the model was not predicted to reduce bird survival or body condition; except in combination with an extreme increase in the number of visitors (disturbance index = 25). Even if the frequency of disturbance that was observed at Baiter Park (8.17 responses per hour) were to occur at all other roost and inland feeding sites, which is unlikely, birds were predicted to be able to compensate for this with a small increase in the proportion of time spent feeding.

5.5.2. Comparison between activity types

Model outputs predicted no impact of wildfowling across the range of frequencies tested. Bird survival, body condition and even proportion of time spent feeding were unrelated to number of wildfowling visits. This was apparent even with the precautionary assumption that birds were excluded from the disturbed intertidal area by the sound of the shotgun for the entire duration of the wildfowling visit, and in combination with both large and extreme increases in the frequency of other activities (disturbance index = 10 and 25 respectively).

Chapter 4 showed that the effect of a single wildfowler (measured in space-time disturbed) is more than an order of magnitude greater than for a single pedestrian due to the differences in duration of each activity and the magnitude of bird responses. However, given that wildfowling represents less than 0.04% of the daily number of potentially disturbing activities in Poole Harbour, it is not surprising that the model predicted no reduction in most birds' survival, body condition or proportion of time spent feeding in response to increased wildfowling intensities, when set in the context of disturbance from all other human activities.

5.5.3. Management implications

Bar-tailed godwit showed the greatest vulnerability to the impacts of disturbance in all of the scenarios tested; however, over-winter survival for this species was predicted to be below 100% even in the absence of disturbance. It is also important to note that the limited availability in Poole Harbour of the sandy habitats (Herbert et al. 2010) that bar-tailed godwits prefer (Summers et al. 2002, Hopper 2008) means that the site does not support large numbers of the species. Only 100 individuals were included in the model so starvation of just one bird represented a one percentage point drop in predicted survival, whereas for example in dunlin, a 1% drop in survival was represented by starvation of 14 birds.

As other researchers have noted, it is likely that the impacts of disturbance are more apparent when birds are already experiencing difficulties in meeting their energetic requirements (Durell et al. 2005, Goss-Custard et al. 2006a). In such situations (e.g. extreme cold weather) birds will have no extra capacity to compensate for the costs of responding to disturbance, except by reducing the magnitude of their responses.

As well as reductions in site quality (relating to availability of foraging and roosting habitat and invertebrate prey), the main reason why birds may experience difficulties in meeting their energetic requirements is due to the weather. Thermoregulatory costs are high during periods of extreme cold (Kersten and Piersma 1987, Piersma and Morrison 1994, Wiersma and Piersma 1994, Kelly et al. 2002) and invertebrate prey become less accessible (Evans 1976, Zwarts and Wanink 1993). High waves and low air pressure during winter storms also make the exposure of intertidal foraging habitats unpredictable (Swennen et al. 1989) as well as further increasing thermoregulatory costs due to the wind chill effect. Management measures to reduce the likelihood of disturbance occurring during prolonged periods of cold weather have been developed over the last three decades with standardised criteria for suspending waterbird shooting in the UK (Stroud et al. 2006, Ellis 2012). When such a ban

comes into force all coastal bird ringing activities must also cease with the exception of exempted weather-related research (Redfern and Clark 2001). Extension of this principle to reduce disturbance from other, more frequent, activities – such as walking and dog walking – would clearly be beneficial, though difficult to implement in practice.

Whilst the model outputs showed that disturbance from high frequencies of human activities (20 or more times current levels) *can* reduce the predicted survival and body condition of birds, environmental changes through for example sea level rise, habitat loss or reductions in prey availability had a greater impact. Therefore to maintain the numbers of birds that can be supported over winter in Poole Harbour, it would be logical to continue to concentrate management efforts on maintaining or improving these aspects of site quality:

- i) Create or extend refuge areas where activities may be restricted and to minimise habitat loss due to development or through coastal squeeze (see Figures 1.9 & 4.2);
- ii) Ensure that clam dredging and bait harvesting do not reduce prey availability below a threshold required by the birds (part of the remit of Southern IFCA); and
- iii) Take steps to reduce pollution, nutrient enrichment and algal mat formation which may alter prey community structure and abundance (an obligation of the EU Water Framework Directive – Ferreira et al. 2007).

5.5.4. Model limitations and improvements

The most useful predictive models are those that capture the key system properties and processes without being overly complicated and they should be designed in such a way that they can be tested for the appropriate degree of complexity (Grimm and Railsback 2005). It was therefore decided not to incorporate all of the complexities of bird responses to disturbance that were discussed in Chapters 2 to 4, but that the consequences of that decision should be tested. Sensitivity analysis showed that estimates of the number of birds that could be supported in Poole Harbour were robust to variations in magnitude of response when values were fixed across the duration of a simulation i.e. the simplification was appropriate. Nevertheless it would be valuable in future to also test how model predictions might vary if these other real world relationships were incorporated e.g. inclusion of variation in FID, flight time and total time lost according to individual body condition and sub-site or under different environmental conditions. Even if model predictions are unchanged, incorporation of such complexities could help to improve the believability of the results for non-modellers.

Sensitivity analysis for the influence of the chosen value for amount of time taken to return to the original distribution of birds after disturbance by a pedestrian (recovery time) and the hourly number of wildfowler shots that result in birds taking flight suggested that model predictions were robust to variations in these parameters for all species except bar-tailed godwit. This would not necessarily be the case at other sites, however, so further research into the recovery times in relation to different disturbance types, species and bird densities would be beneficial

It is likely that the timing of the field observations around low tide and during daylight resulted in an under-estimation of the frequency of some activities. Bait digging and angling often take place at night (Liley et al. 2008, Liley and Fearnley 2012); and pump scoop dredging for clams (Fearnley et al. 2013) and watersports occur when the intertidal area is covered with at least some water. Despite this, the addition of these extra occurrences of potential disturbance would be unlikely to alter the overall conclusions since birds were predicted to be able to cope with relatively large increases in the frequency of human activities (ten or more times current levels).

Lastly, whilst the focus of this research was disturbance to birds during the intertidal foraging period, a logical extension of the work is to gain a better understanding of the frequency of disturbance of roosting and inland-feeding birds and how this varies around Poole Harbour. Roost and field disturbance from wildfowling and other activities at high tide could be modelled in a more spatially-explicit way. The relative importance of different roosts could be captured, along with the costs of moving between roost sites, and recognising that some sites are less likely to experience disturbance than others – for example, Brownsea Island lagoon compared to Baiter Park (Hopper 2008, Morrison 2015).

Chapter 6 – Using individual-based modelling to investigate how site characteristics influence impacts of disturbance on non-breeding waders.

6.1 Abstract

While site-specific individual-based models (IBMs) may offer the most reliable predictions about the impacts of disturbance, their development may not always be feasible. They rely on detailed knowledge of the distribution and abundance of benthic invertebrates and patterns of human activities around the site, and the expertise to develop the models and interpret their outputs. Simpler options would therefore be useful; so that conservation managers can make an initial assessment about whether disturbance is likely to be causing a problem and to judge whether further investigation or management measures may be necessary. An alternative to using percentage survival as a way of determining whether the impact of disturbance is significant is to assess birds ability to balance the energy budget. This was used as the basis for development of a new, generic IBM – using NetLogo modelling software – of a hypothetical estuary. This was then used to investigate whether site characteristics can be used to predict the impacts of disturbance, and to develop rules of thumb for initial site assessment. One important difference between this model and the Morph IBM is that disturbance could be simulated in a more spatially-explicit way so the costs of disturbance were assigned to individual birds rather than being spread across all birds on a patch. In addition to the total number of visitors per day, site characteristics that determined the distribution of those visitors were important explanatory factors in relation to bird predicted ability to balance the energy budget. The number of disturbances that birds experienced and the proportion of visitors that caused a disturbance were predicted to be greater on sites with a large number of access points (so visitors could access all areas equally easily). Birds were also predicted to experience greater number of disturbances on sites where a large proportion of visitors leave the upper shore area (firm, sandy rather than soft, muddy sediments), and on relatively ‘thin’ sites (where the distance between the high and low water marks is short).

6.2 Introduction

6.2.1. Decision making on designated sites

Managers of sites of conservation importance, particularly sites with statutory designations recognising their national or international significance, have a duty to ensure favourable conservation status by preventing, minimising or mitigating the occurrence of damaging activities. This is particularly relevant to estuaries both in the UK and around the world, many of which are recognised because of the large assemblages of migratory waterbirds that they support during the non-breeding season (Ramsar 2016b). Managers of such sites and policy makers often need to make decisions about appropriate courses of action quickly; for example when setting fishing and shellfishing quotas, agreeing wildfowling consents, and assessing planning applications for housing or port developments, whilst ensuring no reduction in site carrying capacity for designated species and no net loss of key habitats. Although the importance of evidence-based decision making is well recognised, there continues to be a reliance on experience-based decision-making or following the status quo (Pullin et al. 2004, Sutherland et al. 2004, Ferraro and Pattanayak 2006, Likens 2010, Cook et al. 2016). There may therefore be a trade-off between undertaking detailed long-term research and employing other effective methods that do not require large commitments of time, money or specific expertise. So whilst developing site-specific IBMs may be the most reliable way of determining the impacts of disturbance, this may not always be feasible since the approach requires detailed knowledge of the distribution and abundance of benthic invertebrates and patterns of human activities around the site, and the expertise to develop the models and interpret their outputs.

This chapter explores a more general method for assessing the predicted impacts of disturbance on wintering birds, based on the physical characteristics of a site and patterns of use by humans. The new approach will be tested by comparing the results with the predictions/patterns that emerged from scenario testing with the Morph model in the previous chapter. This method could be used as a preliminary assessment tool to determine whether or not further investigation using the more detailed modelling approach (Chapter 5) may be warranted on a case-by-case basis.

Table 6.1. Site-specific characteristics that could affect the number of human visitors and the proportion that result in disturbance response flights by birds.

Factor	Rationale
Proximity to residential areas	The closer a site is to residential areas, the greater the number of visitors it is likely to experience (Ode and Fry 2006, Fearnley et al. 2010).
Number of access points	The number and location of car parks and other access points along the shoreline of an estuary is likely to influence where visitors occur and their frequency (Goss-Custard and Verboven 1993). More remote areas with few access points are likely to receive fewer casual visitors such as walkers and dog walkers, though other users such as birdwatchers may specifically seek out the more remote areas.
Site dimensions	Expansive sites with large areas of intertidal habitat and with long distances between the water's edge and upper shore may experience fewer disturbance events than small, narrow sites where people are more likely to be able to approach foraging birds closely enough to cause them to take flight (Coombes et al. 2008).
Sediment type	The proportion of visitors that use the intertidal habitat rather than remaining at the top of the shore will be strongly influenced by sediment type. Soft, muddy sediments that are dangerous to walk on or wide expanses of saltmarsh with tidal creeks are likely to have few visitors compared to more solid, sandy intertidal areas and beaches (Goss-Custard and Verboven 1993). Some activities such as bait digging, however, involve specific use of the intertidal area; and watersports may disturb the intertidal area from both the landward side (when setting up) and the seaward side.
Duration of visit	Average visit duration is likely to vary from site to site, and in reality not all human visitors will remain for the same amount of time. Those that are present for longer may have a greater chance of causing a disturbance or excluding birds for longer (Goss-Custard et al. 2006a). If the routes of longer-staying visitors cover a greater area of intertidal habitat or they are present for long enough to walk all the way to the low tide mark on larger sites, they may disturb birds that would not otherwise have been disturbed by visitors that only stayed for a short period of time.

6.2.2. Visitor patterns and potential for disturbance

In addition to knowledge of bird behavioural responses to predict the impacts of disturbance from human activities on wintering waders, we also need an understanding of the spatial and temporal patterns of occurrence of those activities in relation to the patterns of use by the birds. Chapter 5 showed that human activities are not evenly spread across Poole Harbour or across shore levels so individual visitors do not have equal probability of causing a disturbance. Not all activities, therefore, will result in flight responses by birds: only those that overlap in both time and space with the birds have the potential to cause problems through loss of time and area for feeding or other activities, and the additional energy costs of fleeing a disturber. For example, Liley et al. (2012) found that in Poole Harbour only around 10% of potential disturbance events resulted in a visible flight response by birds. This value, however, is likely to vary from site to site based on a number of key factors (Table 6.1) as well as the species-specific and environmental factors identified in previous chapters.

6.2.3. Energy budgets

As a minimum, birds need to balance their energy intake against energy expenditure over the same time period; otherwise they must rely on stored energy reserves to avoid starvation. Wintering waders maintain fat reserves for this very reason; depositing fat in preparation or response to unpredictable or deteriorating environmental conditions (Pienkowski et al. 1979, Dugan et al. 1981), which can then be mobilised in periods of extreme cold or when poor weather prevents birds from feeding (Davidson and Evans 1982, Summers et al. 1998, Kelly et al. 2002). Small waders at temperate latitudes generally store between 1.5 and 4 days of energy reserves (Castro et al. 1992 and Poot and Piersma 1994 in Kelly et al. 2002). As Pienkowski et al. (1984a) point out, most waders manage to forage at least a little even during severe weather so only some of their energy requirement will need to come from stored fat. Survival is therefore only likely to be affected if a negative energy budget is sustained over a period of several days or weeks.

A negative energy budget could be problematic, however, towards the end of the winter when migratory waders must build up fat reserves to sustain them on long-distance flights and ensure subsequent breeding success (Kvist and Lindström 2003, Atkinson et al. 2007, Morrison et al. 2007). Energy demands can consequently be high throughout the non-breeding season and even when environmental conditions begin to improve (Kersten and Piersma 1987) and anything that prevents birds from achieving their target energy intake has the potential to reduce survival, delay migration and/or limit reproductive success (Baker et

al. 2004, Morrison and Hobson 2004, Morrison et al. 2007). Some researchers, therefore, have taken an energy budget approach to investigating the impacts of disturbance on birds (Riddington et al. 1996, Houston et al. 2012, Lilleyman et al. 2016, Nolet et al. 2016).

Waders feeding in intertidal environments are constrained by the tidal cycle as it periodically exposes and covers their favoured feeding areas (Granadeiro et al. 2006), and the time available to them for feeding is therefore limited. Nevertheless birds do not feed at a constant rate throughout the exposure period (Kersten and Visser 1996b, van Gils et al. 2005). Kersten and Visser (1996a) found that the amount of food consumed by oystercatchers *Haematopus ostralegus* varies greatly between tidal cycles, but that intake and expenditure were balanced over a 24 hour period. This value will also be used in this chapter as the basis for the energy budget calculations.

6.2.4. Using the individual-based modelling (IBM) approach

The IBM modelling framework, Morph, that was used to develop the site-specific model of foraging birds in Poole Harbour (Chapter 5) has the drawback of not being easy to transfer to new sites without detailed knowledge of invertebrate food availability, bird behaviour and patterns of use for human recreation and other activities. Nevertheless, many of the same modelling concepts can still be applied to gain a more general understanding of how the impacts of disturbance may vary from site to site. By using knowledge of wader foraging and disturbance response behaviour, and incorporating real-life variation between individual birds and individual human visitors, the mechanisms by which disturbance may impact wintering waders can be modelled in a relatively simple way. Furthermore, by limiting the model simulations to the 24 hour period over which birds attempt to balance their energy budget, we can explore the finer-scale, spatially explicit responses of birds to disturbance under varying circumstances in a way that was not possible with the Morph model.

A programme called NetLogo (Wilenski 1999) was chosen for development of the IBM of 'hypothetical estuaries' with different physical characteristics. Netlogo is a freely available, programmable, grid-based modelling environment for simulating natural and social phenomena, which is well-suited for modelling complex systems of multiple individuals operating independently (Wilenski 2016).

6.3 Methods

6.3.1. Model development

The model was built using Netlogo (Wilenski 1999) and the results of field observations and experiments described in the previous chapters: it was based on a hypothetical estuary with intertidal patches that are periodically exposed in the tidal cycle, and which have invertebrate resources available to foraging birds. Potential disturbers can be present in the model estuary by walking along a shoreline path or on the intertidal patches when they are exposed. Figure 6.1 shows the interactive model interface with which parameters can be varied to explore the predicted effects on bird energy budgets. Model birds behave in a fitness-maximising way by choosing patches based on perceived fitness (net energy intake after accounting for the costs of flying between patches) and responding to human disturbers that get too close (van Gils et al. 2006).

Many of the concepts, foraging decisions and equations used here are the same as those used in the Morph model described in the previous chapter, which will allow comparisons to be made between the outputs of the two types of model. However, there are four key differences: (1) in this model the intertidal area is divided into many more, smaller patches to incorporate finer-scale movements of foraging birds and their responses to disturbance; (2) movements of potential disturbers are modelled in a more spatially explicit way so the costs of disturbance are incurred by individual birds rather than being averaged across all birds on a patch; (3) for simplicity, only one species of bird is represented and it feeds on just one uniformly distributed size class of worm; and (4) model simulations were only run over the course of a 24 hour period rather than the whole winter season.

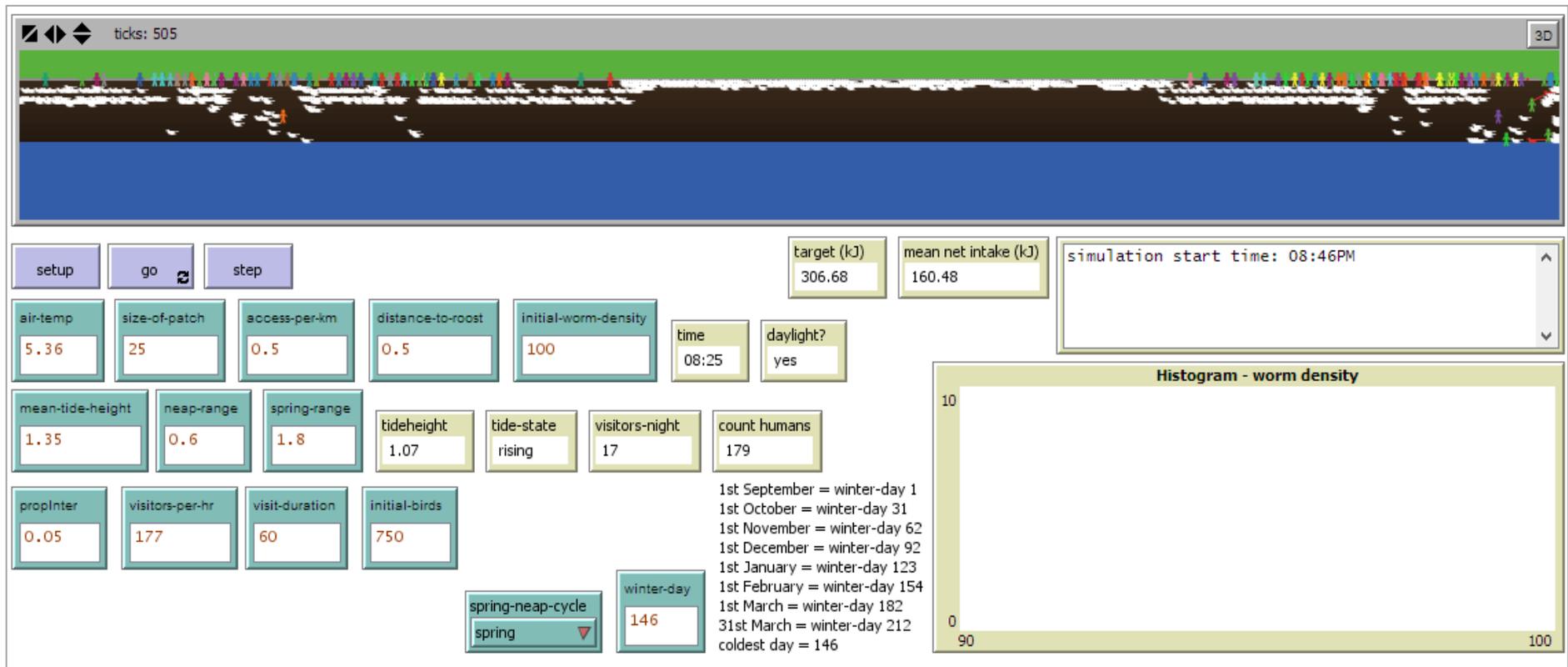


Figure 6.1. The hypothetical estuary NetLogo model interface.

6.3.2. Global parameters

Model time steps

Simulations were split into one-minute time steps and run between 00:00 and 23:59 since 24 hours is the length of time over which birds have been found to attempt to balance their energy budget (Kersten and Visser 1996a). Winter day was included so that air temperature and day length (hours of daylight) could be adjusted for different model runs according to the stage of the season of interest. Winter day 1 = 1 September.

Environmental conditions

Air temperature was set using the same equation for daily temperature as in the Morph model; this temperature was fixed throughout the whole of each 24 hour simulation.

$$T (^{\circ}C) = 0.000579 \times Day^2 - 0.1687 \times Day + 17.65 \quad \text{Equation 6.1}$$

Whether or not it was daylight during each time step was based on the following equation for day length, where D is winter day and which assumes that the number of hours of daylight per day oscillates between 16.5 hours on the longest day (21 June) and 8 hours on the shortest day (21 December) (US Naval Observatory 2015):

$$Day\ length = 12.25 + 4.25 \times \cos\left(2\pi \times \frac{(D + 70)}{365}\right) \quad \text{Equation 6.2}$$

Daylight hours were split equally either side of midday. Tide height was also set using a *cos* curve to give two high tides per day and one neap-spring cycle every 14 days; using the mean tide height (1.35m), spring range (1.8m) and neap range (0.6) values for Poole Harbour reported by Humphreys (2005). The tidal stage for each simulation was set by selecting either “spring” or “neap” on the model interface, and each simulation began at high tide. A variable called ‘distance to roost’ was also included so the contribution of travel costs to bird daily energetic requirements when moving between intertidal patches and high tide roosts could be tested. This was set to 2 km in the base model since all intertidal areas in Poole Harbour are within this distance of one or more known roost sites (Morrison 2015). The base model did not include any disturbance to birds whilst roosting, although this would be straightforward to add for sites where this is known to be a particular problem.

Disturbance-related global variables

The number of visitors per hour, and the proportion of visitors that walk on the intertidal area rather than remaining on the path were fixed throughout each simulation but could be varied between simulations. The base model used values according to the observations described in the previous chapter: a mean of 177 visitors per hour (assuming that each stays for 60 minutes), 12.9% of whom were observed on the intertidal habitat. The number of visitors per hour during evening darkness was calculated from daytime visitor numbers, based on the finding by Stillman et al. (2012) that 6% of coastal visits occur during darkness and Liley et al.'s (2008) finding that most visits after dark in Poole Harbour occur before 10pm.

6.3.3. Patch parameters

Spatial extent and patch availability

The model 'world' was split into a grid of patches each representing an area 25 metres by 25 metres. The exact dimensions of the world depended on the estuary type scenario being modelled (Figure 6.2 and Table 6.2), though the number of intertidal patches was kept constant in all scenarios. Patches were categorised as 'water', 'mud', 'path' or 'roost', and mud patches were only available to birds when their assigned 'exposure height' was equal to or less than the tide height of the current time step.

Birds could not use patches labelled as water or path, but roost patches were always available. The exposure height was assigned to each patch so that the maximum extent of intertidal habitat at low water was equal to 14 km² and all intertidal habitat was covered by water for two hours either side of high water on spring tides.

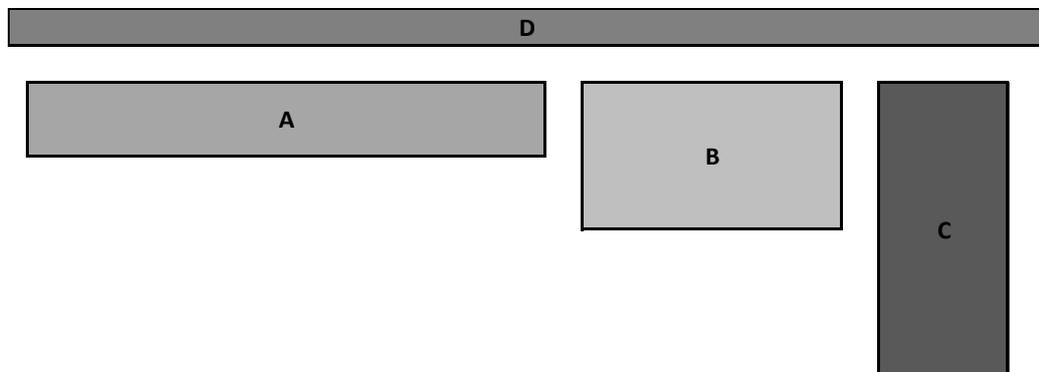


Figure 6.2. Relative dimensions of estuaries 'A', 'B', 'C' and 'D' – all with the same total area of intertidal habitat. See Table 6.2 for details.

