

Ecological and anthropogenic constraints on waterbirds of
the Forth Estuary: population and behavioural responses to
disturbance

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the Forth Estuary: population and behavioural responses to
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Abstract

Disturbance from engineering works is an increasing problem in terrestrial and marine ecosystems throughout the world. Many reported declines in population size, breeding success and body condition have been diagnosed as the result of anthropogenic disturbance, however little is known about the effect of long-term disturbance from large-scale engineering works. Understanding the mechanisms by which animals respond to anthropogenic activities is fundamental to explaining interactions, and resolving potential conflicts between humans and wildlife.

This thesis focuses on the factors affecting the habitat use and foraging decisions in wintering shorebirds and wildfowl. The first half of this thesis considers the direct and indirect impacts on waterbirds of a major engineering project in central Scotland; construction of the new Clackmannanshire Bridge at Kincardine-on-Forth. For individual bird species in close proximity to the bridge site, round-the-clock construction work had consequences ranging from neutral to considerably negative. Cormorant *Phalacrocorax carbo* declined in the area, probably as a result of the disturbance of an important low tide roost. Redshank *Tringa totanus*, previously abundant in the prey-rich areas adjacent to the construction site, were displaced into poorer areas for most of the construction period; where they may also have suffered from increased interference competition and elevated risk from raptorial predators.

Some positive effects of industrial development were also revealed; radio-transmitters combined with tilt-switch posture sensors indicate that Redshank were able to capitalise on the improved nocturnal visibility in areas around Grangemouth docks to assist with foraging and predator detection. Evidence is presented that birds switched foraging strategy (from sight to touch feeding) depending on ambient light levels; whereby artificial light was used in a similar manner to moonlight to assist with prey detection. Redshank also avoided riverine areas at night that were used frequently by day, probably in response to an elevated threat from nocturnal predators. As the predator landscape changes from day into night, birds adopt different strategies to minimise the risk from nocturnal predators. It is clearly important, therefore, that information on nocturnal distributions is available to inform decisions on site management, especially where anthropogenic activity continues throughout the diel cycle.

Behavioural decisions were shown to vary widely within a species depending on individual state, metabolic demands and previous exposure to human disturbance. Prey resources were shown to change dramatically over the course of a winter. In response to this decline, the home range of Redshank contracted over a winter season. Similarly, animals responded less and took greater risks in response to experimental disturbance events later in the winter than earlier in the winter, and on days when the temperature was lower. This effect was strongest for individuals occupying heavily disturbed areas, which were possibly already compensating for lost feeding

time and a negative energy balance. The results were consistent with the hypothesis that those individuals that respond most obviously to human disturbance were those least likely to suffer fitness consequences. This is the opposite from what is commonly assumed when behaviour is used as an index of disturbance impacts, most notably in the use of flush distance in the design of wildlife buffer zones.

In conclusion, this study demonstrated various negative impacts of disturbance, including local displacement, due to construction activity on overwintering waterbirds. It also revealed two key, but poorly understood, phenomena relating to mechanisms for coping with anthropogenic disturbance: routine utilisation of artificial light to extend night-time feeding opportunities amongst Redshank and an adaptive flexibility in escape responses across a range of species under varying conditions of risk.

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Chapter 1

General Introduction

1. General Introduction

1.1. An overview

The effective management of human activities in wildlife areas and the wider landscape is a key issue in conservation biology. Many reported declines in population size, breeding success and body condition have been diagnosed as the result of anthropogenic disturbance (Pierce & Simons 1986; Altmann *et al.* 1993; Gabrielsen & Smith 1995; Blackmer *et al.* 2004; Durell *et al.* 2005; Stankowich 2008). According to Batten *et al.* (1990): 49 out of the 117 species listed as Red Data Birds in the UK were potentially affected or threatened by some form of disturbance. Similarly Tucker and Heath (1994) reported that of the 129 species of European conservation concern, 35 were threatened or affected by disturbance. Despite this, a small number of species thrive in urban areas where they occur at higher densities than those in more natural environments (Gorenzel & Salmon 1995; Blair 1996; Evans *et al.* 2009). Understanding the mechanisms by which animals respond to anthropogenic activities is therefore fundamental to explaining interactions, and resolving potential conflicts between humans and wildlife.

The effects of disturbance are expected to become an increasing issue as the footprint of human influence continues to expand (Janzen 1998; Green *et al.* 2005), and the impacts of human activity (e.g. noise, lighting and pollution) spread into more areas (Madsen 1998; Blumstein *et al.* 2005; Fernandez-Juricic *et al.* 2005; Burton *et al.* 2006; Patricelli & Blickley 2006; Lengagne 2008). Such expanding human activity is widely perceived to lead to negative consequences for wildlife, beyond that of habitat-loss alone (Frid 2003; Higham 1998; Stevens & Boness 2003; Taylor & Knight 2003; de la Torre *et al.* 2000; Wauters, Somers, & Dhondt, 1997). After a decade or more of relative stability, pressure on UK coastlines has increased recently with the passing of the EU Renewable Energy Directive to expand energy production from renewable sources. Given the world-wide demand for renewable energy, it seems likely that for countries with large renewable potential, an increasing proportion of coastal water will be accessed for renewable energy production (Gill 2005; Inger *et al.* 2009). Coastal zones, however, are already under significant pressure from human activity as a result of their high biological productivity and accessibility (Blaber *et al.* 2000), and the exploitation of valuable ecosystem services and functions (Costanza *et al.* 1997). The rate and scale of developments such as offshore wind farms and tidal barrages (Clark 2006; Bright *et al.* 2008), in addition to the continued redevelopment of urban watersides (Burton *et al.* 1996; Marsden 2000), raises questions about the potential impact on wildlife.

In recognition of these concerns, environmental impact assessments currently deal with the habitat loss incurred by development (e.g. through the siting and building of a new industrial plant), but also with the implications of noise and site activity during construction and later use on species richness and diversity. The former represents irreparable damage to the animals

concerned, whereas the latter might be reduced to acceptable levels by mitigating practices (Hockin *et al.* 1992). If wildlife managers and ecological consultants are to exercise their powers wisely, they must ensure the potential impacts that are identified are real and significant. Similarly, it is vital that the successes of mitigation measures are investigated in order to make recommendations to future developments. Such adaptive management schemes provide practitioners a flexible method for improving strategies to achieve and sustain the desired conservation impact.

1.2. Aims

This project sought to understand the factors determining the effect of human disturbance on wintering waterbird populations. Coastal waterbirds are exposed to increasing levels of human disturbance, making them appropriate models to study the mechanisms whereby disturbance influences behaviour and fitness (West *et al.* 2002; Goss-Custard *et al.* 2006). I will argue that (1) although much research has been done on disturbance, little is known about the effect of long-term anthropogenic disturbance (such as large-scale engineering works) on wildlife populations; (2) that a proper understanding requires research into the effects at both the individual level and at the population level; and (3) the effect of disturbance may be elevated during times when animals are energetically stressed.

Firstly, I review the literature reporting on the different effects of human disturbance on animals. Much of the extant literature focuses exclusively on disturbance to birds; consequently many ideas are well developed for this group. For this reason, most examples presented in this review will concern the effects of disturbance on birds; however when available, non-avian examples will be cited. Secondly, I will focus on the study system, giving general information on the ecology and behaviour and motivate the research compiled in this thesis.

1.3. What is disturbance?

The term 'disturbance' has been defined as: "Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White & Pickett 1985). This may refer to the immediate behavioural responses by wildlife to recreational walkers (e.g. Fernandez-Juricic *et al.* 2001), or indirect effects as a result of habitat modification; such as those caused by movement and noise of humans and vehicles, or artificial lighting used to illuminate urbanised areas and industrial developments (Hockin *et al.* 1992). From this definition it is clear that human disturbance may cause a measurable effect, however caution should be taken when assuming that this response will always be negative; the effects of disturbance may be entirely trivial (Marsden 2000; Gill *et al.* 2001a), or may even offer some benefits to particular species (e.g. Gorenzel & Salmon 1995).

There has been considerable study into the effects of disturbance on animal populations (see reviews by Hockin *et al.* 1992; Hill *et al.* 1997; Carney & Sydeman 1999; Gill *et al.* 2001b; Burton 2007; Gill 2007; Sutherland 2007). The principal way in which disturbance can impact on wildlife is by altering the ability of wildlife to exploit important resources (Gill 2007); this is done by directly restricting access to resources such as food supplies, roosting sites or nesting sites, or by altering the actual or perceived quality of a site. Disturbance may impact directly in the short term causing a behavioural response as individuals consume considerable energy fleeing from the disturbance stimuli (Nudds & Bryant 2000), whilst losing valuable feeding time moving to alternative feeding areas (Quinn 1997). If large enough and long-lasting, disturbance may act in a manner similar to habitat loss; forcing animals to feed in poorer quality sites (Hill *et al.* 1997), causing higher competitor densities resulting in increased interference competition (Dolman & Sutherland 1997; Vahl *et al.* 2005). Anthropogenic disturbance may also increase the predation risk directly, by masking auditory cues or distracting attention away from an approaching threat (Quinn *et al.* 2006; Yim-Hol Chan *et al.* In Press); or indirectly, by displacing individuals into 'risky' areas, previously avoided due to a high predatory threat (Cresswell 1994; Cresswell & Quinn 2004).

1.4. Assessing disturbance

1.4.1. Behavioural approach

A variety of approaches has been taken by different researchers to investigate disturbance impacts (Hill *et al.* 1997; Gill 2007), with both comparative and experimental approaches commonly adopted. Assessments of whether disturbance affects a population, and how severe that effect is, currently rely on a proximate measure of disturbance impacts (such as a behavioural approach) to connect the impact of disturbance with a particular group of animals. For example, measurements have been taken on species differences in responses to a standard disturbance stimulus (Blumstein 2003) and, in particular, the distances at which they take flight, are displaced, or return after a disturbance (Pfister *et al.* 1992; Stankowich & Blumstein 2005). Reductions in nest incubation and changes in foraging behaviour have also been adopted to understand the effects of disturbance (de Boer & Longamane 1996). The general assumptions of these studies is that 1) if no behavioural change is apparent, there can be no fitness consequences and 2) those species showing the greatest behavioural response are the most compromised (Burger 1981; Klein *et al.* 1995). However, using behavioural responses to investigate the susceptibility of animals to disturbance can be misleading. Behavioural responses are context-dependent (Keller 1989; Gill *et al.* 2001b) and will reflect the trade-off of the energetic quality of current feeding grounds (Colwell & Landrum 1993), the proximity and relative quality of alternative areas, predation risk (Cresswell & Quinn 2004), energy demands (Goss-Custard 1969; Baker 1981), and competition (Bednekoff & Lima 2004). In this context, it can be very difficult to distinguish between animals that do not respond to disturbance because

they are unaffected by it, or if they are constrained to feed there, despite suffering fitness costs (e.g. reduced foraging time, nest defence or increased predation risk). If researchers are to use behavioural responses as a proximate measure of fitness, such trade-offs must be explored.

1.4.2. *Landscape approach*

A comparative landscape approach is among the most popular methods of determining the impact of a disturbance over a longer time period (Gill *et al.* 2001b). Rather than focusing on behavioural responses to disturbance events, landscape features associated with disturbance are used as surrogates to investigate whether the abundance, distribution or absence of species within a site are influenced by proximity to areas used by humans (Burger 1981; Klein *et al.* 1995; Reijnen *et al.* 1996). Because birds are very mobile, comparisons of a change in density can reveal there is selection or avoidance of particular habitats (Finney *et al.* 2005). This has been demonstrated as reduced densities occurring next to public paths (Fernandez-Juricic *et al.* 2005), roads (Keller 1991), railways and other man-made landscape features (Burton *et al.* 2002). A major flaw in this approach, however, is that very little consideration is given to other factors which may influence species' distributions. As estuaries are heterogeneous habitats, there are many variations in biotic and abiotic factors which may also influence habitat use (Kelsey & Hassall 1989; Nehls & Tiedemann 1993; Yates *et al.* 1993; Johnstone & Norris 2000). Using generalised linear models (GLMs) Burton *et al.* (2002a) included month, count section area, whether the sector bordered the low water mark and the proximity of sections to the nearest footpath access point (car park, town or road). However this analysis was limited as little consideration was made to variation in factors such as substrate penetrability, water depth and food supply. The different landscape features may also have been considerably autocorrelated with other factors, such as the avoidance of the upper intertidal zone due to the risk of predation (Whitfield 2003).

1.4.3. *Experimental approach*

By developing an experimental approach alongside comparative studies, it is possible to vary the rate of disturbance across a number of patches within a site and observe how birds might use a site in the presence or absence of the disturbance (Sutherland & Crockford 1993). Madsen (1998) investigated the effects of hunting on waterfowl, by manipulating areas available to wildfowlers for shooting. The hunting impacts were then investigated by reversing those sites available for hunting with previously restricted sites and allowing birds to redistribute themselves accordingly. The study showed up to fifty-fold increases in bird numbers using hunting-free areas, compared to those when the areas were continuously disturbed by shooting. Burton *et al.* (2002b) used generalised linear models to assess if the sustained impact of the construction of the barrage impacted on the bird densities. The abundance of five of seven species (Eurasian Teal *Anas crecca*, Eurasian Oystercatcher *Haematopus ostralegus*, Dunlin *Calidris alpina*, Eurasian Curlew *Numenius arquata* and Common Redshank *Tringa totanus*)

and feeding activity of all four wader species were depressed in count sectors adjacent to construction work during operations.

1.5. Confounding factors

Although spatial variation in food supply was partially, indirectly, taken into account by Burton *et al.* (2002a) (i.e. by distinguishing between intertidal count sectors which bordered the low water mark), and by Burton *et al.* (2002b) (i.e. by including count section and the presence of construction work as explanatory variables), these studies would be strengthened by including variables describing food availability (Milsom *et al.* 1998) or ideally by direct measurement of food abundance. Gill *et al.* (2001a) found that the presence of footpaths and marinas had no effect on Black-tailed Godwit *Limosa limosa* abundance once bivalve supply had been taken into account. The temporal changes in species numbers may also have been driven by annual variations in food abundance (Bryant & McLusky 1997), rather than by the effect of the construction disturbance itself. If this were the case, the impact of the construction work by Burton *et al.* (2002b) on waterbirds may have been misdiagnosed.

While the redistribution of animals (i.e. avoidance) is widely observed in areas where disturbances are likely (Tarlow & Blumstein 2007), strong evidence of a direct impact of disturbance of any kind on population size is rare in the literature. Furthermore as Gill *et al.* (2001b) illustrate, although animals may appear to avoid human presence, this may not reduce the population size supported by the estuary. Animals may be able to compensate for the losses of time and energy resulting from disturbance by feeding in the most disturbed areas at times when there were few disturbances (e.g. early mornings), or by using the disturbed areas once resources were used up in undisturbed areas. In combination, human disturbance may have additive effects which may actually improve a site for some wildlife. For example, disturbance may also make a site less attractive for avian predators, or alternatively, may improve the availability of benthic prey for foraging birds.

Despite much research being conducted into effects of disturbance on wildlife, many of these results are difficult to interpret. This is because multiple factors in addition to disturbance may affect individuals and hence population dynamics, making it hard to disentangle the effects of different factors (Cayford 1993). Physiological responses have been used to examine the effects of disturbance; where subtle impacts, such as elevated heart rates and stress hormone levels, can reduce survival and fecundity leading to population decline (Weimerskirch *et al.* 2002; Thiel *et al.* 2005; Ellenberg *et al.* 2006; Arlettaz *et al.* 2007). Studies have also demonstrated the direct effects of disturbance on breeding success through observations and modelling (Hockin *et al.* 1992; Hill *et al.* 1997; Carney & Sydeman 1999; Beale & Monaghan 2005). When breeding success has been shown to decline, we can be sure that the disturbance is indeed of conservation concern. Difficulties arise however, when assessing how disturbance impacts a species during

the non-breeding period without the observed effects on fecundity. For migratory animals (especially birds), breeding areas are often thousands of kilometres away from wintering and staging sites, which may be where the effects of disturbance have the greatest impacts (Madsen 1995; Tombre *et al.* 2005; Inger *et al.* 2008). Furthermore, ecological conditions experienced through the winter, particularly winter habitat selection, can be ‘carried over’ into subsequent seasons and have significant impacts on the reproductive success of individuals (Norris *et al.* 2003; Bearhop *et al.* 2004). It is therefore important to monitor the consequences of disturbance on habitat use during the wintering period, in order to highlight the potential impacts of displacement on future breeding success.

1.6. Trade-off mechanisms

In general, it is accepted that the study of behaviour within a conservation context is encouraged, as ultimately most fitness consequences are mediated by behavioural decisions made by the individual (Sutherland 1998; Gill *et al.* 2001b). The risk-disturbance hypothesis synthesises this behavioural approach in order to explain responses of individuals and populations to humans based on the grounds that animals seek a balance between avoiding disturbance and undertaking activities that may increase fitness, such as foraging, mating and parental care (Frid & Dill 2002). To counterbalance the energy deficit of reduced prey consumption and increased energy expenditure during the day, birds confined to disturbed areas can supplement their diet by moving to supratidal habitats to forage during high tides (Goss-Custard 1969), or by increasing nocturnal foraging (Belanger & Bedard 1990; Mouritsen 1994; Kuwae 2007). Similarly, if habituation towards the disturbance occurs, the impact on fitness is likely to be reduced (Sutherland 2007). Burton *et al.* (2002b) concluded that those species which declined were unable to habituate to the irregular noise and activities of the construction work and thus avoided sites adjacent to the disturbance for the duration of the project (Hill *et al.* 1997).

1.6.1. Availability of resources

It is often difficult to distinguish between animals that disperse because the costs of moving are trivial, and those that move because the impacts exceed what may be considerable costs of remaining (Gill *et al.* 2001b, Gill 2007). As Gill *et al.* (2001b) adduce, a lack of behavioural response may not imply a lack of fitness consequence but may instead reflect a lack of choice. Although herbivorous duck species such as Wigeon *Anas penelope*, show strong avoidance of humans (Madsen 1995), the cost of moving at some sites may be low due to the wide range of alternative feeding sites available to them (Gill *et al.* 2001b). If behavioural measures are not necessarily an indication of fitness costs, then the use of these to quantify the impacts of disturbance is therefore not justified.

A better understanding of the trade-offs which shape the response of waterbirds to human or predators may explain the responses of wildlife to human disturbance and the subsequent fitness costs (Gill *et al.* 2001b). This may help managers identify those locations, times or populations which are at most at risk from the negative effects of disturbance (Yasue & Dearden 2006). Disturbance is most likely to have an effect during those periods in the annual cycle when food resources are depleted and animals have difficulty in meeting their energy requirements (Madsen 1995). Difficulties are most likely to arise when a high food intake is required for the build up of nutrient reserves advance of periods of high demand. In the case of shorebirds and wildfowl, energy reserves are accumulated in late autumn and early winter; these are then exhausted throughout the course of a winter and replenished in spring when a rapid accumulation of nutrient stores takes place prior to migration and breeding (Owen & Cook 1977; Pienkowski *et al.* 1984; Fox *et al.* 1992; Owen *et al.* 1992; Ebbinge & Spaans 1995).

1.6.2. Thermoregulatory demands

Severe weather may affect the trade-off between starvation and predation risk in wild animals (Yasue *et al.* 2003). Thermoregulatory demands will increase as weather conditions become more severe (Wiersma & Piersma 1994; Kelly *et al.* 2002). As low temperatures and high wind speeds increase thermoregulatory demands, behavioural trade-offs are expected to shift towards avoiding starvation (McGowan *et al.* 2002). This can force animals to feed in areas previously avoided due to the high perceived risk (Houston *et al.* 1993; Yasue *et al.* 2003). Alternatively, the pressure to accumulate sufficient fat may cause individuals to forage more intensively or react later to an approaching threat (Lima & Dill 1990). Those individuals unable to alter their behaviour may suffer fitness costs and mortality during these severe weather episodes. Thus the impacts of disturbance are expected to be greatest when animals are already struggling to meet energy requirements. Decreased air temperatures and increased wind speeds may also reduce prey activity (Evans 1976) or the availability of prey (Goss-Custard 1976; Dugan *et al.* 1981), exacerbating the effects on energy budgets. Finally, weather can also affect predation risk directly, by increasing the demands on the predator and leading to more attacks (Willem 2001), or reducing the ability of birds to detect or escape from approaching predators (Hilton *et al.* 1999).

1.7. Study area

The Forth estuary, Scotland, is recognised for its nationally and internationally important populations of wintering and passage estuarine bird populations (Newton & Bryant 1991). The extensive intertidal areas of the Forth are known to support up to 80,000 wintering waterfowl, including some 40,000 shorebirds from as far away as the high arctic regions (at least 2.3% of the wintering north-eastern Canada/ Greenland/ Iceland/ north-western Europe Red Knot *Calidris canutus* population) as well as Shelduck (1.2% of wintering north-western Europe population) Pink-footed *Anser brachyrhynchus* and Greylag Geese *Anser anser* and many other

species (Wetland Bird Survey WeBS 1994-95 to 1998-99). The Forth as a whole is of major importance for a rich assemblage of waterbirds in the migration periods and through the winter, including divers, sea-ducks, geese, other ducks, waders and terns, and for breeding seabirds in the summer months.

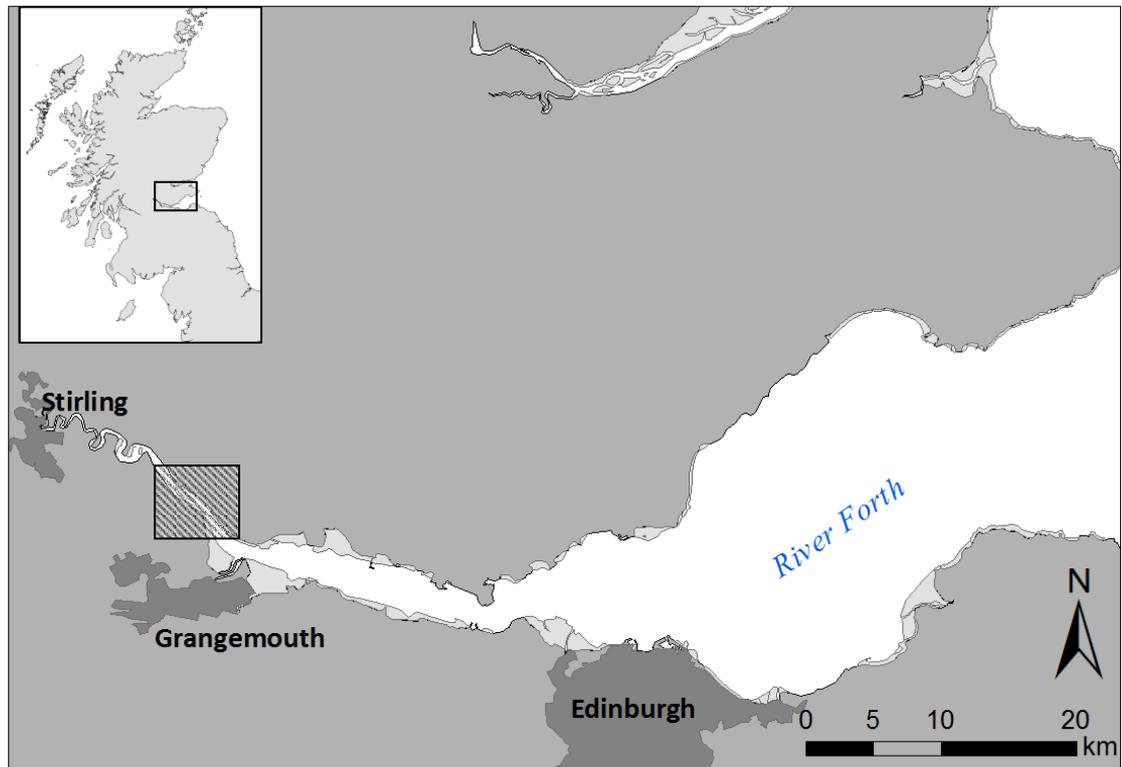


Figure 1.1: Map of the Forth estuary complex. The intertidal area is indicated by light shading and large urban areas on the Forth are indicated by dark shading. The area most likely to be disturbed by the construction of the new Clackmannanshire Bridge is indicated by the shaded box located between Stirling and Grangemouth.

Under pressure to redevelop the existing Kincardine Bridge and to alleviate congestion within the town of Kincardine, a new bridge crossing was proposed adjacent to the existing Kincardine Bridge. However, the Kincardine site forms part of the protected Firth of Forth Special Protection Area (SPA), RAMSAR Site and Site of Special Scientific Interest (SSSI) (Figure 1.1). The construction of the Clackmannanshire Bridge resulted in the loss of roughly half a hectare of intertidal habitat, and contained relatively high levels of noise and movement in areas close to intertidal habitat frequently used by waterbirds (Figures 1.2i, ii).



Figure 1.2: The engineering work in progress: i) construction of drilled pile foundations by the Seacore ® marine drilling station and ii) construction of the bridge deck, launched from the northern bank to minimize the disturbance to feeding and roosting grounds on the south side of the estuary. Photos: David Bryant.

The Scottish Government were obliged under Article 6.3 of the Habitats Directive to conduct a study of impacts, both before (predictive), during and after the construction is completed. Although the construction calendar was arranged in a way to minimise disturbance to wintering and migrating birds (e.g. by limiting heavy engineering work to the summer months), work continued throughout the year. Construction of the Clackmannanshire Bridge began in June 2006, with all works completed by November 2008. In order to mitigate any effects of the bridge, part of the old Scottish Power site in Kincardine was to be flooded creating the ‘Kennet Pans Realignment site’ (hereafter known only as the ‘Realignment site’). This allowed additional mudflats and saltmarsh adjacent to Kennet Pans to be re-created, expanding the roosting and feeding area for wintering birds by 9ha (Babtie Group 2002).

1.8. Thesis outline

In this thesis, I will try to elucidate the factors affecting the habitat use and foraging decisions in wintering shorebirds and wildfowl. This requires accurate estimates of the different costs and benefits induced by industrial disturbance. To obtain these I used a variety of approaches, including focal observations (**chapters 2, 3, 6**), database analysis (**chapter 3**) and radiotelemetry (**chapters 4, 5**). The first two data chapters focus mainly on the impact of the construction of the Clackmannanshire Bridge on local waterbird populations. The construction of the new bridge (and the wealth of historical data on the Firth of Forth) essentially provided an excellent opportunity to conduct a Before-After-Control-Impact (BACI) study on the effects of the construction process. **Chapter 2** is an investigation into spatial and temporal variations in habitat quality within the study area. This was assessed by sampling intertidal invertebrates across the study area and throughout the period of study to assess what factors determine habitat quality and investigate whether neighbouring less disturbed sites were of adequate quality to contain displaced birds. In **chapter 3**, I combine counts undertaken throughout the course of this study with historical data to assess the impact of bridge construction on bird numbers, distribution and habitat use. As in **chapter 2**, here I focus on the new Clackmannanshire Bridge and examine three years of pre-construction counts, two years of development and one year of recovery to gain an understanding of what impact bridge development has on intertidal habitats supporting large numbers of overwintering waterbirds. In this chapter, I was interested in how habitat use compared during bridge construction with the period prior to construction and how bird recovered in the winter after construction.