Table 6.2. Dimensions and details of each hypothetical estuary scenario tested.

Scenario	Dimensions (number of patches)	Patch size	Area of intertidal habitat (km ²)	Length of shoreline footpath
A	560 x 60	25m x 25m	14	14
B	280 x 100	25m x 25m	14	7
C	140 x 180	25m x 25m	14	3.5
D	1120 x 40	25m x 25m	14	28

Invertebrate prey availability

The model was parameterised for redshank *Tringa totanus* feeding on worms of a single size class; 45-60mm, which is the largest available size class of worms within the range eaten by redshank in Poole Harbour (Durell et al. 2006, Goss-Custard et al. 2006b). At the start of each simulation the intertidal patches were all assigned the same density. This density was decreased on selected patches throughout each time step as each bird fed one by one. The base model used a value of 56 worms/m², which is the mean density of worms of this size class in Poole Harbour, based on sampling by Herbert et al. (2010).

Access for humans

At the start of each simulation the patches representing the shoreline footpath were categorised as either containing an access point or not – humans could only enter and leave the model via patches with an access point. The number of access points per kilometre of shoreline could be varied to explore how this may affect the distribution of humans across a site and the resulting disturbance of birds.

6.3.4. Forager parameters

Energy expenditure

Simulations were run with 750 redshank (the same as in the Morph model), based on Wetland Bird Survey (WeBS) data for this species in Poole Harbour (Holt et al. 2015). At the start of each simulation, birds calculated their target energy intake for the next 24 hour period, according to field metabolic rate, FMR (set at 2.1 times the basal metabolic rate, BMR), and any additional costs of thermoregulation if the air temperature was below the birds' lower critical temperature (LCT). As well as the energetic costs of fleeing disturbers, birds incurred costs of travelling to and from the roost, which were deducted from net intake. Energetic costs of flight were set at 12 times BMR (Castro and Myers 1988) and bird's flight

speed was set at 12.46 m/s using the allometric equation given by Alerstam et al. (2007) with a mean body mass for redshank of 153.3g (British Trust for Ornithology 2015):

$$\text{Flight speed (m/s)} = 5.9 \times (\text{Mass}_{kg})^{0.13} \quad \text{Equation 6.3}$$

Choice of patch

At the start of each time step birds chose the patch where they could maximise their net energy intake (using the same equations as in the previous chapter) by assessing their own foraging efficiency and dominance, the density of worms, density of competitors (and therefore susceptibility to interference), and the time and energy costs of travelling to the patch.

Costs of disturbance

Birds did not know, however, whether they would be disturbed until they arrived on a patch. If when a bird selected a patch there was one or more humans present within its flight initiation distance (FID) then the bird fled to a 'safe' patch that could be reached within its 'flight time'. If there were no such patches available, but there were safe patches that could be reached before the end of the time step, the bird moved to the closest of these patches. And if there were none like this available, the bird continued to fly for the remainder of the time step. The energetic costs of responding to disturbance were deducted from net intake according to the length of time spent in flight, and the time costs were deducted from the bird's free time available for feeding. At the start of each time step the free time was reset to 60 seconds.

Energy assimilation

After checking for disturbers and responding if necessary, birds with free time greater than zero foraged for the remainder of the time step and the resulting energy assimilated was added to their net intake for the simulation. At the end of each simulation, each bird's net intake was compared with its target to determine whether it had been able to balance its energy budget over the course of that 24 hour period and whether it had any surplus available for deposition of fat stores. Fat deposition rate (FDR) as a percentage of body mass was calculated following Lindström (1991), where I_{net} is net intake (kJ) at the end of the simulation, I_{target} is target intake (kJ) based on daily energy expenditure, M_{lean} is lean body mass in grams, and 34.3 kJ/g is the energy density of fat.

$$FDR = \left(\frac{I_{net} - I_{target}}{34.3 \times M_{lean}} \right) \times 100 \quad \text{Equation 6.4}$$

When food is abundant, bird food intake may be constrained by the maximum rate at which the gut can process ingested prey, and birds may be forced to take digestive pauses (Zwarts and Dirksen 1990, Zwarts and Blomert 1992, Kersten and Visser 1996b, van Gils et al. 2005). A maximum daily energy assimilation rate was therefore included so model birds only fed when their net intake was below this limit; this was set according to the following equation given by Kirkwood (1983):

$$Assim_{max} (kJ \text{ per day}) = 0.75 \times 1713 \times M^{0.72} \quad \text{Equation 6.5}$$

where M is body mass in kilograms and 0.75 is the assimilation efficiency of converting ingested energy into metabolisable energy (Goss-Custard et al. 2006).

Individual variation

At the start of each simulation the daytime foraging efficiency of each bird was selected from a normal distribution with mean = 1 and standard deviation = 0.125 (Goss-Custard et al. 1995): night time foraging efficiency was set at 0.95 x day time efficiency (the same as used for redshank in the Morph model). Birds varied in their relative dominance (selected from a uniform distribution between 0 and 1), which influenced their susceptibility to interference from competitors. Birds also varied in the shore levels at which they preferred to feed: each was randomly allocated a shore level between the high- and low-water marks at or below which it attempted to feed unless covered by water. This resulted in a more realistic distribution of birds across shore levels rather than birds continually foraging on patches at the top of the shore simply because those were the first to be exposed by the falling tide.

6.3.5. Disturber parameters

Arrival of humans

At the start of each time step new humans entered the model depending on the time of day and the global parameter for frequency of visitors per hour. They could only arrive on a path patch with an access point, and that was set as the human's 'home patch' to which it had to return before departing the system.

Movement of humans

When humans arrived they were assigned a 'route' based on the value of the associated global variable, which determined what proportion of visitors walked along the path or walked on the intertidal habitat. Those that walked on the intertidal set a random heading away from the path and walked towards the water (but not in it); returning to the path and

their home patch as the tide rose or so that they did not stay for longer than one hour (Figure 6.3). Humans on the path also returned to their home patch and departed after an hour. Walking speed was set according to substratum: 4 km/hr on the path and 2.5 km/h on the intertidal patches.

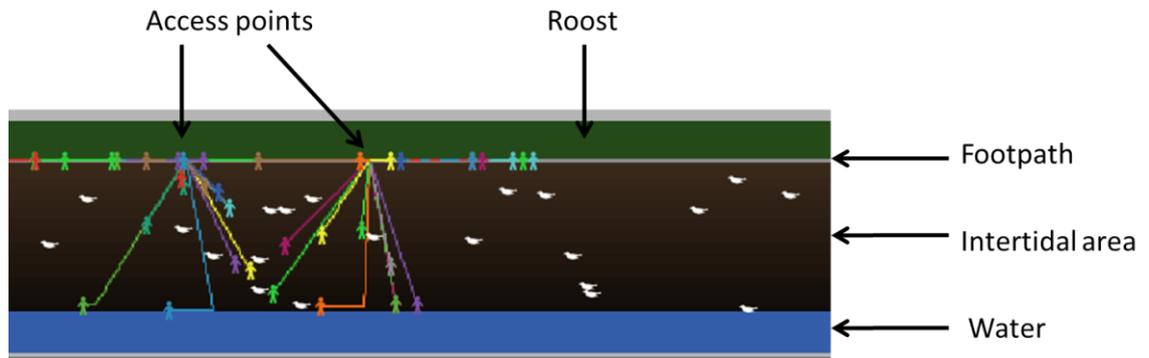


Figure 6.3. Screen shot of part of the model interface showing humans arriving at access points and spreading out across the hypothetical estuary along the footpath or walking towards and alongside the water, with birds feeding on the intertidal area.

6.3.6. Scenario testing

At the end of each simulation the model reported the total number of disturbance responses, bird net intake relative to target intake for the 24 hour period, and the proportion of human visitors that caused disturbance responses by one or more birds. Unless specified, parameter values were fixed at their base values (Table 6.3). The model was used to investigate the predicted outcomes under scenarios of differing site characteristics and environmental factors (Table 6.4); each scenario was run twice.

Table 6.3. Parameter values used in the base model.*a) Estuary*

Parameter	Base mode value	Details/info source
Site dimensions	Scenario A	Similar to Poole Harbour
Number of visitors per hour during daylight	177	Based on observations in this study
Proportion of visitors on the intertidal	0.129	Based on observations in this study
Number of access points per km	0.5	Estimate for Poole Harbour
Distance to roost (km)	2	Morrison (2015)
Winter day	146	Coldest winter day
Initial worm density (number per m ²)	56	Herbert et al. (2010)
Worm mass (gAFDM/worm)	0.0154	Herbert et al. (2010)
Number of birds	750	Holt et al. (2015)
Tidal stage	spring	-

b) Foragers

Parameter	Base mode value	Details/info source
Field metabolic rate (FMR, kJ/day)	233.86	2.1 x BMR (Kersten and Piersma 1987)
Lower critical temperature (LCT, °C)	18.6	Equation 5.6
Thermostatic costs below LCT (kJ/°C/day)	5.5	Equation 5.7
Cost of flight (kJ/s)	0.015	12 x BMR (Castro and Myers 1988)
Flight speed (m/s)	12.46	Equation 6.3
Flight initiation distance (m)	59.09	Table 3.3
Time spent in flight per response (s)	13.89	Table 3.3
Latency time per response (s)	12.96	Poole pedestrian disturbance experiments
Lean mass (g)	90.5	Goss-Custard (unpublished data)
Max energy assimilation rate (kJ/day)	332.97	Equation 6.5

c) Disturbers

Parameter	Base mode value	Details/info source
Visit duration (minutes)	60	Fearnley et al. (2010)
Walking speed – intertidal (km/hr)	2.5	Chapter 2
Walking speed – path (km/hr)	4	Chapter 2

Table 6.4. Parameters and ranges of values tested.

Parameter	Values
Site dimensions	See Table 6.2
Number of visitors per hour	0; 100; 177; 250; 400
Proportion of visitors on the intertidal	0.05; 0.129; 0.5
Number of access points per km of shoreline	0.5; 5; 40 (fully accessible)
Winter day (1 Sep; 24 Jan; 1 Mar)	1; 146; 182
Initial worm density of patches (number/m ²)	25; 56; 100
Tidal stage	spring; neap

6.4 Results

6.4.1. Prey availability

Birds were predicted to achieve a higher net intake and balance their energy budget when there were greater numbers of worms per m^2 , and during neap tides (Figure 6.4) when at least some intertidal habitat was available for the whole 24 hour period (c.f. 16 hours on spring tides). However, the difference in achievable fat deposition rate (FDR) between spring and neap tides was more pronounced when prey density was lower.

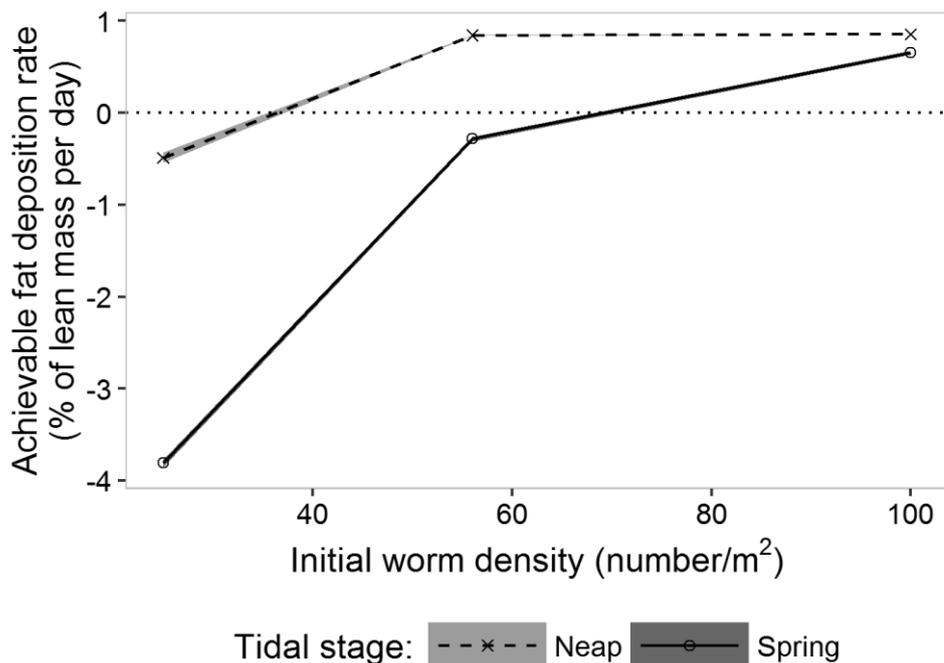


Figure 6.4. Predicted effect of prey availability on daily achievable fat deposition rate (FDR) under two different tidal regimes (spring/neap). All other parameters set at base model values. Horizontal dotted line at FDR = 0 indicates the threshold below which birds were unable to balance their energy budget. Shading indicates the 95% confidence interval around the mean.

6.4.2. Number of visitors and stage of season

Figure 6.5 shows that increased number of visitors across the range tested was only predicted to reduce bird FDR when feeding time was limited (i.e. on spring tides). Although there was a noticeable difference in predicted achievable FDR between autumn (1st September) and winter or spring (24th January/ 1st March). With only an intermediate density of prey available ($56/m^2$) birds were only predicted to be able to balance their energy budget on neap tides in winter and spring.

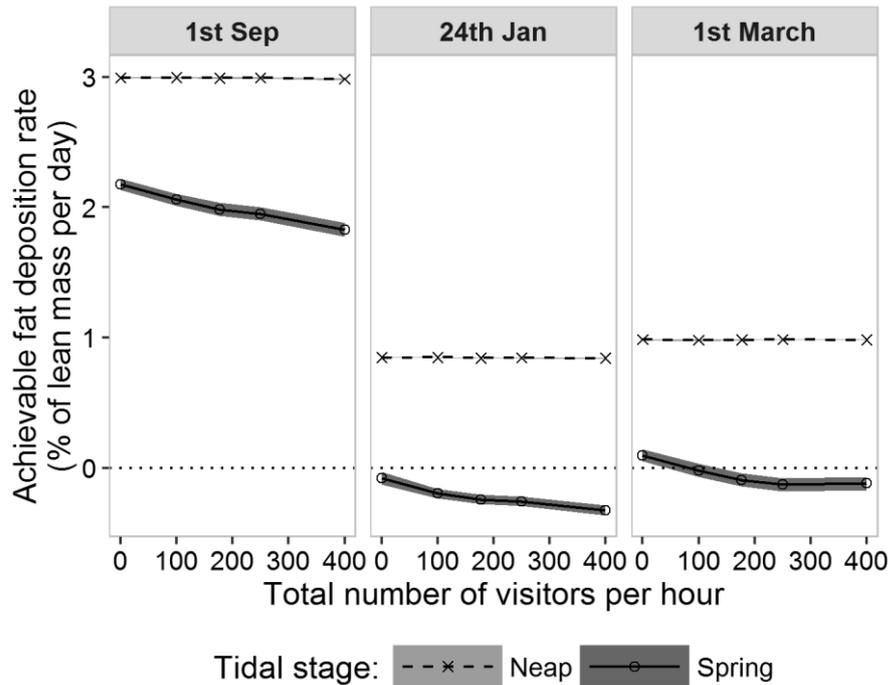


Figure 6.5. Predicted effect of number of visitors on daily achievable fat deposition rate (FDR) at three stages of the non-breeding season and for neap and spring tides. All other parameters set at base model values. Horizontal dotted line at FDR = 0 indicates the threshold below which birds were unable to balance their energy budget.

6.4.3. Number of disturbances

In scenarios where prey availability was high (100/m²) the FDR that birds were predicted to achieve was not reduced by the number of disturbances that they experienced during the 24 hour period (Figure 6.6). This was also the case with an intermediate density of worms (56/m²) on neap tides when available feeding time was not limited. However if prey availability was low, birds were unable to balance their energy budget (except on neap tides in autumn) and FDR was predicted to be lower in birds that experienced a greater number of disturbances.

The total number of disturbances that birds experienced was not solely determined by the number of visitors in the model (Figure 6.6). Number of disturbances was also related to the dimensions of the site, the number of shoreline access points and the proportion of visitors that left the path at the top of the shore. Total number of disturbances was greater on narrower sites with a relatively short distance between the path and low water mark (A and D – see Figure 6.2). Birds also experienced fewer disturbances when there were fewer shoreline access points and the proportion of visitors that left the path was low (top left panel of Figure 6.7 vs. bottom right panel).

The model predicted similar relationships between site characteristics and the proportion of visitors that actually resulted in bird disturbance flights (Figure 6.8). Humans were more likely to disturb bird on narrower sites with more access points and when more people walked on the intertidal area rather than staying on the path.

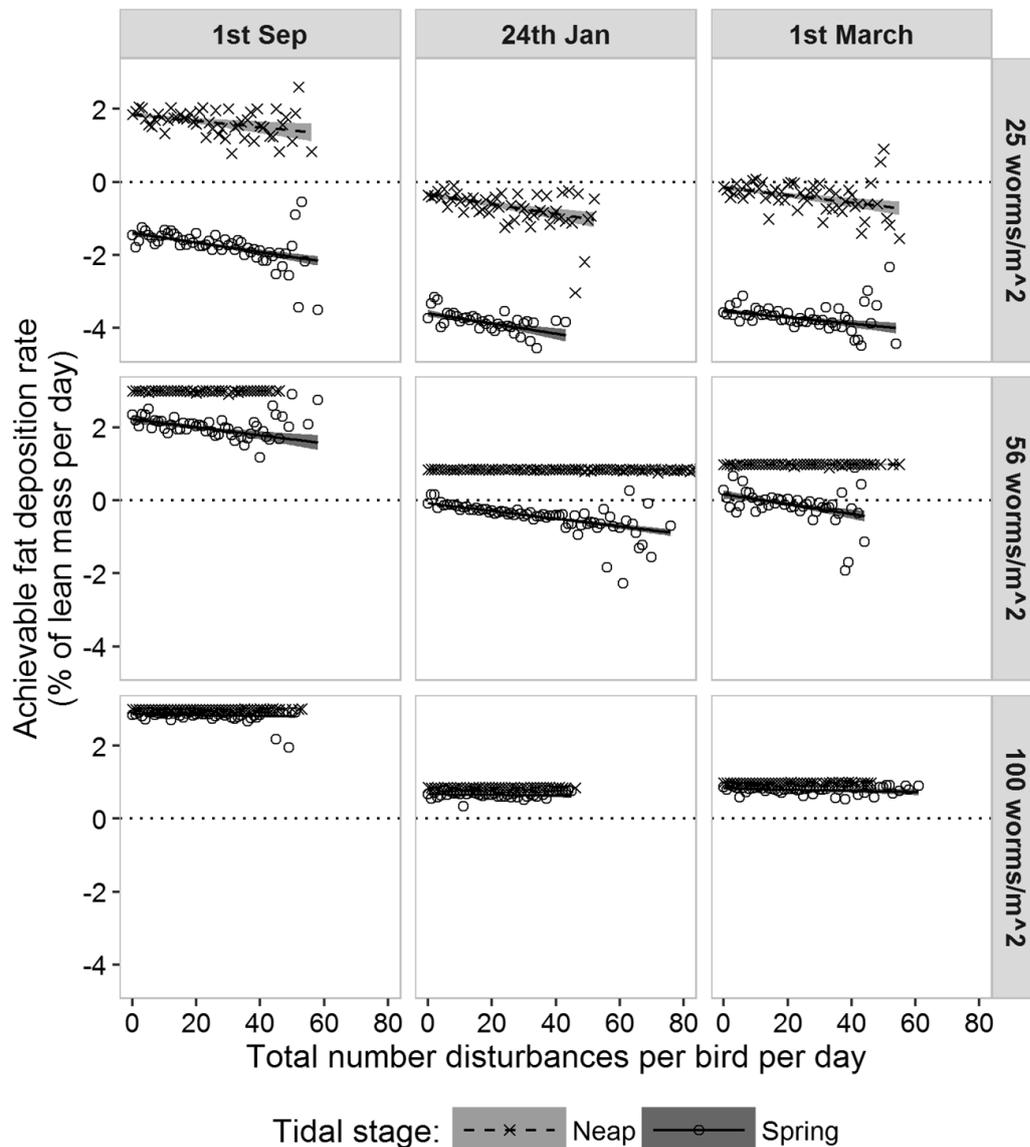


Figure 6.6. Predicted relationships between the number of times a bird is disturbed and its achievable fat deposition rate (FDR) under different scenarios of prey availability and stage of the season. All other parameters set at base model values. Horizontal dotted line at FDR = 0 indicates the threshold below which birds were unable to balance their energy budget.

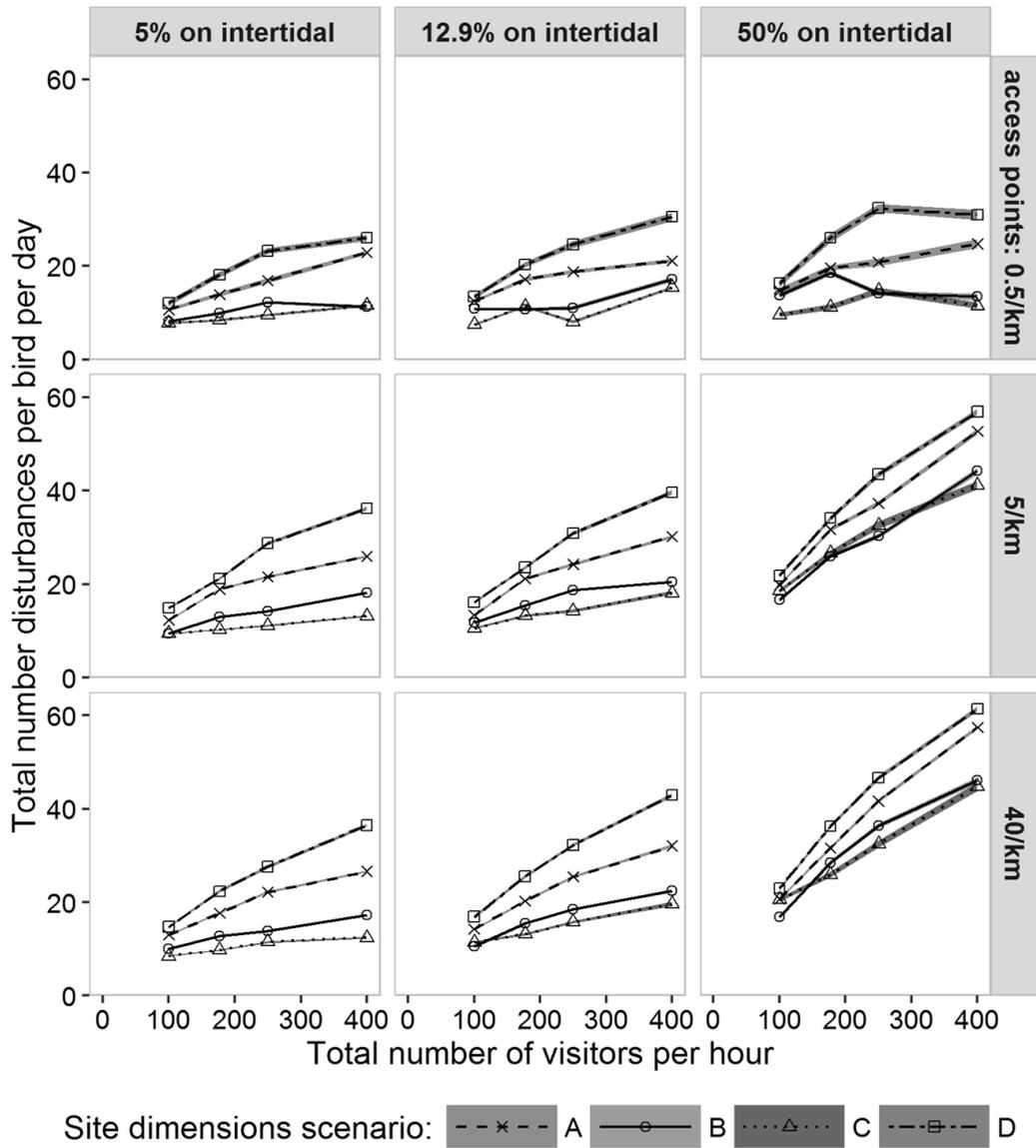


Figure 6.7. Predicted relationships between the number of visitors and the daily number of times a bird is disturbed for different scenarios of visitor access (proportion on the intertidal area and availability of shoreline access points) and site dimensions (see Figure 6.2).

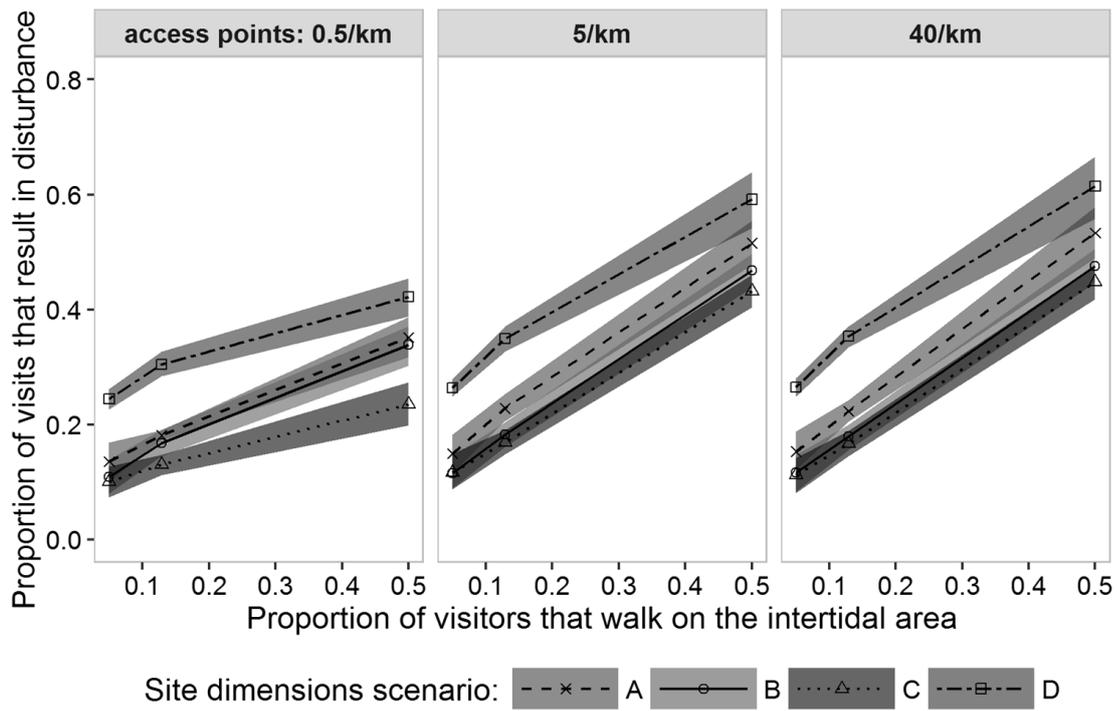


Figure 6.8. Predicted relationships between site characteristics (dimensions; number of access points; and proportion of visitors on intertidal areas) on the proportion of visits that result in disturbance of birds.

6.5 Discussion

This chapter has shown how a new, simple individual-based model (IBM) of wintering waders foraging in an intertidal system can be used to identify patterns of important factors that influence the number of times birds are disturbed and the resulting impact on their daily energy budgets. The predictions relating to key site characteristics and environmental factors will be discussed in this section, and they will be compared with the outputs from the site-specific Morph model for Poole Harbour (Chapter 5). The practical applications of this approach will then be highlighted whilst acknowledging the limitations and potential improvements/extensions.

6.5.1. Balancing the budget

In order to balance the energy budget, bird energy intake must equal or exceed energy expenditure. It is therefore unsurprising that model predictions for achievable fat deposition rate (FDR) were related to: (1) food availability (different intertidal exposure patterns on spring and neap tides, and density of prey); (2) thermoregulatory requirements on top of daily BMR (lower FDR with temperatures in mid-winter and spring compared to autumn); and (3) the number of disturbances that each bird experienced (greater time/area/energy costs associated with an increased numbers of responses). The predictions were supported by the results from the previous chapter, which also found positive relationships between survival/body condition and prey or habitat availability, and negative relationships with frequency of disturbance. Between them, the two models predicted that birds would be better able to partially or completely compensate for the impacts of disturbance over the short- (24 hours) and longer-term (whole non-breeding season) when foraging and environmental conditions were more favourable.

6.5.2. Number of disturbances

One of the benefits of this model over the Morph model used in Chapter 5 is that the movements of people and responses by individual birds could be modelled in a more spatially-explicit way. This demonstrated the importance of understanding how the behaviour of potential disturbers influences the likelihood of birds and people interacting. Whilst bird FDR was predicted to be inversely related to the daily number of disturbance responses, the number of visitors per day was not the only factor that influenced the total number of bird responses. Site characteristics that determined the distribution of visitors were also important explanatory factors. The number of disturbances that birds experienced

and the proportion of visitors that caused a disturbance were predicted to be greater on sites with a large number of access points (so visitors could access all areas equally easily); this is supported by the prediction of the Morph model that increases in visitor numbers would have a greater impact on survival/body condition if visitors were evenly spread around the site rather than concentrated in certain areas as is currently the case. This simpler NetLogo model also predicted that birds would experience a greater number of disturbances on sites where a large proportion of visitors leave the upper shore area (firm, sandy rather than soft, muddy sediments), and on relatively 'thin' sites (where the distance between the high and low water marks is short). Field observations by Goss-Custard and Verboven (1993) showed a similar relationship between disturbance levels and access and habitat type for oystercatchers foraging on the Exe estuary.

6.5.3. Model limitations

This general model is not intended to be a detailed model that captures all of the complexities of the real world system. So although it does not include disturbance at the roost; different types of disturbance; more than one bird species; or more prey types, these should not be considered limitations. The simplifications do not detract from the usefulness of the predictions and general patterns that have emerged.

One simplification, however, may be important to the predictions about how birds and people overlap in time and space and therefore the number of disturbances that birds experience per day. All intertidal patches in the model had an equal density of invertebrate prey at the start of each simulation. In reality this would not be the case (Thrush 1991, Yates et al. 1993, Legendre et al. 1997). Patchy distribution in terms of both the abundance and availability of prey also influences the distribution of birds (Piersma et al. 1993, Yates et al. 1993, Meire 1996, Gawlik 2002, Coleman 2008) and could therefore affect the probability of those birds being disturbed. Additionally, high levels of disturbance in certain areas could exclude birds from more profitable feeding areas (Pfister et al. 1992, Fox and Madsen 1997), and consequently mean that they are less able to compensate for the energetic costs of responding.

These additional real-world differences could be incorporated into an updated version of the model, though for detailed, site-specific modelling exercises it may be more appropriate to use the well-established Morph framework (Stillman 2008).

6.5.4. Applications and further development of the energy budget approach

There are two main ways in which this energy budget/individual-based modelling approach could be applied to decision-making relating to the disturbance of protected species on sites of conservation importance. Firstly, the general patterns identified here could be used to rank sites in order of relative susceptibility to significant disturbance impacts. This method would not necessarily identify sites where disturbance definitely is or is not significantly impacting birds, but would be able to identify priorities for further detailed field study and site-specific modelling to answer that question. The site-specific modelling could then also be used to test and compare proposed management options and make predictions about the most effective course of action. Higher priority sites would be those with:

- high ratio of shoreline length to intertidal area ('long, thin' sites);
- high number of access points relative to the length of shoreline;
- high number of daily visitors;
- high proportion of visitors that leave the shoreline path and walk on the intertidal area; and
- low invertebrate food availability.

Alternatively, the general model could be reparameterised to reflect the anthropogenic, physical and environmental characteristics of other sites of interest, and used to make predictions about the consequences of disturbance for different species using the site. However, in order to derive reliable predictions for the absolute values of FDR, the model outputs would need to be tested with site-specific field data – for example observations relating to the distribution of potential disturbers across the intertidal area and the proportion of visits that result in flight responses. The model would also need to be calibrated to achieve a predicted daily FDR in the absence of disturbance that is close to the median value of 1.3% as reported for waders by Alerstam and Lindström (1990). This could arguably defeat the object of taking this simpler modelling approach; instead, a potential extension of the logic of the energy budget approach to develop a simple, site-specific rapid assessment tool will be discussed in Chapter 7.

Chapter 7 – Discussion

7.1 Human disturbance of wintering waterbirds in an estuarine environment

Human activities are putting ever-increasing pressure on the natural world; threatening the health and functioning of ecosystems and damaging their ability to provide the valuable services upon which we all rely (Millennium Ecosystem Assessment 2005). There is a pressing need, therefore, to better understand the mechanisms behind the impacts of human activities and take action to reverse or mitigate further damage.

This study has focussed on estuarine environments, which provide vital habitat for migratory waders and wildfowl on passage and during the non-breeding season (Davies et al. 2001, Austin et al. 2014). Such habitats are also important for a wide variety of human recreation and economic activities (Barbier et al. 2011) so there are many opportunities for conflict between people and birds – including through disturbance. Conservation managers and policy makers therefore have a duty to prevent or minimise the impacts of disturbance on designated sites and species. In the absence of clear evidence of site-specific or generally applicable thresholds of disturbance that would be expected to cause a conservation problem, managers may take a precautionary approach to the regulation of potentially damaging activities (Rio Declaration Principle 15, United Nations 1992). However, regulations that are perceived as unnecessary and/or unfair risk non-compliance and mistrust of conservation measures in general, regardless of the justification (Glover et al. 2011). With this in mind, the overarching aim of the research was to understand how and when disturbance from human activities would be expected to significantly impact wintering bird populations, so that conservation measures can be put in place where needed.

To this end, fieldwork was undertaken to characterise patterns of occurrence of human activities (Chapter 5), and quantify the responses of birds to two types of disturbance; walking (Chapters 2 and 3) and wildfowling (Chapter 4). The results were then used to inform development and parameterisation of two individual-based models (IBMs). First, a site-specific model of Poole Harbour, to determine whether current or future levels of disturbance are limiting overwintering wader populations (Chapter 5). This was followed with a more generally applicable model to assess estuary characteristics that affect whether disturbance may be a conservation problem; the results of which allowed identification of criteria for prioritisation of sites for conservation action (Chapter 6).

The rest of this chapter summarises key findings; discusses them in the context of existing research and the practical applications; identifies limitations of the study; and makes recommendations for further research.

7.2 Key findings from field observations and experiments

7.2.1. Patterns of human activities

As Fearnley et al. (2012) point out, determining spatial and temporal patterns of site use by humans in relation to use of the site by birds is fundamental to understanding the impacts of disturbance. Only when birds and people try to use the same areas at the same time and when no suitable alternative areas are available is disturbance likely to cause a conservation problem. Observations in Poole Harbour showed that a wide variety of activities occur around the site; the most frequent is walking either with or without a dog (66% of observations). By comparison, the other focal activity of this study – wildfowling – represents less than 0.04% of daily activities (based on data provided by Dorset Wildfowlers' Association).

Human recreation activities are not evenly spread around Poole Harbour or across shore levels. There are obvious concentrations on the north and east side, which have a greater number of access points and are closer to the densely populated conurbation of Bournemouth and Poole. However, most (75% or more) visitors to these busier areas remain on the shoreline footpath or beach areas, where they are unlikely to disturb birds for most of the intertidal exposure period. Furthermore, most of the 'Bird Sensitive Areas' identified in the Poole Harbour Aquatic Management Plan (Drake and Bennett 2011, Figure 1.8) are located in the quieter southern and western parts of the site.

Further surveys are needed to determine whether the patterns that were observed in Poole Harbour are typical of all estuarine sites, though Fearnley et al. (2010) did report similar patterns for a variety of sites on the Solent, Humber and in Kent. They also found that visitor pressure was not consistent between sub-sites; the most frequently reported activities were walking and dog walking; and most people (75-82%) remained on the path at the top of the shore or on the beach. The importance of site-specific, spatially explicit observations of this kind (rather than simply recording total numbers of people) will be discussed in more detail in section 7.3.

7.2.2. Testing predictions of the risk-disturbance hypothesis – behavioural responses to disturbance

The risk-disturbance hypothesis proposed by Frid and Dill (2002) offers a clear theoretical framework for making and testing predictions about animal responses to disturbance due to the similarities with anti-predator behaviour. In the context of wintering waders feeding during the intertidal period, behavioural responses to disturbance can therefore be expected to vary between individuals according to differences in perceived risk and the relative costs and benefits of fleeing or remaining. For example, birds are more likely to respond when environmental conditions are mild and suitable alternative feeding areas are available nearby (i.e. because starvation risk is low). These predictions were supported by the results of pedestrian disturbance experiments on twelve species of waders using the Wash embayment and Poole Harbour. Birds exhibited a great deal of variability in their responses to disturbance (Chapters 2 and 3), which was apparent between and within species; across small and large spatial scales; and according to environmental conditions. The observed relationships also broadly fit the patterns reported for other sites and species around the world. Most other published disturbance studies, however, relate to Australian and North American species so the data presented here make an important contribution to the suite of information available on responses to disturbance for birds of the East Atlantic flyway.

As well as flight initiation distance (FID; the most commonly reported measure of response to disturbance in the literature), in this study, time spent in flight and total feeding time lost were also recorded. These time-related responses have rarely been reported in other studies, yet they make up an important component of the mechanism by which responding to disturbance can be costly for birds. Flight incurs additional energetic costs and total response time reduces the time available to birds for extra feeding to compensate.

When the energetic cost per flight response was expressed as a proportion of daily requirement, it was tiny (less than 0.1%) and the estimated number of disturbances per bird that would result in a 5% reduction in available feeding time was much lower than would be expected to occur based on current patterns of use by humans both in Poole Harbour and on the Wash. Under normal circumstances most birds do not use 100% of their available feeding time (Goss-Custard et al. 1977, Table 3.7) so unless disturbance forces birds to forage in less profitable or more dangerous areas, they are likely to be able to compensate. Such calculations based on experimental data and field observations can give an indication of whether site carrying capacity may be reduced as a result of disturbance, though the

magnitude of impact cannot be determined in this way. Nor can predictions be made about the impacts in combination any future environmental changes that may affect site quality. Simulation modelling, however, can offer more reliable predictions and identify specific circumstances under which disturbance would be considered a conservation problem (Section 7.3).

Despite the worldwide popularity of wildfowling and its close associations with key species and habitats of conservation importance, the impacts – particularly on non-quarry species – are poorly understood. In addition, few disturbance studies have investigated or compared the responses of birds to disturbing activities besides walking or to non-visual stimuli: Chapter 4 therefore helps to address these gaps in knowledge. Factors governing bird responses to disturbance from wildfowling followed similar patterns to those observed in this study in relation to pedestrian disturbance (with differences between species and according to environmental conditions). However in this case, the relationship with species body mass was reversed, with larger birds being less likely to respond to the sound of the shotgun at any given distance. This suggests that the mechanisms governing responses to disturbance may be different for acoustic versus visual stimuli.

Given that wildfowling occurs considerably less frequently than other activities, even though the magnitude of response per disturbance was greater for wildfowling, the cumulative costs over the course of a winter are low compared to the overall costs of disturbance from all other activities. On sites where conservation management objectives include achieving reductions in overall disturbance levels, measures to address currently frequent, yet unregulated, activities could therefore be more meaningful than further restrictions on already infrequent activities such as wildfowling.

7.3 Predicting the impacts of disturbance – modelling insights

Individual-based ecology (Grimm and Railsback 2005) offers a key theoretical framework for understanding the impacts of disturbance. Consequences at the population level (the scale by which most species conservation efforts are measured) cannot be determined based simply on the short-term behavioural and physiological responses of individuals (Gill et al. 2001a, Beale and Monaghan 2004b): individual-based models (IBMs) offer a solution. By simulating individual variation and fitness-maximising behaviour, using knowledge of the real-world system, we can make predictions about the population-level consequences that emerge from individuals' interactions with their environment and with each other (Stillman et al. 2015, 2016).

IBMs have successfully been used to predict the impacts of disturbance and/or environmental change on a variety of birds and mammals (West et al. 2002, Blumstein et al. 2005b, Goss-Custard et al. 2006a, Lusseau et al. 2006, Bennett et al. 2009) and to test alternative management strategies (Bennett et al. 2011). This research adds further support for the IBM approach in both a site-specific and general context (Chapters 5 and 6).

To be confident in the predictions of IBMs, they must be built and parameterised according to a good understanding of the important processes relating to the system being modelled. Chapter 5 therefore used field observations from the preceding chapters to add detailed disturbance-related parameters to an existing site-specific IBM (Stillman 2008, K. M. Bowgen [BU] unpublished data) for Poole Harbour with its internationally important assemblage of wintering waders.

The combined results of multiple simulations of the full non-breeding season (September to March) suggested that current disturbance levels around Poole Harbour are not limiting the numbers supported (carrying capacity) or bird body condition at the end of the season (perhaps with the exception of bar-tailed godwit *Limosa lapponica*). Birds were predicted to be able to increase their time spent feeding and therefore compensate for the additional energy requirements despite reductions in total available feeding time.

In addition, birds were predicted to be able to cope with large increases in the number of visitors to Poole Harbour (ten or more times current values), especially if the relative distribution of activities around the site and across shore levels remained the same. Model outputs also supported the conclusion from Chapter 4 that birds are likely to be able to cope with the relatively minor costs of wildfowling disturbance due to the infrequency of this

activity and their ability to cope with disturbance in general. Results showed no impact on the numbers of birds supported or their body condition with the currently consented number of wildfowling visits (183 per year) nor across the range of increased wildfowling intensities that were tested.

Human-induced environmental changes such as habitat loss or sea level rise and declines in prey availability through over-exploitation were predicted to have a much greater impact than changes in visitor numbers, though the impacts were predicted to be amplified when occurring in combination with each other. This has implications for identifying priorities for conservation management, which will be discussed in the next section.

The new, generally applicable estuary IBM (Chapter 6) supported all of the comparable site specific predictions from Chapter 5. Ability to balance the energy budget and the maximum fat deposition rate (FDR) that could be achieved were predicted to be greater when birds experience fewer disturbances, when more prey was available, and when environmental conditions were more favourable. Model outputs also showed that the probability of birds being disturbed by human activities is not solely dependent on the number of people present. Birds are more likely to experience significant impacts from disturbance when feeding in estuaries with a short distance between the high and low water mark, or where the types of activity or sediment characteristics mean that many visitors access intertidal areas, as well as on sites that have many access points relative the length of the shoreline. These insights can be distilled into the conceptual model shown in Figure 7.1 and are key points to bear in mind when assessing the likelihood of disturbance being a conservation problem at different sites.

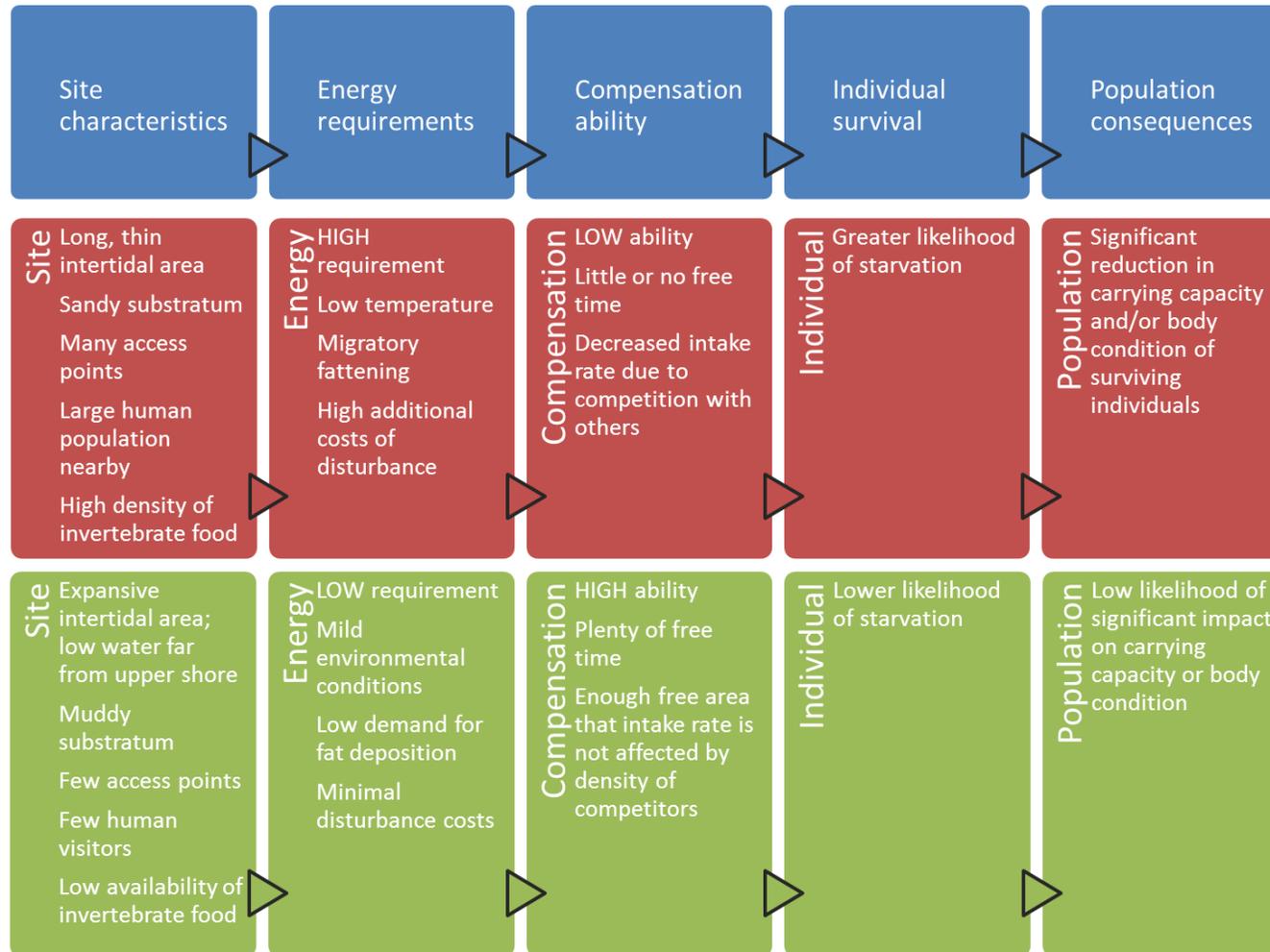


Figure 7.1. Conceptual model showing situations where disturbance may (red) and may not (green) be expected to have a significant impact on wintering wader populations. Insights into key factors (blue) – i.e. site characteristics/energetics/compensation opportunities – derived from simulation modelling.

7.4 Management implications for Poole Harbour and wider applications

Whilst this study has shown that disturbance from very high frequencies of human activities can have a significant impact on survival and body condition, it would be appropriate to focus management efforts in Poole Harbour on non-disturbance-related aspects of site quality in order to improve wading bird resilience and maintain overwintering populations in the face of environmental change. Specifically, model outputs showed that when there is enough suitable intertidal or supratidal habitat available, with sufficient densities of invertebrate food, most birds are able to compensate for the (relatively minor) additional costs of disturbance from human activities.

Given that the degree of impact of disturbance is partly dependent on spatial and temporal patterns of use for different human activities and that present day distributions do not limit bird numbers, this is an argument for continued implementation and communication of the benefits of the current zoning of activities (see Figure 1.9) rather than introducing new measures. This could be combined with monitoring for any changes in patterns of use, particularly any increases in the number of visitors to 'quieter' areas or an increase in the proportion of visitors that access the intertidal area rather than remaining near the top of the shore. Hocking et al. (1992) summarise other potential options for mitigation, including concealment of observers by constructing banks or screens, and careful location of public access points. However, this study found no evidence that additional proactive management such as this is currently necessary in Poole Harbour.

Crucially, birds are most likely to suffer negative consequences due to disturbance in circumstances when they are already experiencing difficulties achieving their energy intake requirements – as demonstrated by the model predictions for bar-tailed godwit. For example Figure 5.8 shows that even in the absence of disturbance over-winter survival was predicted to be below 100% for bar-tailed godwit; and this species showed the steepest decline in predicted final body condition and overall survival in response to increased frequencies of human activities. Similarly, disturbance during prolonged periods of extreme winter weather could be problematic for all species (Davidson and Evans 1982, Camphuysen et al. 1996). When thermoregulatory requirements are particularly high and feeding opportunities are limited, measures to restrict access and reduce disturbance in areas with large numbers of birds would therefore be beneficial. Country-wide cold weather bans like those that already exist for wildfowling and bird ringing (Stroud et al. 2006, Ellis 2012) would admittedly be

difficult to enforce in expansive, publicly accessible areas; though this could be more achievable on smaller nature reserves and areas that already have wardening and communication schemes in place. Koch and Paton (2014) also comment that activity restrictions could be challenging to implement since birds do not consistently forage in a fixed location; instead the authors emphasise the importance of outreach and education to foster appreciation and understanding of the importance of key sites.

Broad management recommendations are shown in Table 7.1. They are based on the results of the site-specific simulation modelling for Poole Harbour, and are supported by the predictions of the more generally applicable IBM. Further work is needed, however, to determine the extent to which they apply to other sites since the ability to cope with current or future frequencies of disturbance depend on between-site variation in many different factors, as already discussed (environmental conditions; patterns of use; estuary size and dimensions; ease of access; sediment type; prey availability etc. – see Figure 7.1).