In **chapters 4-6**, I extend the focus from the areas around the Kincardine and Clackmannanshire Bridges, to an estuary-wide scale to examine the effects of disturbance on an individual level. **Chapter 4** uses radiotelemetry in an attempt to understand how the bridge has affected habitat use in the Common Redshank *Tringa totanus* and if there are any ecological traits in habitat use which affects the susceptibility of Redshank to anthropogenic disturbance. **Chapter 5** investigates the effects of ambient light levels on foraging behaviour throughout the tidal cycle.

Chapter 6 uses an experimental approach to investigate trade-off decisions in the flight response of a subset of waterbird species, and tests how previous experience and individual state may affect behavioural responsiveness to disturbance. **Chapter 7** is a synthesis of this thesis; in this chapter our current knowledge of the Forth system will be reviewed, management guidelines summarised and our findings placed in a wider ecological and conservation perspective.

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Chapter 2

Variation in site quality for foraging waterbirds on the Forth estuary

2. Variation in site quality for foraging waterbirds on the Forth estuary

Food density and the net energetic and nutrient value of foraging grounds are widely thought to be the most important parameter in determining shorebird abundance. As birds may respond to prey in a density dependent manner, any assessment of annual or seasonal fluctuations in bird density should be accompanied by an investigation into their main prey. Crucially, an understanding of this relationship allows any confounding effects of food supplies on the impact of anthropogenic disturbance to be evaluated.

Sites in our study varied greatly in prey quality, with Kennet Pans and Skinflats revealed as the most prey-rich sites for birds. Adjacent sites were poorer in terms of prey quality and may not be capable of sustaining displaced birds from Kennet Pans. Prey density and total prey biomass were negatively related to time. If prey occurs at lower densities and biomass, birds will have to commit more time to searching for food in order to meet daily energy requirements. We recommend that behavioural studies should take this seasonal decline in site quality into account when investigating the impact of disturbance on foraging rates, time budgets and habitat use within the estuary. As little or no variation in invertebrate prey was found between winters, we argue that should evidence for numerical, spatial and behavioural changes amongst waterbirds be found, coincident with bridge construction, that these are likely to be due to anthropogenic factors rather than to substantial changes in the local estuarine environment.

In addition, the breaching of the sea wall and the creation of new mudflat habitat on the Forth also provided the opportunity to investigate the re-colonisation of this site by marine invertebrates. At the managed realignment site, both prey density and biomass increased in the second year following the removal of the sea wall. While only low *Macoma* densities were found in the first winter, all four study species were present in the second winter. The invertebrate species which colonised this site were generally preferred prey and are of suitable size to be exploited by Redshank, Dunlin and Shelduck. We would therefore expect these bird species to move into this area in winter 2008/09 in order to capitalise on this new availability of invertebrate prey.

2.1. INTRODUCTION

Understanding why animals choose to forage where they do has been a main focus of ecological research over many years (MacArthur & Pianka 1966; Stephens & Krebs 1986). To survive, individuals must make economic decisions about where to feed based on balancing the risks of starvation and predation (Lima & Dill 1990; Lima 1998). Habitat selection in non-breeding shorebirds is known to be influenced by many factors such as predation risk (Cresswell 1994; Quinn & Cresswell 2004), human disturbance (Burton 2007), proximity to roost sites (Dias *et al.* 2006; Zharikov & Milton 2009), substrate resistance (Finn *et al.* 2007) and particle size (Yates *et al.* 1993). A number of studies have shown densities of shorebirds are linked directly to their main prey (Bryant & Leng 1975; Goss-Custard *et al.* 1977; Bryant 1979). For example, Bryant (1979) showed densities of *Nereis diversicolor* were closely correlated with bird-feeding hours per km² for Curlew *Numenius arquata*, Redshank *Tringa totanus* and Dunlin *Calidris alpina* and the density of the bivalves (*Mytilus edulus* and *Cerastoderma edule*) with Oystercatcher *Haematopus ostralegus* and Knot *Calidris canutus* respectively. Goss-Custard (1977) showed how Redshank populations on the Ythan estuary concentrate feeding effort where *Corophium volutator* density and body size was greatest. The close relationship between food availability and shorebird abundance has been illustrated over time-scales of a tidal cycle (Burger *et al.* 1977), between seasons (Goss-Custard *et al.* 1984; Goss-Custard *et al.* 2001), between years (Zwarts *et al.* 1992; Colwell & Landrum 1993; Bryant & McLusky 1997) and between areas (Bryant 1979; Goss-Custard *et al.* 1991; Colwell & Landrum 1993; Zwarts & Wanink 1993).

Shorebirds are size-selective feeders with the available prey heavily constrained by bill morphology (Stephens & Krebs 1986; Thrush *et al.* 1994; Durell 2000). This constraint affects the depth of sediment species can reach, and the size and type of prey birds can handle (Zwarts & Wanink 1989; Zwarts & Blomert 1992; Piersma *et al.* 1993; Zwarts & Wanink 1993). Of the total biomass of prey present, only a small fraction is harvestable (i.e. accessible as well as profitable) by shorebirds (Zwarts & Wanink 1993). In Knot, a wading bird specializing on eating hard-shelled prey, 89% of biomass in the intertidal sediment consisted of animals that were too large, too small or lived too deeply to be taken (Zwarts & Blomert 1992; Zwarts & Wanink 1993; Zwarts *et al.* 1996). Direct field observations and diet studies have clearly shown the prey size the shorebird species are targeting (Bryant 1979; Kalejta 1993). The preferred size classes of *Corophium volutator*, *Hydrobia ulvae*, *Macoma baltica* and *Nereis diversicolor* taken by a range of waterbirds is shown in Table 2.1.

Table 2.1: Preferred size classes of prey selected by waterbird species. Sources: Goss-Custard (1969), Goss-Custard (1977), Buxton & Young (1981), Warnes (1981), Moreira (1996), Rippe & Dierschke (1997).

Waterbird species	Invertebrate size (mm)			
	<i>Corophium</i>	<i>Hydrobia</i>	<i>Macoma</i>	<i>Nereis</i>
Redshank (<i>T. totanus</i>)	>4	2.5-4.8	4.8-10.8	<20
Dunlin (<i>C. alpina</i>)	-	0.6-3.5	-	<30
Curlew (<i>N. arquata</i>)	-	-	8-21	>79
Oystercatcher (<i>H. ostralegus</i>)	-	-	11-13	-
Red Knot (<i>C. canutus</i>)	-	4-8	4-10	-
Shelduck (<i>Tadorna tadorna</i>)	>4	3-4.5	<6	-

In soft-bottom marine habitats, the abundance of infaunal animals are more often directly limited by their major predators rather than interspecific competition for space (Virnstein 1977; Peterson 1979; Peterson & Quammen 1982; Wilson 1989; Estes & Peterson 2000). Shorebirds are important predators in marine soft-bottom habitats (Szekely & Bamberger 1992; Thrush *et al.* 1994; Goss-Custard *et al.* 1996; Zharikov & Skilleter 2003). Their high feeding rates and mobility, allow them to quickly respond to variation in prey abundance at large spatial scales (Haig 1998; Lewis *et al.* 2003; Taft & Haig 2006). Warnes (1981) found that at North Skinflats, 25% of the total annual benthic production was consumed by bird predators, with the remainder presumably consumed by invertebrate predators, fish, or 'lost' to decomposers (Baird & Milne 1981; Raffaelli & Milne 1987; Jensen & Andre 1993).

The availability of food resources is well known to be affected by abiotic as well as biotic factors. Tidal cycles form predictable temporal and spatial changes in the foraging environment (Burger *et al.* 1977; Granadeiro *et al.* 2006), and prey availability is influenced by variation in temperature, wind and day length (Evans 1976; Zwarts & Wanink 1993). Invertebrates are known to move deeper in the substrate in cold conditions becoming unavailable to birds with short bills (Esselink & Zwarts 1989; Zwarts & Wanink 1989) and polychaetes, such as *Arenicola marina* and *Nereis*, may leave their burrows altogether in very cold conditions to migrate to deeper water (Zwarts & Wanink 1993). Severe weather can also remove foraging opportunities for waterbirds, for example if mudflats are covered by snow or ice (Clark 2009). Due to their high daily energy requirements (Kersten & Piersma 1987), shorebirds are not able

to survive long periods without food. A change in prey availability can cause extensive fat and muscle loss in birds due to starvation (Davidson & Evans 1982) and high mortality is well documented during severe cold weather episodes (Pilcher *et al.* 1974; Davidson & Evans 1982; Clark 2009). For species such as Redshank which prey on small items, longer periods of feeding are normally required to meet daily energy requirements than birds targeting larger prey, such as Grey Plover *Pluvialis squatarola* or Black-tailed Godwit *Limosa limosa* (Mitchell *et al.* 2000). A reduction in prey availability during severe weather may be more likely to lead to a negative energy balance in Redshank as they have less scope to increase feeding time during a tidal cycle than larger shorebird species (Mitchell *et al.* 2000).

As we have discussed, food density and the net energetic and nutrient value of foraging grounds are widely thought to be the most important parameter in determining shorebird abundance (Bryant 1979; Zwarts *et al.* 1996; Bryant & McLusky 1997). Food availability within estuaries is well known to vary greatly from year to year, with prey populations exhibiting significant annual fluctuations in density, biomass, size or availability (Goss-Custard *et al.* 1995; Bryant & McLusky 1997; Ens *et al.* 2004). The attractiveness of a foraging patch may also change over the course of a season, as depletion reduces the profitability of feeding in some areas and causes individuals to select more risky alternatives in order to meet energy requirements (Lima & Dill 1990; Lima 1998; Hilton *et al.* 1999). As birds typically respond to prey in a density dependent manner, any assessment of annual and seasonal fluctuations in bird density should also be accompanied by an investigation into their main prey. Crucially, an understanding of the relationship between shorebirds and their prey allows any confounding effects of food supplies on the impact of anthropogenic disturbance to be evaluated.

2.2.METHODS

2.2.1. *Description of study area*

The intertidal habitats of the Forth estuary are dominated by fine grained muds and silts with a few rocky outcrops, piers, bridges and reclamation bunds (McLusky 1987). Intertidal sediments above the Kincardine bridge are exclusively muds with a median particle diameter of 0.058-0.027mm, and those sediments below the bridge at Skinflats having a median particle diameter of 0.034mm (Warnes 1981). In the upper estuary, the horizontal distance from mean low water spring tide level to mean high water spring tide level ranges from 5m up to 100m (McLusky 1987). The interstitial salinity increases markedly downriver from Alloa to Kincardine Bridge, reaching a mean of 26‰ at Kincardine (McLusky 1987). This is accompanied by a marked increase in the density and diversity of intertidal fauna seawards of Alloa (McLusky 1987).

Historic land claim for agriculture and industry has resulted in the loss and degradation of large areas of intertidal habitats in estuaries (Davidson *et al.* 1991; Moser *et al.* 1996). Intertidal habitats on the Forth have been reduced by approximately 50% over the past 200 years

(McLusky 1987). Managed realignment is one method which is increasingly being used to mitigate habitat loss and restore intertidal habitats (Atkinson *et al.* 2004). New areas of tidal mudflats and saltmarsh are created by the removal of all or a section of the embankment, re-establishing tidal conditions in this area. The breaching of the sea wall to the north east of the Kincardine Bridge in 2008 provided an excellent opportunity to investigate the re-colonisation of this site by marine invertebrates. In NW Europe the experience of creating new habitat, especially mudflats, is fairly limited and the use of managed realignment to create or restore areas has often been haphazard with little or no monitoring (Atkinson 2003). An important aspect of the success of these realignment sites is to ensure harvestable invertebrate prey is available to foraging birds (Atkinson *et al.* 2001). The speed at which invertebrates colonise sites is usually in line what can be predicted through knowledge of life history traits (Atkinson 2003). It is predicted that mobile species such as *Corophium* and those that have a planktonic larval phase (such as *Nereis* and *Hydrobia*) should be first to colonise these sediments. Bivalves may be present as settled larvae after the first breeding season (Atkinson 2001) however, because they take longer than other species to grow to harvestable sizes, adults should occur in low densities (Evans *et al.* 1998). Species with no planktonic larval phase, such as oligochaetes, should be absent or present at very low densities (Atkinson *et al.* 2004).

2.2.2. *Sampling methods*

Sampling of benthic fauna was conducted at seven intertidal flats (sites) on the Forth estuary to assess variation in invertebrate prey density and composition (Figure 2.1). The area of each site ranged between 61,458m² and 418,763m², with sites spaced between 0.36km and 3.96km apart. At each site, ten core samples were extracted from the mud. Sampling stations were located on transects which began from the edge of saltmarsh and ran perpendicular to the shoreline down to the low water mark (Figure 2.1). Sampling stations were spaced evenly along its length and the distance between each station depended on the width of each site. Samples were taken between 1.5 hours before and after low water in order to cover the maximum tidal range at each mudflat. Substrate resistance of each site was measured using a penetrometer. At each sample station, a 1m length of wood was dropped into the sediment from 0.3m above the surface and the depth (mm) penetrated by the instrument scored (Table 2.2). Intertidal area at MLWS, and the length of shore at each site was measured in ArcGIS (ESRI 2009) (Table 2.2).

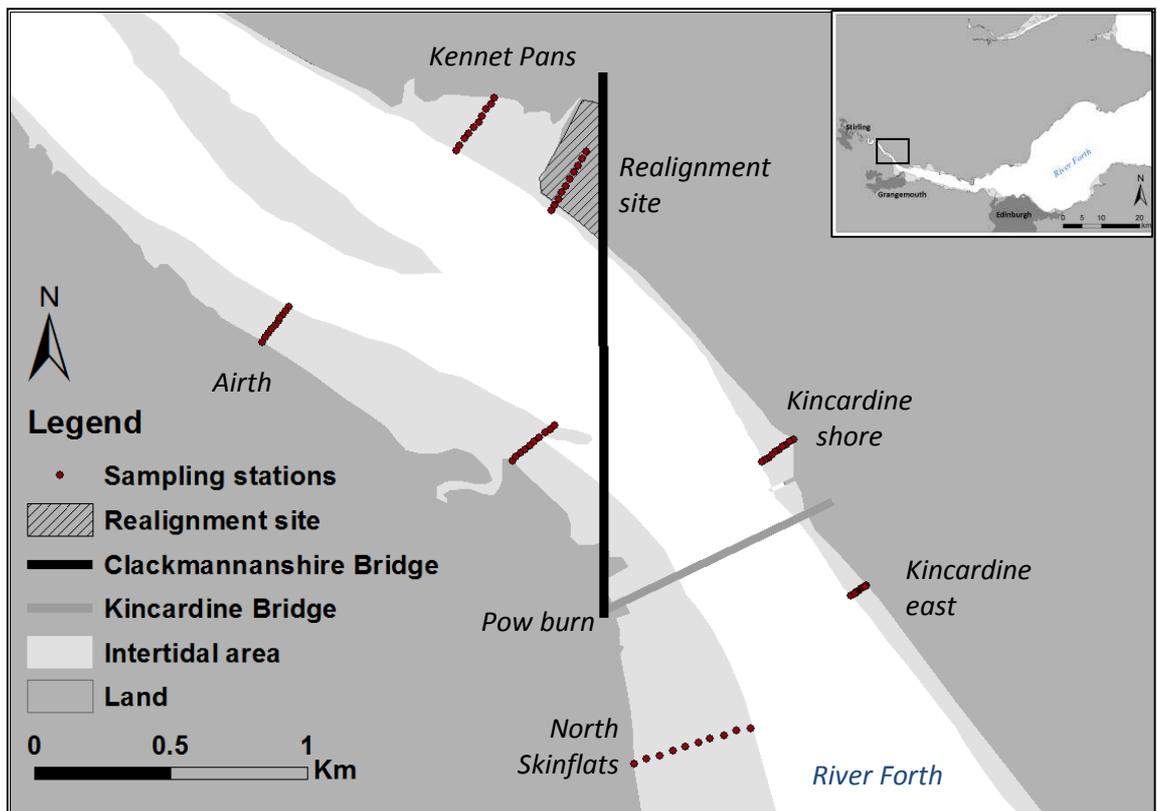


Figure 2.1: An overview of the study area in the Forth estuary, Scotland showing the road bridges, the seven intertidal sampling sites, and the ten sampling stations within each site. The intertidal area indicated by light shading is bordered by the mean low-water mark at spring lows.

Table 2.2: Names and physical characteristics of study sites.

Site	Location	Shore	Sediment resistance (mm)	Width (m)	Length (m)	Area (m ²)	Shape
Airth	upriver	south	63.2 ± 4.0	161	2,853	320,066	strip
Kennet Pans	upriver	north	133.8 ± 7.6	261	592	131,563	trapezoid
Realignment site	upriver	north	265.0 ± 61.3	172	176	61,458	trapezoid
Pow burn	upriver	south	116.6 ± 13.9	130	1030	233,351	strip
Kincardine shore	downriver	north	127.5 ± 6.1	111	878	57,584	strip
Kincardine east	downriver	north	211.1 ± 11.8	59	1,587	108,420	strip
North Skinflats	downriver	south	52.9 ± 3.6	466	1,044	418,763	trapezoid

To investigate temporal variation in prey density and the depletion of invertebrate prey throughout the course of a winter, monthly core samples were taken at Kennet Pans (kp, NS 917887) and North Skinflats (henceforth called Skinflats, sk; NS 922862) between September 2007 and March 2008. Bamboo stakes inserted on previous visits enabled replicate positioning. Samples were also collected in March 2008 from five other sites: Kincardine shore (ks; NS 927875), Airth (ai; NS 929870), Pow burn (po; NS 917874), Kincardine east (ke; NS 929870), and the recently flooded Realignment site on the north shore adjacent to the Clackmannanshire Bridge (re; NS 919885), to investigate how prey density and quality varies across sites. In addition, samples were collected from Kennet Pans and Skinflats in January and March 2009 and from the Realignment site in March 2009, to investigate annual variability in invertebrate biomass. The substrate was sampled using a 5cm diameter cylindrical core pushed 5cm (98cm³) into the benthos and the contents carefully transferred into a sealable plastic bag (Sherfy *et al.* 2000). This depth was chosen as only invertebrates in the top 50mm layer of sediment were considered to be available to most birds (Bryant 1979; Mouritsen & Jensen 1992; Kalejta 1993; Zwarts & Wanink 1993). Samples were wet sieved through a 600µm mesh (Chambers & Milne 1975) within 12 hours of collection and all material retained by the sieve was transferred into plastic vials and stored under 70% ethanol. Samples were identified under a binocular microscope and counted and measured to the nearest 0.01mm using SPOT *Basic* digital imaging software (Windows Version 4.1). The shells of *Hydrobia* and *Macoma* were cracked using fine forceps after measurements were taken to see if shells were empty. In order to quantify the

biomass available for birds, the shell length of the gastropod *Hydrobia ulvae* (Moreira 1996), the shell width of the bivalve *Macoma baltica* (Speakman 1984), the body length of the amphipod *Corophium volutator* (Speakman 1984), and the jaw length of the polychaete *Nereis diversicolor* (Speakman 1984; Zwarts & Esselink 1989; Moreira 1996) were measured. As worms can often become damaged by the corer during sampling, distorted, or shrink during preservation, jaw length of *Nereis* was chosen over body length (Chambers & Milne 1975; Esselink & Zwarts 1989). To assess the energetic quality of foraging sites, these measurements were used to estimate biomass ash-free-dry-weight (AFDW) from allometric equations derived from studies conducted by Speakman (1984) and Warnes (1981) (Table 2.3).

Table 2.3: Equations used to predict prey biomass (DW: Dry weight; AFDW: Ash-free dry weight) from measurements of prey size (x).

Prey type	Size variable (x)	Function	Correction for calculating AFDW (Moreira 1996)	Source
<i>Nereis diversicolor</i>	Jaw length (mm)	Log DW (g) = 2.943 log(x) +1.286	AFDW=0.771DW	Chambers & Milne (1975)
<i>Hydrobia ulvae</i>	Shell length (mm)	Log AFDW(mg) = 2.855 log(x) -1.561	Corrected for 12.5% organic matter in the shell	Warnes (1981)
<i>Macoma baltica</i>	Shell width (mm)	Log AFDW(mg) = 1.24 log(x) -0.741	-	Speakman (1984)
<i>Corophium volutator</i>	Shell length (mm)	Log AFDW(mg) = 1.83 log(x) -3.22	-	Speakman (1984)

2.2.3. Analysis

The two indices measuring prey quality within each site were: 1) mean prey density (individuals m⁻²), calculated as the mean number of invertebrates among core samples at each site, and 2) mean prey biomass (g AFDW m⁻²) calculated as the mean estimated invertebrate ash-free biomass among cores in a site. All predictions were tested using generalised linear models (GLMs), and analysis was carried out in R version 2.9.2 (R Development Core Team 2009). To investigate the role of disturbance on the rate of depletion of foraging grounds, GLMs were fitted to data collected between October 2007 and March 2008 from Kennet Pans (disturbed) and Skinflats (undisturbed). GLMs were constructed using a quasi-Poisson error distribution. *Site*, *Month* and *Month squared* (to control for possible nonlinear seasonal effects) were included as explanatory variables. All invertebrates were combined in the first analysis before species were considered individually. Annual variability in density and biomass was compared using a paired t-test.

It was important to explore the nature of each site to investigate which habitat characteristics influenced the abundance of invertebrates on these intertidal mudflats. We defined five predictors describing seven sites in our study: *site area*, *site length*, *site width*, *substrate resistance*, *site shape* and whether the sites were upriver or downriver of the new bridge (*'site location'*) (Table 2.2). Because the Realignment site was only created in 2008, this site was omitted from the model. Generalised linear models (GLMs) were used to evaluate the influence of each of these predictors on the response variables (mean prey density and mean prey biomass). Density was modelled using a quasi-Poisson distribution and biomass was log-transformed ($\ln+1$) to satisfy model assumptions. Non-significant variables ($p>0.05$) were removed through stepwise deletion and the most parsimonious model was chosen to determine the most important factors influencing invertebrate density. All invertebrates were combined in the first analysis and then species were considered separately to investigate the factors influencing distribution. All analysis were conducted in the R programming language (R Development Core Team 2009).

2.3.RESULTS

2.3.1. *Spatial variation in site quality and species composition*

The overall density of potential invertebrate prey species varied between the sites ($F_{5,63}=4.042$, $p=0.002$) with Kennet Pans and Skinflats holding the highest densities of invertebrates, and Kincardine shore and the Realignment site harbouring the lowest densities (Figure 2.2i). Neither Skinflats nor Kennet Pans held significantly greater densities than Airth (*paired t-test*: $t_9=1.307$, $p=0.196$ and $t_9=1.787$, $p=0.079$ respectively). Sites were also found to vary significantly in terms of total biomass (Figure 2.2ii; $F_{5,63}=6.457$, $p<0.001$). Kennet Pans was the most profitable with significantly greater prey biomass (gAFDW) than Airth ($t_9=-2.436$, $p=0.018$), Kincardine east ($t_9=-2.733$, $p=0.008$), Kincardine shore ($t_9=-3.232$, $p=0.002$), Pow burn ($t_9=-2.987$, $p=0.004$) and the Realignment site ($t_9=3.258$, $p=0.002$). Biomass was significantly greater at Skinflats than at Pow burn ($t_9=-2.197$, $p=0.032$), Kincardine shore ($t_9=-2.507$, $p=0.015$) and the Realignment site ($t_9=-2.935$, $p=0.005$).

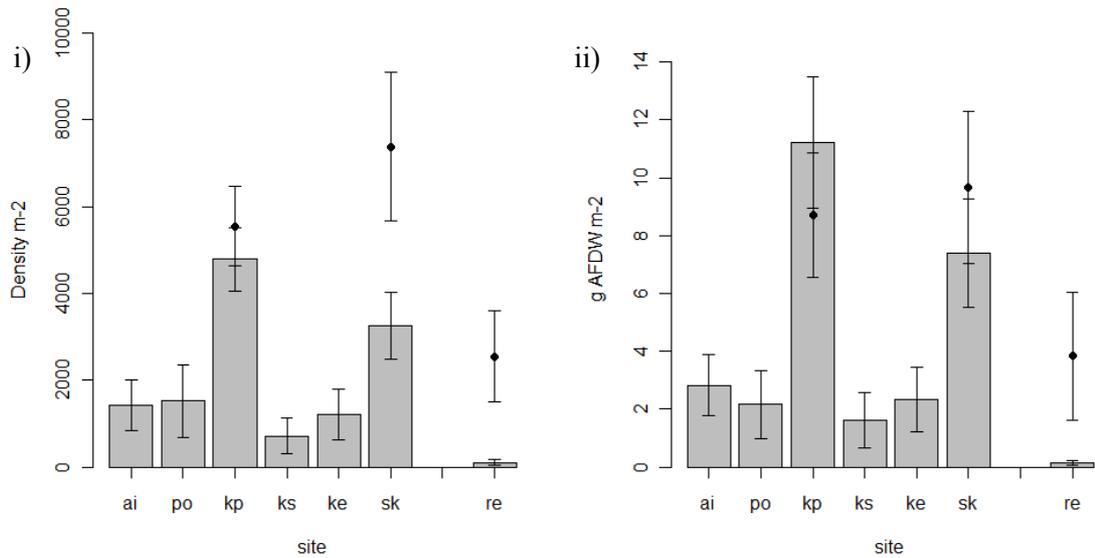


Figure 2.2: Total invertebrate density (i) and biomass (g AFDW) (ii) in the Forth estuary study area (\pm SE). Sites are positioned from upriver (Airth: ai) to the most downriver (Skinflats: sk). The Realignment site (re) is considered separately. Bars represent samples collected in March 2008 and points represent samples collected in 2009.

Hydrobia density (Figure 2.3i) and biomass (Figure 2.3ii) varied between sites ($F_{5,63}=5.002$, $p<0.001$; $F_{5,63}=9.550$, $p<0.001$, respectively). *Hydrobia* density was greatest at Kennet Pans ($2720\text{m}^{-2} \pm 1705$) and no *Hydrobia* were found at Kincardine east or at the Realignment site in 2007/08 (Figure 2.3i). Densities at Kennet Pans and Skinflats, and Skinflats and Airth were similar ($p>0.05$). Sites varied significantly in the density and biomass of *Macoma* found in cores ($F_{5,63}=2.807$, $p=0.017$; $F_{5,63}=2.300$, $p=0.045$). *Macoma* was the only species found in cores collected at Kincardine east and were also common at Kennet Pans and Pow burn where they were found at similar densities. Kennet Pans held significantly greater densities of *Macoma* and at greater biomass at than Airth ($t_9=2.357$, $p=0.022$; $t_9=2.392$, $p=0.020$).