Data from studies such as this that record bird behavioural responses to disturbance have frequently been used to inform protective measures such as ‘buffer zones’ or ‘set-back distances’ (Glover et al. 2011; Weston et al. 2012; Chatwin et al. 2013; Schlacher et al. 2013a; Koch and Paton 2014). The size of such buffers is usually based on the largest FID value recorded for the group of species of interest – in fact a database was recently published by Livezey et al. (2016) precisely for this purpose. However, such measures are arguably overly precautionary on most expansive estuarine sites; where large areas of intertidal mud already act as a buffer zone for most of the exposure period, and birds are not usually confined to a particular foraging location. Using FID in this way ignores the biotic and abiotic factors that influence bird responses and the fact that FID is not a good measure of vulnerability to suffering negative impacts from disturbance. Efforts to prevent or reduce the impacts of disturbance in estuarine areas would be better placed using the management measures already outlined (and see Table 7.1).

Table 7.1. Key management measures to prevent significant impacts of disturbance in Poole Harbour and maintain the number of birds that the site can support. The principles are the same for other sites, though the threshold level for significant impact of disturbance will vary from site to site.

Action	Details	Rationale
Maintain existing habitat, along with creation or extension of refuge areas/ nature reserves	Restore/protect habitats from loss due to development or coastal squeeze.	Figure 5.11: even small reductions in the availability of intertidal habitat (due to simulated sea level rise) were predicted to reduce site carrying capacity and the ability of birds to cope with increased frequencies of human activities.
Harvest management	Identify how much of the invertebrate resource is required to sustain birds throughout the non-breeding season, and put limits on shellfish and baitworm extraction in order to achieve this.	Figures 5.12 and 6.4: achievable fat deposition rate, body condition and survival were all predicted to be greater under scenarios of higher invertebrate prey availability i.e. birds were better able to meet their energy requirements and compensate for the costs of disturbance.
Pollution control	Minimise nutrient inputs and associated algal mat formations which can alter prey communities and bird foraging behaviour.	Also linked to ensuring sufficient invertebrate prey availability to enable birds to meet daily energy intake requirements or compensate for additional costs of disturbance responses (see above).
Cold weather restrictions/ communication of potential impacts of disturbance	Encourage visitors to alter their behaviour at times when birds are likely to be particularly vulnerable.	Figure 6.5: achievable fat deposition rates were predicted to be lower in winter and spring compared to autumn, in part due to the additional thermoregulatory costs associated with lower temperatures and when feeding time was limited by the tidal stage. Severe weather would be expected to negatively impact energy budgets, which would be further exacerbated by disturbance costs.
Zonation	Identify sensitive/priority areas where greater emphasis should be put on implementing the above actions, and other areas where restrictions can be relaxed.	Figures 5.8, 6.7 and 6.8: model simulations demonstrated how the spatial patterns of occurrence of potential disturbers influence predicted fat deposition rate, body condition and overwinter survival.

7.5 Study limitations and recommendations for further work

7.5.1. General applicability and unexplained variability

Whilst most of the field data and detailed modelling exercises from this study were for a single site, Poole Harbour, the results were also supported by data from a second study site (the Wash) and the general model simulations. Further work to add detailed disturbance-related parameters to existing IBMs for other estuarine sites would therefore help to demonstrate the extent to which the findings are more widely applicable. Additional field work with an IBM in mind could also benefit from more detailed consideration of the patterns of visitor use: specifically time of day; weekends versus weekdays; and variability in visitor numbers though the season between September and March.

As was shown here for pedestrian and wildfowling disturbance and elsewhere in the literature (e.g. Burger 1981, Glover et al. 2011, Lafferty 2001b), there may be important differences in the way that birds respond to different types of human activity. So whilst a focus on responses to pedestrians is logical (since walking is the most frequently occurring activity), there is a need to understand the relative impacts of other activities. This could for example inform appropriate management of shellfish and bait harvesting or address, if necessary, the increasing popularity of other activities like kite surfing (Davenport and Davenport, 2006) and flying drones (Allport 2016; McEvoy et al. 2016; Rümmler et al. 2016).

Much of the unexplained variability in bird responses that were observed in relation to experimental disturbance is likely to be due to between-individual differences in experience and body condition, so any research that can measure this alongside controlled experimental disturbance would make an important contribution to knowledge. This could also help to address the crucial point that the results of experimental studies such as those described in Chapters 2-4 still cannot tell us at what level of disturbance there will be a population impact. Full time budget surveys, for example, that determine the proportion of available time that key species spend feeding would give an indication of the difficulty with which they are achieving their daily energy requirements (Goss-Custard et al. 1977), and thus their capacity to cope with the costs of responding to disturbance at different stages of the winter period. For example Bell et al. (1991) used radio tracking to show that wigeon on the Ouse Washes (UK) spent over 16 hours per day feeding, and would therefore be particularly vulnerable to experiencing negative consequences of disturbance disrupting their feeding patterns and increasing their energy requirements since they would have little available time with which to compensate.

Abundance and accessibility of intertidal invertebrates are inherently patchy in both time and space so not all foraging areas that are available to birds are equally attractive. Disturbance that excludes birds from the most profitable areas could therefore be relatively more problematic than the same amount of disturbance in more uniform or poorer quality habitat. This needs to be acknowledged or accounted for when making predictions about impact. The distinction was incorporated into the Morph model using data from detailed surveys of the invertebrate communities in Poole Harbour; however in the interest of general applicability and model parsimony, such variability was not included in the simple IBM. There is scope to address this alongside further development of the model for additional scenario testing and investigating further patterns in site- and bird-related predictors of the impacts of disturbance.

7.5.2. Tools for conservation decision making

Chapter 5 demonstrated how site-specific modelling can offer detailed insights into the impacts of disturbance (or lack of) and suitable management. However, there is also a need for an effective rapid assessment method for determining whether such detailed investigation should be a priority given limited resources. The general IBM (Chapter 6) to test bird ability to balance energy expenditure against intake showed that the energy budget approach can be a useful way to judge whether survival is likely to be significantly impacted as a result of disturbance. The next step following on from this research, therefore, would be to develop, test and ultimately communicate the effectiveness of an energy budget rapid assessment tool (Figure 7.2).

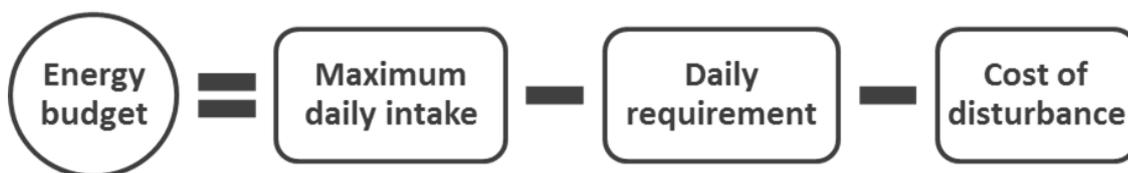


Figure 7.2. The key elements of an energy budget calculation that incorporates the energetic costs of responding to disturbance.

The maximum daily intake that birds could achieve can be estimated using knowledge of intertidal exposure time for a site; details of invertebrate prey availability (mean ash-free dry mass per individual within the size range consumed by each bird species); and the functional response equations given by (Goss-Custard et al. 2006b). Daily energetic requirements would be calculated in the same way as described in Chapters 5 and 6, according to BMR and the

additional energetic costs of thermoregulation. And as shown in this study, the expected cost of disturbance is related to the number of potentially disturbing activities, the probability of them overlapping in time and space with foraging birds, and the behavioural responses of birds (time spent in flight and lost feeding time).

If the results of this rapid assessment can be shown to be consistently accurate when tested against the predictions of site-specific IBMs for a range of sites, it could be a very useful tool for quickly identifying management priorities in relation to mitigation of disturbance impacts. Users should bear in mind, however, that this is likely to be a more precautionary assessment, since survival will only be affected when birds suffer a negative energy budget for a prolonged period of time i.e. days or weeks (Pienkowski et al. 1984a).

7.6 Final remarks

Human disturbance of birds (and wildlife in general) can be an emotive topic and the subject of heated debate as to whether it is 'morally acceptable'. However from a biological point of view, the issue may not be as problematic as many people think. Sites that support large numbers of birds during the non-breeding season are likely to be of sufficiently high quality to allow birds to cope with the relatively minor costs of responding to disturbance. Since bird ability to compensate for those costs is related to habitat quality (availability of feeding areas where birds can achieve high intake rates) and available feeding time, it follows that disturbance during the non-breeding season is only likely to have a significant population impact under circumstances where birds are already having difficulty in meeting their energy requirements (such as during prolonged periods of extreme cold weather or after considerable loss of suitable habitat).

By investigating wildfowling as well as pedestrian disturbance, this research has added to our understanding of bird responses to noise stimuli and the potential impacts of hunting on non-target species. It provides evidence to allow less-precautionary approaches to be taken regarding management of disturbance in the context of other threats to key species and habitats.

This study has also shown how field data and simulation modelling can be combined to give site-specific and general recommendations for conservation management, with applications not just for birds and estuarine environments. The patterns, predictions and assessment tools that have been discussed are also applicable to a wide variety of systems where management of human-wildlife interactions might be necessary.

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Parkstone Bay 04/03/2014

Appendices

Appendix 1. Preliminary analysis revealed no effect of winter year on a) FID, b) flight time or c) latency time, and that only one interaction term (Site:WinterDay) should be included in the global models for multi-model inference testing.

a)

```
Call:
lm(formula = log(FID) ~ z.SpMass * z.windChill + z.SpMass * z.ShoreLevel +
    Site + z.SpMass * z.WinterDay + Site:z.WinterDay + z.WinterYear +
    c.IsItOC + c.IsItPlover, data = data)
```

```
Residuals:
    Min       1Q   Median       3Q      Max
-1.94155 -0.28532  0.02335  0.28781  1.61603
```

Coefficients: (1 not defined because of singularities)

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.428505	0.035069	126.280	< 2e-16 ***
z.SpMass	1.242445	0.052448	23.689	< 2e-16 ***
z.windChill	0.098183	0.044116	2.226	0.026380 *
z.ShoreLevel	-0.166977	0.042068	-3.969	8.00e-05 ***
Site2-Maretail	-0.110784	0.219572	-0.505	0.614046
Site3-Breast Sand	0.110221	0.127162	0.867	0.386379
Site4-Stubborn Sand	-0.361535	0.042938	-8.420	2.34e-16 ***
z.WinterDay	-0.129668	0.075554	-1.716	0.086589 .
z.WinterYear	-0.036778	0.046494	-0.791	0.429215
c.IsItOC	-0.512430	0.061200	-8.373	3.35e-16 ***
c.IsItPlover	0.488813	0.061513	7.947	8.29e-15 ***
z.SpMass:z.windChill	0.119596	0.086022	1.390	0.164910
z.SpMass:z.ShoreLevel	0.015544	0.084897	0.183	0.854780
z.SpMass:z.WinterDay	0.005905	0.087933	0.067	0.946483
Site2-Maretail:z.WinterDay	-0.236508	0.348730	-0.678	0.497884
Site3-Breast Sand:z.WinterDay	NA	NA	NA	NA
Site4-Stubborn Sand:z.WinterDay	0.313813	0.088296	3.554	0.000406 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.4907 on 661 degrees of freedom
Multiple R-squared: 0.6017, Adjusted R-squared: 0.5926
F-statistic: 66.57 on 15 and 661 DF, p-value: < 2.2e-16

b)

```
Call:
lm(formula = log(FlightTime) ~ z.SpMass * z.windChill + z.SpMass *
    z.ShoreLevel + Site + z.SpMass * z.WinterDay + Site:z.WinterDay +
    z.WinterYear + c.IsItOC + c.IsItPlover, data = data)
```

```
Residuals:
    Min       1Q   Median       3Q      Max
-1.60092 -0.38003  0.00709  0.39324  1.47614
```

Coefficients: (1 not defined because of singularities)

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	2.9162885	0.0388360	75.092	< 2e-16 ***
z.SpMass	0.5552171	0.0580814	9.559	< 2e-16 ***
z.windChill	0.1579749	0.0488549	3.234	0.001283 **
z.ShoreLevel	-0.1635865	0.0465865	-3.511	0.000476 ***
Site2-Maretail	-0.2696744	0.2431579	-1.109	0.267812
Site3-Breast Sand	0.2033731	0.1408216	1.444	0.149160

```

Site4-Stubborn Sand      -0.2638803  0.0475507  -5.549  4.15e-08  ***
z.WinterDay              -0.2423223  0.0836701  -2.896  0.003902  **
z.WinterYear             -0.0324933  0.0514888  -0.631  0.528210
c.IsItOC                 -0.2057459  0.0677738  -3.036  0.002493  **
c.IsItPlover             0.2120478  0.0681202   3.113  0.001933  **
z.SpMass:z.WindChill     0.0438667  0.0952628   0.460  0.645322
z.SpMass:z.ShoreLevel    -0.0709289  0.0940166  -0.754  0.450860
z.SpMass:z.WinterDay     0.0002832  0.0973781   0.003  0.997680
Site2-Maretail:z.WinterDay -0.0940819  0.3861896  -0.244  0.807604
Site3-Breast Sand:z.WinterDay      NA          NA          NA          NA
Site4-Stubborn Sand:z.WinterDay  0.3205609  0.0977810   3.278  0.001099  **

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.5434 on 661 degrees of freedom
Multiple R-squared: 0.253, Adjusted R-squared: 0.2361
F-statistic: 14.93 on 15 and 661 DF, p-value: < 2.2e-16

c)

```

Call:
lm(formula = log(TotalTime) ~ z.SpMass * z.WindChill + z.SpMass *
  z.ShoreLevel + Site + z.SpMass * z.WinterDay + Site:z.WinterDay +
  z.WinterYear + c.IsItOC + c.IsItPlover, data = data)

```

```

Residuals:
    Min       1Q   Median       3Q      Max
-1.31732 -0.30585  0.00614  0.29032  1.29050

```