The density of *Nereis* varied significantly across the seven sites (Figure 2.3i; $F_{5,63}=3.396$; $p=0.006$) with the highest densities found at Kennet Pans ($255\text{ indiv. m}^{-2} \pm 136.87$). No significant difference in *Nereis* biomass was found between sites (Figure 2.3ii; $F_{5,63}=1.199$, $p=0.319$). *Corophium* density differed significantly between sites ($F_{5,63}=3.160$ $p=0.009$), where it only occurred at Airth and Kennet Pans. No intersite variation was found for *Corophium* biomass ($F_{5,63}=0.915$, $p=0.490$), possibly due to the low sample size and small body length. The low density of this species found in our study suggests that *Corophium* is not a main prey species for waterbirds on the Forth within the study area.

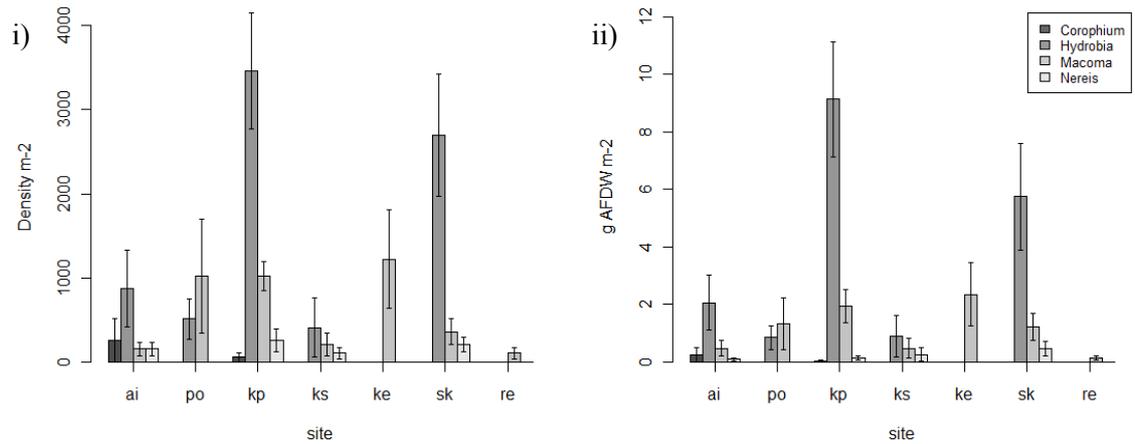


Figure 2.3: Species density (i) and biomass (\pm SE) (ii) in the Forth estuary study area in March 2008. Sites are sequenced from upriver (Airth: ai) to the most downriver (Skinflats: sk). The Realignment site (re) is considered separately.

Skinflats and Pow burn were both dominated by *Hydrobia* under 2mm long March 2007 (Figure 2.4i). Kennet Pans held the highest densities of *Hydrobia* >2mm while Airth and Kincardine shore were dominated by *Hydrobia* between 2mm and 3mm. Although all sites held populations of *Macoma*, few individuals were larger than 4mm (Figure 2.4ii). Kennet Pans and Pow burn were dominated by small *Macoma* (<4mm) while the downriver sites Skinflats and Kincardine east held greater densities of a middle size class (4-8mm) while Kennet Pans held the greatest densities of >8mm *Macoma*. *Nereis* collected upriver of the Clackmannanshire Bridge at Airth and Kennet Pans, occurred in size classes smaller than 30mm (Figure 2.4iii). *Nereis* grew larger at Skinflats and Airth while smaller worms (<20mm) and medium sized worms (20-60mm) were not recorded at Skinflats and Airth.

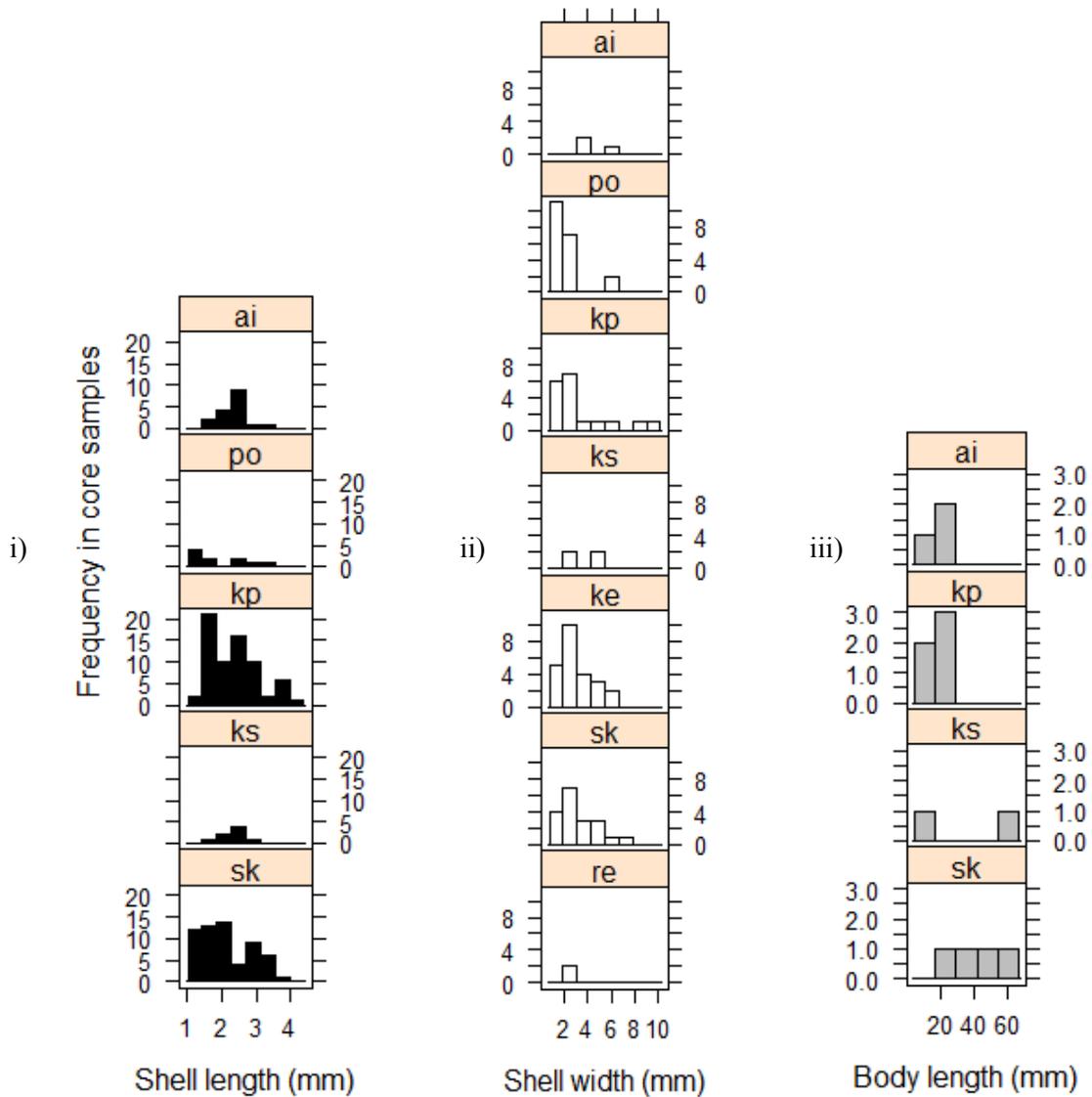


Figure 2.4: Size-frequency histograms of i) *Hydrobia* (black), ii) *Macoma* (white) and iii) *Nereis* (grey) at all sample sites on the Forth estuary in March 2007/08. Sites sequenced from upriver-downriver. The Realignment site is considered separately. *Nereis* body length was calculated using regression equation: Body length (mm) = 48.417*(jaw length (mm))^{1.5674} (Chambers & Milne 1975).

2.3.2. Temporal variation in prey quality

There was no evidence that the rate of depletion varied between Kennet Pans and Skinflats for total prey density (*interaction*; $F_{1,116} < 0.001$, $p = 0.979$) or prey biomass (*interaction*; $F_{1,116} = 0.504$, $p = 0.479$). Prey density and total prey biomass were negatively related to time ($F_{1,118} = 4.355$, $p = 0.039$; $F_{1,118} = 5.301$, $p = 0.023$). Prey density and biomass were similar between sites ($F_{1,117} = 0.493$, $p = 0.473$; $F_{1,117} = 0.366$, $p = 0.547$). Total prey density was similar between winters at both Kennet Pans and Skinflats (Figure 2.2i; $t_9 = 0.559$, $p = 0.59$; $t_9 = -2.194$, $p = 0.056$), as was total prey biomass (Figure 2.2ii; $t_9 = 0.639$, $p = 0.539$; $t_9 = -0.736$, $p = 0.48$).

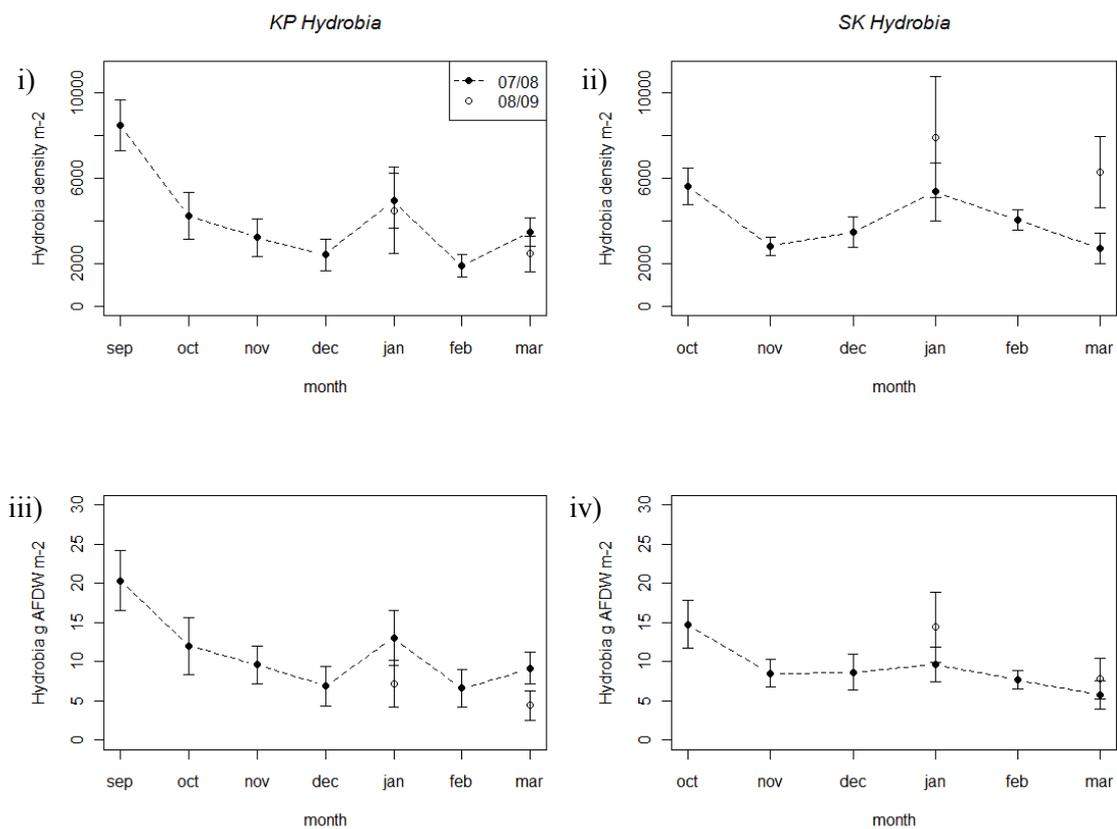


Figure 2.5: Mean *Hydrobia* density (\pm SE) at Kennet Pans (i) and Skinflats (ii) and mean *Hydrobia* biomass (\pm SE) at Kennet Pans (iii) and Skinflats (iv) from monthly sampling in winter 2007/08 (solid points) and winter 2008/09 (open points).

There was no evidence to suggest that *Hydrobia* density or biomass depletion rates differed between sites (*interaction*; $F_{1,116} = 0.053$, $p = 0.818$; *interaction*; $F_{1,116} = 1.128$, $p = 0.290$). *Site* had no significant effect on either *Hydrobia* density ($F_{1,118} = 1.492$, $p = 0.224$) or biomass ($F_{1,118} = 0.075$, $p = 0.785$) suggesting *Hydrobia* were similar at Kennet Pans and Skinflats. Although depletion over time was not evident for *Hydrobia* density (Figures 2.5i and ii; $F_{1,117} = 1.176$, $p = 0.184$), *Hydrobia* biomass decreased with time (Figures 2.5iii and iv; $F_{1,118} = 4.819$, $p = 0.030$). There was no annual variation in *Hydrobia* density at Kennet Pans in January or March sampling (Figure 2.5i; $t_9 = 0.144$, $p = 0.888$; $t_9 = 1.736$, $p = 0.117$). *Hydrobia*

densities were also similar between winters in January and March sampling at Skinflats (Figure 2.5ii; $t_9=1.284$, $p=0.231$, $t_9=-0.491$ $p=0.635$). Similarly, *Hydrobia* biomass did not vary between winters at either Kennet Pans (Figure 2.5iii; $t_9=0.932$, $p=0.364$; $t_9=2.089$, $p=0.052$) or Skinflats (Figure 2.5iv; $t_9=0.257$, $p=0.803$, $t_9=-0.477$, $p=0.645$).

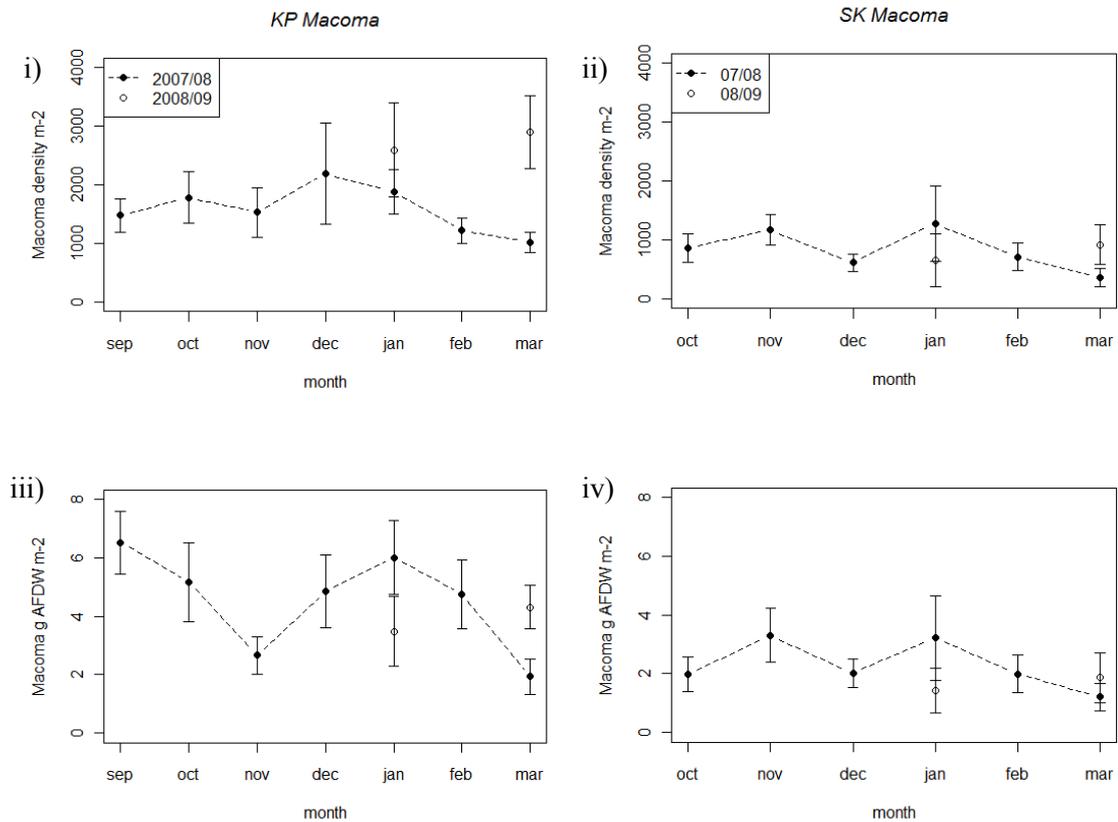


Figure 2.6: Mean *Macoma* density (\pm SE) at Kennet Pans (i) and Skinflats (ii) and mean *Macoma* biomass (\pm SE) at Kennet Pans (iii) and Skinflats (iv) from monthly sampling in winter 2007/08 (solid points) and winter 2008/09 (open points).

Over the course of a winter, Kennet Pans held consistently more *Macoma* (Figures 2.6i and iii) and at a greater biomass (Figures 2.6ii and iv) than Skinflats ($F_{1,118}=11.202$, $p<0.001$; $F_{1,118}=11.873$, $p<0.001$). *Macoma* biomass showed a marginally negative relationship with $month^2$ ($F_{1,117}=4.141$, $p=0.041$), with numbers remaining relatively constant until January when biomass decreased in late winter. Density however, did not vary significantly with $month$ ($F_{1,117}=4.141$, $p=0.064$) or $month^2$ ($F_{1,116}=4.141$, $p=0.081$). As with *Hydrobia*, there was no evidence that *Macoma* numbers were depleted at a faster rate at Skinflats than at Kennet Pans (*interaction*; $F_{1,115}=0.035$, $p=0.852$). At Kennet Pans, *Macoma* density was similar between winters in both January or March sampling (Figure 2.6; $t_9=-0.126$, $p=0.903$; $t_9=-0.431$, $p=0.677$). Although *Macoma* biomass was similar in January sampling at Kennet Pans (Figure 2.6iii; $t_9=1.553$, $p=0.155$), biomass was significantly greater in March 2009 than in 2008 ($t_9=-2.798$, $p=0.021$). *Macoma* density (Figure 2.6ii) and biomass (Figure 2.6iv) did not vary

between winters at Skinflats in either January ($t_9=0.475$, $p=0.646$; $t_9=0.726$, $p=0.468$) or March sampling ($t_9=-0.548$, $p=0.597$; $t_9=-0.341$, $p=0.741$).

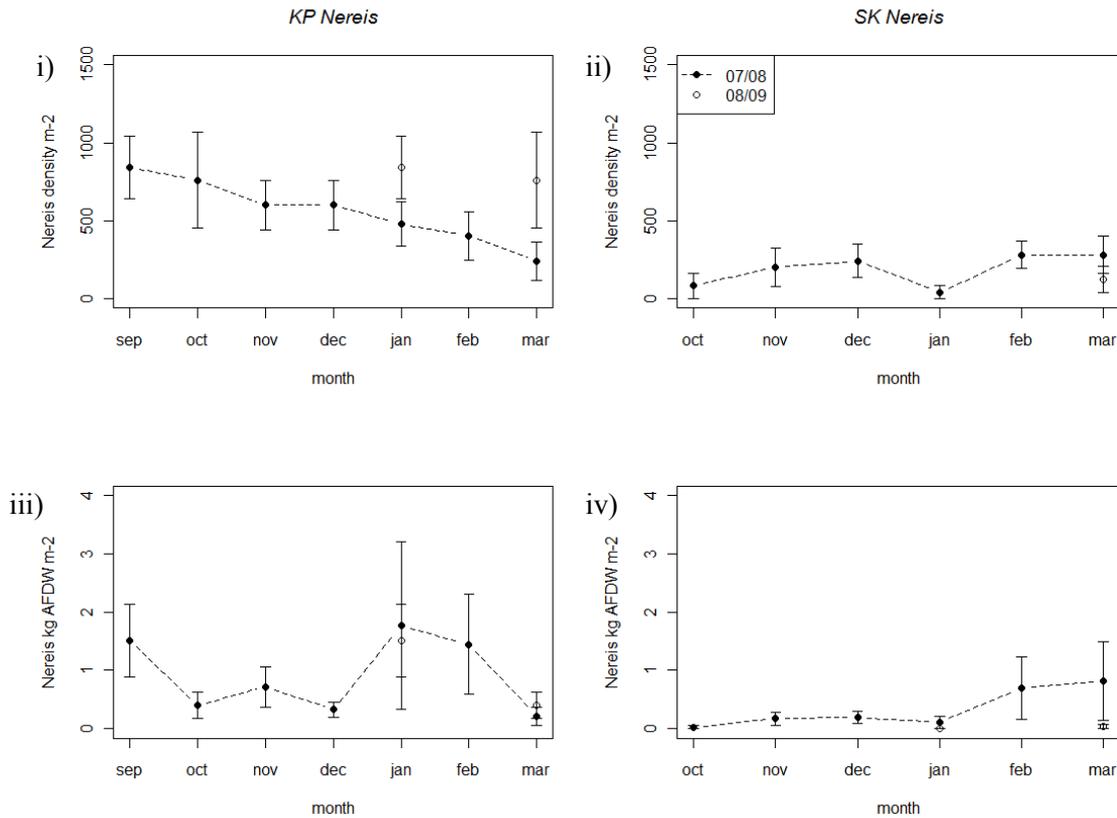


Figure 2.7: Mean *Nereis* density (\pm SE) at Kennet Pans (i) and Skinflats (ii) and mean *Nereis* biomass (\pm SE) at Kennet Pans (iii) and Skinflats (iv) from monthly sampling in winter 2007/08 (solid points) and winter 2008/09 (open points).

Nereis density were depleted at a significantly greater rate at Kennet Pans (Figure 2.7i) than at Skinflats (Figure 2.7ii; *interaction*; $F_{1,116}=5.136$, $p=0.025$). Kennet Pans held 580 more *Nereis* m⁻² in October but whereas *Nereis* density remained at low densities throughout the winter at Skinflats, prey was depleted throughout the winter until prey were at similar densities midway between February and March 2008. No evidence of biomass depletion was found for *Nereis* at either site (*interaction*; $F_{1,118}=1.153$, $p=0.221$). There was no significant annual variation in *Nereis* density in January or March samples at Kennet Pans ($t_9=-0.390$, $p=0.701$; $t_9=0.452$, $p=0.657$). Similarly, biomass did not vary between winters in either January or March sampling ($t_9=0.530$, $p=0.606$; $t_9=0.092$, $p=0.928$). Similarly, there was no annual variation in *Nereis* density at Skinflats in either January or March sampling ($t_9=-1.497$, $p=0.169$; $t_9=0.002$, $p=0.963$). *Nereis* biomass was also similar between winters for both January and March sampling ($t_9=-0.439$, $p=0.666$; $t_9=0.970$, $p=0.350$).

2.3.3. Colonisation of managed realignment site

The Realignment site was re-sampled in March 2009 to monitor the development of the site with respect to prey quality. Total invertebrate density was significantly greater in winter 2008/09 than winter 2007/08 (Figure 2.2i; $t_9=-2.296$, $p=0.036$). Total biomass also increased in the second year following the removal of the sea wall (Figure 2.2i; $t_9=-2.402$, $p=0.038$). In the first sampling year (2007/08), only low densities of *Macoma* were collected in core samples (Figure 2.8i). These individuals were collected from sampling stations located on pre-existing mudflats between the old sea wall and the MLWS. No *Hydrobia*, *Corophium* or *Nereis* were collected at any station within the Realignment site in the first winter following the breach (winter 2007/08). In the second winter, all four study species were found within the Realignment site.

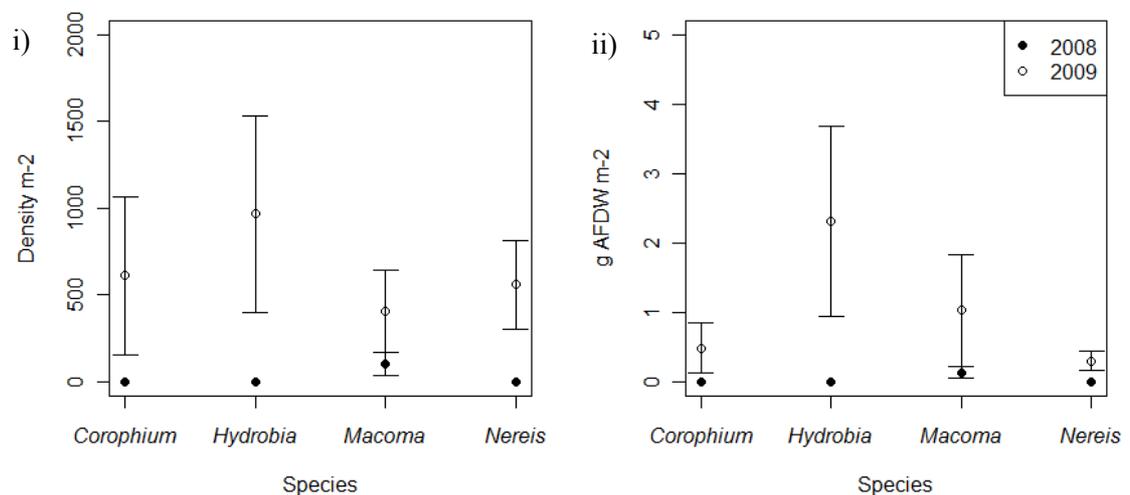


Figure 2.8: Species density (i) and biomass (\pm SE) (ii) at the Realignment site in March 2008 (first winter) and March 2009 (second winter).

Hydrobia were found in significantly higher densities in the second winter following the breach (Figure 2.8i; $t_9=-2.407$, $p=0.004$) although the increase in AFDW was non-significant (Figure 2.8ii; $t_9=-2.037$, $p=0.072$). *Nereis* density and biomass increased significantly within the Realignment site in the second winter ($t_9=-2.978$, $p=0.016$; $t_9=-2.325$, $p=0.045$). There was no evidence to suggest *Macoma* density or AFDW differed in the two winters following the sea wall breach at the Realignment site ($t_9=-0.727$, $p=0.485$; $t_9=-1.106$, $p=0.297$). Although *Macoma* were generally larger in the second winter (shell width= $3.69\text{mm} \pm 0.78\text{SE}$) than in the first winter (shell width= $2.23\text{mm} \pm 0.11\text{SE}$), this increase was non-significant ($F_{1,8}=0.396$, $p=0.547$) with the largest individual 7.37mm wide. There was no evidence to suggest *Corophium* density and biomass was any greater in this second winter ($t_9=-1.942$, $p=0.084$; $t_9=-1.557$, $p=0.154$), however nine *Corophium* were collected from a single sample station in March 2009 (length= $5.05\text{mm} \pm 0.48\text{SE}$), illustrating their often patchy distribution.