```

Coefficients: (1 not defined because of singularities)
              Estimate Std. Error t value Pr(>|t|)
(Intercept)   3.798442   0.032125 118.238 < 2e-16 ***
z.SpMass      0.505669   0.048045  10.525 < 2e-16 ***
z.WindChill   0.117532   0.040413   2.908 0.003757 **
z.ShoreLevel -0.129354   0.038537  -3.357 0.000834 ***
Site2-Maretail -0.036983   0.201142  -0.184 0.854178
Site3-Breast Sand  0.245100   0.116489   2.104 0.035750 *
Site4-Stubborn Sand -0.144054   0.039334  -3.662 0.000270 ***
z.WinterDay  -0.284009   0.069213  -4.103 4.58e-05 ***
z.WinterYear -0.148172   0.042592  -3.479 0.000537 ***
c.IsItOC      0.020871   0.056063   0.372 0.709803
c.IsItPlover  0.318822   0.056350   5.658 2.28e-08 ***
z.SpMass:z.WindChill  0.072659   0.078802   0.922 0.356844
z.SpMass:z.ShoreLevel -0.002636   0.077771  -0.034 0.972972
z.SpMass:z.WinterDay -0.038420   0.080552  -0.477 0.633545
Site2-Maretail:z.WinterDay  0.055688   0.319459   0.174 0.861668
Site3-Breast Sand:z.WinterDay      NA          NA          NA          NA
Site4-Stubborn Sand:z.WinterDay  0.323716   0.080885   4.002 6.99e-05 ***

```

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.4495 on 661 degrees of freedom
Multiple R-squared: 0.332, Adjusted R-squared: 0.3168
F-statistic: 21.9 on 15 and 661 DF, p-value: < 2.2e-16

Appendix 2. Standardised, model averaged, species-specific parameter estimates for predictors of wader responses to experimental disturbance by an approaching pedestrian.

a) logFID

Predictor	Species									
	Curlew		Oystercatcher		Bar-tailed godwit		Grey plover		Redshank	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	5.913	0.061	4.705	0.051	4.344	0.039	5.046	0.073	4.245	0.046
1 WindChill	0.118	0.153	0.160	0.056	0.231	0.079	-0.053	0.091	0.112	0.116
2 ShoreLevel	0.004	0.049	-0.160	0.064	-0.317	0.082	-0.363	0.116	-0.017	0.056
3 Site ^a										
Site2-Maretail	0.213	0.227	-0.053	0.124	-	-	-1.721	4.475	-	-
Site3-Breast Sand	-	-	0.147	0.148	-	-	-	-	-	-
Site4-Stubborn Sand	-0.484	0.104	-0.336	0.064	-0.162	0.119	-0.470	0.099	-0.811	0.109
4 WinterDay	0.191	0.162	0.016	0.041	0.069	0.084	-0.226	0.200	-0.007	0.043
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	-	-	-	-	-	-	-1.105	4.922	-	-
Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	-	-
Site4-Stubborn Sand:WinterDay	-	-	-	-	-	-	0.459	0.349	-	-

Predictor	Species									
	Knot		Turnstone		Ringed plover		Sanderling		Dunlin	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	4.153	0.068	3.296	0.175	3.658	0.063	3.081	0.112	3.609	0.054
1 WindChill	-0.009	0.055	0.395	0.209	0.233	0.157	-0.014	0.109	-0.077	0.116
2 ShoreLevel	-0.264	0.107	-0.694	0.184	0.010	0.072	-0.023	0.114	0.034	0.080
3 Site ^a										
Site2-Maretail	0.064	0.139	0.575	0.667	-	-	-	-	-	-
Site3-Breast Sand	0.198	0.283	-	-	-	-	-	-	-	-
Site4-Stubborn Sand	0.001	0.068	-0.056	0.184			-0.042	0.186		
4 WinterDay	-0.313	0.106	0.088	0.166	0.004	0.061	0.051	0.151	0.208	0.144
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	-	-	-	-	-	-	-	-	-	-
Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	-	-
Site4-Stubborn Sand:WinterDay	-	-	-	-	-	-	-	-	-	-

b)logFlightTime

Predictor	Species									
	Curlew		Oystercatcher		Bar-tailed godwit		Grey plover		Redshank	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	3.439	0.075	2.983	0.094	2.841	0.057	3.232	0.110	2.637	0.088
1 WindChill	0.016	0.092	0.232	0.085	0.303	0.125	-0.036	0.099	-0.008	0.090
2 ShoreLevel	-0.044	0.110	-0.099	0.108	-0.224	0.144	-0.052	0.115	0.037	0.118
3 Site ^a										
Site2-Maretail	<0.001	0.073	-0.121	0.192	-	-	0.065	0.413	-	-
Site3-Breast Sand	-	-	-0.127	0.212	-	-	-	-	-	-
Site4-Stubborn Sand	0.005	0.041	-0.080	0.116	-0.047	0.110	-0.487	0.151	-0.600	0.195
4 WinterDay	-0.012	0.090	0.007	0.047	0.011	0.060	0.053	0.119	-0.085	0.157
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	-	-	-	-	-	-	-	-	-	-
Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	-	-
Site4-Stubborn Sand	-	-	-	-	-	-	-	-	-	-

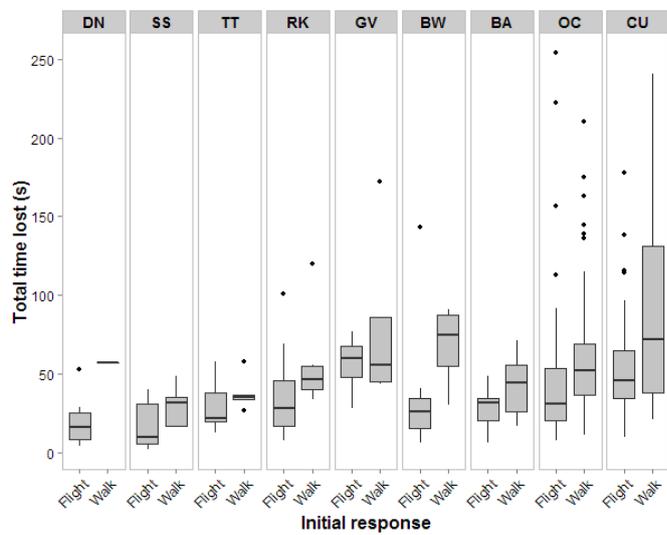
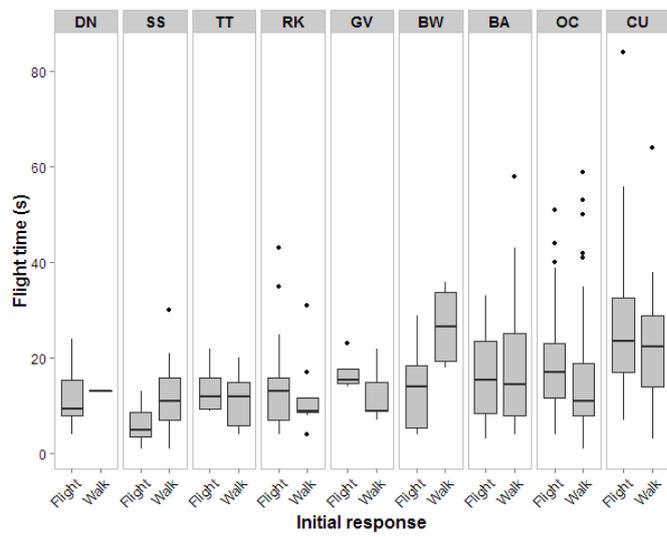
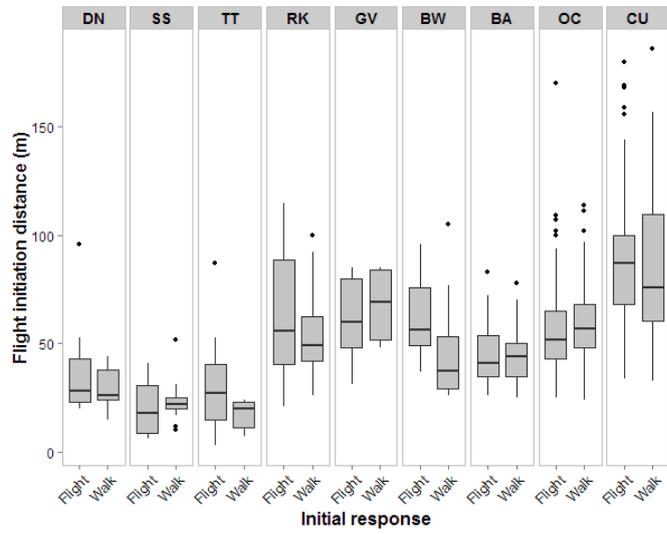
Predictor	Species									
	Knot		Turnstone		Ringed plover		Sanderling		Dunlin	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	2.853	0.089	2.680	0.307	2.401	0.090	2.156	0.100	2.502	0.084
1 WindChill	0.003	0.055	0.149	0.218	0.199	0.213	0.310	0.280	0.086	0.110
2 ShoreLevel	-0.005	0.056	-0.221	0.251	0.008	0.107	-0.122	0.202	-0.044	0.085
3 Site ^a										
Site2-Maretail	2.063	3.548	0.884	0.750	-	-	-	-	0.55881	0.41408
Site3-Breast Sand	0.371	0.403	-	-	-	-	-	-	0.32452	0.21671
Site4-Stubborn Sand	-0.022	0.101	-0.444	0.339	-	-	-0.231	0.336	-0.1248	0.11029
4 WinterDay	-0.340	0.334	0.030	0.132	-0.020	0.097	0.148	0.237	-0.002	0.055
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	3.78731	5.90756	-	-	-	-	-	-	-	-
Site3-Breast Sand:WinterDay	0	0	-	-	-	-	-	-	-	-
Site4-Stubborn Sand	0.24417	0.33877	-	-	-	-	-	-	-	-

c) logTotalTimeLost

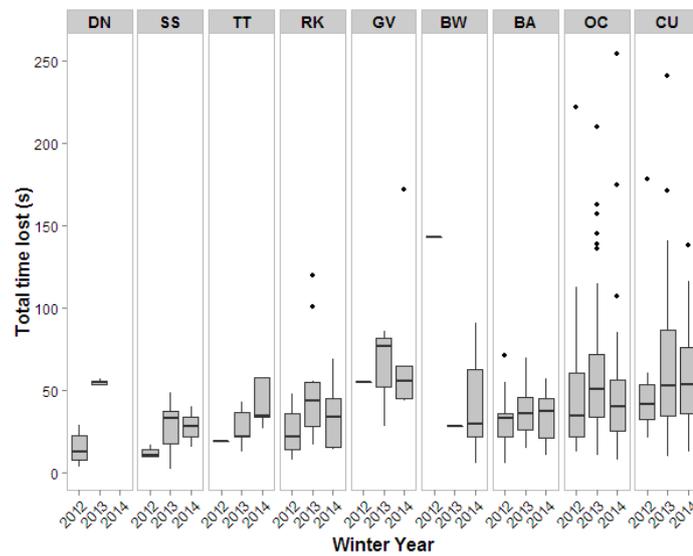
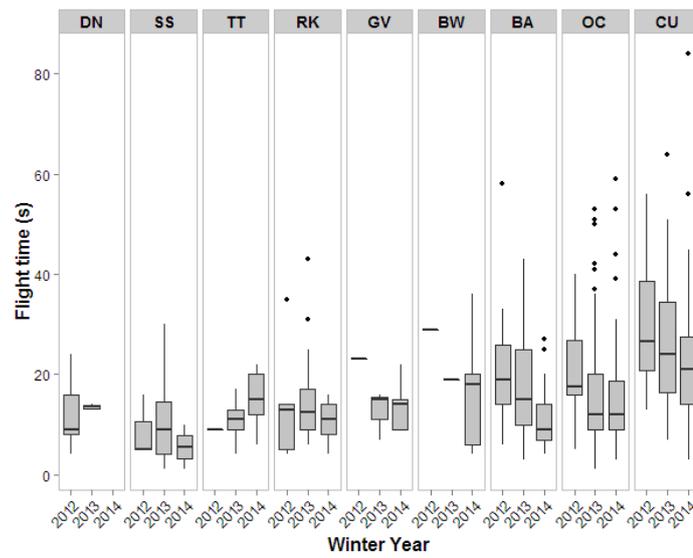
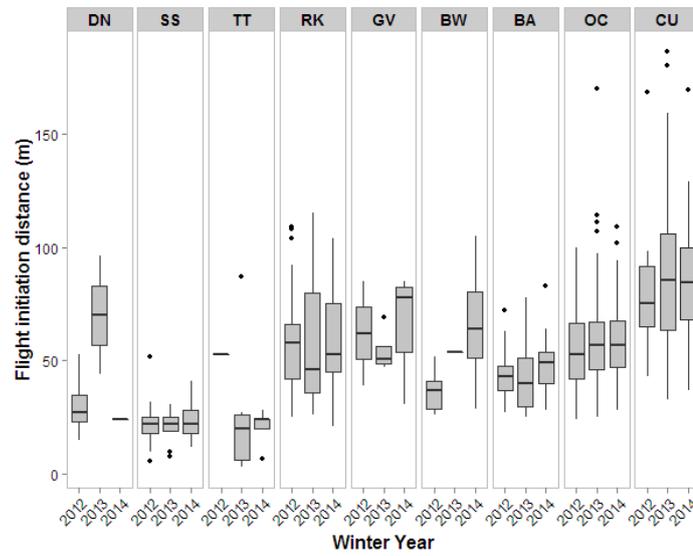
Predictor	Species									
	Curlew		Oystercatcher		Bar-tailed godwit		Grey plover		Redshank	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	4.239	0.070	4.022	0.046	3.736	0.049	4.132	0.092	3.673	0.074
1 WindChill	0.014	0.088	0.281	0.070	0.232	0.113	-0.023	0.071	0.054	0.121
2 ShoreLevel	-0.046	0.107	-0.085	0.080	-0.134	0.121	-0.015	0.067	0.006	0.074
3 Site ^a										
Site2-Maretail	0.000	0.072	0.024	0.086	-	-	0.160	0.315	-	-
Site3-Breast Sand	-	-	-0.015	0.141	-	-	-	-	-	-
Site4-Stubborn Sand	0.007	0.046	-0.019	0.052	-0.028	0.083	-0.307	0.135	-0.159	0.184
4 WinterDay	-0.020	0.092	-0.0025	0.031	0.014	0.057	0.061	0.108	-0.046	0.110
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	-	-	-0.015067	0.0841063	-	-	-	-	-	-
Site3-Breast Sand: WinterDay	-	-	-0.057848	0.4003784	-	-	-	-	-	-
Site4-Stubborn Sand:WinterDay	-	-	0.0010851	0.0304808	-	-	-	-	-	-

Predictor	Species									
	Knot		Turnstone		Ringed plover		Sanderling		Dunlin	
	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e	Estimate	s.e
Intercept	3.676	0.084	3.544	0.224	3.502	0.075	3.180	0.078	3.353	0.069
1 WindChill	0.007	0.053	0.014	0.082	0.357	0.179	0.045	0.116	0.060	0.090
2 ShoreLevel	-0.010	0.056	-0.240	0.204	0.043	0.131	-0.449	0.187	-0.136	0.110
3 Site ^a										
Site2-Maretail	2.633	3.478	0.588	0.578	-	-	-	-	0.345	0.374
Site3-Breast Sand	0.440	0.382			-	-	-	-	0.237	0.217
Site4-Stubborn Sand	-0.020	0.099	-0.231	0.248	-	-	-0.250	0.287	-0.044	0.087
4 WinterDay	-0.426	0.327	0.053	0.124	0.069	0.136	0.078	0.150	0.002	0.050
5 Site:WinterDay ^b										
Site2-Maretail:WinterDay	4.803	5.767	-	-	-	-	-	-	-	-
Site3-Breast Sand: WinterDay	0	0	-	-	-	-	-	-	-	-
Site4-Stubborn Sand:WinterDay	0.359	0.355	-	-	-	-	-	-	-	-

Appendix 3. No effect of initial response (walk or fly) on FID, flight time or total time lost so data can be combined.



Appendix 4. No effect of winter year on responses to disturbance so all data can be combined.



Appendix 5. Model selection tables – top five AIC_c-ranked models in each candidate set.

a) Global model = log(FID)~Approach+IsItOC+IsItPlover+FlockSize+SpMass+StartDist+VisitFreq+WindChill+WinterDay+SpMass:VisitFreq

Variables in top five candidate models										adjR ²	AIC _c	Δ _i	ω _i
Approach	IsItOC	IsItPlover	FlockSize	SpMass	StartDist	VisitFreq	WindChill	WinterDay	SpMass:VisitFreq				
x	x	✓	x	✓	✓	✓	✓	✓	✓	0.6398	476.743	0	0.088
x	x	✓	x	✓	✓	✓	✓	x	✓	0.6370	477.204	0.461	0.070
✓	x	✓	x	✓	✓	✓	✓	✓	✓	0.6415	477.322	0.579	0.066
x	✓	✓	x	✓	✓	✓	✓	✓	✓	0.6412	477.553	0.810	0.059
x	✓	✓	x	✓	✓	✓	✓	x	✓	0.6386	477.794	1.051	0.052

b) Global model =

log(FlightTime)~Approach+IsItOC+IsItPlover+FlockSize+SpMass+StartDist+VisitFreq+WindChill+WinterDay+Approach:SpMass+FlockSize:SpMass+WindChill:WinterDay

Variables in top five candidate models													adjR ²	AIC _c	Δ _i	ω _i
Approach	IsItOC	IsItPlover	FlockSize	SpMass	StartDist	VisitFreq	WindChill	WinterDay	Approach: SpMass	FlockSize: SpMass	WindChill: WinterDay					
x	✓	x	✓	✓	✓	✓	✓	✓	x	✓	✓	0.1895	753.474	0	0.039	
x	✓	x	✓	✓	✓	✓	x	x	x	✓	x	0.1718	753.995	0.520	0.030	
x	✓	x	✓	✓	✓	✓	x	✓	x	✓	x	0.1751	754.811	1.337	0.020	
x	✓	x	✓	✓	✓	✓	✓	x	x	✓	x	0.1740	755.248	1.774	0.016	
x	x	x	✓	✓	✓	✓	✓	✓	x	✓	✓	0.1794	755.282	1.808	0.016	

c) Global model =

$\log(\text{TotalLost}) \sim \text{Approach} + \text{IsItOC} + \text{IsItPlover} + \text{FlockSize} + \text{SpMass} + \text{StartDist} + \text{VisitFreq} + \text{WindChill} + \text{WinterDay} + \text{FlockSize:SpMass} + \text{VisitFreq:WinterDay}$

Variables in top five candidate models											adjR ²	AIC _c	Δ _i	ω _i
Approach	IsItOC	IsItPlover	FlockSize	SpMass	StartDist	VisitFreq	WindChill	WinterDay	FlockSize:SpMass	VisitFreq:WinterDay				
x	x	✓	✓	✓	✓	✓	x	✓	✓	✓	0.2222	717.226	0	0.089
x	✓	✓	✓	✓	✓	✓	x	✓	✓	✓	0.2269	717.479	0.253	0.079
x	x	✓	✓	✓	✓	✓	✓	✓	✓	✓	0.2251	718.182	0.956	0.055
✓	✓	✓	✓	✓	✓	✓	x	✓	✓	✓	0.2302	718.282	1.056	0.053
✓	x	✓	✓	✓	✓	✓	x	✓	✓	✓	0.2248	718.300	1.074	0.052

Appendix 6. Estimating Effective Disturbance Distance (EDD) – a worked example.

Effective disturbance distance (EDD) is an FID-like measure of the distance over which birds are disturbed by an activity. It is calculated using modelled probabilities of a disturbance response occurring at a given distance from the disturbance stimulus. Following Stillman et al. (2012), this method was used to calculate EDDs for each species of wader and wildfowl in response to the sound of a wildfowler’s shotgun (Chapter 4).

This worked example for curlew shows how the calculations used the results of the binary logistic regression analyses and model averaging. The probability of any response occurring was estimated for each 1 metre interval up to the maximum recorded response distance (850 m). These predicted probabilities could then be summed to give the EDD value for each species as shown in Table 4.7. Each probability value was calculated for the mid-point in the wildfowling season (winter day = 117), based on the mean flock size observed for that species, and using the mean wind chill equivalent temperature for the study period (5.3°C).

$$EDD = P_{Any}(1) + P_{Any}(2) + P_{Any}(3) \dots \dots + P_{Any}(849) + P_{Any}(850)$$

$$EDD (curlew) = 431.36m$$

CURLEW EDD calculation

Distance	SpMass	FlockSize	IsItOC	IsItPlover	WinterDay	WindChill	P _{Any}
1	782	10.467	No	No	117	5.333	0.90524
2	782	10.467	No	No	117	5.333	0.90480
3	782	10.467	No	No	117	5.333	0.90435
4	782	10.467	No	No	117	5.333	0.90389
5	782	10.467	No	No	117	5.333	0.90344
6	782	10.467	No	No	117	5.333	0.90298
7	782	10.467	No	No	117	5.333	0.90252
8	782	10.467	No	No	117	5.333	0.90206
9	782	10.467	No	No	117	5.333	0.90160
10	782	10.467	No	No	117	5.333	0.90114
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
⋮	⋮	⋮	⋮	⋮	⋮	⋮	⋮
845	782	10.467	No	No	117	5.333	0.10449
846	782	10.467	No	No	117	5.333	0.10401
847	782	10.467	No	No	117	5.333	0.10352
848	782	10.467	No	No	117	5.333	0.10304
849	782	10.467	No	No	117	5.333	0.10256
850	782	10.467	No	No	117	5.333	0.10208
						SUM=	431.35616

Appendix 7. Model selection tables – top five AIC_c-ranked models in each candidate set for waders: a) probability of any response, b) probability of flight, c) probability of flight with abandonment; and wildfowl: d) probability of any response, e) probability of flight, f) probability of flight with abandonment.

a) Global model = $\text{glm}(\text{AnyResponse} \sim \text{SpMass} + \text{Distance} + \text{FlockSize} + \text{WindChill} + \text{WinterDay} + \text{IsItOC} + \text{IsItPlover}, \text{family} = \text{binomial}, \text{data} = \text{waders})$

Variables in top five candidate models							adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	IsItOC	IsItPlover	SpMass	WindChill	WinterDay				
✓	✗	✓	✗	✓	✓	✓	0.2843	196.614	0	0.131
✓	✗	✓	✗	✓	✗	✗	0.2538	197.367	0.753	0.090
✓	✗	✓	✗	✓	✓	✗	0.2638	197.848	1.234	0.071
✓	✓	✓	✗	✓	✓	✓	0.2879	198.182	1.568	0.060
✓	✗	✓	✓	✓	✓	✓	0.2847	198.707	2.093	0.046

b) Global model = $\text{glm}(\text{FlightResponse} \sim \text{SpMass} + \text{Distance} + \text{FlockSize} + \text{WindChill} + \text{WinterDay} + \text{IsItOC} + \text{IsItPlover}, \text{family} = \text{binomial}, \text{data} = \text{waders})$

Variables in top five candidate models							adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	IsItOC	IsItPlover	SpMass	WindChill	WinterDay				
✓	✗	✗	✗	✓	✓	✓	0.2649	229.647	0	0.206
✓	✗	✓	✗	✓	✓	✓	0.2754	229.913	0.267	0.180
✓	✗	✗	✓	✓	✓	✓	0.2682	231.197	1.551	0.095
✓	✗	✓	✓	✓	✓	✓	0.2779	231.617	1.971	0.077
✓	✗	✗	✗	✓	✓	✓	0.2657	231.636	1.990	0.076

c) Global model = glm(Abandon~SpMass+Distance+FlockSize+WindChill+WinterDay+IsItOC+IsItPlover,family=binomial,data=waders)

Variables in top five candidate models							adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	IsItOC	IsItPlover	SpMass	WindChill	WinterDay				
x	x	x	x	x	x	x	0.0000	232.018	0	0.071
x	x	x	✓	x	x	x	0.0061	233.236	1.218	0.039
x	x	x	x	x	✓	✓	0.0208	233.320	1.303	0.037
x	x	x	x	x	✓	x	0.0028	233.679	1.661	0.031
x	x	x	x	x	x	✓	0.0028	233.681	1.663	0.031

d) Global model =

glm(AnyResponse~SpMass+Distance+FlockSize+WindChill+WinterDay+QuarryUK,
family=binomial, data=wildfowl)

Variables in top five candidate models						adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	QuarryUK	SpMass	WindChill	WinterDay				
✓	✗	✗	✗	✓	✓	0.0957	134.608	0	0.073
✓	✗	✗	✗	✗	✗	0.0395	134.845	0.238	0.065
✗	✗	✗	✗	✗	✓	0.0361	135.106	0.499	0.057
✓	✗	✗	✗	✗	✓	0.0596	135.369	0.761	0.050
✗	✗	✗	✗	✓	✓	0.0591	135.411	0.803	0.049

e) Global model =

glm(FlightResponse~SpMass+Distance+FlockSize+WindChill+WinterDay+QuarryUK,
family=binomial, data=wildfowl)

Variables in top five candidate models						adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	QuarryUK	SpMass	WindChill	WinterDay				
✓	✗	✗	✗	✗	✗	0.0504	146.764	0	0.087
✓	✗	✗	✗	✗	✓	0.0710	147.155	0.391	0.072
✗	✗	✗	✗	✗	✓	0.0399	147.634	0.870	0.056
✓	✗	✗	✗	✓	✓	0.0883	147.852	1.088	0.051
✓	✓	✗	✗	✗	✗	0.0602	148.066	1.302	0.045

f) Global model =

glm(Abandon~SpMass+Distance+FlockSize+WindChill+WinterDay+QuarryUK,family=binomial,
data=wildfowl)

Variables in top five candidate models						adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	QuarryUK	SpMass	WindChill	WinterDay				
✗	✓	✗	✗	✓	✓	0.0267	122.299	0	0.239
✗	✓	✗	✗	✗	✓	0.0154	124.140	1.841	0.095
✓	✓	✗	✗	✓	✓	0.0279	124.175	1.876	0.093
✗	✓	✓	✗	✓	✓	0.0271	124.253	1.954	0.090
✗	✓	✗	✓	✓	✓	0.0266	124.486	2.187	0.080

Appendix 8. Model selection tables – top five AIC_c-ranked models in each single-species candidate set for curlew, oystercatcher and redshank.

Curlew:

a) Global model = glm(AnyResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✓	✗	✗	✗	0.4393	44.461	0	0.232
✓	✓	✗	✗	0.4839	44.595	0.134	0.217
✓	✗	✗	✓	0.4680	45.380	0.919	0.147
✓	✗	✓	✓	0.5010	46.152	1.690	0.100
✓	✓	✓	✗	0.4962	46.393	1.932	0.088

b) Global model = glm(FlightResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✓	✗	✓	✓	0.4331	52.192	0	0.294
✗	✗	✓	✓	0.3723	52.660	0.468	0.232
✗	✗	✗	✓	0.2950	53.781	1.589	0.133
✓	✓	✓	✓	0.4391	54.434	2.242	0.096
✓	✗	✗	✓	0.3242	54.818	2.626	0.079

c) Global model = glm(Abandon~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✗	✗	✓	0.1424	49.817	0	0.271
✗	✗	✓	✓	0.1531	51.760	1.943	0.103
✗	✓	✗	✓	0.1475	51.947	2.130	0.093
✓	✗	✗	✓	0.1467	51.973	2.155	0.092
✗	✗	✗	✗	0.0000	52.146	2.329	0.085

Oystercatcher:

d) Global model = glm(AnyResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✗	✓	✓	0.1223	77.601	0	0.209
✗	✗	✗	✗	0.0000	78.560	0.959	0.129
✗	✗	✓	✗	0.0362	79.176	1.576	0.095
✓	✗	✓	✓	0.1376	79.216	1.615	0.093
✓	✗	✗	✗	0.0284	79.514	1.913	0.080

e) Global model = glm(FlightResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✗	✓	✓	0.1173	77.827	0	0.156
✗	✗	✓	✗	0.0511	78.538	0.711	0.110
✗	✗	✗	✗	0.0000	78.560	0.733	0.108
✓	✗	✓	✗	0.1007	78.580	0.753	0.107
✓	✗	✓	✓	0.1459	78.829	1.002	0.095

f) Global model = glm(Abandon~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✓	✓	✓	0.2884	61.499	0	0.236
✗	✓	✓	✗	0.2298	61.919	0.420	0.191
✗	✓	✗	✗	0.1741	62.176	0.677	0.168
✓	✓	✓	✓	0.3013	63.294	1.796	0.096
✓	✓	✗	✗	0.1842	63.967	2.469	0.069

Redshank:

g) Global model = glm(AnyResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✓	✗	✗	✗	0.3679	18.443	0	0.166
✗	✗	✗	✓	0.3357	19.021	0.578	0.125
✓	✗	✗	✓	0.4580	19.197	0.754	0.114
✓	✗	✓	✗	0.4448	19.449	1.006	0.101
✗	✗	✓	✗	0.2894	19.833	1.391	0.083

h) Global model = glm(FlightResponse~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✓	✗	✓	0.2678	42.907	0	0.191
✗	✓	✓	✗	0.2560	43.258	0.351	0.160
✗	✓	✓	✓	0.2970	44.620	1.713	0.081
✗	✓	✗	✗	0.1200	44.634	1.727	0.081
✗	✗	✓	✗	0.1042	45.048	2.141	0.066

i) Global model = glm(Abandon~Distance+WindChill+WinterDay+FlockSize, family=binomial)

Variables in top five candidate models				adjR ²	AIC _c	Δ _i	ω _i
Distance	FlockSize	WindChill	WinterDay				
✗	✗	✗	✓	0.1424	49.817	0	0.271
✗	✗	✓	✓	0.1531	51.760	1.943	0.103
✗	✓	✗	✓	0.1475	51.947	2.130	0.093
✓	✗	✗	✓	0.1467	51.973	2.155	0.092
✗	✗	✗	✗	0.0000	52.146	2.329	0.085

Appendix 9. NetLogo model code © C Collop

```
;; Model settings
; location of origin Corner, bottom left
; world wrapping OFF
; patch size 2
; font size 10
; world dimensions:
; A: max-pxcor=559, max-pycor=60
; B: 279, 100
; C: 139, 180
; D: 1119, 40

globals [ time daylength daylight? visitors-night tideheight temp tide-state speed-mud speed-path worm-mass max-assim
roost-distance last-x last-y fid fltime flight-speed latency propSpring total-visitors disturbers]
; other globals on interface [ air-temp size-of-patch mean-tide-height spring-range neap-range spring-neap-cycle
winter-day initial-birds access-per-km distance-to-roost
; visitors-per-hr propInter visit-duration initial-worm-density ]

; time = hour of the day (time hh:mm also reported on interface)
; daylength = hours of daylight (see set-daylight)
; daylight? = yes/no (see set-daylight)
; visitors-night = number of humans per hour during evening darkness (between sunset and 10pm)
; tideheight (m)
; temp = temperature fixed for whole simulation (based on same equation as used in Morph)
; tide-state = rising or falling
; speed-mud = walking speed of humans on intertidal habitat (km/hr)
; speed-path = walking speed of humans on path (km/hr)
; worm-mass = gAFDM per worm (I've chosen to use worms 45-60mm => 0.01538895 gAFDM per worm as used in Morph)
; max-assim = daily maximum energy assimilation (based on gut constraints)  $0.75 * 1713 * \text{Mass}(\text{kg})^{0.72}$  kJ/day (Kirkwood
1983 in Lindstrom 1991) 0.75 = assimilation efficiency when feeding on worms
; roost-distance = distance (km) birds must fly to get from roost to intertidal habitat
; last-x = previous x co-ordinate of a bird (used in some distance calculations)
; last-y = previous y co-ordinate of a bird (used in some distance calculations)
; FID = species-specific flight initiation distance
; fltime = species-specific mean time spent in flight in response to approaching pedestrian
```

```

; latency = species-specific mean time spent latent after flight in response to approaching pedestrian
; flight-speed = flight speed of a bird (using allometric relationship in Alerstam et al 2007 => 12.46 m/s for
redshank)
; propSpring = used to calculate tide height based on position in relation to the spring-neap cycle (see set-
tideheight)
; total-visitors = total number of humans that arrived on site
; disturbers = number of humans that have resulted in a disturbance of one or more birds
; size-of-patch = scale of world e.g. one patch is 25m wide
; mean-tide-height = what it says!
; spring-range/neap-range = difference in tideheight between high and low tide on spring and neap tides
; spring-neap-cycle = chooser to determine the tidal curve for the simulation
; winter-day = chooser to determine winter-day (winter day 1 = 1st September) - this determines air-temp and daylength
; initial-birds = number of birds included in simulation
; access-per-km = number of access points per km of shoreline from which humans can arrive
; visitors-per-hour = number of humans that arrive per hour between 6am and sunset (based on my daylight
observations)
; propInter = proportion of visitors that leave the path and walk on the intertidal habitat
; visit-duration = length of time (in minutes) that each visitor stays
; initial-worm-density = number of worms per m2 that all intertidal patches have at the start of the simulation

breed [ birds bird ]

breed [ humans human ]

birds-own [ Species Target ProgressNet MetRate LCT ThermoCosts ShoreLevelPref ForagingEff NightEff Eff Dom Intake
FreeTime CostOfFlight
LastPatch DisturbCost TotalResponses MaxDist]
; Species = bird species being simulated (I have chosen to use redshank feeding on worms of 45-60mm)
; Target = intake (kJ assimilated) that birds need to achieve in order to balance their energy budget (i.e. based on
metabolic rate and thermoregulation costs)
; ProgressNet = total energy assimilated minus travel costs and costs of disturbance (kJ)
; MetRate = metabolic rate of a bird (2.1 * BMR) same as used in Morph (kJ/day)
; LCT = lower critical temperature of a bird (same as used in Morph)
; ThermoCosts = cost of thermoregulation kJ per day per degree below LCT (same as in Morph)
; ShoreLevelPref = randomly selected y coordinate of the shore level at which a bird "wants" to forage
; ForagingEff = daytime foraging efficiency of birds follows random normal distribution like in Morph

```

```

; NightEff = species-specific relative efficiency when feeding at night (same as used in Morph)
; Eff = bird's efficiency in the current time step depending on whether day or night
; Dom = relative dominance of bird follows uniform distribution (used to calculate susceptibility to interference like
in Morph)
; FreeTime = seconds of time available for travel between patches/responding to disturbance/foraging
; CostOfFlight = energetic cost of flight kJ/s
; LastPatch = the previous location of a bird (used to calculate distance moved)
; DisturbCost = the additional energetic costs (kJ) due to responding to disturbance in a time step
; TotalResponses = total number of disturbance response flights made by a bird in the course of a simulation
; MaxDist = maximum distance (proportion of a patch) a bird can fly in one timestep

```

```

patches-own [ area habitat patch-type exposure-height available? access? worm-density IFIR attract ]
; area = m2 (size-of-patch ^ 2)
; habitat = roost, path, intertidal, or water
; patch-type = intertidal or not
; exposure-height = when tideheight is equal to or below exposure height, the patch becomes exposed
; available? = yes/no i.e. whether birds can use a patch (roost patches are always available; intertidal only when
exposed)
; access? = yes/no whether a path patch can "create" humans
; worm-density = number of worms per m2
; IFIR = interference-free intake rate that a bird could achieve if it used the patch
; attract = measure of attractiveness to birds based on IFIR and density of birds

```