2.3.4. Impact of site factors on invertebrate density and biomass

In the GLM, *site width* and *substrate resistance* positively affected both total invertebrate density ($F_{1,56}=9.088$, $p=0.004$) and total invertebrate biomass ($F_{1,56}=9.088$, $p=0.004$). Substrate resistance increased with increasing site width suggesting that narrow mudflats also have the greatest penetrability. There were no convincing effects of *site area*, *length*, *location* or *site shape* on invertebrate density or biomass. The interaction between *substrate resistance* \times *site width* remained highly significant for *Hydrobia* biomass, with broad sites with low penetrability holding the greatest biomass ($F_{1,55}=6.840$; $p=0.011$). Sites south of the Clackmannanshire Bridge also held greater *Hydrobia* biomass than those sites north of the bridge ($F_{1,56}=6.141$, $p=0.016$). Significant interactions within the *Hydrobia* density model between *substrate resistance* \times *site width* ($F_{1,52}=10.556$, $p=0.002$), *resistance* \times *site length* ($F_{1,52}=10.202$, $p=0.002$) and *resistance* \times *area* ($F_{1,52}=8.530$, $p=0.005$) suggests *Hydrobia* density was greatest in large, broad mudflats with low substrate penetrability. Although *location* was important for *Hydrobia* biomass, it had no significant effect on *Hydrobia* density. There was no correlation with any of the site factors for *Macoma* density, suggesting that there must be some other factor affecting *Macoma* numbers in our study area. *Macoma* biomass was positively correlated with *substrate resistance* and *site width*, with a significant interaction present between the two ($F_{1,56}=4.304$, $p=0.043$). *Site width* was the only term significantly associated with *Nereis* density ($F_{1,58}=5.289$, $p=0.025$), with higher densities found on broader mudflats. However, the picture for *Nereis* biomass was more complex with significant interactions present between *substrate resistance* \times *width* ($F_{1,52}=5.450$, $p=0.024$), *resistance* \times *site shape* ($F_{1,52}=8.031$, $p=0.007$) and *resistance* \times *site area* ($F_{1,52}=6.973$, $p=0.011$). There was no correlation with any of the site factors for *Corophium* density or biomass. The most parsimonious model for *Corophium* was the null model with no effect of *site*, *shape*, *width*, *length*, *area*, *location* or *penetrability*.

In summary, *site width* and *substrate resistance* proved to be the most important factors governing invertebrate abundance. On an individual species level, *site width* and *substrate resistance* was also important for *Hydrobia*, *Nereis* and *Macoma*. Those sites downriver of the Clackmannanshire Bridge held greater *Hydrobia* biomass but densities were similar. From our results, it would appear that the least profitable foraging grounds for birds were found in narrow sites with high substrate penetrability.

2.4.DISCUSSION

2.4.1. Prey types and their distribution on foraging substrates

Because shorebirds on estuaries are usually aggregated in areas with abundant food supplies (Bryant 1979), we would expect shorebirds to distribute themselves at greater densities at these sites (Sutherland 1983). Accordingly, any impacts of anthropogenic disturbance must be considered alongside the concurrent effects of variation in site quality. The density and biomass of prey varied greatly between the component sites in our study area. Kennet Pans and Skinflats held the highest concentrations of benthic invertebrates, whilst prey density was lowest at Kincardine shore. The most abundant inhabitant of Kennet Pans was the gastropod *Hydrobia*, with many individuals in the size range preferred by Shelduck, Redshank and Dunlin. Lower densities of *Macoma*, *Nereis* and *Corophium* were collected at this site, in a broad range of size classes fitting dietary preferences of Curlew, Oystercatcher, Knot, Redshank, Shelduck and Dunlin. We would therefore expect these waterbirds to be abundant on Kennet Pans if birds on the Forth illustrate a numerical response to prey density. A similar pattern was found for Skinflats, although *Nereis* occurred at greater body lengths so we would expect feeding Curlew densities to be greater there. *Macoma* were fewer at Skinflats but more abundant in the 4-6mm size category preferred by Redshank, Knot and Shelduck.

Airth and Pow burn held similar densities of prey, however this was around 50% of those present at Kennet Pans and Skinflats. Due to the relatively small size of prey items, furthermore, the inter-site differences in ash-free biomass were even greater. Small prey may also be rejected because of their low profitability (Piersma *et al.* 1993). The *Hydrobia* and *Macoma* found at Pow burn were mostly under the range favoured by Redshank, and *Nereis* were absent from this site altogether. Airth held greater densities of *Nereis* and *Hydrobia* than at Pow burn and Kincardine shore, and in the size classes favoured by Redshank, Dunlin and Shelduck. Our data fits well with previous sampling between Dunmore and Airth where small numbers of bivalve spat *Macoma* were found but did not appear to grow into adult populations (McLusky 1978). Accordingly, we would expect Pow burn to hold relatively low overall densities of feeding birds and Airth to hold relatively high densities of Redshank, Dunlin and Shelduck, but few feeding Oystercatcher or Curlew.

Kincardine shore held very low densities of *Hydrobia* and *Macoma* in the size range harvestable by Redshank, Dunlin and Shelduck. *Nereis* also occurred at low densities there, however Curlew may have profited from the large worms present here. High densities of *Macoma* were found at Kincardine east in the size classes favoured by Redshank, Shelduck and Knot. *Nereis*, *Corophium* and *Hydrobia* however were all absent from this site. Steeper mud slopes and lower substrate resistance were typical of the poorer foraging habitat for shorebirds as they also held the lowest densities and biomass of benthic prey. The low densities of surface dwelling

invertebrates such as *Hydrobia* and *Corophium* at Kincardine east and Kincardine shore may also be explained by the rapid water flow around the area of the bridges due to the natural bottleneck in the coastline.

The correlative nature of our study, the small number of sites and close proximity of these sites, however, places constraints on our ability to generalise about the influence of habitat characteristics on prey availability. While this may reduce confidence for the application of optimal habitat characteristics on intertidal areas outside the Forth complex, our aim was to collect a representative sample from those areas surrounding the Kincardine and Clackmannanshire Bridges. While future study should incorporate a broader suite of sampling locations from a number of UK and European estuaries, our findings have practical applications for the creation of intertidal habitat on the Forth estuary through managed realignment.

At some localities, *Corophium* is an important prey item for Redshank and is preferred to *Nereis* where it occurs at greater densities (Goss-Custard 1977). *Corophium* occurred at very low densities in our study, and was absent from several sites including North Skinflats where they are known to be present (Warnes 1977). This species are known to be patchily distributed at Skinflats and on the Forth as a whole (Warnes 1977; McLusky *et al.* 1976). Positive associations of *Corophium* densities with feeding distributions of Redshank have been indicated on the Forth (Bryant 1979), however samples of Redshank pellets from Skinflats roost sites show *Hydrobia*, *Nereis* and *Macoma* were the most frequent prey harvested by birds (Warnes 1977). Our study fits in well with previous literature that regards *Corophium* as of low or of very localised importance on the Forth estuary.

McLusky (1987) found *Corophium*, *Hydrobia* and *Macoma* to be lower than expected upriver of the Kincardine Bridge. This was due to high levels of organic loading from Stirling, Cambus and Alloa creating organic enrichment and severe oxygen depletion in this part of the estuary (Leatherland 1987). Our study found prey densities up- and downriver of the bridges were similar, with only *Hydrobia* biomass dependent on the location relative to the Clackmannanshire Bridge. Although our study sampled only a small part of the estuary, our findings suggests that organic loading is no longer a problem on the upper Forth, due to improved water quality and tighter regulations on farming practices (McLusky *et al.* 1993). Increasing prey densities in upper Forth, over time, could cause a shift in the distribution of birds from downriver to upriver. Investigation of historical data on estuary wide counts such as WeBS high tide counts (BTO) for the Forth estuary should reveal if this is the case.

2.4.2. Annual variation in intertidal invertebrates

Apart from *Macoma* biomass, which was greater at Kennet Pans in March 2009, there was no evidence to suggest invertebrate density or biomass varied between years. Annual variation in benthic invertebrates is common on the Dutch and German Wadden Sea (Zwarts & Wanink

1993). However, fluctuations may be smaller in more sheltered estuaries with higher average winter temperatures (Ens *et al.* 2004). For example, cockle stocks in the eastern Schelde, an estuary in the southern Netherlands, exhibit very low annual variation (Ens *et al.* 2004); similarly the Exe estuary in south west England shows little variation in mussel biomass between winters (McGrorty *et al.* 1990). For the purpose of our study, we can assume there was little or no variation in invertebrate prey between winters. It is unlikely, therefore, that annual differences in shorebird abundance in the study area are a consequence of substantial changes in invertebrate food supplies.

2.4.3. Seasonal variation in intertidal invertebrates

As predicted, our study showed a general pattern of prey depletion across seasons. The maximum densities of *Hydrobia*, *Nereis* and *Macoma* all occurred in early winter, becoming scarcer as the winter progressed. Between September and February, for example, the density of *Hydrobia* at Kennet Pans declined from 6640m⁻² to 1480m⁻². If prey occurs at lower densities and biomass, birds will have to commit more time to searching for food in order to meet daily energy requirements. For example, Bryant and Leng (1975) found Shelduck at Skinflats spent more time feeding as food availability declined. In addition, the body condition of prey is typically 30-60% lower in winter than in summer (Zwarts & Wanink 1993), consequently more prey must be eaten per unit time to obtain a given energy intake rate. Behavioural studies should take this seasonal decline in site quality into account when investigating the impact of disturbance on foraging rates, time budgets and habitat use within the estuary.

If waterbirds used Skinflats preferentially, the rates of prey depletion would have been higher in this site than in Kennet Pans. Both sites, however, held similar total prey densities and biomass and were depleted at comparable rates throughout the winter. Although *Hydrobia* and *Macoma* biomass were negatively correlated with time, there was no evidence of depletion of *Hydrobia* and *Macoma* density. This suggests the larger *Hydrobia* were being depleted faster than the smaller size classes. As smaller size classes are generally rejected by waterbirds, whereas no size selectivity is expected from weather-related mortality, it is therefore likely that this decline was due to predation.

In October, Kennet Pans held almost 600 more *Nereis* m⁻² than Skinflats and was rapidly depleted throughout the winter. In contrast, densities at Skinflats remained relatively constant until February when they became more abundant. Curlew feeding on *Nereis* achieve their highest intake rates in late winter, and not, as expected, in summer or autumn when prey densities are highest (Zwarts & Esselink 1989). Whereas in summer *Nereis* mostly remain in their burrows to filter food from the overlying water, in winter they feed more frequently on the substrate around their burrows, especially on sunny days in late winter and early spring (Esselink & Zwarts 1989). A switch in behaviour to feed at the surface of the mud in February

and March may result in an increase in worm availability in late winter. Although the sampling procedure in this study was adequate to estimate the densities of most intertidal invertebrates, it was probably not adequate to estimate the densities of polychaetes, which may be able to retract up to 30cm into burrows when sampling (Muus 1967; Goss-Custard 1977). Although *Nereis* burrows on the Forth seldom exceed 15cm long (Speakman 1984), by taking 15cm diameter core samples at least 40cm deep, this change in vertical distribution would not have affected estimates of *Nereis* density.

2.4.4. Success of the Realignment site

The rate of colonisation of the Realignment site should depend on the life history traits of the species concerned. We would expect the first species to colonise the site to be the most mobile, short-lived and have a long breeding season (Atkinson *et al.* 2004; Crowther 2007). Contrary to predictions, the only species found in sampling in the first winter was the bivalve *Macoma*, a species whose adult stages are considered to be relatively immobile. Evans and others (1998; 2001) found *Macoma* to be rare at the Seal Sands Managed Realignment Site in Teeside seven years after its creation. Similarly, Atkinson and others (2001; 2004) found no bivalves in the four years after the creation of Orplands Managed Realignment site in Essex, despite being abundant on adjacent mudflats. Mature *Macoma* however, were found to have colonised Nigg Bay (Cromarty Firth) in the first year after the site was created (Crowther 2007). The *Macoma* found in our study were at stations located between MLWS and the original sea wall. Stations located on the dredged earth north of the original sea wall were absent of invertebrates in the first winter. It is possible that the *Macoma* found at the Realignment site, therefore, were present before the breach; rather than immigrants driven from other parts of the Forth by wind or wave action, as was the case at the restored habitat at Nigg Bay (Crowther 2007).

Hydrobia, *Nereis* and *Corophium* were all present at the Realignment site in the second winter following the breach (2007/08). Many of these individuals were also found at stations located behind the line of the original sea wall. *Corophium* and *Nereis* are both mobile species (Goss-Custard *et al.* 1984; Atkinson *et al.* 2001) capable of moving into the site from the ingress of the first tide. Colonisation of this site by larval *Hydrobia* and *Nereis* is therefore likely to have occurred during summer 2008. Adults may also colonise new areas and exploit resources by migrating in the water column (Armonies 1994) or floating on the surface using mucosal rafts (Jackson 2000). *Corophium* usually favour muddy sands rather than the fine-grained mud sediments found in the upper Forth (McLusky 1987; Mouritsen *et al.* 1998), the coarse sediment and the absence of competitors in the Realignment site (Jensen & Mouritsen 1992; Jensen & Andre 1993) may have encouraged the rapid settlement of this species.

Often, there is a tendency for created coastal habitats to lack the diversity seen in natural habitats and support only generalist species (Atkinson 2003). Atkinson (2004) found that even

after five years, the waterbird and invertebrate assemblages on the Blackwater estuary Realignment sites were still developing. Because of the close proximity of the Realignment site to Kennet Pans, the highest quality site sampled, we would expect recruitment to be high and the Realignment site to be rapidly colonised. The invertebrate species which colonised this site were generally preferred prey and are of suitable size to be exploited by Redshank, Dunlin and Shelduck. We would therefore expect these waterbirds, already present on neighbouring mudflats, to move into the Realignment site in winter 2008/09 in order to profit on these prey species.

2.5.CONCLUSIONS

Studies of disturbance often demonstrate that wildlife regularly show strong avoidance towards humans, however the effect of confounding factors are rarely checked. Here, we conclude that due to the negligible variation in invertebrate prey during the study period, should evidence for numerical, spatial and behavioural changes amongst waterbirds be found, coincident with bridge construction, these are likely to be due to anthropogenic factors rather than to substantial changes in the local estuarine environment. Sites in our study varied greatly in prey quality, with Kennet Pans and Skinflats revealed as the best sites for birds in terms of prey densities and biomass. Low quality sites such as Kincardine east, Airth and Kincardine shore may not be capable of sustaining displaced birds from Kennet Pans, and, at least, would provide a less profitable site to exploit.

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Chapter 3

The impacts of disturbance related to bridge construction work on numbers, distribution and behaviour of waterbirds of the Forth estuary

3. The impacts of disturbance related to bridge construction work on numbers, distribution and behaviour of waterbirds of the Forth estuary

This study forms part of a governmental report to Babbie Group and SNH investigating the direct and indirect impacts on waterbirds of a major engineering project in central Scotland; construction of the new Clackmannanshire Bridge at Kincardine-on-Forth. The impact of disturbance from construction work around the bridge site on waterbird densities was studied over a six-year period. The impact of construction disturbance on Common Redshank and Common Shelduck feeding behavior was also examined.

Contrary to our predictions, waterbird numbers increased in our wider study area during the construction phase. Although ducks are widely thought to be the most prone to human disturbance, our study showed that duck numbers increased in the areas adjacent to the construction site during construction. This was partly due to an increase in Eurasian Teal at Kennet Pans, which may have benefited from the reduced public access to the site during the construction phase. Oystercatcher also increased in the areas bordering the construction site, where they benefited from the installation of the new roosting area at the managed realignment site. Cormorant and Redshank were least tolerant of the disturbance and total numbers within the study site declined during the construction period. The greater densities of feeding Redshank and roosting Cormorant occurring on the higher flats near Kincardine Bridge, consequently made them vulnerable to habitat disturbance in this area. Evidence is also presented whereby displaced Redshank were forced to use an arguably more dangerous and less profitable site, in preference to those which are prey-rich, have lower competitor densities and have a reduced risk of attack from land-based raptors.

Both Redshank and Shelduck dedicated more time to foraging during the winter with bridge construction compared to the winter without construction. Foraging was negatively related to increasing temperatures and a greater proportion fed at low temperatures during construction work. Our findings suggest Shelduck were able adapt to disturbance by spending more time feeding in the water than on land. This may further explain why duck numbers increased within the study in areas surrounding the bridges, while wader species, unable to take advantage of new or supratidal roosts or find greater security on the water, declined.

3.1. INTRODUCTION

Many estuaries in the UK and elsewhere have been affected by anthropogenic activities, including agriculture, industry and transport (Davidson 1991). Some of these activities involve landscape-scale engineering, leading to land-claim, changes in land use, drainage and sometimes modification of adjacent habitats (Smart *et al.* 2006; Burton 2007). After a period of relative stability, pressure on UK estuaries has increased in recent years with the passing of the EU Renewable Energy directive to extend energy production from renewable sources. The rate and scale of developments such as offshore wind farms and tidal barrages raises questions about possible negative impacts of these structures on wildlife (Clark 2006; Bright *et al.* 2008). This impact may be direct, such as when feeding grounds or habitats are permanently lost, or indirect, when natural areas become unavailable, in the short or longer term, because of increased human disturbance (Hockin *et al.* 1992; Marsden 2000; Burton *et al.* 2002).

While the direct effect of anthropogenic activity has been widely examined (Williams & Hall 1987; Lambeck *et al.* 1989; Percival *et al.* 1998; Durell *et al.* 2005; Burton *et al.* 2006; Dias *et al.* 2006; West & Caldow 2006), the scale and implications of indirect effects are less well known. Studies have shown how proximity to man-made landscape features such as roads, paths and cycle routes can affect spatial variation in bird numbers or densities (Burton *et al.* 2002). Others have quantified levels of human disturbance, such as hunting pressure or visitor number at wildlife reserves, and related them to bird usage and species richness within sites (Burger & Gochfeld 1998; Beale & Monaghan 2005). With respect to new engineering projects, disturbance from works can play a significant role in reducing the attractiveness of a habitat (Hockin *et al.* 1992; Burton *et al.* 2002). Prater (1981) states that shorebirds, and to a greater extent wildfowl, will move away from the vicinity of active workings, concluding that construction effects may be significant locally and engineering operations should avoid proximity to established roost sites. In a study delta in south-west Netherlands, Meire (1989) found the densities of diving ducks to be unrelated to food supply but negatively affected by coastal engineering works. In a study investigating the impact of eight estuarine bridge crossings in Scotland on shorebird density and behaviour, however, Logie & Bryant (1994) found no evidence of reduced densities or restricted movements of estuarine waterbirds in areas surrounding bridges.

However, estuaries are heterogeneous habitats and waterbird distributions may be due to variations in factors such as food supply, substrate type and proximity to roost sites. There is also likely to be considerable autocorrelation between the effects of different landscape features such as the proximity to footpaths and the distance to predator-concealing cover (Burton 2007). Because of these factors, few studies of displacement due to disturbance are conclusive, often due to a lack of before-after-control-impact (BACI) assessments (Drewitt & Langston 2006). By introducing new sources of disturbance to an area, a better understanding of the role of human

disturbance may be achieved (Burton 2007). In a study on Galveston Bay, Texas, Mueller & Glass (1988) found that drilling at oil wells adjacent to waterbird colonies, reduced the number of returning nesting wading birds the following year. Birds were thought to be most susceptible during the early spring, when individuals were selecting nest sites and establishing territories. Burton *et al.* (2002) found disturbance from the construction of the Cardiff Bay barrage caused a reduction of Oystercatcher *Haematopus ostralegus*, Dunlin *Calidris alpina*, Curlew *Numenius arquata*, Shelduck *Tadorna tadorna* and Redshank *Tringa totanus* on adjacent intertidal mudflats. The feeding activity of Redshank, Oystercatcher and Dunlin were also reduced in adjacent count sections.

Studies have shown that when people are present, animals may attempt to decrease risk by spending less time foraging and more time scanning for approaching humans (Burger & Gochfeld 1991; Thomas *et al.* 2003). Burger (1988) found that the activities associated with demolition work reduced the feeding efficiency of waterbirds throughout the day. Long-term effects are manifested through continued high-level disturbance reducing available feeding time and raising energy expenditure above a threshold, beyond which the site becomes unprofitable as a feeding area (Hockin *et al.* 1992).

This study considers the direct and indirect impacts on waterbirds of a major engineering project in central Scotland; construction of the new Clackmannanshire Bridge at Kincardine-on-Forth (56°38'N, 2°37'W). Construction of the 1.2km bridge and its associated infrastructure began in June 2006 with all major works completed by November 2008. Rather than concentrate on individual disturbance events, we were interested in the long-term effects of construction disturbance, in particular whether waterbirds were affected in the immediate vicinity of the bridge. In this way, we would be able to ascertain if the disturbance caused by construction works depressed local habitat quality and therefore the overall carrying capacity of the estuary. Long-term monitoring maximises the probability of capturing those individuals which habituate rapidly to disturbance, and those individuals which may only tolerate disturbance as a last resort once food resources are depleted (Owens 1977). If there is a decline in species number within the vicinity of works, then those individuals may not have become habituated to the nature of the noise and activities associated with construction work.

3.1.1. Study aims

The principal aim of this study was to investigate the indirect impact of the construction of the new Clackmannan Bridge on waterbird populations and on the integrity of the Firth of Forth SPA. This will include an assessment of whether there has been a depression in bird numbers or a reduction in access by waterbirds to important roosting sites, intertidal foraging areas or open waters around the new and existing bridges. This study considered how bridge construction altered the perception of site quality, how the temporal pattern of site usage changed with bridge

construction and how this affected the behaviour of shorebirds and wildfowl within the vicinity of the bridge.

3.1.2. Study area

The study area comprised the intertidal area around the two Kincardine bridges, known to hold substantial populations of Pink-footed Geese *Anser brachyrhynchus*, Shelduck, Knot *Calidris canutus*, Dunlin and Redshank during the winter months (Bryant 1976; Newton & Bryant 1991). Surveys were conducted upriver of the bridges, west towards Dunmore on the south shore (NS 896893) and Kennet Pans on the north shore (NS 888912) (Figure 3.1). Downriver, the study area extended east as far as Powfowlis on the Skinflats SSSI (NS 859923) and a comparable section of the intertidal habitats on the north shore (NS 860939). Birds found in the area of mud, mid-channel between Pow burn and Dunmore village which was exposed during low-water spring tides, were included in the 'Airth' sector counts (Figure 3.1). A full description of the intertidal habitats of the Forth estuary can be found in the Environmental Statement (Babtie Group 2003). A list of waterbird and raptor species found in the study area during the six-year survey can be found in Appendix 3.1.

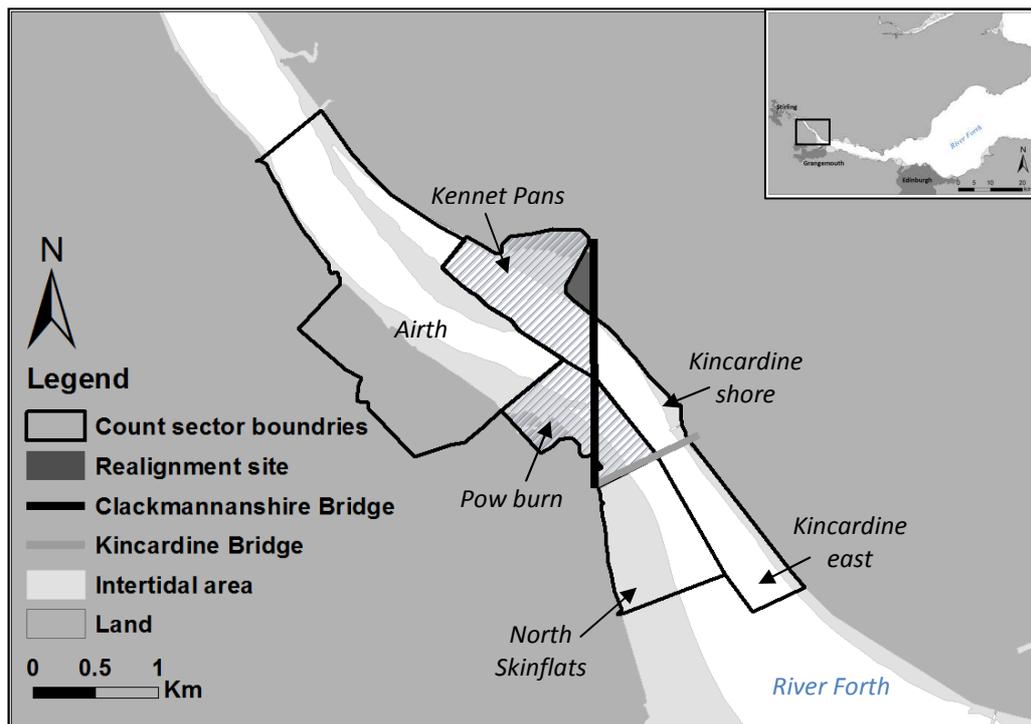


Figure 3.1: Map of study site showing count sector boundaries, the realignment site and the two bridges. The new Clackmannanshire Bridge lies between the Realignment site and Kincardine shore; and intersects the Pow burn count sector. The Kincardine Bridge divides the Pow burn and Kincardine shore sectors from the Skinflats and Kincardine east count sectors. Sectors likely to be disturbed by construction activity (i.e. those bordering the construction site) are shaded grey.

3.1.METHODS

Permission was granted to use population data collected prior to bridge construction (Babtie Group 2003; 2006; 2006; 2007). Counts began in November 2003 and continued between November and March each year until the works began in July 2006 (Jacobs UK Ltd, *unpublished*). These data were combined with monitoring data collected between November 2006 and March 2009 by R.G. Dwyer to build a complete picture of habitat use in the area of the bridges over the past six years.

The abundance and distribution of all waterbirds were sampled using a type of through-the-tide count (TTTC) performed three times per week covering ebb, flow, spring and neap tides. TTTCs sample intertidal areas at different tidal heights to create a complete picture of bird usage and each species' dependence on all levels of mudflats across all tidal states. The type of TTTC used in this study allowed several count sectors to be observed per day, rather than a single sector as with standard through-the-tide counts (Babtie Group 2003). Surveys were conducted from vantage points with a wide view which also allowed the observer to count the entire sector while remaining concealed from feeding and roosting birds. Recreational use of the study area by walkers, cyclists, bird watchers, wildfowlers, as well the disturbances from the construction work itself, road, boat, and air traffic were recorded during TTTCs (Table 3.1). These disturbances were recorded only when birds were put to flight in response to the disturbance (see Belanger & Bedard 1989, Kirby *et al.* 1993, for justification of this selection criterion). Rates of disturbances (number of disturbances/visit) were calculated for all winter surveys from November 2006. Because predation risk can have an important role in habitat choice (Cresswell 1994; Hilton *et al.* 1999), the occurrence of raptor species within the study area and the proportion of attacks on birds by raptors were also recorded.

The area covered was divided into six counting sectors to assist with the collection, synthesis and interpretation of results and the sectors were counted sequentially (Figure 3.1). The design of the study ensured the full tidal range at each count sector was covered. The positions of waterbirds on mudflats, saltmarsh, and in open water were recorded onto 1:10,000 scale maps in the field using landscape features and fixed structures to plot accurately their position on the estuary. Each full TTTC across six sectors was performed within a two hour period to ensure minimum movement of birds between sectors. Where bird movements were observed, observations were allocated to the first sector to be counted. TTTCs between November 2003 and March 2006 were performed three times per day (Babtie Group 2004, 2005, 2006). Counts between November 2006 and March 2009 were performed at the same six sectors, using the same methodology as those conducted previously. However, a single daily TTTC over a greater number of days was used instead of a series of TTTCs counts completed on a single day. As the variances in tide height did not differ between serial (n=334) and daily (n=162) TTTCs (*Fishers test*, $F=1.14$, $p=0.333$), and serial counts were performed on only marginally higher tides than

Table 3.1: Names, physical characteristics and disturbance frequency of individual count sectors.

<i>Count sector</i>	<i>Proximity</i>	<i>Width (m)</i>	<i>Length (m)</i>	<i>Area (km²)</i>	<i>Walkers</i>	<i>Wildfowler</i>	<i>Raptors</i>	<i>Raptor attacks</i>	<i>Construction</i>	<i>Train</i>	<i>Boat</i>	<i>Aircraft</i>
Airth	distant	161	2,853	0.320	0.20	0.02	0.23	0.06	0.01	0	0.02	0.01
Kennet Pans	border	261	592	0.132	0.09	0.01	0.09	0.01	0.6	0	0.01	0.01
Realignment site	border	172	176	0.061	0.02	0.01	0	0	0.01	0	0.01	0
Pow burn	border	130	1030	0.233	0.15	0.02	0.02	0	0.03	0	0.02	0.01
Kincardine shore	Distant	111	878	0.058	0.72	0	0.09	0.05	0.01	0	0.03	0
Kincardine east	distant	59	1,587	0.108	0.13	0	0.03	0.01	0.02	0.022	0.01	0
Skinflats	Distant	466	1,044	0.419	0.04	0	0.06	0.04	0.01	0	0.01	0.01

singular counts ($2.96m \pm 0.07SE$, $3.26m \pm 0.10SE$; *Wilcoxon test*, $W=23473$, $p=0.011$), for the purpose of this study we assume the counts were directly comparable.

To investigate the role of construction disturbance on waterbird behaviour, Redshank and Shelduck were chosen, as complementary species, for focal animal sampling. Behavioural observations were recorded in 2008 and 2009 at the same time as TTTCs in order to compare behaviours during and after bridge construction. Behaviours were categorised as resting (land), loafing (water), walking, swimming, preening, land-foraging, water-foraging, vigilant and flying (Bryant & Leng 1975; Yasue *et al.* 2003). The position and behaviour of each bird was plotted onto 1:10,000 scale maps in the field using landmarks as above and the date and time of each observation was recorded. Tidal data were obtained later from the British Oceanographic Data Centre (BODC) collected by tidal gauge site located at Leith docks, Edinburgh (NT 263781).

Behavioural observations of Redshank and Shelduck were made in the winter of 2007/08 on 27 days between 04/01/08 and 04/03/08 and in the winter of 2008/09 on 27 days between 29/12/08 and 05/03/09. We tested the following hypotheses: 1) that birds inhabiting areas bordering the construction site during works will spend less time foraging than birds inhabiting the same area once works have ceased; 2) disturbance will cause birds to be more alert and 3) birds will spend more time active (i.e. 'startled' running, swimming or flying) in response to disturbance related to bridge construction. As wildfowl species were regularly seen to take to the water when disturbed, we also investigated whether Shelduck spent more foraging time in water in response to increased disturbance related to bridge construction. Because Shelduck were absent from Kincardine shore and Kincardine east in winter 2008/09, these count sectors were removed from the analysis for this species. Similarly, due to the small numbers of Shelduck and Redshank at the Realignment site in both winters, this sector was also excluded from the analyses.

3.1.1. Analysis

Count sectors were at first combined to investigate any large scale changes in bird number across the study site. Subsequently, each sector was analysed separately to assess localised effects of construction work on bird populations. To assess whether total bird numbers had changed, bird counts were averaged over the week in which they were conducted, and the means compared using an analysis of deviance to test whether winters varied in bird number. Winters were then sub-divided into those performed 'before' (2003/04, 2004/05, 2005/06), 'during' (2006/07, 2007/08) or 'after' construction was completed (2008/09); or whether counts were performed in *construction* or *non-construction* winters. The GLMs assumed a Poisson distribution for the number of birds, with quasi-likelihoods to compensate for overdispersion.

In order to investigate spatial and temporal patterns, we used generalised linear mixed-effect models (*GLMMs*) with Poisson errors and quasi-likelihoods. *Construction* (i.e. construction vs.

non-construction winters), *proximity* (bordering vs. distant count sectors; Table 3.1) and *season* (early winter: Nov 1st – Dec 31st vs. late winter: Jan 1st – Mar 5th) were included in our model as fixed effects. As it was important to investigate the impact of the bridge on habitat use, *tide* was included as a fixed effect to investigate the impact on birds at low ($\leq 2\text{m}$), mid ($>2\text{m}$ and $<4.5\text{m}$) and high tide ($\geq 4.5\text{m}$). In order to test whether disturbance had the greatest impact in sectors bordering the construction site and during metabolically stressful periods, the 3-way interactions between *winter*, *proximity* and *season*, and *winter*, *proximity* and *temperature* were included in the model. Similarly to test whether the effects of construction disturbance were strongest at particular tidal heights, the 3-way interaction between *winter*, *proximity* and *tide height* was included within the model. Statistical analysis of bird count data is often difficult as successive counts from the same sector may lead to data that are non-independent (Gill *et al.* 2001). Because these counts were repeated measures from the same six count sectors over time, *sector* was included within the model as a random effect. The *week* in which counts were conducted was included as a continuous random effect to acknowledge temporal pseudoreplication within each sector count. Unimportant variables were removed from both the GLM and the GLMM by stepwise deletion, until only those variables that were significant at the 5% level at explaining variation in bird numbers were retained in the final model.

Generalised linear mixed models (GLMMs) with binomial errors and quasi-likelihoods were used to determine the effects of construction disturbance on Redshank and Shelduck time budgets. In all models, *winter* (2007/08 or 2008/09), *tide height* (m), *temperature* ($^{\circ}\text{C}$) and *proximity* (border vs. distant) were included as fixed effects. As with the bird density models, the 3-way interactions between *winter*, *proximity* and *tide height*, and *winter*, *proximity* and *temperature* were included in our behaviour models to investigate the effects of disturbance on Redshank and Shelduck behaviours at various tide heights and at low temperatures. *Count sector* was included as a random effect to control for spatial autocorrelation. As with count data, unimportant variables ($p > 0.05$) were removed by stepwise deletion until the most parsimonious model was achieved. GLMMs were constructed using the ‘lme4’ package (Bates & Maechler 2009) and all analysis was conducted in the R programming language (R Development Core Team 2009).

3.2. RESULTS

3.2.1. Comparison of count data

Over a period of 292 days, 1752 counts were carried out at six individual sectors. Between 17/11/03 and 05/03/09, 38 waterbird species and 4 raptor species were recorded on the Forth, including 11 duck and 16 wader species (Appendix 3.1). For the purpose of this study, wader species (order *Charadriiformes*) were pooled into the group ‘waders’ and all diving and dabbling ducks along with Shelduck were pooled into the group ‘ducks’ (Appendix 3.1). The

impact of disturbance on these two groups and on individual species was investigated. Wader and duck species, plus geese (genera *Anser* and *Branta*), swans (genus *Cygnus*), Cormorant, Heron, divers (family *Gaviidae*), grebes (family *Podicipedidae*) and auks (family *Alcidae*) were referred to under the larger group: ‘waterbirds’.

3.2.2. Large-scale distribution

Waterbird, duck and wader counts differed significantly between years ($F_{5,88}=7.64$, $p<0.001$; $F_{5,88}=63.66$, $p<0.001$; $F_{5,88}=6.30$, $p<0.001$). After a steady rise in wader numbers in the study area, numbers fell in the fifth winter, during the second year of construction (Figure 3.2i). Waders were significantly fewer in counts during this winter than in winters 2005/06, 2006/07 and 2008/09 ($F_{3,68}=5.71$, $p=0.002$). However, there was no evidence to suggest the 2007/08 winter held fewer waders than winters 2003/04 or 2004/05 ($F_{2,37}=1.88$, $p=0.168$).

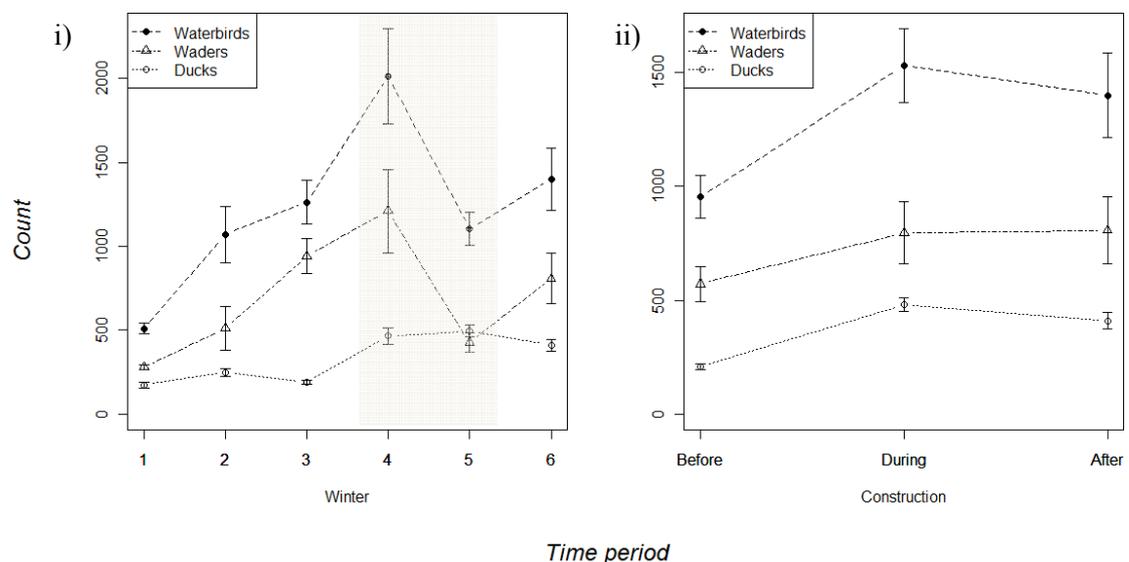
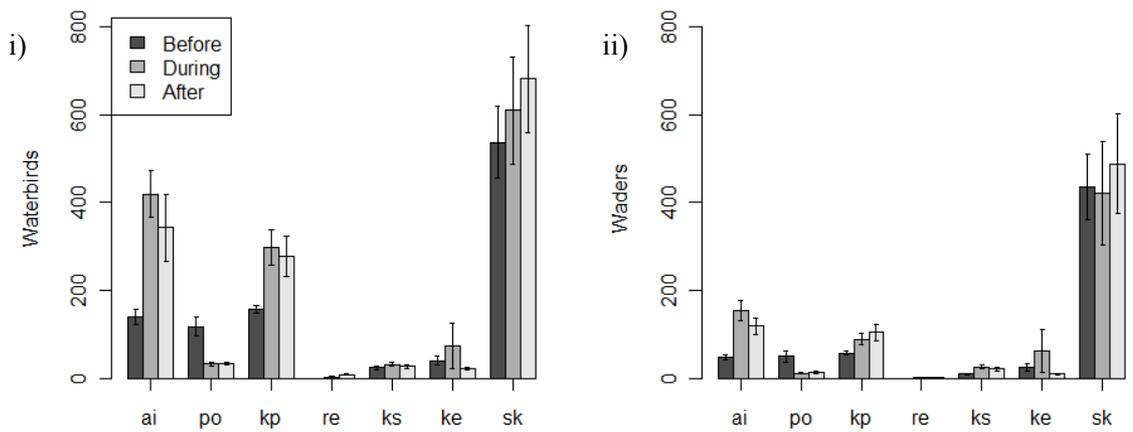


Figure 3.2: (i) Annual trends (\pm SE) in waterbird, wader and duck populations in the Kincardine-on-Forth study area between November 2003 (winter 1) and March 2009 (winter 6). Dark shading represents period where bridge construction is taking place. (ii) Trends in waterbird, wader and duck populations (\pm SE) before (Nov 2003-Mar 2006), during (Nov 2006-Mar 2008) and after bridge construction (Nov 2008-Mar 2009).

Contrary to our predictions, there were significantly more waterbirds in the study area during bridge construction compared with before and after (Figure 3.2ii; $F_{1,88}=4.73$, $p=0.032$). Duck numbers were greater during construction winters than non-construction winters ($F_{1,88}=34.75$, $p<0.001$), however there was no evidence to suggest total wader numbers differed between construction and non-construction winters ($F_{1,88}=1.01$, $p=0.319$). Waterbirds were significantly fewer in counts made before bridge construction began than in those counts conducted during bridge construction work and after works ceased ($F_{2,88}=5.15$, $p=0.008$). Duck numbers were

significantly greater during construction than before or after construction ($F_{2,88}=37.06$, $p<0.001$). There was no evidence to suggest wader numbers varied before, during and after construction ($F_{2,88}=1.18$, $p=0.313$).

Airth, Kennet Pans and Skinflats held the greatest numbers of waterbirds in our study area (Figure 3.3i). Prior to construction work, Pow burn previously held similar numbers as Kennet Pans. However, since construction began in 2006, bird numbers were reduced at this sector by more than 30%. This reduction can be attributed mainly to the decline in wader numbers at this sector (Figure 3.3ii). As populations did not increase in the winter post-construction, it appears this sector may have been compromised by the installation of the bridge. Bird numbers increased at Airth and Kennet Pans, as these sectors lay adjacent to Pow burn; it is possible this increase could be partly due to the displacement of birds from Pow burn.



Count sector

Figure 3.3: Before, during and after construction counts (\pm SE) of i) waterbirds and ii) waders within each count sector (ai=Airth, po=Pow burn, kp=Kennet Pans, re=Realignment site, ks=Kincardine shore, ke=Kincardine east, sk=Skinflats). Pow burn and Kennet Pans are classed as ‘bordering’ count sectors, Airth, Kincardine shore, Kincardine east and Skinflats are classed as ‘distant’ count sectors.

In the GLMM, the 3-way interaction between *construction*, *proximity* and *season* was significantly associated with waterbird, duck and wader counts ($X^2_1=1153.30$, $p<0.001$; $X^2_1=7.10$, $p=0.008$; $X^2_1=475.44$, $p<0.001$). Waterbird numbers increased only during late winter at distant sectors driven by the increase in wader numbers in these areas at these times. Duck numbers were greater in both early and late winter at distant sectors but only in early winter at bordering sectors. This suggests that large numbers of waterfowl arrived later in the season during construction years.

The 3-way interaction between *construction*, *proximity* and *tide* was associated significantly with total waterbird and duck counts ($X^2_1=109.33$, $p<0.001$; $X^2_1=37.48$, $p<0.001$). Waterbird numbers in distant sectors increased during construction across all tidal stages (Figure 3.4i); numbers were similar, however, in bordering sectors across all tidal stages. Duck numbers also increased in distant sectors during construction, and numbers were greater in bordering sectors at high tide (Figure 3.4ii). Although this three-way interaction was not significant for waders ($X^2_1=2.56$, $p=0.109$), the interaction between *construction* and *tide* was significant ($X^2_1=16.99$, $p<0.001$). During construction there was a greater increase in wader numbers across the estuary at mid tide (non-construction: $136\pm 10SE$; construction: $106\pm 29SE$) and at high tide (non-construction: $161\pm 20SE$; construction: $128\pm 48SE$).

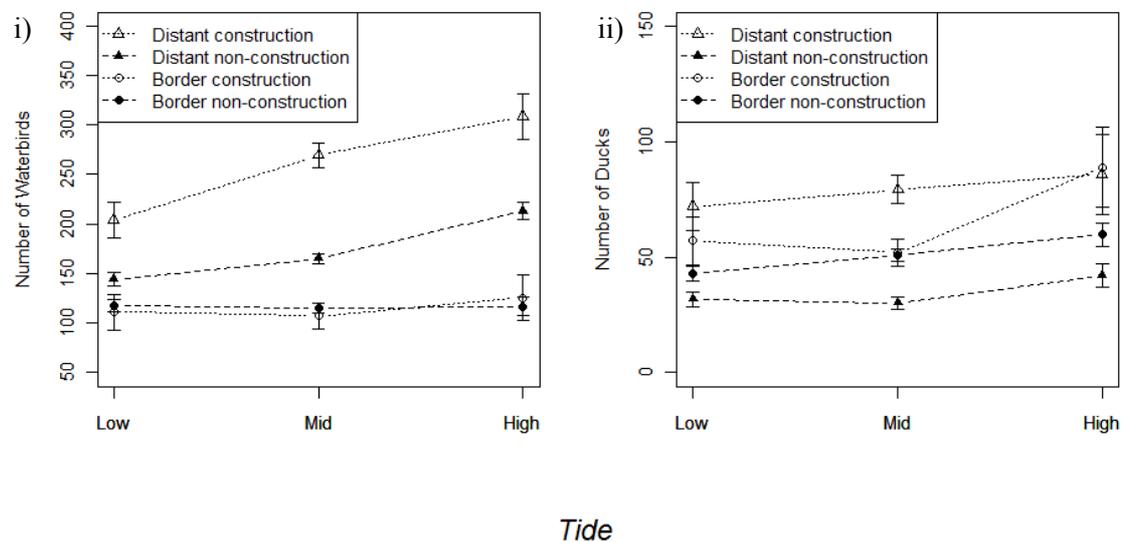


Figure 3.4: Comparison of waterbird (i) and duck (ii) counts ($\pm SE$) across tidal stages (low, mid, high) during non-construction and construction winters in distant and bordering sectors.

3.2.3. Species-level factors

All waterbird species apart from Pink-footed Geese showed significant changes between winters. Redshank, Bar-tailed Godwit, Cormorant and Lapwing were significantly fewer in the study area in construction winters than non-construction winters ($p>0.05$). During construction, Redshank densities were reduced at Kennet Pans, Pow burn and Skinflats, while numbers increased at Airth and Kincardine shore (Figure 3.5i). Contrary to predictions, Dunlin, Curlew, Shelduck, Teal, Wigeon, Red-breasted Merganser and Goldeneye numbers increased in the study area during construction. There was no significant change in the numbers of Knot, Oystercatcher, Black-tailed Godwit, Pink-footed Geese during bridge construction compared to winters when there was no construction occurring. Cormorant and Lapwing were fewer in the study area during construction and in the year post-construction than before construction began.

Oystercatcher, Bar-tailed Godwit and Mallard increased in the year post-construction. Dunlin, Curlew, Teal, Wigeon and Red-breasted Merganser were all more abundant during construction years than in either pre- or post-construction counts.

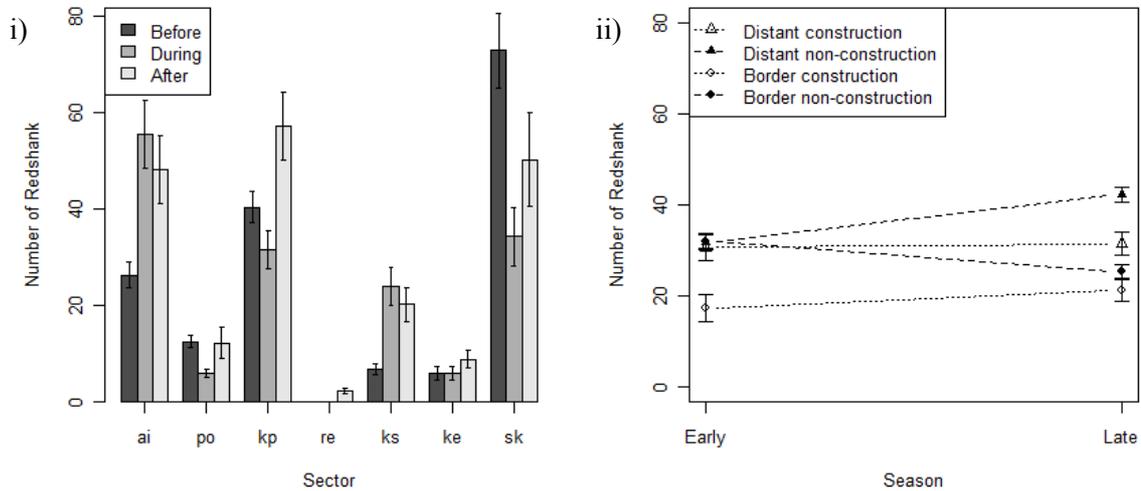


Figure 3.5: Comparison of Redshank counts (\pm SE) by individual count sector (i) and across early and late winter during non-construction and construction winters in distant and bordering sectors (ii).

3.2.4. Temporal patterns

The 3-way interaction between *construction*, *proximity* and *season* was associated significantly with Redshank ($X^2_1=256.13$, $p<0.001$), Dunlin ($X^2_1=44.51$, $p<0.001$), Curlew ($X^2_1=231.13$, $p<0.001$), Oystercatcher ($X^2_1=30.21$, $p<0.001$), Wigeon ($X^2_1=15.90$, $p<0.001$), Teal ($X^2_1=57.83$, $p<0.001$), Mallard ($X^2_1=7.25$, $p=0.007$), Red-breasted Merganser ($X^2_1=4.99$, $p=0.026$), and Cormorant counts ($X^2_1=142.22$, $p<0.001$). The decline in Redshank and Cormorant within the study area can be mainly attributed to a large decline in these species at those areas bordering the construction site in early winter (Figure 3.5ii). Curlew, Wigeon and Mallard numbers fell in the areas around the construction site, but increased at distant sectors during late winter. Conversely, Oystercatcher increased their usage at bordering sectors, especially during late winter and Dunlin increased at bordering sectors in both early and late winter and increased at distant sectors during late winter. There was no significant 3-way interaction between *construction*, *proximity* and *season* with Shelduck counts ($p>0.05$) however the 2-way interactions between *construction* and *season* and *construction* and *proximity* were significant ($X^2_1=138.16$, $p<0.001$; $X^2_1=68.25$, $p<0.001$). The large increase in Shelduck numbers within the study area during the construction period occurred mainly during the early part of the winter and in areas distant from the construction site.

3.2.5. Tidal patterns

The 3-way interaction between *construction*, *proximity* and *tide* was significantly associated with Redshank ($X^2_1=61.10$, $p<0.001$), Dunlin ($X^2_1=646.24$, $p<0.001$), Curlew ($X^2_1=53.73$, $p<0.001$), Oystercatcher ($X^2_1=24.29$, $p<0.001$), and Cormorant counts ($X^2_1=6.29$, $p=0.012$). Redshank avoided areas bordering the construction site at mid-tide (Figure 3.6i). The largest decline in occurred around the bridges at low tide (Figure 3.6ii). Dunlins were more abundant around the bridges during low and mid-tide but numbers declined at high tide roosts. Curlew used bordering sectors more at high tide and less at low tide during construction and Oystercatcher used bordering sectors more and distant sectors less during high tide. Curlew also used high tide roosts at distant sectors more during construction than in non-construction winters.

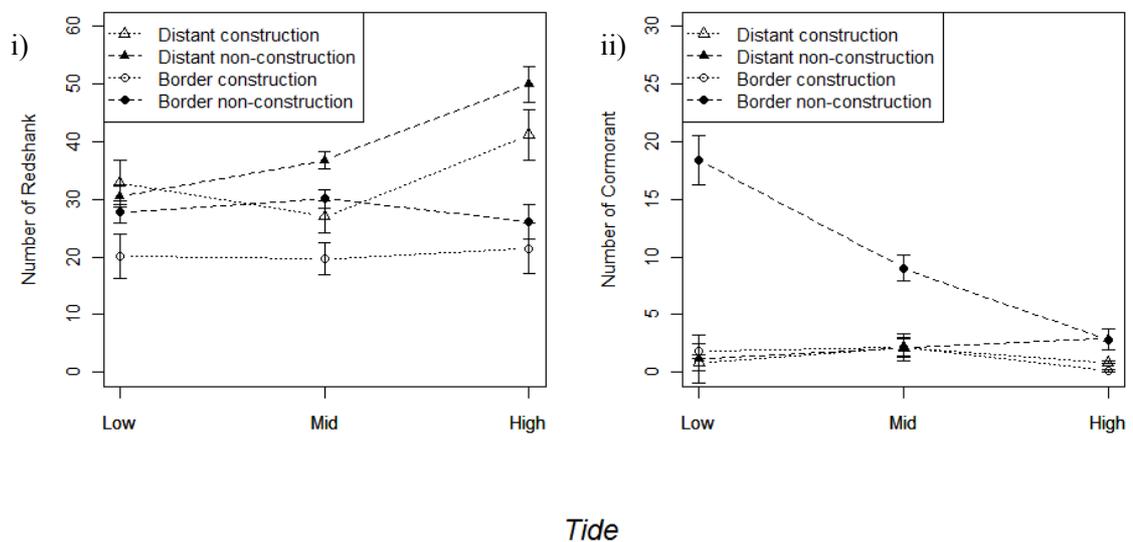


Figure 3.6: Comparison of Redshank (i) and Cormorant (ii) counts (\pm SE) across tidal stages (low, mid, high) during non-construction and construction winters in distant and bordering sectors.

There was no significant 3-way interaction between *construction*, *proximity* and *tide* with Shelduck, Wigeon, Teal, Mallard, Red-breasted Merganser counts ($p>0.05$). The 2-way interaction between *construction* and *tide* was however significant for Wigeon ($X^2_1=44.19$, $p<0.001$), Teal ($X^2_1=152.84$, $p<0.001$), Mallard ($X^2_1=23.245$, $p<0.001$), and Shelduck counts ($X^2_1=104.51$, $p<0.001$). During construction, Wigeon numbers increased in the study area at mid and high tide. The greatest rise in Mallard and Teal numbers occurred at high tide whilst the increase for Shelduck was greatest at low tide. There was no relationship between *construction* and *tide* for Red-breasted Merganser abundance.

3.2.6. Behavioural patterns

In the GLMM, the two-way interactions between *winter* x whether or not the sector bordered the construction site ($X^2_1=208.79$, $p<0.001$); *winter* x *temperature* ($X^2_1=208.79$, $p<0.001$; Appendix 3.3i) and *winter* x *tide height* ($X^2_1=142.96$, $p<0.001$; Appendix 3.3ii) were all significant in predicting foraging time in Redshank. In distant sectors, the proportion of Redshank foraging was greater during construction (07/08: $0.74\pm 0.03SE$; 08/09: $0.41\pm 0.24SE$), however the proportion foraging in bordering sectors were similar between winters (07/08: $0.45\pm 0.03SE$; 08/09: $0.43\pm 0.19SE$). During bridge construction (07/08) the proportion of Redshank foraging was greater at lower temperatures and at lower tide heights than in the year post construction (08/09). Across all sectors, Redshank were most vigilant and spent the least proportion of time feeding at Kincardine east during construction (Figure 3.7i). In the GLMM, there was no evidence that vigilance varied between winters in the study site as a whole ($X^2_1=1.19$, $p=0.660$), in bordering or distant sectors (interaction, $X^2_1=3.11$, $p=0.078$), across particular tides (interaction, $X^2_1=1.18$, $p=0.278$) or temperatures (interaction, $X^2_1=3.19$, $p=0.074$). Similarly, the proportion of time Redshank spent active was similar between winters ($X^2_1=0.61$, $p=0.433$), in bordering or distant sectors (interaction, $X^2_1=1.38$, $p=0.24$), across particular tides (interaction, $X^2_1=2.32$, $p=0.128$) or temperatures (interaction, $X^2_1=0.10$, $p=0.754$).