```

humans-own [ route speed dist remaining home-patch disturber]

```

```

; route = whether the human stays on the path or goes onto the intertidal habitat
; speed = walking speed according to route chosen (converted to metres per minute)
; dist = distance (proportion of a patch) that a human can cover in a time step => based on walking speed
; remaining = number of time steps remaining until human leaves (based on visit-duration)
; home-patch = location of path patch where human started - they return back to this patch before leaving

```

```

to setup
  file-close-all
  clear-all
  reset-ticks

```

```

set-daylight
set air-temp precision (17.65 + (-0.1687 * winter-day) + (0.000579 * winter-day * winter-day)) 2
set temp air-temp
set-tideheight

set FID 59.09 ; metres
set fltime 13.89 ; seconds of flight per disturbance
set latency 12.96 ; latent seconds after flight before feeding
set flight-speed 12.46 ; m/s (Alerstam et al 2007)

set speed-mud 2.5 ; km/hr
set speed-path 4 ; km/hr
set roost-distance distance-to-roost ; km

set worm-mass 0.01538895 ;gAFDM per worm
create-patches
ask patches [ set-available-patches ]

create-foragers

let evening-dark (22 - (12 + (daylength / 2))) ; hrs of darkness between sunset and 10pm
set visitors-night (((visitors-per-hr * daylength) / 0.94) * 0.06) / evening-dark ; number of humans per hour during
evening darkness

set max-assim 0.75 * 1713 * ((153.3 / 1000) ^ 0.72) ; kJ/day (using body mass 153.3g)

end

to set-daylight
set daylength (16.5 + 8) / 2 + ((16.5 - 8) / 2) * cos(2 * pi * (winter-day + 70) / 365 * 57.2957795) ; day length
oscillates between 16.5hrs on the longest day (21 June)
; and 8hrs on the shortest day (21 Dec). 1 Sep is 71 days after 21 June.
ifelse (time >= (12 - (daylength / 2))) and (time <= (12 + (daylength / 2))) ; daylight hours are split equally
either side of midday.
[ set daylight? "yes" ]

```

```

[ set daylight? "no" ]

end

to set-tideheight

  let propHigh 0.5 * (cos(2 * pi * 2 * (ticks) / 60 / 24 * 57.2957795) + 1) ; the second "2" makes two high-low
  cycles per day. Multiply by 57.2... for radians to degrees
  ; conversion. (ticks) / 60 / 24 = time step (in minutes) as a proportion of the daily cycle

  if spring-neap-cycle = "spring" [ set propSpring 0.5 * (cos (2 * pi * (ticks) / 60 / 24 / 14 * 57.2957795) + 1) ] ;
  (ticks) / 60 / 24 / 14 = time step (in minutes) as a proportion of the 14-day spring-neap cycle. Multiply by 57.2...
  for radians to degrees conversion.
  if spring-neap-cycle = "neap" [ set propSpring 0.5 * (cos (2 * pi * (ticks + 10080) / 60 / 24 / 14 * 57.2957795) +
  1) ]

  if spring-neap-cycle = "intermediate" [ set propSpring 0.5 * (cos (2 * pi * (ticks + 4320) / 60 / 24 / 14 *
  57.2957795) + 1) ]

  let dayRange neap-range + propSpring * (spring-range - neap-range)
  set tideheight mean-tide-height + (propHigh - 0.5) * dayRange

  ifelse ticks < 360 ;or (ticks > 720 and ticks <= 1080)
  [ set tide-state "falling" ]
  [ ifelse ticks >= 1080
  [ set tide-state "rising" ]
  [ ifelse ticks < 720
  [ set tide-state "rising" ]
  [ set tide-state "falling" ]
  ]
  ]

end

```

```

to create-patches ; patches set their exposure height according to their perpendicular distance from the shore.
; Set exposure height at top of shore so that everything is covered for two hours either side of high tide on spring
tides
; use different AreaScenarios according to dimension of the world
ask patches
[ if AreaScenario = "A" [ set exposure-height precision (0.45 + 0.0349 * (pycor - 10)) 2 ] ; 0.45 = low water
springs. tide height 2hrs after high tide = 1.81. (1.81-0.45)/39 = 0.0349
if AreaScenario = "B" [ set exposure-height precision (0.45 + 0.017 * (pycor - 10)) 2 ] ; (1.81-0.45)/79 = 0.017
if AreaScenario = "C" [ set exposure-height precision (0.45 + 0.00855 * (pycor - 10)) 2 ] ; (1.81-0.45)/159 =
0.00855
if AreaScenario = "D" [ set exposure-height precision (0.45 + 0.0716 * (pycor - 10)) 2 ] ; (1.81-0.45)/19 = 0.0716
set area size-of-patch ^ 2 ; sq metres
]

if AreaScenario = "A"
[ ask patches with [pycor = 50] [set pcolor 5 set habitat "path"] ; path at the top of the shore
ask patches with [pycor > 50] [set pcolor green set habitat "roost"] ; roost is effectively "far away" from the
path and shore
ask patches with [pycor < 50 and pycor > 9] [ set worm-density initial-worm-density set patch-type "intertidal" ]
; number of worms per m2
]

if AreaScenario = "B"
[ ask patches with [pycor = 90] [set pcolor 5 set habitat "path"] ; path at the top of the shore
ask patches with [pycor > 90] [set pcolor green set habitat "roost"] ; roost is effectively "far away" from the
path and shore
ask patches with [pycor < 90 and pycor > 9] [ set worm-density initial-worm-density set patch-type "intertidal" ]
; number of worms per m2
]

if AreaScenario = "C"
[ ask patches with [pycor = 170] [set pcolor 5 set habitat "path"] ; path at the top of the shore
ask patches with [pycor > 170] [set pcolor green set habitat "roost"] ; roost is effectively "far away" from the
path and shore
ask patches with [pycor < 170 and pycor > 9] [ set worm-density initial-worm-density set patch-type "intertidal" ]
; number of worms per m2
]

```

```

]
if AreaScenario = "D"
[ ask patches with [pycor = 30] [set pcolor 5 set habitat "path"] ; path at the top of the shore
  ask patches with [pycor > 30] [set pcolor green set habitat "roost"] ; roost is effectively "far away" from the
path and shore
  ask patches with [pycor < 30 and pycor > 9] [ set worm-density initial-worm-density set patch-type "intertidal" ]
; number of worms per m2
]

ifelse (((max [pxcor] of patches + 1) * size-of-patch) / 1000) * access-per-km) >= count patches with [habitat =
"path"]
[ ask patches with [habitat = "path"] [ set access? "yes" set pcolor 15 ]
]
[ ask n-of (((max [pxcor] of patches + 1) * size-of-patch) / 1000) * access-per-km) patches with [habitat = "path"]
[ set access? "yes" set pcolor 15 ]
]

ask patches with [patch-type = "intertidal"] [ set-IFIR ]

end

```

to set-available-patches ; Mud patches are available when exposed by the tide. Roost patches are always available. Birds don't land on the path.

; Patches are coloured according to whether it is daylight and whether they are water, mud, path, path with an access point, or roost.

```

ifelse tideheight <= exposure-height
[ set available? "yes" ]
[ set available? "no" ]
if habitat = "roost" [set available? "yes" ifelse daylight? = "yes" [set pcolor green] [set pcolor 52]]
if habitat = "path" [set available? "no"]
if available? = "no" and habitat != "path" [ifelse daylight? = "yes" [set pcolor blue] [set pcolor 101] set
habitat "water" ]
if available? = "yes" and habitat != "roost" [set pcolor scale-color brown exposure-height 0 10 set habitat "mud"]

```

```

end

to create-foragers
  create-birds initial-birds
  [
    set shape "bird side"
    set color white
    set size 5
    move-to one-of patches with [habitat = "roost"] ; at the start of the simulation (midnight) all birds are on the
    roost, randomly distributed across the roost patches.
    set-foraging-eff ; birds vary in their feeding efficiency
    set Species "Redshank"
    set MetRate 233.8623 ; kJ per day
    set NightEff 0.95
    set LCT 18.6
    set ThermoCosts 5.5 ; kJ per degree per day
    set CostOfFlight 1336.356 / 24 / 60 / 60 ; kJ per second (12 times BMR)
    ifelse temp < LCT
    [ set Target MetRate + (ThermoCosts * (LCT - temp)) ]
    [ set Target MetRate ] ; target intake for the 24hr simulation
    set Dom random-float 1 ; randomly assigned relative dominance
    if AreaScenario = "A" [ set ShoreLevelPref 10 + random 40 ]
    if AreaScenario = "B" [ set ShoreLevelPref 10 + random 80 ]
    if AreaScenario = "C" [ set ShoreLevelPref 10 + random 160 ]
    if AreaScenario = "D" [ set ShoreLevelPref 10 + random 20 ]
    set MaxDist (flight-speed * 60) / size-of-patch
    ;pd
  ]
end

to set-time ; the hour of the day
  set time ((ticks + 1) mod 1440) / 60
end

```

```

to go
  if ticks = 0 [ output-type "simulation start time: " output-type substring date-and-time 0 5 output-print substring
date-and-time 13 15 ] ; report simulation start time on interface
  if ticks >= 1440 or count birds = 0 ; at end of simulation report end time, total number of bird responses, mean
number of responses per bird, and % of birds that did not meet their target
  [ output-type "simulation end time: " output-type substring date-and-time 0 5 output-print substring date-and-time
13 15
    output-type "total number of bird responses = " output-print sum [TotalResponses] of birds
    output-type "mean number of responses per bird = " output-print precision (mean [TotalResponses] of birds) 1
    output-type precision (((count birds with [ProgressNet < target]) / initial-birds) * 100) 2 output-print "% of
birds unable to balance energy budget "
    if total-visitors > 0 [ output-type precision (disturbers / total-visitors * 100 ) 1 output-print "% of visitors
caused a disturbance" ]
    ask patches with [patch-type = "intertidal" and worm-density < initial-worm-density] [set pcolor yellow ]
    draw-plots ; show birds' net intake
;   file-open "Results.csv"
;   ask birds [file-write ProgressNet]
;   file-close
    export-world (word "D:/NetLogo/Run2/Graph2D/" behaviorspace-experiment-name "ResultsTest" (behaviorspace-run-
number + 0) ".csv")
    stop ]
  set-time
  set-daylight
  set-tideheight
  ask patches with [patch-type = "intertidal"] [ set-available-patches ]

  if count patches with [access? = "yes"] > 0 [ enter-humans ] ; humans enter and move before birds make foraging
decisions
  move-humans

  ask birds [choose-patch-and-forage] ; scheduling: each bird moves, checks for humans, reponds and then feeds if it
has time, and then the next does the same etc.

  tick

end

```

to-report hh:mm ; displays time using 24hr clock

```

let mm ticks mod 60
let hh (floor (ticks / 60)) mod 24
ifelse hh < 10
[ifelse mm < 10
 [report (word 0 (hh) ":0" (mm))]
 [report (word 0 (hh) ":" (mm))]]
[ifelse mm < 10
 [report (word (hh) ":0" (mm))]
 [report (word (hh) ":" (mm))]]
end

```

to set-foraging-eff ; birds vary in their feeding efficiency compared to eachother, following a normal distribution with mean = 1 and s.d. = 0.125

```

set ForagingEff random-normal 1 0.125
while [ ForagingEff < 0 or ForagingEff > 20 ] ; ensures no negative numbers or excessively high foraging
efficiencies
[ set ForagingEff random-normal 1 0.125 ]

```

end

to enter-humans

let new-visitors 0 ; humans only arrive between 6am and 10pm; and at a lower frequency (6% of total daily visits) during evening darkness compared to during the day (same as in Morph)

```

ifelse (time >= 6 and time < 12) or daylight? = "yes"
[ set new-visitors visitors-per-hr ]
[ if time > 12 and time < 22 [ set new-visitors visitors-night ]
]

```

```

ifelse (new-visitors / 60) < 1
[ if random-float 1 < (new-visitors / 60) ; if number of visitors per minute is less than one, use a random number
to determine whether a visitor arrives in the current time step
[ ask one-of patches with [access? = "yes"]

```

```

    [ sprout-humans 1
      [ set total-visitors total-visitors + 1
        set remaining visit-duration
        set shape "person"
        set size 5
        set home-patch patch-here
        ifelse random-float 1 < propInter
          [ set route "intertidal"
            set heading 91 + random 179 ; humans that are going to walk on the intertidal select a random heading
            away from the path
          ]
          [ set route "path"
            set heading one-of (list 90 270) ; humans on the path set their heading either "E" or "W"
          ]
        set-speed
        if [pxcor] of patch-here = 0 [set heading 90]
        if [pxcor] of patch-here = (max [pxcor] of patches with [habitat = "path"]) [set heading 270]
      ]
    ]
  ]
]
[ repeat (new-visitors / 60)
  [ ask one-of patches with [access? = "yes"]
    [ sprout-humans 1
      [ set total-visitors total-visitors + 1
        set remaining visit-duration
        set shape "person"
        set size 5
        set home-patch patch-here
        ifelse random-float 1 < propInter
          [ set route "intertidal"
            set heading 135 + random 91
          ]
          [ set route "path"
            set heading one-of (list 90 270)
          ]
        ]
    ]
  ]
]

```

```

        set-speed
        if [pxcor] of patch-here = 0 [set heading 90]
        if [pxcor] of patch-here = (max [pxcor] of patches with [habitat = "path"]) [set heading 270]
    ]
]
]
if random-float 1 < ((new-visitors / 60) mod 1) ; accounts for the fact that the above code does not allow for
fractions of visitors per time step
[ ask one-of patches with [access? = "yes"]
  [ sprout-humans 1
    [ set total-visitors total-visitors + 1
      set remaining visit-duration
      set shape "person"
      set size 5
      set home-patch patch-here
      ifelse random-float 1 < propInter
        [ set route "intertidal"
          set heading 135 + random 91
        ]
        [ set route "path"
          set heading one-of (list 90 270)
        ]
      set-speed
      if [pxcor] of patch-here = 0 [set heading 90]
      if [pxcor] of patch-here = (max [pxcor] of patches with [habitat = "path"]) [set heading 270]
    ]
  ]
]
]
end

to move-humans
  ask humans

```

```

[ if remaining < 1 and patch-here = home-patch ; when humans have been present for the total visit duration and they
get back to their starting point, they leave
  [ if disturber = "yes" [ set disturbers disturbers + 1 ]
    die
  ]
  ifelse route = "path"
  [ ifelse (dist * (remaining - 1)) > distance home-patch ; if humans still have time to get back 'home' the keep
walking away from home
    [ ifelse can-move? dist
      [ fd dist ]
      [ set heading (heading + 180) ; when humans get to the end of the path, they turn around and go back
        fd dist
      ]
    ]
  ]
  [ ifelse distance home-patch <= dist ; humans walk towards home so that they do not stay longer than visit-
duration
    [ move-to home-patch ]
    [ face home-patch fd dist ]
  ]
]
[ if [habitat] of patch-here = "water" [ face home-patch fd dist ] ; humans that have reached the water's edge
head for home when the tide starts to rise
  ifelse can-move? dist and [habitat] of patch-ahead dist != "water" and (dist * (remaining - 1)) > distance home-
patch
    [ fd dist ]
    [ if (dist * (remaining - 1)) <= distance home-patch
      [ ifelse distance home-patch <= dist
        [ move-to home-patch ]
        [ face home-patch fd dist ]
      ]
    ]
    if patch-ahead dist = nobody
    [ ifelse xcor > (((max [pxcor] of patches + 1) / 2) - 1)
      [ set heading 180 + random 91 ] ; when humans reach the water, they walk parallel with it
      [ set heading 180 - random 91 ]
    ]
  ]
  if [habitat] of patch-ahead dist = "water"

```

```

    [ ifelse tide-state = "rising"
      [ face home-patch fd dist ]
      [ set heading one-of (list 90 270) ]
    ]
  ]
]
set remaining remaining - 1
if [habitat] of patch-here = "roost" [setxy xcor ([pycor] of one-of patches with [habitat = "path"]) face home-
patch] ; if humans overshoot the path and end up on the roost

; they reposition on path.
]

end

```

```

to set-speed ; walking speed (metres per minute) depends on whether walking on the path or on mud
  if route = "path" [ set speed speed-path * 1000 / 60]
  if route = "intertidal" [ set speed speed-mud * 1000 / 60]
  set dist speed / size-of-patch ; distance (proportion of patch) that a human can travel in one time step
end

```

```

to set-IFIR ; kJ per timestep - same calculation as in Morph
  ifelse patch-type = "intertidal"
  [ set IFIR precision (22 * worm-mass * (0.06 * (e ^ (-1.434063 + 0.36542 * ln (1.05 * 1000 * worm-mass)))) / (worm-
mass + (0.761 / worm-density)))) 5 ] ; (based on 22 kJ/gAFDM)
  [ set IFIR 0 ]
end

```

```

to choose-patch-and-forage
  ;if ProgressNet >= max-assim [ show "full" ]
  set color white

```

```

set FreeTime 60
set Intake 0
ifelse daylight? = "no"
[ set Eff ForagingEff * NightEff ]
[ set Eff ForagingEff ]
set LastPatch patch-here
set last-x xcor
set last-y ycor
let max-dist MaxDist

ifelse [habitat] of patch-here = "roost" ; if birds are on the roost and the tide is rising, they stay on the roost
[ ifelse tide-state = "falling"
  [ let available-patches patches with [ habitat = "mud" ]
    ifelse count available-patches > 0 and ProgressNet < max-assim
      [ move-to patch xcor ([pycor] of one-of patches with [habitat = "path"])
        let best-patch max-one-of available-patches [attractiveness-for myself] ; birds on the roost leave when the
first mud patches become available
        ; and move to the patch where they can maximise intake.
        move-to best-patch

        roost-travel ; account for the flight costs of travelling between the roost and intertidal habitat
; (assumes birds have at least enough time to travel between roost and intertidal twice during high tide)

        check-humans

        eat-worms

        account-for-costs

      ]
    [ account-for-costs ]
  ]
[ account-for-costs ]
]

```

```

[ let available-patches patches with [ habitat = "mud" and distancexy last-x last-y <= max-dist ] ; if already on
the mud, birds only move if covered by water or there is a better patch than the current one (based on predicted
intake rate and travel costs)
  ifelse count available-patches > 0
  [ let preferred-y ShoreLevelPref
    let favourites patches with [pycor <= preferred-y]
    ifelse count favourites with [habitat = "mud" and distancexy last-x last-y <= max-dist] > 0
    [ set favourites favourites with [habitat = "mud" and distancexy last-x last-y <= max-dist]
      let best-patch max-one-of favourites [attractiveness-for myself]
      ifelse member? patch-here favourites
      [ set-current-patch-attract ; assess whether the current patch is the best place to be
        ifelse [attract] of patch-here >= [attractiveness-for myself] of best-patch
          [ check-humans

            eat-worms

            account-for-costs
          ]
          [ move-to best-patch

            set-travel-costs

            check-humans

            eat-worms

            account-for-costs
          ]
        ]
      [ move-to best-patch

        set-travel-costs

        check-humans

        eat-worms
      ]
    ]
  ]

```

```

    account-for-costs
  ]
]
[ ifelse count favourites with [habitat = "mud"] > 0
  [ face min-one-of favourites [distancexy last-x last-y]
    fd MaxDist

    set-travel-costs
  ]
  [ ifelse tide-state = "falling"
    [ face patch last-x ShoreLevelPref
      ;face min-one-of favourites [distancexy last-x last-y]
      ifelse can-move? MaxDist and [habitat] of (patch-ahead MaxDist) != "water"
      [ fd MaxDist

        set-travel-costs
      ]
      [ let favourite patch last-x ShoreLevelPref
        ;let favourite min-one-of favourites [distancexy last-x last-y]
        let chosen-patch min-one-of patches with [habitat = "mud"] [distance favourite]
        ifelse chosen-patch = patch-here
        [ check-humans

          eat-worms

          account-for-costs
        ]
        [ move-to chosen-patch

          set-travel-costs

          check-humans

          eat-worms
        ]
      ]
    ]
  ]
]

```

```

        account-for-costs
      ]
    ]
  [ set-current-patch-attract ; assess whether the current patch is the best place to be
    let best-patch max-one-of available-patches [attractiveness-for myself]
    ifelse [attract] of patch-here < [attractiveness-for myself] of best-patch
      [ move-to best-patch
        set-travel-costs

        check-humans

        eat-worms

        account-for-costs
      ]
      [ check-humans

        eat-worms

        account-for-costs
      ]
    ]
  ]
]
[ move-to one-of patches with [habitat = "roost" and pxcor = last-x] ; birds return to roost when there are no
intertidal patches available
  roost-travel
  account-for-costs
]
end

```

to set-current-patch-attract ; use same calculation as in Morph to determine susceptibility to interference based on number of competitors present redshank feeding on worms only have to consider weak-klepSTI

```
let birds-efficiency Eff
let compareDom dom
let rankDom count (birds-here with [dom < compareDom]) + 1
let STI 1
ifelse (count birds-here / area) > 0.0319
  [ set STI (((count birds-here) / area) / 0.01) ^ (-0.08 + 0.08 * (rankDom / count birds-here)) ]
  [ set STI ((0.0319 / 0.01) ^ (-0.08 + 0.08 * (rankDom / count birds-here)))]

ifelse [habitat] of patch-here = "mud"
[ ask patch-here [ set attract (birds-efficiency * STI * IFIR) ] ]
[ ask patch-here [ set attract 0 ] ]
```

end

to account-for-costs ; adjust net progress by subtracting energetic costs of flight in response to disturbance

```
set ProgressNet (ProgressNet - DisturbCost)
set DisturbCost 0
```

end

to-report attractiveness-for [a-bird] ; attractiveness depends on quality (density of worms), the number of other birds already there, and the travel costs (time and energy) of getting there

```
let birds-efficiency [Eff] of a-bird
let flight-cost [CostOfFlight] of a-bird ; mgAFDM intake required per second of flight
let distnce distncexy ([xcor] of a-bird) ([ycor] of a-bird)
let compareDom [dom] of a-bird
let rankDom count (birds-here with [dom < compareDom]) + 1
let competitors (count birds-here)
let STI 1
```

```
ifelse ((competitors + 1) / area) > 0.0319
```

```

[ set STI (((competitors + 1) / area) / 0.01) ^ (-0.08 + 0.08 * (rankDom / (competitors + 1))) ]
[ set STI ((0.0319 / 0.01) ^ (-0.08 + 0.08 * (rankDom / (competitors + 1))))]

let attractiveness birds-efficiency * STI * IFIR * (1 - ((distnce / flight-speed) / 60)) - ((distnce / flight-speed)
* flight-cost) ; adjust IFIR by foraging efficiency, interference, time lost flying to patch and energy costs of
flying to patch

report attractiveness

end

to roost-travel ; energetic cost (kJ) of flying between roost and intertidal area

let TravelTime ((distance-to-roost * 1000) / flight-speed)
ifelse [habitat] of patch-here = "mud"
[ set TravelTime TravelTime + (distance patch ([pxcor] of patch-here) ([pycor] of one-of patches with [habitat =
"path"])) / flight-speed ]
[ set last-x [pxcor] of LastPatch
set last-y [pycor] of LastPatch
set TravelTime TravelTime + ([ distance patch last-x ([pycor] of one-of patches with [habitat = "path"]) ] of
patch last-x last-y) / flight-speed
]

set ProgressNet ProgressNet - (TravelTime * CostOfFlight)

end

to set-travel-costs ; energetic cost (kJ) of travelling between patches when foraging
if patch-here != LastPatch
[ let TravelTime (distancexy last-x last-y) / flight-speed
let TravelCost TravelTime * CostOfFlight
set ProgressNet ProgressNet - TravelCost

set FreeTime FreeTime - TravelTime

```

```
]
```

```
end
```

```
to check-humans ; check for disturbance before foraging
```

```
  if FreeTime > 0
```

```
    [ if [habitat] of patch-here != "roost" and count humans in-radius (FID / size-of-patch) > 0 [ flee ]] ; birds  
    check for human disturbers that are closer than their FID.
```

```
end
```

```
to flee
```

```
  set last-x xcor
```

```
  set last-y ycor
```

```
  let free FreeTime
```

```
  set color red ; change colour to show that birds have moved to a non-preferred patch due to disturbance.
```

```
  ;pen-down ; show where birds have fled from
```

```
  let the-disturber min-one-of humans [distance myself] ; if there are one or more humans present within the bird's  
  FID, it flees from the closest human and moves as far as it can from the disturber within the usual flight time for  
  that species, to a 'safe' patch.
```

```
  ask the-disturber [set disturber "yes"]
```

```
  let available-patches patches with [habitat = "mud" and distanceexy last-x last-y <= fltime * flight-speed / size-of-  
  patch and count humans in-radius (fid / size-of-patch) = 0]
```

```
  ifelse count available-patches > 0
```

```
  [ move-to max-one-of available-patches [distance the-disturber]
```

```
    set FreeTime FreeTime - fltime - latency
```

```
    set DisturbCost fltime * CostOfFlight
```

```
    set TotalResponses TotalResponses + 1
```

```
    set color yellow
```

```
  ]
```

```
  [ set available-patches patches with [habitat = "mud" and distance myself <= ((free - latency) * flight-speed /  
  size-of-patch) and count humans in-radius (fid / size-of-patch) = 0]
```

```
  ifelse count available-patches > 0 ; if there's nowhere 'safe' available that can be reached within FlightTime,  
  the bird flies to the closes 'safe' patch that can be reached within the time step.
```

```

[ move-to min-one-of available-patches [distance myself]
  let flight-time (distancexy last-x last-y) * size-of-patch / flight-speed
  set FreeTime FreeTime - flight-time - latency
  set DisturbCost flight-time * CostOfFlight
  set TotalResponses TotalResponses + 1
  set color yellow
]
[ ifelse tide-state = "rising" ; if there's nowhere 'safe' that can be reached within the time step and the tide
is rising, the bird returns to the roost
  [ move-to one-of patches with [habitat = "roost" and pxcor = last-x]
    ;show "fled to roost"
    set TotalResponses TotalResponses + 1
    roost-travel ; if nowhere is 'safe', it goes to the roost
    set color yellow
  ]
  [ ;show "out of time" ; if there's nowhere 'safe' that can be reached within the time step and the tide is
falling, the bird flies for the rest of the time step waiting for humans to move away or more mud to become exposed
  set heading one-of (list 90 270)
  ifelse can-move? (free * flight-speed / size-of-patch)
  [ fd (free * flight-speed / size-of-patch)
    set DisturbCost FreeTime * CostOfFlight
    set TotalResponses TotalResponses + 1
    set FreeTime 0
  ]
  [ set heading heading + 180
    fd (free * flight-speed / size-of-patch)
    set DisturbCost FreeTime * CostOfFlight
    set TotalResponses TotalResponses + 1
    set FreeTime 0
  ]
]
]
]
;pen-up

```

end

to eat-worms ; one birds have finished responding to disturbance they use the rest of the time step to feed i.e. calculate their intake and then the patch updates its worm availability and predicted IFIR.