As with Redshank, the two-way interactions between *winter* x proximity to the construction site ($X^2_1=75.30$, $p<0.001$); *winter* x *temperature* ($X^2_1=71.61$, $p<0.001$; Appendix 3.4i) and *winter* x *tide height* ($X^2_1=37.64$, $p<0.001$; Appendix 3.4i) were all significant in predicting foraging time in Shelduck. The proportion of Shelduck feeding was greater in bordering sectors (07/08: $0.44\pm 0.14SE$; W6: $0.33\pm 0.14SE$) and less in distant sectors (07/08: $0.61\pm 0.19SE$; 08/09: $0.85\pm 0.19SE$) during construction compared to the winter post-construction. Shelduck also fed more when it was colder and during low tides compared with the Shelduck in the post-construction winter. Vigilance varied significantly between winters in bordering and distant sectors ($X^2_1=16.24$, $p<0.001$). During construction, a greater proportion were vigilant in bordering sectors (07/08: $0.05\pm 0.02SE$; 08/09: $0.02\pm 0.02SE$) compared to W6. In contrast, a smaller proportion were vigilant in distant sectors during construction (07/08: $0.003\pm 0.02SE$; 08/09: $0.04\pm 0.01SE$). Although there was no effect of temperature, vigilance was greatest across higher tides during construction (two-way interaction; $X^2_1=7.48$, $p<0.001$). The proportion of Shelduck flying, running or swimming in our study area was greater in bordering sectors (07/08: $0.41\pm 0.14SE$; 08/09: $0.17\pm 0.14SE$) and fewer in distant sectors (07/08: $0.11\pm 0.19SE$; 08/09: $0.71\pm 0.19SE$) during construction (interaction: $X^2_1=52.95$, $p<0.001$).

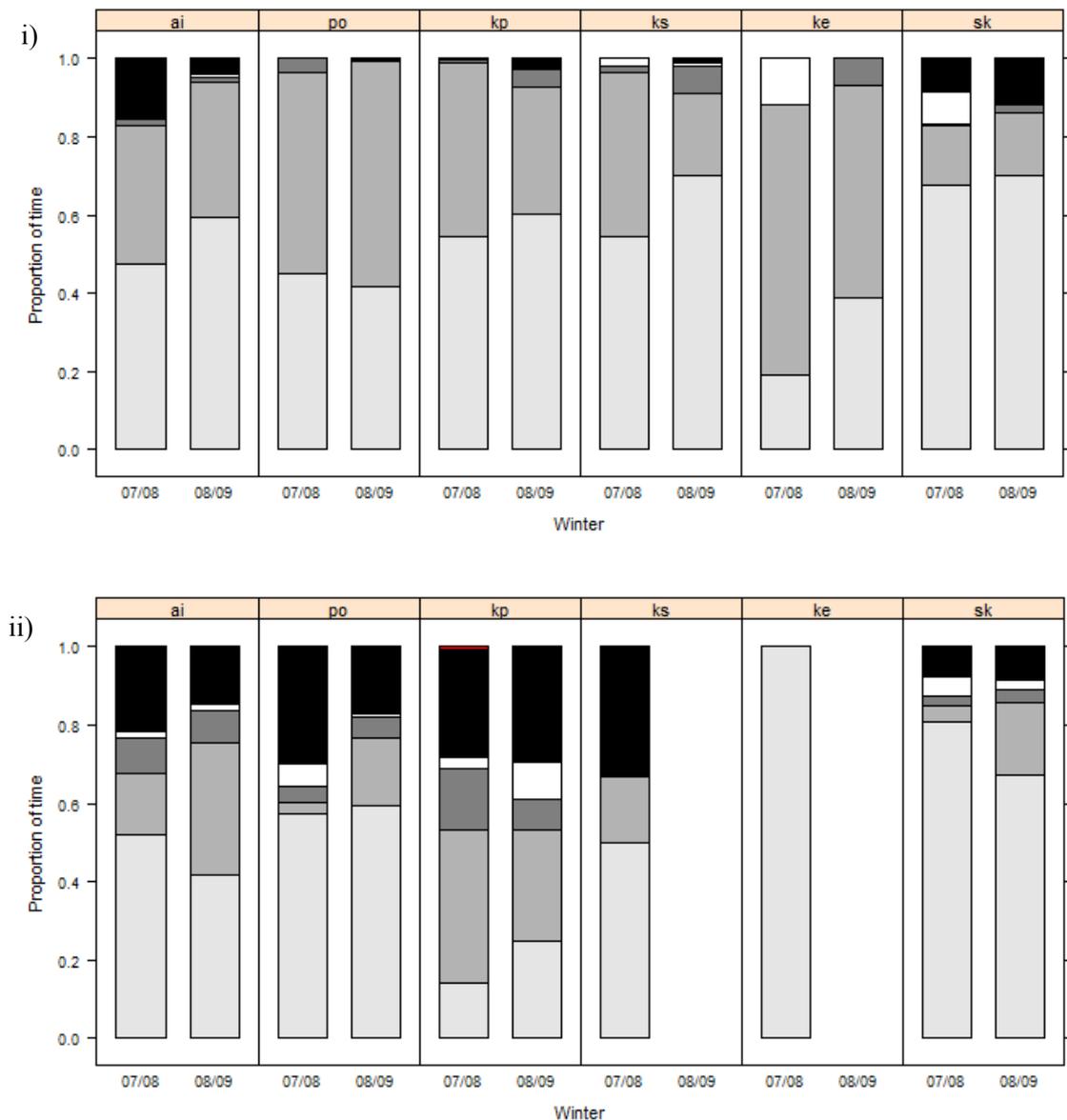


Figure 3.7: Time budget data for Redshank (i) and Shelduck (ii) inhabiting count sectors in winters during construction (07/08) and after construction (08/09) throughout late winter (light grey= feeding, grey= roosting, dark grey= preening, white= alert, black= active). Count sectors labelled as follows: ai=Airth, po=Pow burn, kp=Kennet Pans, ks=Kincardine shore, ke=Kincardine east, sk=Skinflats). As before, Pow burn and Kennet Pans are classed as ‘bordering’ count sectors and Airth, Kincardine shore, Kincardine east and Skinflats are classed as ‘distant’ count sectors.

During construction, there was a greater proportion of Shelduck foraging in the water, compared to foraging on the land, in sectors bordering the construction site (Figure 3.8i; $X^2_1=8.24$, $p=0.004$) than in the post-construction winter. The opposite was found in distant sectors with a greater proportion of birds water-feeding in the winter post-construction than during bridge construction. Below 4m, Shelduck spent a greater amount of foraging time in the water during construction compared to the winter post construction (Figure 3.8ii; $X^2_1=127.23$, $p<0.001$). Shelduck also spent a greater amount of foraging time in the water at lower temperatures ($X^2_1=27.21$, $p<0.001$).

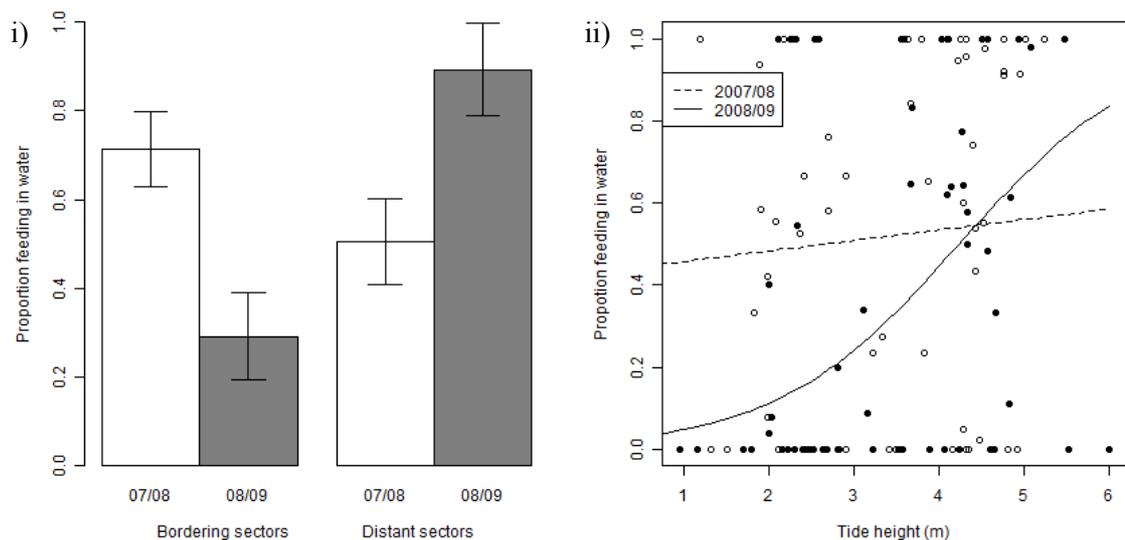


Figure 3.8: i) Between-winter differences (\pm SE) in the proportion of time Shelduck spent foraging in water compared to foraging on land in bordering and distant count sectors. ii) Model predictions (lines) against actual values (dots) for those proportions of Shelduck feeding in water compared to those foraging on land across all tidal heights (*interaction*: $X^2_1=127.23$, $p<0.001$). Empty dots: winter 2007/08, solid dots: winter 2008/09.

3.3.DISCUSSION

3.3.1. *Waders, ducks and waterbirds*

We asked if the sustained disturbance related to bridge construction reduced a site's overall carrying capacity for waterbirds. Contrary to our predictions, waterbird numbers increased in our wider study area during the construction of the new Clackmannanshire Bridge (Figure 3.2i). Furthermore, our study shows that there was little change in numbers in the areas around the bridges, however there were large increases at distant sectors, especially at higher tides (Figure 3.4i). Previous studies have demonstrated that the Forth is susceptible to large fluctuations in waterbird numbers (Bryant 1987; Bryant & McLusky 1997), which can make the detection of changes through time a difficult task (Bryant 2003). However, in a review of count data dating

back over 100 years, Bryant (2003) concluded that the species represented in the vicinity of the Kincardine Bridge have been relatively consistent during this time. The increase in bird numbers during this study was mainly driven by a large increase in waders using high tide roosts at the fringes of the study site. Although ducks are widely thought to be the most prone to human disturbance, our study shows that duck numbers increased in the areas next to the construction site during construction (Figure 3.4ii). As was the case with waders, the increase in ducks was most pronounced towards high tide when species such as Shelduck are known to move progressively upriver (Bryant & Leng 1975; Newton & Bryant 1991) joining the birds present over the low tide period.

3.3.2. *Species-level changes*

This study has shown that bridge construction affected the distribution of some waterbird species more than others. Cormorant and Redshank were least tolerant of the disturbance related to the engineering works and total numbers within the study site declined during the construction period. The areas bordering the construction site were previously known to be important as low tide roosts for Cormorant (Ader & Bryant 2003), and for both feeding and roosting at high tide for Redshank (Newton & Bryant 1991). The greater densities of feeding Redshank occurring on the higher flats near Kincardine Bridge, especially on the rising tide on high water neaps, consequently make them vulnerable to habitat disturbance in this area. Furness (1973) found that disturbance of the roost site was the most conspicuous determinant of roost quality on the Forth estuary. He went further to suggest that the numbers of Redshanks, as observed at the sites, might be limited by disturbance which he observed caused birds to spend less time feeding in food-rich areas.

Disturbance during high tide may reduce the use of roosts around the bridge site, which would be most significant for those species which tend, if possible, to avoid energetically costly flights to distant roosts, such as Redshank or Dunlin (Newton & Bryant 1991). Redshank on the Forth are known to show a high level of fidelity to foraging and/or roosting sites (Furness & Galbraith 1980; Symonds *et al.* 1984). As a result, they may have been less able to adapt to the increased disturbance at sectors bordering the construction site, compared to wide-ranging species, such as Dunlin or Knot, which may have a broader suite of alternative habitat to choose from (Burton 2000).

The impact of disturbance at the population level depends on the availability of alternative habitat (Burton *et al.* 2002). If neighbouring areas were below carrying capacity for a species, then the overall impact of disturbance on mortality rates will be reduced (Hill *et al.* 1997; Gill *et al.* 2001). In our study, while the numbers of Redshank were reduced at Pow burn and Kennet Pans, densities at Airth and Kincardine shore increased. This may suggest that these areas were below the carrying capacity, and were able to accommodate some of the displaced Redshank

from bordering sectors. However, these areas also experienced a high incidence of disturbance from recreational walkers, and the greatest predation risk from Sparrowhawks *Accipiter nisus* (Table 3.1). Sparrowhawks were identified by Whitfield (1985) as the principal predator of wader species on the Forth estuary. The high frequency of sightings of this species, and the close proximity to predator-concealing cover makes relocation to this area, by displacement, a risky option for Redshank. In chapter 2, Kincardine shore was also found to have among the lowest prey densities of the seven count sectors. Hill *et al.* (1997) postulated that disturbance may cause a greater proportion of birds to be forced to use suboptimal feeding habitat. Similarly, Burger (1988) in a study of foraging gulls on mudflats, showed a shift from preferred to less preferred habitat is likely to affect foraging efficiency. A shift to these alternative habitats may therefore have directly impacted on the survival or fitness of the species.

The large densities of Redshank present in the area around the bridges (Newton & Bryant 1991), in combination with their high site fidelity, may have made disturbance easier to detect in this species. In our study, Redshank declined during the period of construction work, but recovered to previous densities in the year following the completion of works. The largest decline in Redshank occurred in areas bordering the construction site and although the impact was possibly greatest at higher tides (Furness 1973); numbers were reduced across all tidal heights (Figure 3.6i). This localised effect, in combination with the “remarkable” long term stability of Redshank on the Forth (Newton & Bryant 1991), suggests that it was the disturbing factor of the bridge construction which reduced the attractiveness and overall carrying capacity of this area, and not some external factor or habitat loss which affected Redshank densities.

Although measures were taken during the construction of the Clackmannanshire Bridge, as not to remove to low tide roost between Pow burn and the Kincardine Bridge, Cormorant avoided this roost site from the commencement of works (Figure 3.6ii). Despite being present in nationally important numbers, Cormorant were assessed as being at less risk from disturbance of their roosts than other species. This was due to the transient nature of Cormorant feeding and roosting sites within the Forth related to tidal movements (Bryant 1978; Newton & Bryant 1991), and the requirement to only feed for a small part of each day (Gremillet *et al.* 2003). Unlike Redshank, Cormorant could adapt to this disturbance by loafing elsewhere on the estuary (Ader & Bryant 2003), continuing to use the Kincardine Bridge area for feeding even if their preferred roost was routinely disturbed.

Contrary to our predictions, Oystercatcher and Curlew numbers increased at high tide in areas around the bridge. Oystercatcher probably benefited most from the newly-created intertidal habitat at Kennet Pans, particularly regarding use of the man-made island as a high tide roost. Counts were similar within our study area in construction and non-construction winters. The increase in areas bordering the construction site and a decrease in distant areas, coupled with the

small home range of Oystercatcher on the Forth (Symonds *et al.* 1984), suggest that Oystercatcher have moved from sectors such as Skinflats and Airth, into the area around the bridge to capitalise on the installation of the new roosting area. Curlew numbers also increased in roosting areas in sectors bordering the bridge. However Curlew were able to take advantage of supratidal foraging grounds located behind the sea wall and away from the construction site. We believe that in these areas, more distant from, or out of sight of construction activity, Curlew would be relatively unaffected by construction disturbance.

Newton & Bryant (1991) predicted that a tidal-power development affecting the mudflats in the direct vicinity of the present Kincardine Bridge was likely to have the greatest impact on Dunlin due to the high densities foraging and roosting at north Skinflats. In areas bordering the bridge, Dunlin numbers declined at high tide but increased at low and mid tide. This suggests that the roost sites next to the construction works became less attractive to roosting birds but the birds were still able to take advantage of foraging grounds up until high tide. As is the case for Redshank, Dunlin can be strongly affected by disturbance at a high tide roosts (Furness 1973i; 1973ii). Dunlin are known to make routine movements from Skinflats, east to Kinneil at both low water and high water (Bryant 1979). Earlier studies showed a greater fall off in numbers at low tide with peaks in feeding numbers on the ebb and flow, probably linked to the higher proportion of birds moving to Kinneil or South Skinflats for the low tide period (Bryant 1979).

Although duck species responded differently to disturbance at different tidal levels, the effect of tide was not significant at near or distant sectors for individual duck species. Wigeon numbers within the study area increased in the areas far from the construction site where Wigeon were previously present at relatively high densities. There was a slight decrease in Wigeon number in areas adjacent to the construction site. In contrast, Teal numbers increased in areas bordering the construction site during construction winters. Reduced public access along a path on the eastern flank of Kennet Pans has prevented recreational walkers from accessing the site and disturbing birds roosting and feeding by Canal Burn, a tidal creek along the east boundary of the count sector.

For those species which increased in areas next to the construction site, disturbances may have been common and regular enough in nature for birds to habituate (Keller 1989; Marsden 2000). Vehicles and vehicle movements are tolerated much more readily than people at the sources of disturbance (Hill *et al.* 1997). This is probably because disturbance from road traffic is restricted spatially and, compared to that of walkers, is relatively predictable (Klein *et al.* 1995; Burton *et al.* 2002).

3.3.3. *Temporal patterns in habitat use*

Our study found that during construction, the greatest decline in Redshank (Figure 3.5ii) and Cormorant occurred in the sectors bordering the construction site in early winter. Birds are known to become more tolerant of human disturbance in late winter, as a result of deteriorating feeding conditions and increased thermoregulatory energy demands (Wiersma & Piersma 1994; Stillman & Goss-Custard 2002; Beale & Monaghan 2004). As preferred foraging grounds become depleted, birds may be forced to feed in 'riskier' areas, despite the increased perceived risk of feeding there (Houston *et al.* 1993; Gill *et al.* 2001; Frid & Dill 2002). Similarly, the apparent tolerance to a disturbance will vary according to the availability of alternative resources and the physiological state of the individual (Burton 2007). Our findings support those of Yasue, Quinn and Cresswell (2003) who found Redshank (mainly juveniles) fed in saltmarsh areas closer to predator concealing cover when they were more energetically stressed, despite the increased predation risk of feeding there (Cresswell & Whitfield 2008). Historically, the mudflats at Kincardine shore were only used later in the winter by Redshank, however during construction, the use of this sector significantly increased in early winter. The construction of the bridge appears to have shifted the perceived quality of the Redshanks habitat: individuals now use an arguably more dangerous and less profitable feeding site where interference competition may be much greater, in preference to those which are prey-rich, have lower competitor densities and have a lower risk of attack from land-based raptors.

3.3.4. *Impact on animal behaviour*

In this study, both Redshank and Shelduck dedicated more time to foraging during the winter with bridge construction compared to the winter without construction. These findings contrast with those of Burton *et al.* (2002), who found that construction work reduced feeding activity in three wader species (including Redshank) and had negligible on foraging in Shelduck. No attempt was made in their study, however, to control for the effects of temperature on metabolic demands. On the Forth, foraging was negatively related to temperature and a greater proportion fed at low temperatures during construction work. Unless animals are able to compensate for a negative energy balance, disturbance is likely to have a negative effect on bird survival (Goss-Custard 1969; Belanger & Bedard 1990).

Shelduck also spent significantly more time active (i.e. running, swimming or flying) during operations in sectors bordering the construction site. When disturbed birds will often leave their chosen feeding grounds, consuming considerable energy fleeing the disturbance (Nudds & Bryant 2000) whilst sacrificing valuable feeding time moving to alternative feeding areas (Quinn 1997). Higher energy costs will have a negative effect on survival unless individuals are able to compensate for lost foraging time by increasing foraging during the day or at night (Goss-Custard 1969; Belanger & Bedard 1990). Although this chapter contained only observations collected by day, our findings suggest that birds dedicated more time to searching

for food at lower tides in order to counterbalance the energy deficit. If birds were already compensating for a negative energy balance, we would expect this effect to be most pronounced at lower temperatures when more foraging time was necessary to meet energy requirements.

Although the proportion of birds foraging was similar between winters in bordering sectors, Redshank increased feeding time in distant sectors during construction. The displacement of birds to alternative feeding areas may increase competitor densities and increase the rate of prey depletion in these neighbouring mudflats (Goss-Custard *et al.* 2006). An increase in interference competition may not only further reduce foraging efficiency (Goss-Custard 1970; Goss-Custard 1980; Triplet *et al.* 1999), but may also cause birds to forage in more dangerous areas. In contrast, Shelduck increased feeding time in bordering sectors during bridge construction. Our findings suggest Shelduck were able to adapt to disturbance by spending more time feeding in the water than on land (Figures 3.8i, ii). This may also explain why duck numbers increased within the study in areas surrounding the bridges, while wader species, unable to take advantage of new or supratidal roosts, or find greater security on the water, declined. If the interpretation of risk from construction disturbance is reduced when ducks are in water, they would be able to compensate for a negative energy balance by increasing water-based foraging. Although thermoregulatory costs, especially during colder temperatures, may be higher for birds foraging on water compared to foraging on land (Humphreys *et al.* 2007), this may allow ducks to take advantage of prey unavailable to disturbed waders.

Vigilance in Shelduck increased in bordering sectors, but decreased in distant count sectors during bridge construction. Similarly, although there was no evidence of increased vigilance in Redshank in response to bridge construction, the refurbishment of the Stirling-Alloa-Kincardine railway line adjacent to the Kincardine east count sector caused an increase in the time spent vigilant, from 0% in 2008/09 to 12% in 2007/08 (Figure 3.7i). In areas of an elevated predation risk, such as close proximity to raptor concealing cover, birds will respond by increasing scanning and vigilance (Cresswell 1994; Cresswell & Quinn 2004). In a similar way, vigilance is known to increase and foraging rates decrease in response to an elevated human threat (Burger 1991; Goss-Custard *et al.* 2006; Yasue 2006) and competitor density (Cresswell 1998; Vahl *et al.* 2005). In our study, the increased vigilance in response to workers and work vehicles on the railway, resulted in a reduction in foraging time (from 38% in 2008/09 to 19% in 2007/08). Unless birds were able to increase foraging efficiency in these areas, they may be unable to acquire enough resources to maintain their energy reserves (Belanger & Bedard 1990; Burger 1997), which may reduce an individual's chances of surviving cold weather (Clark 2009).

3.4. CONCLUSIONS

Ours is the first major study investigating the impact of a bridge crossing on waterbird abundance and behaviour. As with Burton and others (2002b), we have demonstrated that construction-related disturbance on an estuary can depress habitat quality. This caused birds to move to alternative sites where they may have suffered an increased predation risk, increased competitor densities and reduced prey densities. Those which appeared most tolerant to disturbance were vagile shorebird species, and ducks which, as we demonstrated in Shelduck, may have compensated for a negative energy balance by increasing water-based foraging. Although detailed study revealed some negative effects of the construction process on a sample of bird species, the mitigation measures put in place by Jacobs Group Ltd, SNH and Transport Scotland to minimise the impact of the bridge development probably allowed populations to recover in the winter following the cessation of works. Disturbance from large engineering projects is an increasing concern not just in the UK, but on estuarine sites worldwide. As a result, there is a growing body of environmental legislation and growing importance placed on bird conservation at local, regional national and international levels (Hill *et al.* 1997). Monitoring is needed to indicate whether further remedial measures are required in the event of unpredicted impacts occurring. It is also required to help increase the understanding of actual impacts and the testing of mitigation measures, which can then be used to improve future assessments.

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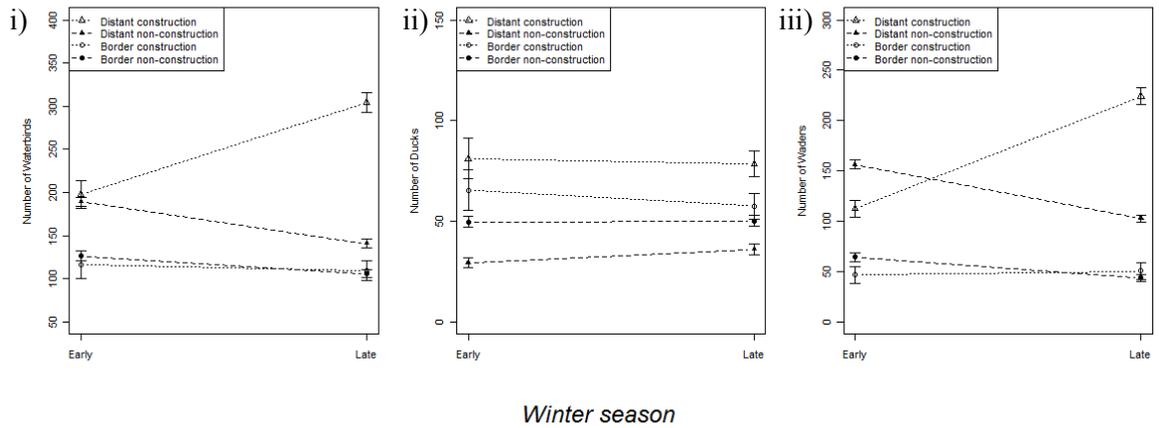
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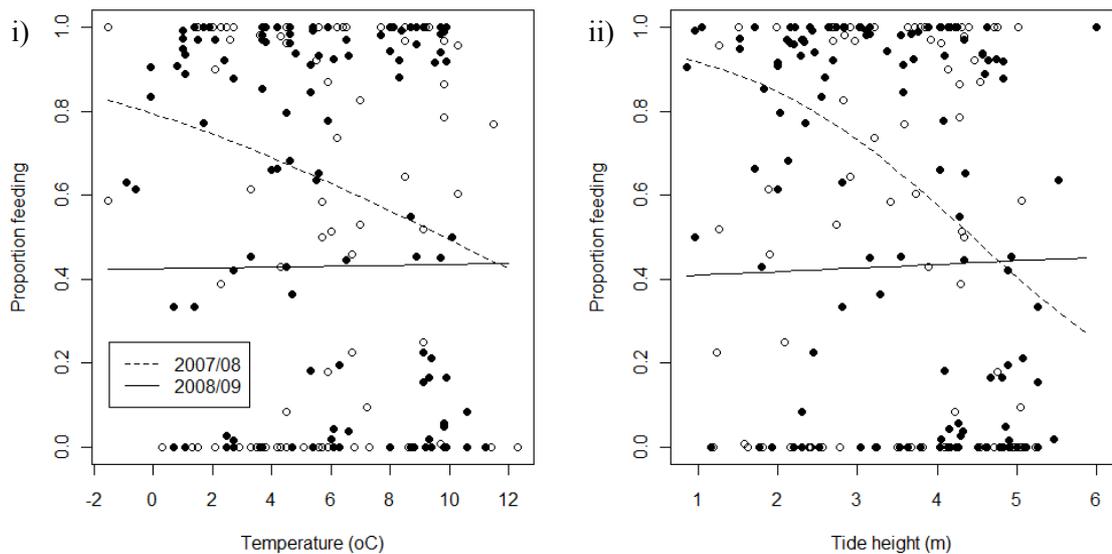
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Appendix 3.1: Table of waterbird and raptor species present in 2003-2009 surveys.

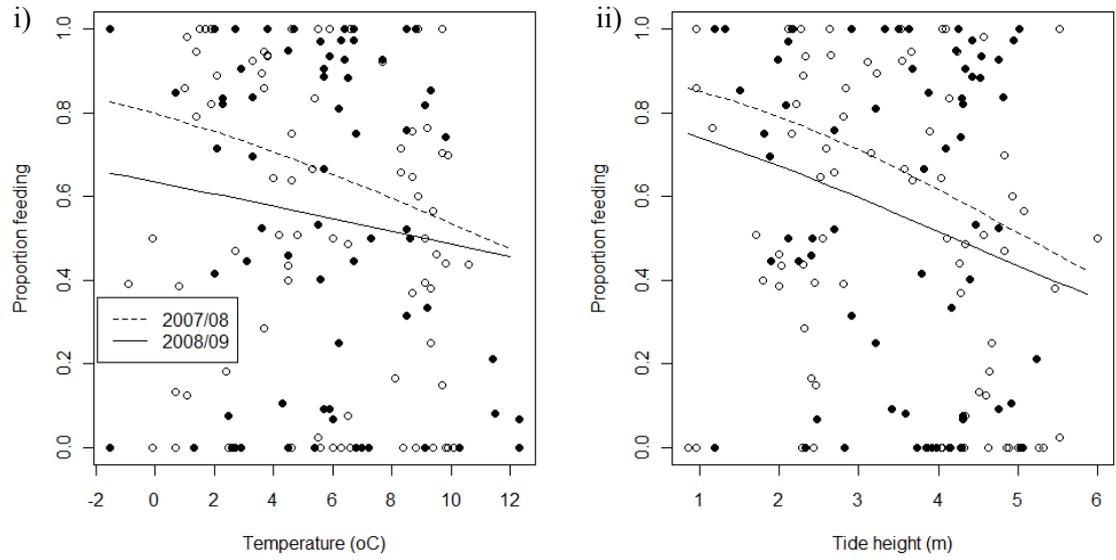
Common Name	Scientific name		
Red-throated Diver	<i>Gavia stellata</i>		
Black-throated Diver	<i>Gavia arctica</i>		
Great-crested Grebe	<i>Podiceps cristatus</i>		
Cormorant	<i>Phalacrocorax carbo</i>		
Grey Heron	<i>Ardea cinerea</i>		
Mute Swan	<i>Cygnus olor</i>		
Whooper Swan	<i>Cygnus cygnus</i>		
Pink-footed Goose	<i>Anser brachyrhynchus</i>		
Greylag Goose	<i>Anser anser</i>		
Canada Goose	<i>Branta canadensis</i>		
Dark-bellied Brent Goose	<i>Branta bernicla bernicla</i>		
Common Shelduck	<i>Tadorna tadorna</i>	}	
Eurasian Wigeon	<i>Anas penelope</i>		
Eurasian Teal	<i>Anas crecca</i>		
Mallard	<i>Anas platyrhynchos</i>		
Northern Pintail	<i>Anas acuta</i>		
Garganey	<i>Anas querquedula</i>		
Tufted Duck	<i>Aythya fuligula</i>		
Common Eider	<i>Somateria mollissima</i>		
Common Goldeneye	<i>Bucephala clangula</i>		
Red-breasted Merganser	<i>Mergus serrator</i>		
Goosander	<i>Mergus merganser</i>		
Eurasian Oystercatcher	<i>Haematopus ostralegus</i>		}
Ringed Plover	<i>Charadrius hiaticula</i>		
European Golden Plover	<i>Pluvialis apricaria</i>		
Grey Plover	<i>Pluvialis squatarola</i>		
Northern Lapwing	<i>Vanellus vanellus</i>		
(Red) Knot	<i>Calidris canutus</i>		
Dunlin	<i>Calidris alpina</i>		
Jack Snipe	<i>Lymnocyptes minimus</i>		
Snipe	<i>Gallinago gallinago</i>		
Black-tailed Godwit	<i>Limosa limosa</i>		
Bar-tailed Godwit	<i>Limosa lapponica</i>		
Eurasian Curlew	<i>Numenius arquata</i>		
Whimbrel	<i>Numenius phaeopus</i>		
Common Redshank	<i>Tringa totanus</i>		
Greenshank	<i>Tringa nebularia</i>		
Ruddy Turnstone	<i>Arenaria interpres</i>		
Eurasian Sparrowhawk	<i>Accipiter nisus</i>		
Common Buzzard	<i>Buteo buteo</i>		
Common Kestrel	<i>Falco tinnunculus</i>		
Peregrine Falcon	<i>Falco peregrinus</i>		



Appendix 3.2: Comparison of waterbird (i), duck (ii) and wader (iii) counts (\pm SE) across early and late winter during non-construction and construction winters in distant and bordering sectors.



Appendix 3.3: Model predictions (lines) against actual values (dots) for those proportions of Redshank feeding compared to those not feeding by temperature (i; *interaction*: $X^2_1=208.79$, $p<0.001$) and over all tidal heights (ii; *interaction*: $X^2_1=142.96$, $p<0.001$). Empty dots: winter 2007/08, solid dots: winter 2008/09.



Appendix 3.4: Model predictions (lines) against actual values (dots) for those proportions of Shelduck feeding compared to those not feeding by temperature (i; *interaction*: $X^2_1=71.61$, $p<0.001$) and over all tidal heights (ii; *interaction*: $X^2_1=37.64$, $p<0.001$). Empty dots: winter 2007/08, solid dots: winter 2008/09.

Chapter 4
Patterns of range use in Common Redshank on the Forth
estuary

4. Patterns of range use in radiomarked Common Redshank on the Forth estuary

In coastal areas, little is known of how individuals alter their daily movements and habitat use to endure in a habitat where predation risk and food availability may change dramatically over time. Using radio-telemetry, the movements of fourteen Common Redshank *Tringa totanus* overwintering on the Forth estuary were examined. Our objectives were to investigate space use and ask if habitats are used differently through time and by night. Our study found that space use varied according to the time of day, the stage of the season and both the shape of the intertidal flat and its proximity to high tide roosting sites. Redshank occupied smaller home ranges later in the winter and home ranges were roughly 20% smaller by night than by day, due to the avoidance of certain riverine areas by night. The reduction of range size with time may be explained by declining body condition or increased habitat awareness. Our study reveals the importance of whole season and nocturnal distributions to inform decisions on site management and protection. The strong site fidelity, limited movements and small home range size of Redshank also emphasize the potential for exposure to long term disturbance. If individuals are forced to compete for fewer habitats due to continuing disturbance of tidal flats, survival of Redshank wintering within this region could decline.

4.1. INTRODUCTION

Disturbance of terrestrial and marine habitats is widespread in most parts of the world, and its negative effects have been well documented (e.g. Sutherland 2007). Although population studies can provide information on how animals redistribute or change their behaviour in response to human disturbance, they often fail to describe fully how habitats are used both spatially and over time (Symonds *et al.* 1984; Drake *et al.* 2001; Butler *et al.* 2002; Warnock & Takekawa 2003). In coastal areas, which are exposed to increasing levels of disturbance (Inger *et al.* 2009), a number of studies have examined the effects of human use and prey availability on waterbird abundance and distributions (Bryant 1979; Meire 1991; Schekkerman *et al.* 1994; Meire 1996; Burton *et al.* 2002). Less is known, however, regarding how shorebirds alter their daily movements and habitat use to endure in a habitat where food availability may change dramatically over the course of a season. Such information on movements and an individual's dependency on smaller areas within larger sites is essential for conservation planning and site management (Symonds *et al.* 1984; Petit 2000).

Knowledge of such movements may be obtained from re-sightings of birds marked with colour dye (e.g. Furness & Galbraith 1980; Symonds *et al.* 1984; Dias *et al.* 2006) or individually-marked with colour rings (e.g. Burton *et al.* 2006; Cresswell *et al.* 2007). By marking birds individually, it also allows investigation into whether behaviour and movement is related to age, sex, size or body condition (Kenward 2001). In contrast to marking techniques, radio-telemetry allows individuals to be located remotely, without the need for re-sighting. This allows accurate, systematic and unbiased information on individual movements and habitat-use to be obtained because individuals can be located on a regular basis and tracked over time (Krementz *et al.* 1994; Warnock & Takekawa 1996). Provided a transmitter remains intact, individuals may be located in conditions when it would be otherwise impossible to distinguish visual markings, such as during inclement weather, at night, or over large distances (Beyer & Haufler 1994; Kenward 2001).

Home range has rarely been used as an instrument to detect the influence of disturbance on an individual's movement patterns. Sitters (2000) found Eurasian Oystercatcher *Haematopus ostralegus* on the Exe estuary made more between-mudflat movements during daytime than at night, due to increased intraspecific interference and greater human disturbance by day. In contrast, Burton & Armitage (2005) found Redshank nocturnal home ranges to be larger, due to the avoidance of a heavily disturbed foraging site located adjacent to a busy heliport during the day. These studies also illustrate the importance of collecting nocturnal as well as diurnal distributions in order to inform decisions on site management and protection. If individuals behave differently at night, the importance of sites used mainly at night and the total extent of the areas used may be underestimated (Beyer & Haufler 1994; Burton & Armitage 2005).

Having determined home range estimates, many researchers have given little attention to their internal structure and patterns of use. For example, areas within ranges may be avoided or used less due to human disturbance (Burton & Armitage 2005), low prey availability (Dugan 1981; Robert & McNeil 1989; Burton & Armitage 2005), exposure during inclement weather (Mouritsen 1993; van Gils *et al.* 2000), predation risk (Mouritsen 1992; Cresswell 1994) and during high spring tides (McConkey & Bell 2005). In addition, most shorebirds are forced to make frequent and often distant flights between foraging grounds and high-tide roosts (Symonds *et al.* 1984; Piersma *et al.* 1993). Dias *et al.* (2006) found the overall density of Dunlin on suitable intertidal foraging grounds declined with the distance to the nearest roost, while individuals avoided foraging in areas of intertidal flats far from their spring high-tide roost. This association between roosts and foraging grounds is probably in response to the need to minimise energy costs of flying between them (Luís *et al.* 2001; Rogers 2003). If the distance to high tide roosts influences the access to foraging areas by shorebirds, then the loss of roosts may affect the carrying capacity of estuaries, with negative consequences for shorebird populations (Furness 1973; Tubbs *et al.* 1992; Burton *et al.* 1996).

In this study we used radio-telemetry to examine the winter movements of the Common Redshank *Tringa totanus*, a species known to be highly site-faithful both within and between winters (Furness & Galbraith 1980; Moss 1985; Burton 2000; Rehfish *et al.* 2003). Our objectives were to investigate local space use and ask if habitats are used differently through time and by night. As avian species are known to regulate fat reserves over the course of a winter (Houston *et al.* 1993; MacLeod *et al.* 2005) and home range size is known to be positively affected by body size (Harestad & Bunnell 1979; Rees 1988; Relyea *et al.* 2000), the influence of body mass on home range size was also investigated. Documenting such a response would not only contribute to our understanding of how organisms interact with coastal landscapes, but may also identify categories of individuals, or periods in their seasonal residency, which may be particularly susceptible to disturbance or habitat loss.

4.1. METHODS

4.1.1. Capture and transmitter attachment

Redshank were caught at five high tide roosts on the Forth estuary by mist-netting, between 17 November 2007 and 15 February 2009 (Figure 4.1). Captures were most successful at night on a rising tide and when a tape lure played a recording of roosting wader calls (Wetlands and Coastal Ecology Unit, British Trust of Ornithology, Thetford, UK). Birds were aged according to Prater (1977), distinguishing between those less than 1 year old (i.e. juveniles, Euring codes 3 and 5) or birds greater than 1 year old (i.e. adults, Euring codes 4 and 6). Standard biometric data were collected. Lengths were measured to the nearest 1mm with a stopped ruler (wing-length and tarsus plus toe-length) or 0.1mm with callipers (bill-length and total head-length).

Mass was measured to the nearest 1g with a Pesola balance. In total, one adult and 28 first winter Redshanks were captured and fitted with backpack-mounted transmitters weighing 2.4g (Figure 4.2; model Pip2 with Ag393 cell battery; Biotrack UK Ltd, Wareham, Dorset, UK). Transmitters were fitted with both a 250mm whip antenna and a ground-plane antenna to maximise range; required for locating birds on distant mudflats. Following the methods of Warnock and Warnock (1993) and Burton and Armitage (2005), tags were fixed to a small sheet of gauze and attached to a small area of clipped feathers on the lower back using cyanoacrylate glue (Loctite® Super Glue, Henkel Consumer Adhesives, Cheshire, UK). To avoid overloading birds and to minimise the risk of premature detachment, each transmitter weighed no more than 2% of an individual's body mass (mean=1.48%, max=1.95%, n=29), as recommended by Kenward (2001). Every Redshank fitted with a transmitter was also given a unique combination of Darvic plastic colour-rings to aid subsequent visual identification in the field. Radio-tagged and ringed birds were normally found foraging and roosting among flocks of non-tagged birds.

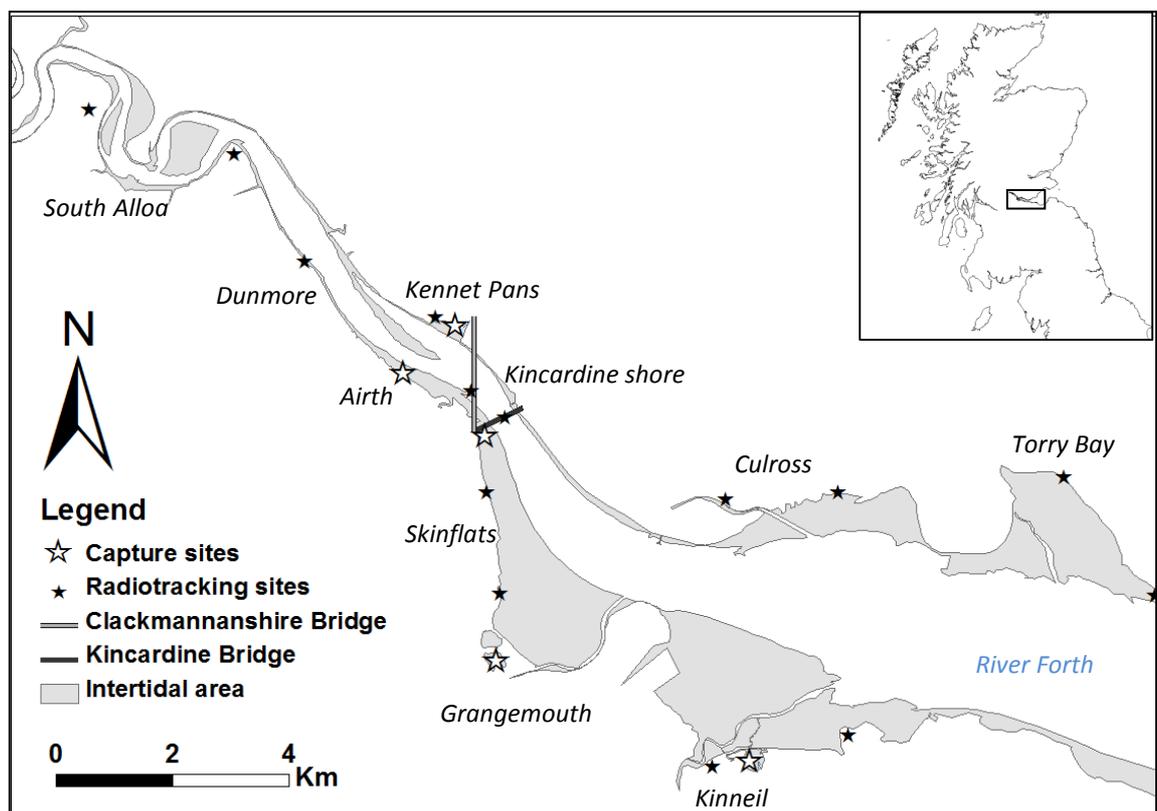


Figure 4.1: The study area on the Forth estuary, Scotland: Location map with capture sites (white stars), radiotracking sites (black stars), Clackmannanshire Bridge, Kincardine Bridge and areas mentioned in text. The intertidal area indicated by dark shading is bordered by the mean low-water mark at spring lows.



Figure 4.2: A juvenile Common Redshank fitted with radio-transmitter and Darvic colour rings.

To control for body-size in the analysis of body mass, equations adapted from Mitchell *et al.* (2000) for Common Redshank wintering at Teesmouth, NE England (54°37'N, 1°12'W), were used as a correcting factor for individual size differences:

$$S = (0.501wl) + (0.543bl) + (0.614tt) \quad (1)$$

$$BM' = BM + (1.98 (16.5-S)) \quad (2)$$

where S = body size, wl = wing-length (mm), bl = bill-length (mm), tt = tarsus-toe (mm), BM' = Size adjusted body mass (g), BM = body mass (g). For all 29 Redshank captured during this study, individuals caught later in the winter were significantly lighter in terms of size adjusted body mass (BM') than those individuals caught earlier in the winter (*Regression*, $F_{1,28}=6.224$, $p=0.019$; Figure 4.3).

4.1.2. Data collection

All tracking of Redshank was done with a Televilt model RX-81 receiver (Televilt/TVP Positioning AB, Lindesberg, Sweden) at the 173.000–173.999 MHz range with a hand-held three-element Yagi antenna. Birds were located via triangulation (Heezen & Tester 1967; White & Garrott 1990; Kenward 2001) both by day and night by scanning from elevated vantage points around the estuary (Figure 4.1). The transmitter's signal could be detected up to 1.5km away on flat ground, but by using the Kincardine Bridge or hills bordering the river, this range could be extended up to 5km under optimal conditions. Location fixes were derived by taking 2-

three bearings as quickly as possible, to reduce the chance a focal bird had moved (White & Garrott 1990). When birds were not observed visually, positions were evaluated using the LOAS positioning software (Ecological Software Solutions, Sacramento, CA, USA) to estimate the locations of individuals (Taft *et al.* 2008). Scans were conducted six days per week and divided into two mornings (0600-1200), two afternoons (1400-2000) and two night searches (2100-0300) per week. The order in which sites were visited within the time allocated was alternated to provide a more representative sample of Redshank movements throughout the tidal cycle, and across spring and neap tides (Appendices 4.2i, ii). Day and night were later separated into discrete categories by morning and evening nautical twilight; nautical dawn and nautical dusk times were obtained from the Astronomical Applications Department, U.S. Naval Observatory. Tracking commenced on the day following release and terminated when the transmitter's signal could not be detected after several intensive large-scale searches of the estuary (Figure 4.4).

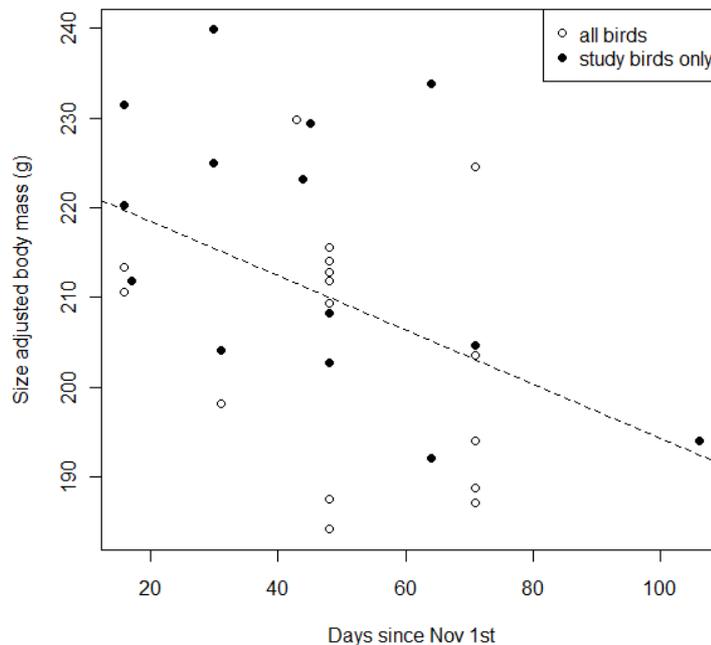


Figure 4.3: Seasonal changes in size adjusted body mass (BM') of juvenile and adult Redshank on the River Forth (2007-2009). Nine Redshank were captured in winter 2007/08 and 20 were captured in winter 2008/09. The dotted line represents the predicted values of a linear regression between BM' of all Redshank captured during our study ($n=29$) and the date of capture ($F_{1,28}=6.224$, $p=0.019$).

Between 14/12/07 - 04/02/08 (W1) and 17/11/08 - 19/03/09 (W2), a total of 114 daily searches for birds on the Forth estuary were conducted. Of the 29 Redshank captured, nine were caught in W1 with the remainder captured using similar methods in W2. Four transmitters were lost or failed less than one day after release. A single transmitter was recovered from a predated

Redshank at Kinneil lagoon in 2009. Once activated, transmitters lasted up to 79 days with the mean lifetime of 36 days for each transmitter (Figure 4.4). Over the period of study, 526 radiolocations were made, with approximately 62% of locations obtained during daylight conditions, including dawn and dusk hours, and approximately 60% of all locations were collected during neap tides. The number of location fixes obtained for each individual was approximately one location every two days.

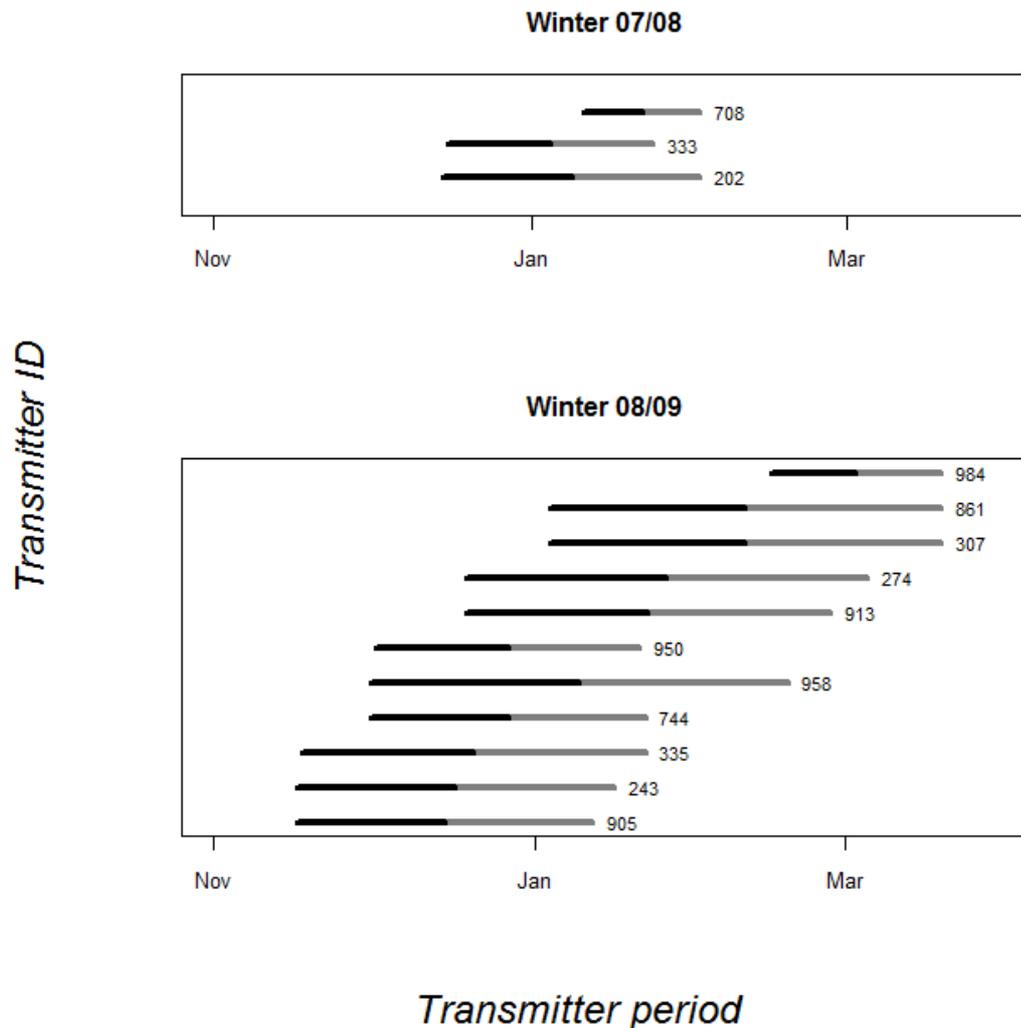


Figure 4.4: Radio-tagged Redshank on the Forth estuary between November 2007 and March 2009. Black bars represent 'early' winter, grey bars represent 'late' winter. For each individual bird, 'early' and 'late' winter ranges contain equal number of locations per range to maintain independence of seasonal elements.

4.1.3. Home range measurements

Prior to calculating home ranges, we selected no more than two location fixes for an individual in a single day, and then only used locations separated by more than three hours to minimise non-independence between successive radiolocations. As independence is an important assumption in statistical measures of animal movement and home range size (Swihart & Slade 1985; Worton 1987), the methods of Swihart & Slade (1985) were used on a subsample of continuous tracking data to determine the level of time-autocorrelation in the data. The sample standard deviation, s , of t^2/r^2 was used to calculate the critical values to determine whether the calculated Schoener's (1981) index (V), was significantly different from 2. From these analyses, minimum interval required to achieve statistical independence between successive locations was 90 minutes (Appendix 4.3). In most cases, time between successive locations was much greater than 3 hours (e.g. mean = 49h \pm 3.49), with 59.3% of observations separated by more than 24 hours, and 87.5% of observations separated by at least one complete tidal cycle (12 hours).

We used the 'adehabitat' library of functions written by Calenge (2006) in the R programming language (R Development Core Team 2009) to produce kernel density estimates of the animal's utilisation distribution (UD; i.e. the probability distribution of defining the animal's use of space). Fixed kernel home ranges (Worton 1989) were calculated for each volume contour, i.e. the lines within which there would be a 50% or 95% chance of finding the individual concerned (Figure 4.5). By using conditional 95% UDs to describe 'home range' for each individual, the effect of very small, non-zero estimates of the UDs near the boundary of the observations were eliminated (Fieberg & Kochanny 2005). Unlike minimum convex polygons, kernel techniques allow for ranges to be split into more than one activity centre, an important consideration in this study due to the discontinuous nature of the intertidal habitat and the likely patchiness of resources within continuous habitat patches (Burton and Armitage 2005). Kernel estimators are nonparametric so are therefore robust to violations of independence and are less sensitive to autocorrelated data and outlying point locations (Seaman & Powell 1996; Swihart & Slade 1997).