```
if FreeTime > 0 and ProgressNet < max-assim
[ set-current-patch-attract
  set Intake ((FreeTime / 60) * [attract] of patch-here)
  let total-biomass ([worm-density] of patch-here) * ([area] of patch-here) * worm-mass
  let new-worm-density (total-biomass - (Intake / 22)) / worm-mass / [area] of patch-here
  ask patch-here [ set worm-density new-worm-density ] ; updates worms on patch based in bird's intake
  set Intake Intake * 0.75 ; (0.75 = assimilation efficiency when feeding on worms)
]
if Intake > 0
[ set ProgressNet ProgressNet + Intake
  ask patch-here [set-IFIR]
]
```

end

```
to draw-plots ; to show how much energy birds have assimilated
set-current-plot "Histogram - birds' net intake (kJ)"
clear-plot
let min-x floor min [ProgressNet] of birds
let max-x ceiling max [ProgressNet] of birds
set-plot-x-range floor min-x max-x
set-histogram-num-bars 10
histogram [ProgressNet] of birds

set-current-plot "Birds' net intake (kJ)"
clear-plot
foreach sort-on [ProgressNet] birds
```

```
[ ask ?  
  [ set-current-plot-pen "Target"  
    set-plot-x-range 0 count birds  
    plot mean [Target] of birds  
    set-current-plot-pen "95% of target"  
    plot 0.95 * mean [Target] of birds  
    set-current-plot-pen "50% of target"  
    plot 0.5 * mean [Target] of birds  
    set-current-plot-pen "Progress"  
    plot ProgressNet  
  ]  
]
```

end

Appendix 10. Published version of Chapter 2.

Collop, C., Stillman, R. A., Garbutt, A., Yates, M. G., Rispin, E. and Yates, T. (2016). Variability in the area, energy and time costs of responding to disturbance for wintering waders. *Ibis* 158(4):711-725.



Variability in the area, energy and time costs of wintering waders responding to disturbance

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Birds' responses to human disturbance are interesting due to their similarities to anti-predator behaviour, and understanding this behaviour has practical applications for conservation management by informing measures such as buffer zones to protect priority species. To understand better the costs of disturbance and whether it will impact on population size, studies should quantify time-related responses as well as the more commonly reported flight initiation distance (FID). Using waders wintering on an estuarine area, we experimentally disturbed foraging birds on the Wash Embayment, UK, by walking towards them and recording their responses (FID, alert time, time spent in flight, time taken to resume feeding, and total feeding time lost). We present data for 10 species of conservation concern: Curlew *Numenius arquata*, Oystercatcher *Haematopus ostralegus*, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Redshank *Tringa totanus*, Knot *Calidris canutus*, Turnstone *Arenaria interpres*, Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba* and Dunlin *Calidris alpina*. Larger species responded more strongly, response magnitude was greater under milder environmental conditions, and responses varied over both small and large spatial scales. The energetic costs of individual responses, however, were low relative to daily requirements and disturbance events were unlikely to be frequent enough to seriously limit foraging time. We suggest, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period. This is also likely to be the case at other estuarine sites with comparable access levels, visitor patterns, invertebrate food availability and environmental conditions.

Keywords: anti-predator behaviour, flight initiation distance, non-breeding season, shorebirds.

Disturbance can mean, in its broadest sense, any event that leads to a change in behaviour or physiology. This might be for example due to natural events, such as attack by a predator, or anthropogenic disturbance whereby recreation or industry brings humans and birds into close proximity, or indirect disturbance through pollution events or noise impacts. For the purposes of this paper in relation to wintering waders, we use the definition adopted by signatories to the African-Eurasian

Waterbirds Agreement (AEWA 2015), as given by Fox and Madsen (1997): 'Any human-induced activity that constitutes a stimulus (equivalent to a predation threat) sufficient to disrupt normal activities and/or distribution of waterbirds relative to the situation in the absence of that activity'.

As recognized in this definition and according to the widely accepted risk-disturbance hypothesis (Frid & Dill 2002, Beale & Monaghan 2004, Blumstein *et al.* 2005), animals respond to the perceived risk from human disturbances in the same way that they respond to predation risk, i.e. by making trade-offs between avoidance of the risk

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and prioritizing other fitness-maximizing activities such as feeding, mating or parental care (Frid & Dill 2002). Birds' responses to disturbance can therefore be expected to vary between individuals according to a variety of factors related to the perceived risk, the individual's current state and the costs of responding (Gill *et al.* 2001a, Beale & Monaghan 2004).

For day-to-day survival, particularly in winter, birds must optimize their daily energy intake to avoid starvation, while minimizing the risk of predation and disease. Consequently, human activities can impact a bird's energy budget, as responding to disturbance events results in both reduced time and area available for feeding (Gill *et al.* 1996) as well as increased energy expenditure through locomotion (Houston *et al.* 2012) or physiological responses (Ackerman *et al.* 2004). Survival will be reduced as a result if the birds are unable to compensate, for example by moving to other sites and/or increasing feeding time or efficiency (Urff *et al.* 1996, Gill *et al.* 2001a,b, Stillman *et al.* 2001, West *et al.* 2002, Navedo & Masero 2007).

We can investigate birds' responses to disturbance and test the relative importance of potential explanatory factors using experimentally collected field data. Walking towards animals and recording characteristics of their response is a frequently used and effective method for studying disturbance avoidance behaviour, and the most commonly reported measure of response to disturbance is FID – flight initiation distance. Also known as 'escape distance' or 'flush distance', FID measures the distance between the disturbance source and animal when it begins to flee (Bonenfant & Kramer 1996, Blumstein *et al.* 2003). The method has been used for a range of taxa including mammals (Li *et al.* 2011), birds (Van Dongen *et al.* 2015), reptiles (Cooper 2009), fish (Gotanda *et al.* 2009) and amphibians (Rodriguez-Prieto & Fernandez-Juricic 2005). However, FID does not quantify the full time and potential energy costs incurred between the point that an animal detects a disturber and when it returns to its original behaviour and physiological state. Very few researchers have studied or reported these time- or energy-related measures, which is a clear knowledge gap that we seek to address here.

Other studies have identified a variety of potential explanatory factors, including species or body size (Blumstein *et al.* 2003, 2005, Glover *et al.*

2011), flock size (Ikuta & Blumstein 2003, Glover *et al.* 2011), habituation (Urff *et al.* 1996, Ikuta & Blumstein 2003, Lin *et al.* 2012), whether birds are quarry species (Laursen *et al.* 2005), environmental conditions (Stillman & Goss-Custard 2002), type of disturbance (Glover *et al.* 2011), starting distance (Ikuta & Blumstein 2003) and individual condition (Beale & Monaghan 2004). Although this shows that FID has been relatively well studied in waders, much of the research has been carried out in Australia and North America (Blumstein *et al.* 2003, 2005, Ikuta & Blumstein 2003, Glover *et al.* 2011, Koch & Paton 2014), with multi-species studies of the birds of the East Atlantic Flyway being limited to the Dutch and Danish Wadden Sea (Smit & Visser 1993, Laursen *et al.* 2005). By focusing our research on the Wash Embayment in eastern England, we are therefore adding new understanding to the suite of information available on birds' responses to disturbance around the world. Estuarine sites, given their importance for both wildlife and human activities (Ramsar Convention 1971, Millennium Ecosystem Assessment 2005), offer useful study systems for such research. We focus on waders (Charadriiformes) as they comprise a relatively long-lived group of species and many are migratory, so survival during the non-breeding period is an important part of the annual cycle with regards to the long-term persistence and viability of populations (Recher 1966, Saether *et al.* 1996, Piersma & Baker 2000, Piersma *et al.* 2016).

Measuring physiological responses to disturbance was beyond the scope of this study and flushing behaviour is a good indicator of acute physiological changes associated with experimental disturbance (Ackerman *et al.* 2004), so we chose to focus on visible behavioural responses. We use our field data to explore the differences in those responses between species, identify key explanatory variables and test four expectations: (1) all aspects of the visible response to disturbance are positively correlated with each other; (2) FID, time spent in flight and total time lost to disturbance differ between species and increase with body size; (3) the magnitude of response (FID, time spent in flight and total time lost) decreases under harsher weather conditions; and (4) responses (FID, time spent in flight and total time lost) vary from site to site and over time (number of days through the winter season).

METHODS

Study site

The study took place on the Wash (52°56'16"N, 00°17'16"E), a large embayment in eastern England on the North Sea coast with extensive intertidal sand and mudflats. Its conservation importance is recognized through several national and international designations including Site of Special Scientific Interest, Special Area for Conservation, Special Protection Area and Ramsar site status (Doody & Barnet 1987, JNCC 2014). 'In terms of total numbers, the Wash is the key site for wintering waterbirds in the UK' (Austin *et al.* 2014) and supports internationally important wintering populations of all the species that we included in this study: Curlew *Numenius arquata*, Oystercatcher *Haematopus ostralegus*, Bar-tailed Godwit *Limosa lapponica*, Grey Plover *Pluvialis squatarola*, Redshank *Tringa totanus*, Knot *Calidris canutus*, Turnstone *Arenaria interpres*, Ringed Plover *Charadrius hiaticula*, Sanderling *Calidris alba* and Dunlin *Calidris alpina*.

The intertidal flats used for the disturbance experiments (Fig. 1) were selected because of the wide range of wader species that were known to feed at low tide (Goss-Custard *et al.* 1988, Goss-Custard & Yates 1992, Yates *et al.* 2004) and the relatively even distribution of the birds within them. We also selected these areas on the basis of local knowledge of their differing distances from

human populations, ease of access and resulting frequencies of human activities (walkers, dog-walkers, wildfowlers, bait diggers, etc.) on the intertidal area and sea wall. Sites 1–3 can be characterized as areas of low disturbance, with a visitor frequency in the order of around three times per week; whereas the more easily accessible Site 4, on the eastern side of the Wash, had a comparatively high frequency of disturbance on a daily basis (M.G. Yates pers. obs.). Together the areas encompassed all shore levels and both regularly disturbed and undisturbed parts of the Wash and so can be considered to be representative of the whole embayment.

Field experiments

All experiments took place during mid-December to late March of winters 2002/2003, 2003/2004 and 2004/2005 and within the period of minimal tidal movement 2 h either side of low water on spring tides, which on the Wash occur around midday. The intention was to survey all sites in all years, although circumstances dictated that Site 2 was not used in 2002/2003 and Site 3 was used only in 2003/2004. Two observers worked together using binoculars to observe the birds and digital stopwatches were used to time the birds' behavioural responses to the nearest second.

The procedure was to agree mutually on a target bird, which remained unobscured from view for the duration of the observation, and then to

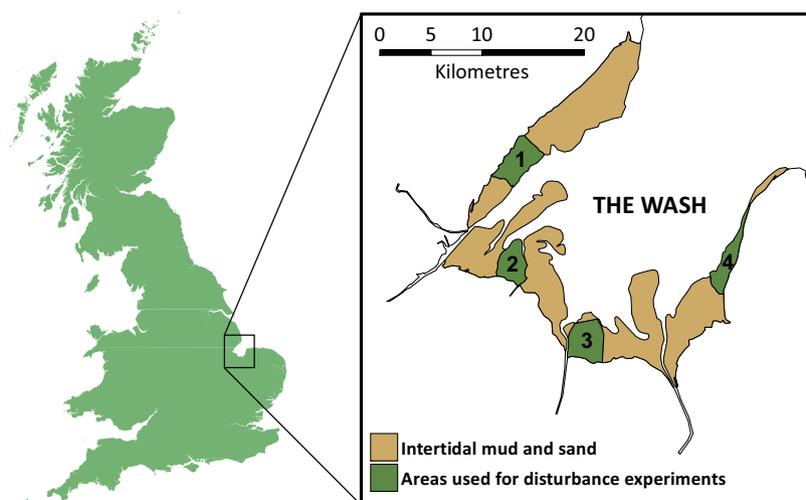


Figure 1. The intertidal areas of the Wash on which disturbance observations were made in winter and early spring of 2002/2003, 2003/2004 and 2004/2005. Site 1 – Wrangle; Site 2 – Maretail; Site 3 – Breast Sand; Site 4 – Stubborn Sand. Reproduced using Ordnance Survey map data © Crown Copyright/database right 2016. An Ordnance Survey/EDINA supplied service.

walk side-by-side directly towards it at a comfortable pace on the soft substrate (approximately 2.5 km/h). The length of time for which the bird was visibly alert was noted and when the bird took flight both observers stopped walking. One observer timed the 'flight time' (the period from taking off to landing) and the 'latency time' (length of time between landing and the first attempt at feeding). Total time lost was calculated by summing alert time, flight time and latency time. The second observer kept their eyes on the place from which the bird had taken off and waited until the other observations had been completed before pacing out the FID. Distances were measured by counting paces which were later converted to metres after calibrating against a known distance in similar walking conditions. Isolated individuals of species that would normally be expected to feed in small groups or flocks were not selected for observation, as their behaviour was considered unrepresentative of the usual behaviour of individuals of that species. Disturbance experiments took place on 38 separate survey days and the number of disturbances during each low tide survey period varied from three to 37 (median = 17.5; median for same species on same day = 3), depending on the number of birds present and how many experiments could be completed in the time available. Care was taken to ensure that the same birds were not disturbed more than once during a single survey, by searching for each target bird in a direction at least 90° from that taken by the previous target bird when it flew off and landed. We also only selected birds that were at least 200 m further away than the anticipated FID. Daily replicates were therefore well spread out in time and space so as to avoid order effects in the data.

In addition to the behavioural response parameters listed, a variety of environmental measurements were recorded relating to factors that may affect birds' responses: air temperature and wind speed (using a hand-held thermometer and anemometer) and the shore level (the part of the shore at which each disturbance took place). This was assigned by dividing each site equally on a three-point scale from 'low' (1), through 'mid' (2) and 'upper' (3) shore, as an indication of the relative proximity to the saltmarsh or sea wall (the most likely source of human disturbance), i.e. upper shore is closest. Shore width (distance between sea wall or marsh and the low tide mark) was approximately 2.5 km at Site 4 and 3–4.5 km

at the other three sites. We also converted the date of each survey to the continuous variable 'winter day': with winter day 1 = 1 August.

As warm bodies lose heat to the surrounding environment at faster rates when exposed to greater wind speeds (Williamson 2003), measurements of air temperature and wind speed from each disturbance experiment were converted to a wind chill equivalent temperature index (WCTI) using the following equation:

$$\text{WCTI} = 13.12 + 0.6215T - 11.37V^{0.16} + 0.3965T \times V^{0.16}$$

where T is the air temperature in °C, and V is the wind speed in km/h (Williamson 2003, Oszcewski & Bluestein 2005). We consider this to be a more appropriate independent variable, in relation to thermoregulation and energy budgets of birds, than records of air temperature alone (Wiersma & Piersma 1994).

Energy and time costs of responding to disturbance

To set birds' time-related responses in the context of daily energy requirements, we calculated energy cost per flight using the following equation from Kvist *et al.* (2001):

$$\text{Cost (kJ)} = \frac{10^{0.39} \times M^{0.35} - 0.95}{1000} \times S$$

and used Nagy *et al.*'s (1999) equation for the birds' thermoneutral requirements:

$$\text{Energy requirement (kJ)} = 10.5 \times M^{0.681}$$

S = time spent in flight in seconds, and M = body mass in grams.

We also estimated the number of disturbances that would result in a 1, 5 and 10% reduction in available feeding time based on our data for total time lost per disturbance (assuming that disturbance events do not overlap). Numbers are presented as a range based on the fact that birds are able to feed throughout the tidal cycle on neap tides but not for 2 h either side of high tide on spring tides (Goss-Custard *et al.* 1977). We used data from Goss-Custard *et al.* (1977) on how much of the available feeding time is used by each species during the winter as an indicator of their likely capacity to compensate for the costs of responding to disturbance.

This is also presented as a range according to the spring–neap tidal cycle and reflecting the reduced number of daylight hours and increased thermoregulatory requirements of smaller species in mid-winter (Dawson & O'Connor 1996).

Model selection and data analysis

We used general linear models in a multi-model inference approach (Symonds & Moussalli 2011, Pap *et al.* 2013) to find variables with high explanatory power for our three different response variables (FID, flight time and total time lost). Preliminary analyses showed no effect of winter year, so the data from all three winters were combined (Table S1). When deciding on the global models to be tested for each response variable, we initially included all biologically plausible two-way interactions in addition to the potential explanatory variables as main effects. Interactions that were found to be non-significant were subsequently excluded from the candidate model set, as recommended by Schielzeth (2010). In situations where the Akaike weight of the best-ranked model (using corrected Akaike information criterion, AIC_c) in the candidate set was considerably higher than that of the next best model, inferences were made based on that model alone (Symonds & Moussalli 2011). However, if this was not the case, model averaging was undertaken using all models with $\Delta_i < 4$ to estimate the relative importance of the predictor variables under consideration. This involves summing the Akaike weights for each model in which that variable appears (Symonds & Moussalli 2011). The larger the sum of the Akaike weights (up to a maximum value of 1), the more important the variable is relative to the others in the global model (Burnham & Anderson 2002). Burnham and Anderson (2002) suggest ranking variables according to their relative importance, so in our analyses, variables with a relative importance value greater than 0.9 were considered to have high explanatory power, those with values between 0.6 and 0.9 were considered moderate, and variables with relative importance less than 0.6 were considered to have low explanatory power.

The candidate models that we tested included 'site' as a fixed factor, with 'shore level', 'wind chill index', 'winter day' and 'species mass' in grams (using Wash-specific data from Johnson 1985) as covariates. We also included two binary variables indicating whether the species was an Oystercatcher or whether it was a plover, as these

species are in different families to the others (Haematopidae and Charadriidae, respectively, as opposed to Scolopacidae) and have different feeding ecologies (Goss-Custard *et al.* 2006). Before carrying out the analyses we centred and standardized the input variables (following Gelman 2008 and Grueber *et al.* 2011) to facilitate interpretation of the relative strength of parameter estimates, particularly where interaction terms were involved. The three response variables were \log_e -transformed, which helped to achieve a better distribution of the model residuals in relation to the assumptions of the statistical tests used.

To assess the relationships between our different response variables we used Spearman's rank correlation tests along with visual inspection of the bivariate scatterplots. We visually inspected diagnostic plots of the residuals for the statistical tests performed, as recommended by Zuur *et al.* (2010). This showed no issues with lack of normality, heterogeneity of variance, collinearity or undue leverage; however, as is often the case with ecological studies, the assumption of independence was not met. Therefore inferences beyond the sample space are made with care, and we will discuss the possibility that this could be an indication that an important covariate was not measured (Zuur *et al.* 2010). Details of preliminary data exploration and statistical tests not reported in the main text can be found in Table S1. Analyses were carried out in R (R Core Team 2015) using functions available in 'arm' (Gelman & Su 2015) to standardize model predictors, and the multi-model inference package 'MuMIn' (Barton 2015) for model selection and averaging; plots were produced using 'ggplot2' (Wickham 2009) and 'PerformanceAnalytics' (Peterson & Carl 2014). Means are presented ± 1 se.

RESULTS

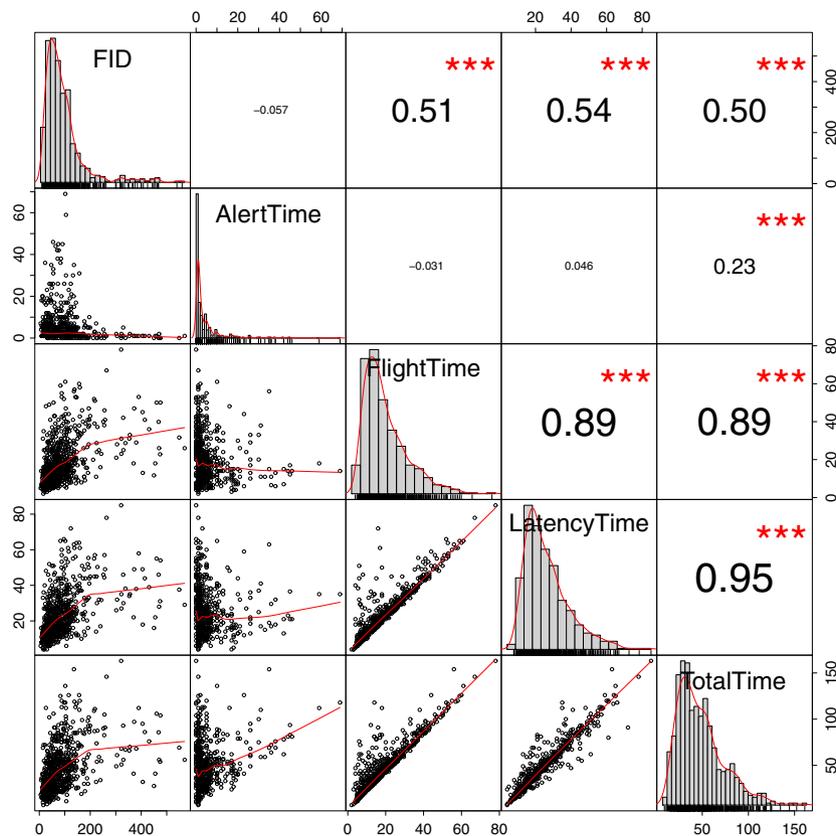
We approached waders a total of 677 times and the birds' responses to the experimental disturbances are summarized in Table 1. During the survey period, the wind chill index ranged from -4.74 °C up to a maximum of 14.27 °C, which is within the range of typical winter temperatures for the area after accounting for wind speed (Met Office 2016).

Following Frid and Dill (2002), we predicted that all measures of response to disturbance would be correlated with each other; Figure 2 shows that

Table 1. Mean, maximum and minimum responses to an approaching pedestrian for each species. Species are presented in order of decreasing body size.

Species	Mass (g)	<i>n</i>	FID (m)				Flight time (s)				Total time lost (s)			
			Mean	se	Min	Max	Mean	se	Min	Max	Mean	se	Min	Max
Curlew (CU)	751	39	340.33	18.23	88	570	34.20	2.35	12	78	75.27	4.8	28	163
Oystercatcher (OC)	500	147	97.28	2.97	30	228	21.17	0.94	6	61	59.86	2.0	21	136
Bar-tailed Godwit (BA)	297	92	84.36	3.93	32	225	20.07	1.20	5	53	47.03	2.4	14	118
Grey Plover (GV)	215	55	132.27	6.81	35	251	22.82	1.65	6	56	58.22	3.4	19	154
Redshank (RK)	143	53	79.83	5.95	28	187	17.44	1.67	4	58	45.16	3.4	11	120
Knot (KN)	134	78	71.83	3.92	20	240	19.58	1.26	6	59	43.71	2.6	15	125
Turnstone (TT)	105	40	31.50	3.00	5	75	12.84	1.49	2	41	32.79	2.8	7	85
Ringed Plover (RP)	64	30	41.07	2.55	20	74	12.35	1.16	4	32	36.15	2.7	11	72
Sanderling (SS)	54	26	25.00	2.65	9	51	10.08	1.27	3	34	26.69	2.6	10	72
Dunlin (DN)	48	117	43.93	2.68	9	194	13.61	0.69	3	41	32.05	1.4	8	85

FID, flight initiation distance; Flight time, time spent in flight; Total time lost, time taken to resume feeding after becoming alert, flying and landing.

**Figure 2.** Correlation matrix for all recorded measures of birds' responses to experimental disturbance. Bivariate scatterplots are presented with a fitted line, and Spearman's rank correlation coefficients, along with stars to indicate significance level. Significance codes: ***0.001, **0.01, *0.05.

this was well supported by our data. Flight time and latency time were strongly positively correlated both with each other and with total time

lost, although alert time was not significantly correlated with flight time or latency time and was only weakly correlated with total time lost.

Individuals that exhibited greater FIDs spent longer in flight and took longer to resume feeding (particularly at FIDs below 200 m) and consequently lost more time in total. However, there was no correlation between FID and alert time.

Mean FID for all species was $89.7 \text{ m} \pm 3.1$ (5–570 m, $n = 677$) but was significantly different between species ($F_{9,667} = 122.1$, $P < 0.001$). There was also a significant difference between species in flight time ($F_{9,667} = 20.9$, $P < 0.001$) and total time lost ($F_{9,677} = 29.5$, $P < 0.001$). Model selection and ranking by AIC_c (Table 2) revealed clear support for the top model, with all potential predictors included, when explaining both FID and time spent in flight (each with a model weight (ω_i) > 0.8). In the case of total time lost, the top model only had a model weight of 0.727, although the cumulative model weight of the top two models (acc ω_i) was 0.993, setting them well apart from the lower ranked models in the candidate set. Standardized and model averaged parameter estimates are shown in Table 3, and with all the coefficients being positive for 'species mass' and 'wind chill', these results support expectations that FID, time spent in flight and total time lost increase with body size (Fig. 3), and that response magnitude decreases under harsher environmental conditions (i.e. lower values of

wind chill equivalent temperature; Fig. 4). There is also support for the expectation that responses vary both between sites and over time; a mixture of positive and negative coefficients indicates differences in birds' responses between sub-sites (Fig. 5) and negative coefficients for the relationships with 'winter day' indicate that response magnitude decreases as the season progresses, although the 95% confidence interval for FID includes zero. In addition to the between-site differences in response we also found within-site differences, with the negative coefficients for 'shore level' indicating a trend for greater response magnitudes when birds were feeding closer to the low water mark.

Inclusion of the two binary variables indicating whether the species was an Oystercatcher or a plover demonstrated additional between-species differences over and above the species mass relationship described. With positive and negative coefficients, respectively, plovers had larger magnitude responses than expected for their size, and Oystercatchers were relatively more tolerant, exhibiting shorter FIDs and spending less time in flight, although any relationship was poorly supported for total time lost (Table 3: relative importance = 0.267, and the 95% confidence interval includes zero).

Table 2. Model selection tables – top five AIC_c -ranked models in each candidate set for (a) FID, (b) flight time and (c) total time lost.

	Candidate models	adj R^2	AIC_c	Δ_i	ω_i	acc ω_i
(a) Global model = log(FID)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay						
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.6656	971.23	0	0.916	0.916
2	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.6608	976.40	5.166	0.069	0.985
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.6568	980.33	9.096	0.010	0.995
4	SpMass+Site+ShoreLevel+WinterDay+IsItOC+IsItPlover	0.6537	982.90	11.669	0.003	0.997
5	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.6533	983.58	12.348	0.002	0.999
(b) Global model = log(FlightTime)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay						
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.2967	1107.02	0	0.892	0.892
2	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.2810	1112.77	5.749	0.050	0.943
3	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover	0.2811	1114.78	7.757	0.018	0.961
4	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.2833	1115.19	8.170	0.015	0.976
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+Site:WinterDay	0.2827	1115.63	8.605	0.012	0.988
(c) Global model = log(Total time lost)~SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay						
1	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover+Site:WinterDay	0.3972	860.50	0	0.727	0.727
2	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItOC+IsItPlover+Site:WinterDay	0.3972	862.52	2.016	0.265	0.993
3	SpMass+Site+ShoreLevel+WindChill+IsItPlover	0.3756	871.25	10.749	0.003	0.996
4	SpMass+Site+ShoreLevel+WindChill+IsItOC+IsItPlover	0.3759	873.08	12.578	0.001	0.998
5	SpMass+Site+ShoreLevel+WindChill+WinterDay+IsItPlover	0.3757	873.27	12.767	0.001	0.999

Δ_i , difference in AIC_c between model and top model; ω_i , Akaike model weight; acc ω_i , cumulative model weight; SpMass, species mass (g); WindChill, wind chill equivalent temperature ($^{\circ}\text{C}$); IsItOC, Oystercatcher vs. other species; IsItPlover, plover vs. other species.

Table 3. Standardized parameter estimates and confidence intervals for eight potential predictors of waders' responses to disturbance. Dependent variables have been natural log-transformed. See Tables 1 and 2 for parameter abbreviations.

	Predictor	Log FID ^a				Log flight time ^a				Log total time lost ^b			
		Estimate	se	95% confidence interval		Estimate	se	95% confidence interval		Estimate	se	95% confidence interval	
				Lower limit	Upper limit			Lower limit	Upper limit			Lower limit	Upper limit
	Intercept	4.430	0.035	4.361	4.499	2.915	0.039	2.839	2.991	3.796	0.032	3.732	3.859
1	SpMass	1.263	0.050	1.165	1.361	0.564	0.055	0.456	0.673	0.512	0.039	0.435	0.589
2	WindChill	0.109	0.041	0.029	0.189	0.163	0.045	0.075	0.252	0.163	0.038	0.089	0.237
3	ShoreLevel	-0.165	0.040	-0.244	-0.086	-0.164	0.044	-0.251	-0.077	-0.154	0.037	-0.226	-0.081
4	Site ^c												
	Site2-Maretail	-0.093	0.210	-0.506	0.320	-0.245	0.232	-0.702	0.211	-0.111	0.194	-0.492	0.270
	Site3-Breast Sand	0.098	0.126	-0.150	0.345	0.208	0.140	-0.066	0.482	0.237	0.116	0.009	0.464
	Site4-Stubborn Sand	-0.361	0.042	-0.445	-0.278	-0.257	0.047	-0.350	-0.165	-0.137	0.039	-0.214	-0.061
5	WinterDay	-0.101	0.073	-0.244	0.042	-0.229	0.080	-0.366	-0.071	-0.222	0.067	-0.354	-0.091
6	IsItOC ^d	-0.533	0.060	-0.651	-0.416	-0.211	0.066	-0.340	-0.081	0.004	0.029	-0.054	0.061
7	IsItPlover ^d	0.487	0.061	0.367	0.606	0.219	0.067	0.087	0.351	0.330	0.056	0.220	0.440
8	Site:WinterDay ^e												
	Site2-Maretail:WinterDay	-0.228	0.333	-0.882	0.426	-0.072	0.368	-0.795	0.652	-0.099	0.308	-0.703	0.504
	Site3-Breast Sand:WinterDay	-	-	-	-	-	-	-	-	0	0	0	0
	Site4-Stubborn Sand:WinterDay	0.298	0.087	0.127	0.469	0.324	0.096	0.135	0.514	0.321	0.080	0.163	0.479

^aBased on top model only. ^bResults of model averaging top two models. ^cReference category is 'Site1-Wrangle Flats'. ^dReference category is 'No'. ^eReference category is 'Site1-Wrangle Flats:WinterDay'.

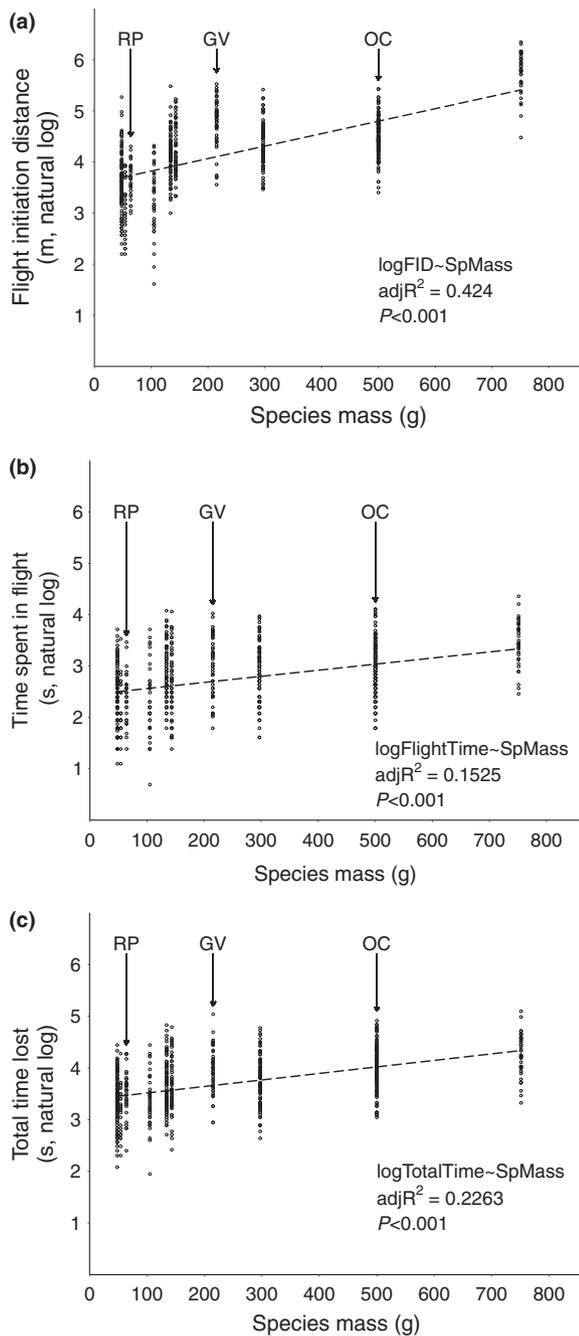


Figure 3. Relationships between species mass and three measures of responses to disturbance: (a) FID, (b) flight time and (c) total time lost. Dependent variables have been log-transformed.

Using our data on mean flight time and mean total time lost, we looked in more detail at the energetic consequences and the lost feeding opportunity costs of responding to disturbance for each species (Table 4). A 5% reduction in birds' daily

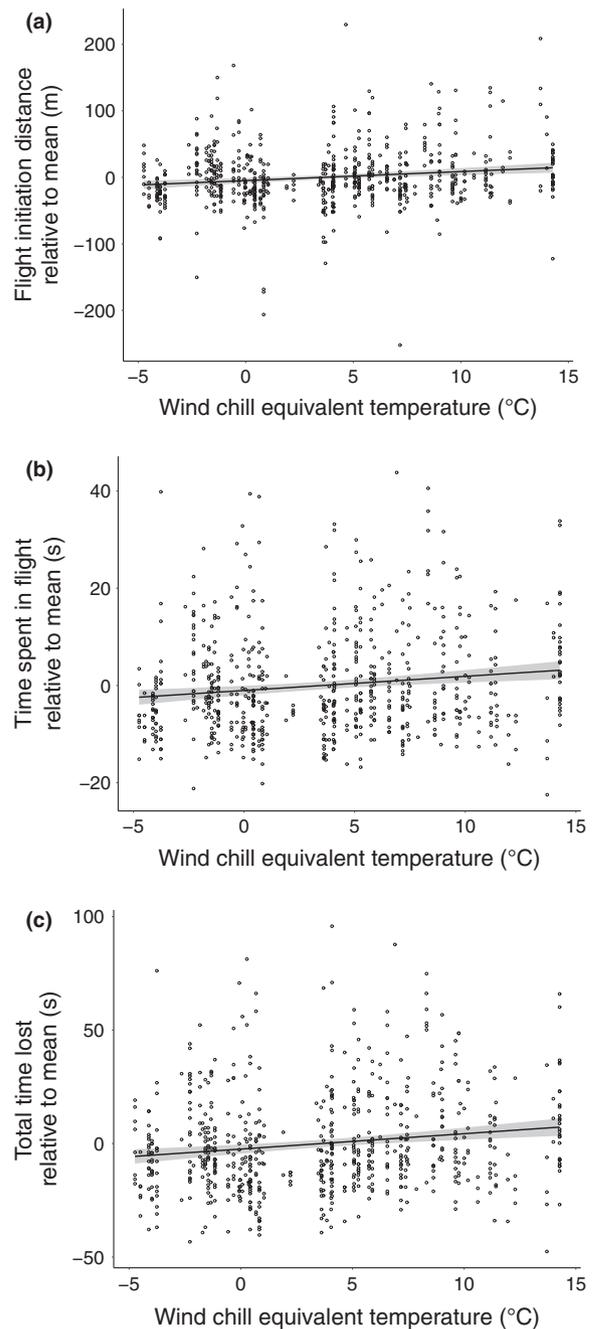


Figure 4. Relationships between wind chill equivalent temperature and three measures of response to disturbance, adjusted relative to the mean response of each species: (a) FID, (b) flight time and (c) total time lost. Regression lines with 95% confidence intervals.

available feeding time would be expected to result from responding to between 38 and 162 separate disturbance events (depending on species and tidal stage). The mean cost per individual flight

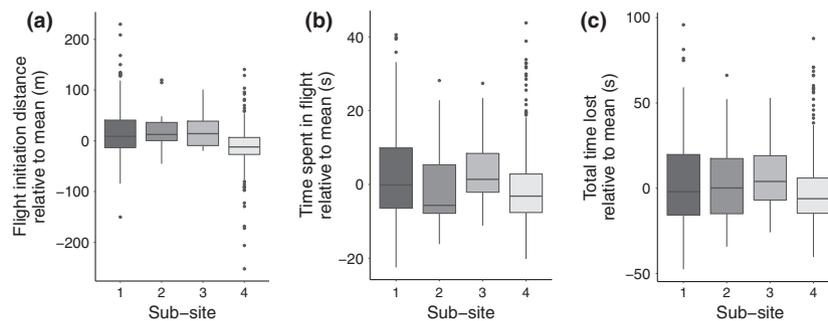


Figure 5. Variation between sub-sites in birds' responses to disturbance, adjusted relative to the mean response of each species: (a) FID, (b) flight time and (c) total time lost. Site codes: 1 = Wrangle; 2 = Maretail; 3 = Breast Sand; 4 = Stubborn Sand.

Table 4. An assessment of the time and energy costs incurred by waders per disturbance response, and the number of disturbances that would be expected to reduce available feeding time by 1, 5 and 10%. See text for a description of the calculations involved. Data reproduced from Goss-Custard *et al.* (1977) give an indication of birds' likely capacity to compensate by extending their feeding time.

Species	Cost per flight response (kJ) ^a	Thermoneutral daily energy requirement (kJ) ^b	Cost per flight as % of daily intake requirement	Number of disturbances that would reduce available feeding time (day and night) by:			% available daylight time spent feeding in winter ^c
				1%	5%	10%	
Curlew	0.820	953.89	0.086	8–11	38–57	77–115	50–80
Oystercatcher	0.437	723.08	0.060	10–14	48–72	96–144	50–70
Bar-tailed Godwit	0.342	507.15	0.068	12–18	61–92	122–184	70–85
Grey Plover	0.345	406.99	0.085	10–15	49–74	99–148	70–80
Redshank	0.227	308.30	0.074	13–19	64–96	128–191	90–100
Knot	0.248	294.95	0.084	13–20	66–99	132–198	97–100
Turnstone	0.148	249.82	0.059	18–26	88–132	176–263	not recorded
Ringed Plover	0.118	178.32	0.066	16–24	80–120	159–239	not recorded
Sanderling	0.090	158.84	0.057	22–32	108–162	216–324	not recorded
Dunlin	0.117	146.59	0.080	18–27	90–135	180–270	95–100

^aUsing cost per second of flight from Kvist *et al.* (2001). ^bUsing Nagy *et al.*'s (1999) allometric equation. ^cAs observed by Goss-Custard *et al.* (1977).

response represented less than a tenth of a per cent of each species' daily energy requirements: Figure 6 shows there was no significant relationship between body mass and energetic cost of responding to a single disturbance when expressed in this way ($F_{1,675} = 0.565$, $P = 0.45$).

DISCUSSION

Our study provides data for 10 species of wader on FID, flight time and total time lost, along with associated energy costs, when birds flee an approaching pedestrian during the non-breeding season. Based on the findings of other studies from around the world (Urfi *et al.* 1996, Stillman &

Goss-Custard 2002, Blumstein *et al.* 2003, 2005, Ikuta & Blumstein 2003, Glover *et al.* 2011, Lin *et al.* 2012), we identified four expectations about how birds' responses to disturbance vary: all four were supported by our results. Waders show a great deal of variation in their responses and much of that variation can be explained by species, body mass, environmental conditions and site differences on both small and larger spatial scales.

Relationships between response measures

With the exception of alert time, all of the time- and distance-related measures of response that we

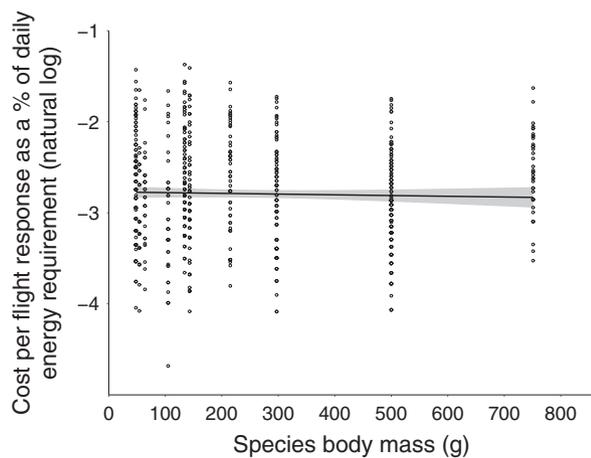


Figure 6. Relationship between species body mass and energetic costs of flight in response to disturbance.

recorded were inter-correlated. This supports the expectation that disturbance avoidance behaviour depends on the relative costs of fleeing and remaining (Frid & Dill 2002): when starvation risk is lower, birds fly from further away (FID), flee further (longer flight time) and spend more time being vigilant (alert and latency time). The lack of a strong relationship between alert time and the other variables could be due to the fact that this was more difficult to record accurately, especially at greater distances. Alternatively, it may be that alert time is simply not a useful measure of response to disturbance in this case, as it is likely to be related to speed of approach, which was approximately constant in our experiments.

Between-species differences

Larger species had greater FIDs, spent more time in flight and lost more feeding time overall than did smaller species. Møller *et al.* (2013) suggest that longer FIDs in larger species are due to the aerodynamic cost of large body size: this explanation may work for FID but does not explain the additional body mass relationships with flight time and total time lost. Another explanation could be that because smaller birds generally spend a greater proportion of the available time feeding (Goss-Custard *et al.* 1977) and have proportionally lower body fat reserves upon which they can rely if they are unable to meet their daily intake requirements (Piersma & Vanbrederode 1990), they have a smaller capacity to compensate for the costs of responding to disturbance. Indeed, the

trade-off becomes apparent when the energetic cost per flight response is expressed as a percentage of the species' daily requirements, and the body mass relationship disappears.

Effect of environmental conditions

One prediction of the risk-disturbance hypothesis is that 'fleeing probability and FID increase when ... environmental conditions are mild' (Frid & Dill 2002), because when birds are able to meet their daily energetic requirements easily, the balance in the trade-off between avoidance of starvation and predation shifts towards greater FIDs. We found this to be the case: birds also spent significantly longer in flight and lost more time overall when conditions were milder (i.e. higher wind chill equivalent temperatures).

Within- and between-site differences

The magnitude of all three measures of response varied on both small and larger spatial scales; birds responded less strongly to disturbance when feeding further from the low water mark and at the site with easiest access, closest proximity to residential areas and highest frequency of potential disturbers. The site effect may thus be attributable to habituation. However, it is not possible to rule out alternative explanations without detailed knowledge of the differences between sites and individual birds, which we unfortunately do not have. For example, if birds feeding on high disturbance sites are in poorer condition, they will prioritize feeding more than higher quality birds feeding on low disturbance sites. Or with any differences between sites in food availability and competitive ability of birds, birds feeding at lower quality sites would be expected to be more tolerant of disturbance because of a lack of alternatives (Frid & Dill 2002). Similar arguments and explanations relating to habitat quality and individual differences could also apply to the observed relationship with shore level. While it was also beyond the scope of this study to collect detailed information on types and frequencies of human activities, we suggest that future studies consider using an objective measure of disturbance (such as number of visitors per day), which lends itself better to comparisons between sites and shore levels.

Costs of responding to disturbance

In addition to the energetic costs of flight, responding to disturbance reduces birds' available feeding time. Feeding intensity data (Goss-Custard *et al.* 1977) show that most birds on the Wash are likely to be able to cope with at least a 5% reduction, which we calculate would be caused by between 38 and 162 separate disturbance events per day depending on species and tidal stage. Curlew, Oystercatcher, Bar-tailed Godwit and Grey Plover may even be able to cope with a more serious reduction of 10% (caused by between 77 and 184 daily disturbance events). Although objective data on visitor frequencies and distribution across the intertidal habitat in our study area are lacking, we believe from experience that current levels on most parts of the embayment are well below these values, especially at lower shore levels (in the order of around three visitors per week; M.G. Yates pers. obs.), perhaps with the exception of the more easily accessible eastern area around Site 4 on busier weekend days. As an example, the popular RSPB Titchwell Marsh Nature Reserve (7 km east of Site 4) receives on average 217 visitors per day (Visit England 2015), and as few as 10% of visitors might cause disturbance events (Liley & Fearnley 2012). We suggest, therefore, that wintering wader populations on the Wash are not currently significantly negatively impacted by human disturbance during the intertidal foraging period.

Further work to quantify disturbance of high tide roosts would complement this study and allow a more confident assessment of the overall impacts of disturbance (or lack thereof) on wintering waders on the Wash. As well as requiring suitable high tide refuges upon which to rest and preen (Rogers *et al.* 2006), some species are known to rely on supratidal habitats for foraging when they are not able to meet their energy requirements during the intertidal exposure period, for example due to increased requirements for thermoregulation during extreme cold weather or reduced intertidal exposure during storm events (Goss-Custard 1969, Milsom *et al.* 1998, Smart & Gill 2003). In such situations, the time and energy costs associated with responding to disturbance could be particularly problematic, especially if birds are forced to fly long distances to alternative roost or foraging sites (Rehfishch *et al.* 1996).

The data that we present here do not take account of the potential additional energetic costs

of physiological responses (increased heart rate, stress hormones, etc.) that may be incurred even when birds do not flee, and which can last longer than visible response behaviours (Ackerman *et al.* 2004, Elliott *et al.* 2016). More research is needed in this area; however, Ackerman *et al.* (2004) found that the largest increase in heart rate occurs during the period immediately before and after initiation of flight, so we expect that the contribution made by physiological changes not associated with flight is small compared with that due to the costs of flight and lost feeding time.

CONCLUSIONS

The few published studies with comparable data to ours show that there can be considerable between-estuary variation in responses (Smit & Visser 1993, Urfi *et al.* 1996, Fitzpatrick & Bouchez 1998, Laurson *et al.* 2005), as well as the within-estuary variation that we observed. We would therefore caution against making direct inferences from our data about the magnitude of birds' responses to disturbance at other sites if those sites do not also have large areas of intertidal habitat that are relatively inaccessible (for humans), where the width of the shore tends to be much greater than our largest observed FID, and where potentially disturbing activities are largely restricted to the upper shore. Similarly, given the influence of environmental conditions, it is important to note the temperature range over which experiments take place – for example, during an abnormally cold winter, FIDs would be lower than those exhibited under more commonly experienced conditions. Our study on the Wash adds to the suite of available data from a range of sites, providing more options for informed comparisons with new sites.

Finally, greater emphasis needs to be placed on recording time-related measures of responses to disturbance – to understand better the constraints on birds' time and energy budgets – rather than simply reporting FID. Doing so would also add value by providing the information necessary for parameterizing simulation models for understanding population-level impacts of different levels of disturbance and to predict the effectiveness of proposed management options (e.g. Blumstein *et al.* 2005, Stillman *et al.* 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Preliminary analysis revealed no effect of winter year on FID, flight time or latency time, and that only one interaction term (Site: WinterDay) should be included in the global models for multimodel inference testing.