The spread of the kernels is determined by a smoothing parameter and, in this study, this was estimated by least-squares cross-validation (LSCV), a method which tends to reduce over-smoothing of the data and results in more accurate estimates of home ranges (Worton 1995; Seaman & Powell 1996; Seaman *et al.* 1999). The LSCV smoothing parameter value h was then standardised by taking the mean h for all home ranges and applying this value across all UDs.

Previous work has shown a negative bias in Kernel and MCP area when employing low numbers of locations (White & Garrott 1990; Mazur *et al.* 1998). To determine the minimum number of locations necessary to achieve stability in home range size, the 95% and 50% UD were plotted against the number of locations (Kenward 1982; Parish & Kruuk 1982; Kenward

2001). Location data from birds captured at Kennet Pans, Skinflats and Kinneil were then chosen to investigate how many locations were required in order for the 95% and 50% UD to reach an asymptote. Stable estimates of range size were found using at least 20 radio locations per range (Appendix 4.4). Of the 29 transmitters deployed on birds, 15 were excluded from our analysis after failing to meet the 20 independent radio locations required to create stable estimates of home range (Appendix 4.1). Further to this test, the effect of location number and the length of the observation period on the 95% and 50% UD were investigated using linear regression. Using a minimum of 20 radio locations per range, there was no significant effect of the number of locations on either 95%, or 50% UD (F_{1,12}=1.587, p=0.232; F_{1,12}=0.895, p=0.363). Similarly there was no effect of observation duration on either 95% or 50% UD (F_{1,11}=3.513, p=0.088; F_{1,11}=2.130, p=0.172).

4.1.4. Statistical analysis

This study used a combination of general linear models (GLMs) and general linear mixed models (GLMMs) to describe patterns in home range use in Common Redshank. To investigate the role of environmental variables on range estimates, GLMs were fitted to the 14 home range (95% UD) and core area (50% UD) estimates. *Tag duration* (days), *capture date* (days after Nov 1st), *body size* (*S*), *size adjusted body mass* (*BM'*) and whether birds were captured upriver or downriver of the Kincardine Bridge ('*site location*') were included as explanatory variables

Separate diurnal and nocturnal ranges were calculated for all individuals with >8 telemetry fixes within each time category (*n*=12 birds). General linear mixed-effect models (*GLMMs*) were used to investigate diurnal vs. nocturnal home range and core area use. *day|night* (diurnal vs. nocturnal) and the *location number* were included in our model as fixed effects and *Bird ID* was included as a random factor. To examine the effects of seasonality on individual range use, locational data from each individual was divided into two categories with equal sample sizes: an 'early' and 'late' winter season (Figure 4.4). This was done to maintain independence of seasonal elements. The respective home ranges were then calculated to see if home range remained constant throughout the winter. We again used GLMMs with *Bird ID* as a random factor to investigate differences in area use. *Season* (early vs. late), *capture date* (days after Nov 1st) and *transmitter period* (days) were included as fixed effects.

Unimportant variables were removed from both the GLM and the GLMM by stepwise deletion, until only those variables that were significant at the 5% level at explaining variation in bird numbers were retained in the final model. GLMMs were constructed using the 'nlme' package (Pinheiro *et al.* 2009) and all analysis was conducted in the R programming language (R Development Core Team 2009).

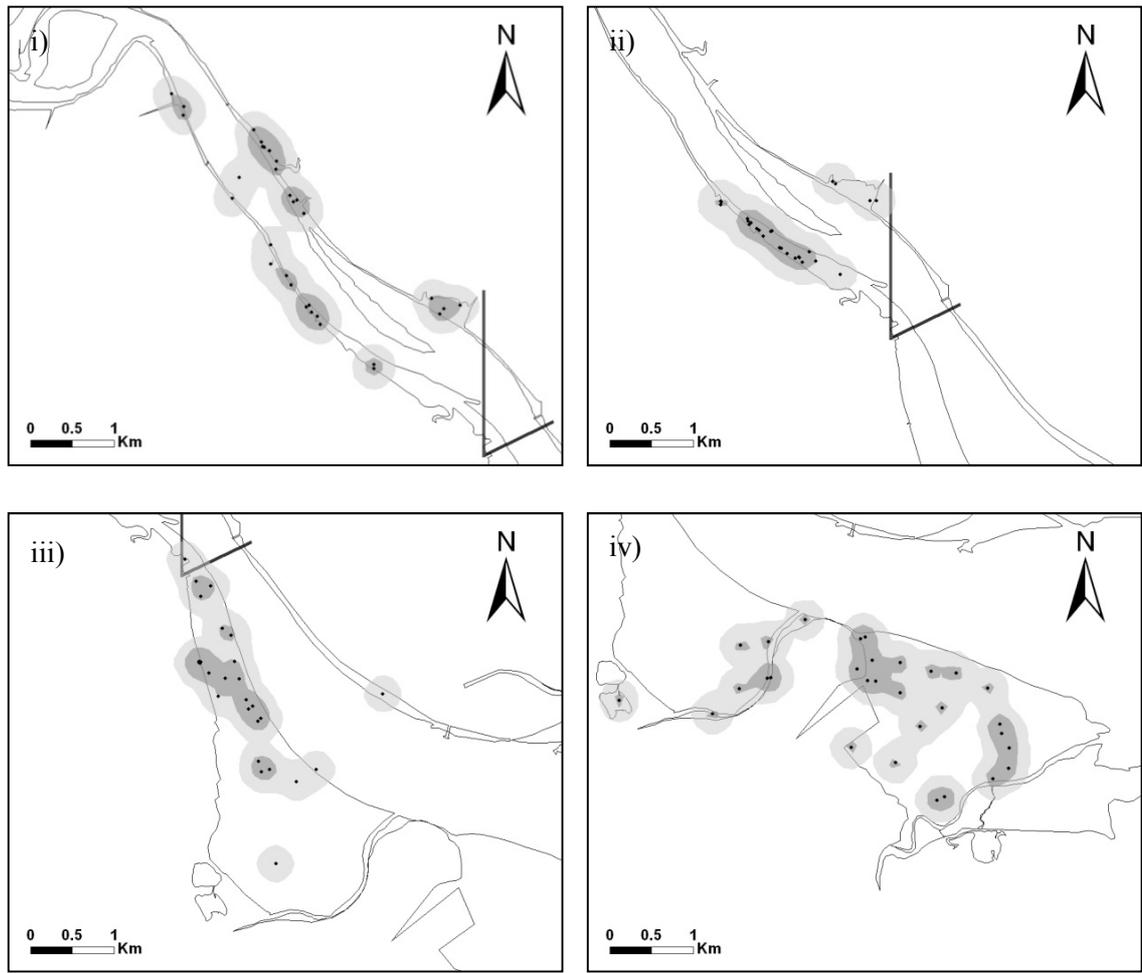


Figure 4.5: The radio-locations and estimated ranges of (i) Redshank ID 333, captured at Kennet Pans on 15/12/2009; (ii) Redshank ID 861, captured at Airth on 04/01/2009; (iii) Redshank ID 950, captured at north Skinflats on 17/11/2008; (iv) Redshank ID 905, captured at Skinflats lagoons on 02/12/2008. Light shading indicates the extent of the 95% home range and the dark area represents the 50% core area. Dark lines in Figures 4.5i, ii and iii represent the line of the Clackmannanshire Bridge (north) and the Kincardine Bridge (south).

4.2.RESULTS

For 14 first-winter Redshank, an average of 31 location fixes (minimum 20, maximum 47) were included in the analysis of home range size. The sizes of ranges varied greatly; one individual captured in the lagoon at Skinflats had a home range of 419ha while an individual captured at Kennet Pans had a home range of 143ha. In our GLM, *Capture date* (i.e. days after Nov 1st) had a negative effect on both home range (Figure 4.6i; $F_{1,11}=10.734$, $p=0.007$) and on core area size (Figure 4.6ii; $F_{1,12}=5.698$, $p=0.034$). This suggests that birds occupied smaller areas later in the winter (i). Home range or core area estimates did not differ significantly for body size (*S*) (home range: $F_{1,9}=0.216$, $p=0.653$; core area: $F_{1,8}=0.072$, $p=0.796$), size adjusted body mass (*BM'*) (home range: $F_{1,10}=1.382$, $p=0.267$; core area: $F_{1,9}=0.459$, $p=0.515$) or the duration of time the transmitters were operational (home range: $F_{1,8}=0.480$, $p=0.508$; core area: $F_{1,10}=0.503$,

$p=0.494$). Home range estimates upriver of the Kincardine Bridge were smaller than those downriver of the bridges ($F_{1,11}=8.349$, $p=0.015$), however core areas were marginally non-significant ($F_{1,11}=3.238$, $p=0.099$).

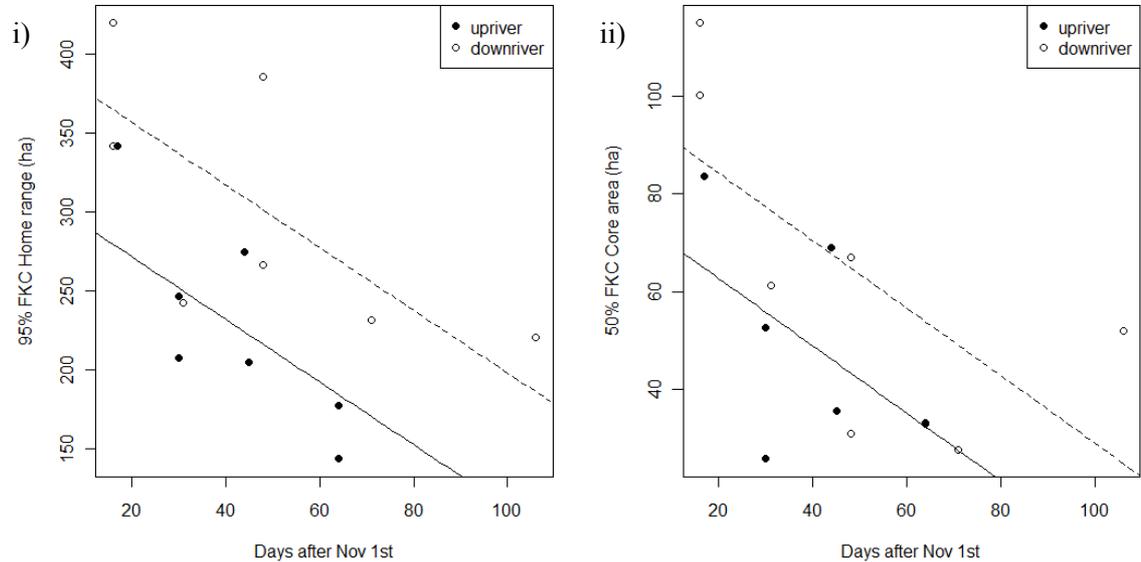


Figure 4.6: Relationship between i) home range and ii) core area size by capture date (days after November 1st) and the location where individuals were first captured for those individuals with ≥ 20 locations ($n=14$). Fitted lines represent upriver (solid line) and downriver birds (dashed line).

Individuals held larger home ranges during the day than at night ($X^2_1=7.243$, $p=0.007$; Figure 4.7i), however core areas were similar by day and by night ($X^2_1=3.434$, $p=0.064$). The number of locations had no impact on the size of an individual's home range or core area (home range: $X^2_1=0.001$, $p=0.972$; core area: $X^2_1=0.310$, $p=0.578$). Individuals were only found feeding at Kincardine shore (NS 292687), Dunmore village (NS 289419) and the east side of Kennet Pans during the day, while a greater proportion fed underneath the Kincardine Bridge (NS 292686), at the sewage works at Airth (NS 290688) and at the west edge of Kennet Pans at night.

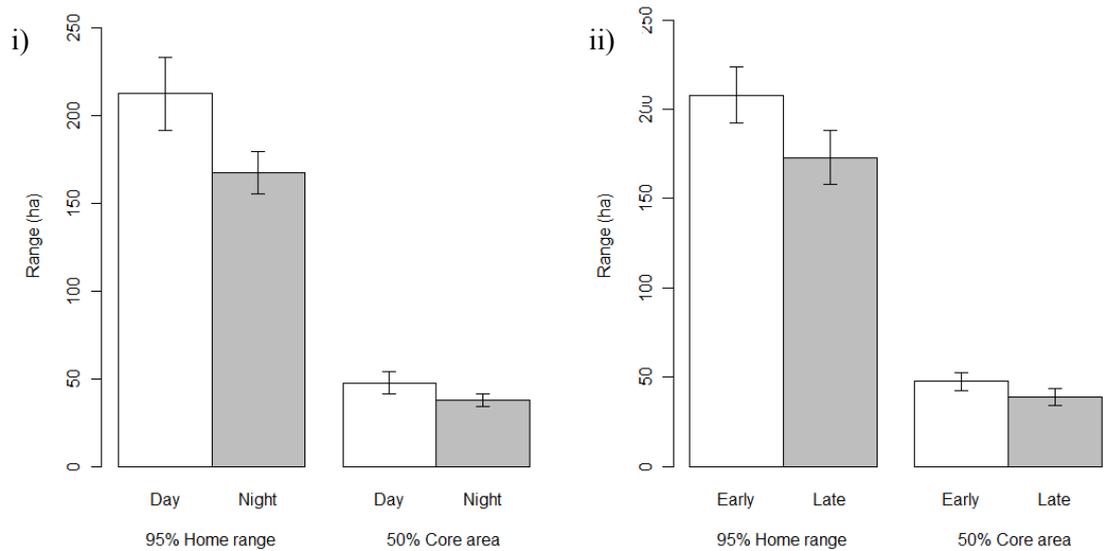


Figure 4.7: Comparison of (i) day vs. night home range and core area estimates (\pm SE) and (ii) early winter vs. late winter home range and core area estimates (\pm SE) for Common Redshank overwintering on the Forth estuary.

Individuals' home ranges and core areas were significantly larger in the early period of monitoring than they were later in the winter (home range: $X^2_1=6.772$, $p=0.009$; core area: $X^2_1=3.922$, $p=0.048$; Figure 4.7ii). Date of transmitter attachment was negatively correlated with home range ($X^2_1=11.549$, $p<0.005$) and core area size ($X^2_1=8.752$, $p=0.003$). Transmitter duration had no significant effect on home range size ($X^2_1=0.108$, $p=0.742$), but had a negative effect on core area size ($X^2_1=3.922$, $p=0.048$). Kennet Pans (NS 291688) was used extensively in early winter, however individuals caught at this site (e.g. ID 202, ID 333, ID 335) dispersed upriver to Dunmore (NS 289689) and to Alloa Inch (NS 286692) later in the winter (Figures 4.8i, iii). Another individual (ID 958) also caught at Kennet Pans moved across the river to Airth (NS 291687) then to Skinflats (NS 292686) before settling at Kincardine shore (NS 292687). This suggests that individuals move around more in the early part of the winter before becoming more sedentary later in the winter.

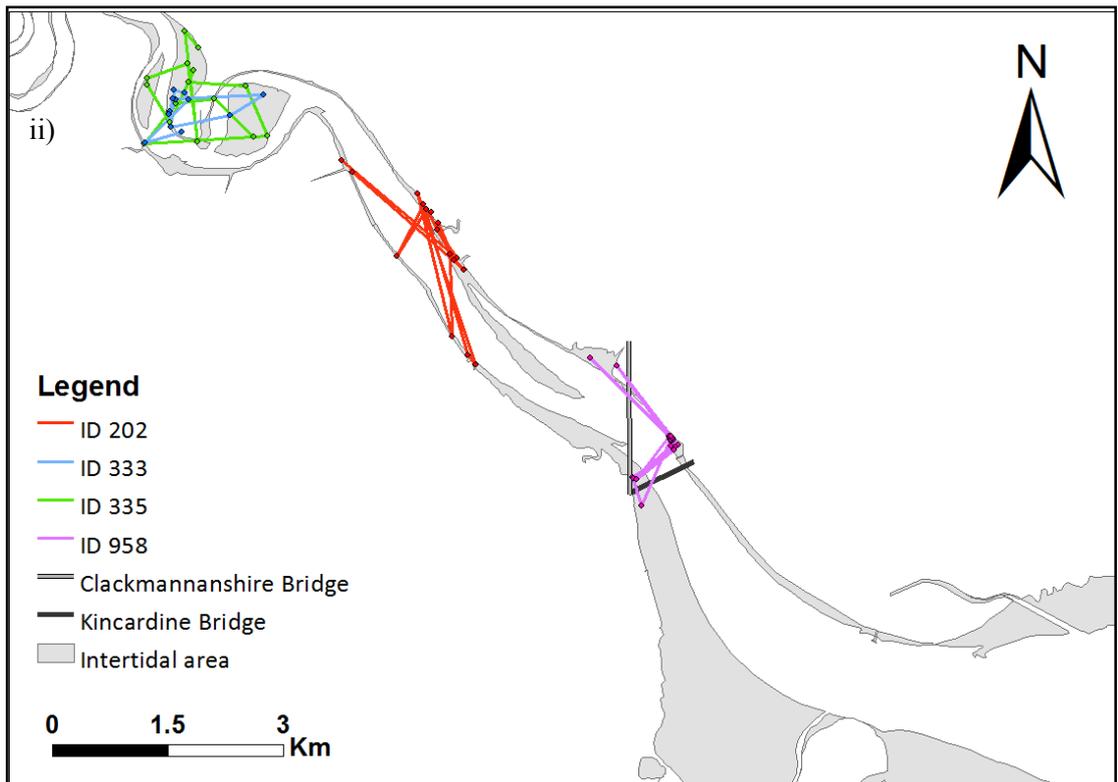
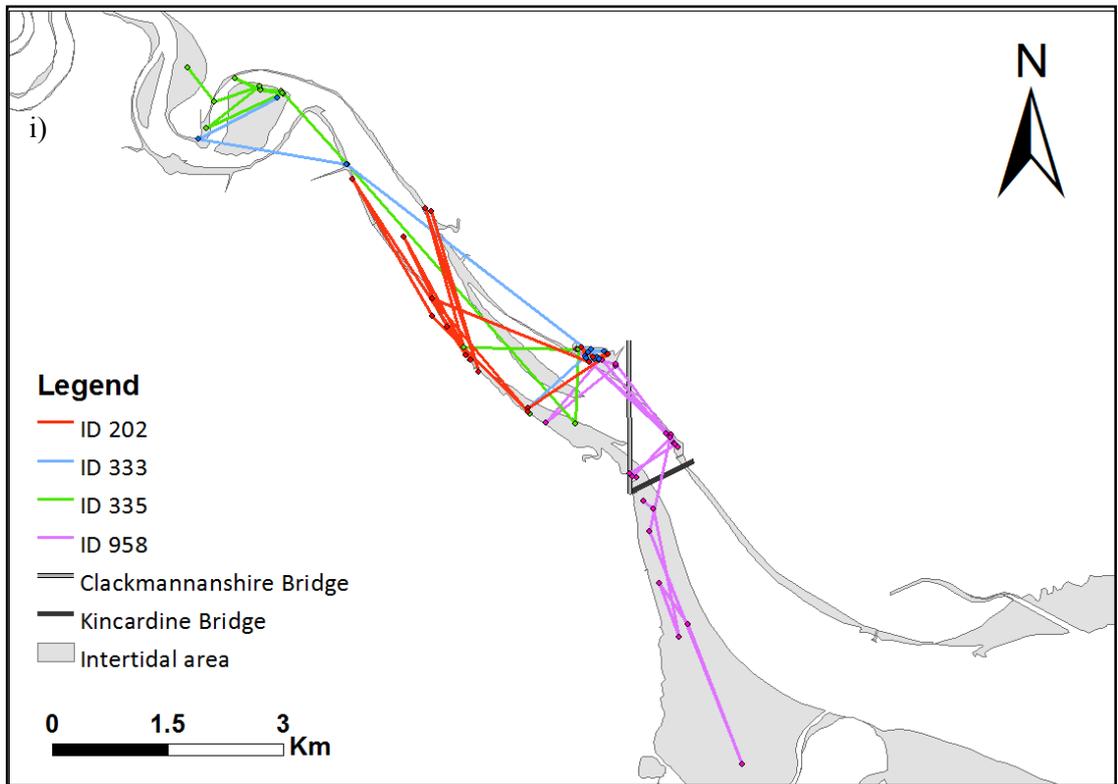


Figure 4.8: Plots of all fixes for selected individuals in ‘early’ (i) and ‘late’ (ii) winter, connected in sequence by lines to show course of winter habitat use. All birds were initially tagged at Airth (ID 202 (red), ID 333 (blue) and ID 335 (green)) or Kennet Pans (ID 958 (fuchsia)).

4.3. DISCUSSION

4.3.1. Seasonal patterns

In our study, Redshank showed substantial losses in body mass during the course of the winter (Figure 4.3). Such seasonal changes in reserves, normally involving changes in fat, have been well documented in several shorebird species (Pienkowski *et al.* 1979; Scott *et al.* 1994; Mitchell *et al.* 2000; Summers *et al.* 2010) as well as some passerines (Rogers 1987; Cresswell *et al.* 2009). An increase in body mass may act as an insurance against unpredictable foraging opportunities (Rogers 1987; Houston *et al.* 1993; Thomas & Cuthill 2002) and the possibility of encountering severe weather conditions in winter (Evans & Smith 1975; Dugan *et al.* 1981). Following mid-winter, reserves were apparently allowed to fall as the chance of encountering prolonged severe weather decreased as winter progressed. An increased mass reduces a bird's ability to accelerate quickly at take-off or when flying away from an attacking predator (Kullberg *et al.* 1996; Brodin 2000; 2001; Krams 2002). This reduction in mass is widely thought to be in response to the trade-off between the risk of starvation, the costs of carrying (especially flying with) an additional load (Witter & Cuthill 1993), and the elevated risk of predation (Lima 1986; Houston & McNamara 1993; Houston *et al.* 1993; Gosler *et al.* 1995).

Redshank occupied smaller home ranges in late winter compared to early winter. A contraction in home range size through winter has previously been demonstrated in Willet *Tringa semipalmata* (Gabbard *et al.* 2001), as well as for Common Redshank (Crowther 2007). For birds wintering on temperate intertidal habitat, food resources may change dramatically over the course of a season (Bryant 1979; Bryant & McLusky 1997). It seems likely, therefore, that shorebirds would correspondingly adjust their use of habitat throughout a period of winter residency. It is less clear, what the nature of this adjustment might be. Shorebirds have been found to respond less to raptorial predators (McGowan *et al.* 2002) and to human disturbance (Stillman & Goss-Custard 2002; Beale & Monaghan 2004) when they were more energetically stressed and the fitness costs of reacting to the disturbance is generally greater. If individuals were more stressed in late winter, with an elevated risk of starvation or disease, they may be reluctant to expend extra energy in travelling between patches, thus resulting in a smaller home range (Bernstein *et al.* 1991; De Leeuw 1997).

Another explanation for this seasonal contraction in range size may be a result of increasing individual awareness of the surrounding habitat. Recently arrived birds, especially juveniles, will have limited experience of their wintering grounds and will thus explore adjacent habitats in order to acquire a knowledge of resource distribution and habitat quality more generally (Metcalf & Furness 1985; Myers *et al.* 1988; Baccetti *et al.* 1995; Rehfish *et al.* 2003). Intra-specific competition with dominant individuals will exclude subordinate individuals from prime foraging sites (Goss-Custard *et al.* 1984). Those individuals unable to compete with dominant

birds will be displaced until a suitable site is found. As our study concerned juvenile birds, these individuals are likely to be sub-dominants, or comprise a higher proportion of sub-dominants, have poor knowledge of the habitat and experience high interference competition from dominant birds (Goss-Custard & Durell 1984; van der Have *et al.* 1984; Summers *et al.* 1990; Cresswell 1994). Consistent with this interpretation, individual juveniles captured at Kennet Pans (a high quality site in terms of prey and predation-risk; chapter 2) gradually dispersed to poorer quality habitat with low prey content, higher levels of human disturbance and/or a high risk of predation in terms of distance to cover and frequency of observed attacks.

In our study, the reduction in an individual's late winter range could be argued as evidence of an increasing unwillingness to fly due to the costs of carrying an extra load, rather than a result of increased habitat awareness or prey depletion. It is recognized that negative effects associated with instrumentation cannot be completely avoided. Not only is handling likely to cause stress, but there is also some energetic cost associated with carrying an excess load (Murray & Fuller 2000; Kenward 2001; Wilson & McMahon 2006). In order to minimize the negative effects of instrumentation, our study applied the '3% rule', a commonly accepted standard that the mass of an instrument should not exceed 3% of the body mass for a species which depends greatly on flight (Caccamise & Hedin 1985; Aldridge & Brigham 1988; Gessaman & Nagy 1988; Kenward 2001; Phillips *et al.* 2003). However such a universal rule has been argued as being too simplistic and does not account for the complexity and specificity of each situation (Casper 2009). An impact may be evident in the instrumented bird itself, for example reduced body mass or increased foraging trip durations leading to increased flight metabolism (Gessaman & Nagy 1988; Sohle *et al.* 2000). Instruments and attachments may additionally cause feather damage (Sykes *et al.* 1990; Foster *et al.* 1992; Wilson *et al.* 1997), disrupt waterproofing and increase heat loss at the attachment site (Godfrey *et al.* 2003; Ackerman *et al.* 2004). However, this relationship between season and range size was consistent for all individuals by capture date (Figures 4.4i, ii), as well as for comparisons of 'early' and 'late' winter ranges for each individual (Figure 4.5ii). Although there may have been some unavoidable negative effects associated with the instrumentation, we argue that this is unlikely to affect our previous conclusions.

4.3.2. *Spatial patterns*

According to models of optimal foraging - metabolic requirements, quality of habitat and the density of food should be important factors influencing home-range size of birds and mammals (McNab 1963; Schoener 1968; Jenkins 1981; Mace & Harvey 1983; Schoener 1983). Redshank occupying the more productive downriver stretch of intertidal habitat had larger home ranges than birds in the less productive upriver sites. These upriver sites also suffered higher frequencies of disturbance due to their narrow mudflat width and their close proximity to recreational paths. This pattern is consistent with our previous argument; that individuals in

good condition are more capable of bearing the costs associated with movements between foraging areas, than individuals in poorer condition for whom movements to alternate foraging grounds may be considered too costly.

Over two winters, Redshank made very few trips across the Kincardine Bridge, remaining faithful to their upriver and downriver habitat. The segregation of birds by the Kincardine Bridge suggests this structure may act as a division between two populations of Common Redshank. During the construction of the Clackmannanshire Bridge in winter 2007/08, no tagged individual was observed to move across this structure while the site was operational and engineers were working on and around the new bridge. If this was a more general pattern, it may have negative survival implications if the birds had to look for novel foraging opportunities during severe weather episodes.

The largest home ranges were amongst those individuals inhabiting the intertidal mudflats at south Skinflats and Kinneil. The wide shallow mudflats at these sites and the relatively few and dispersed high tide roosts may cause birds to move greater distances while following the tide. The removal or disturbance of important roosting sites at such sites could have negative consequences (via elevated travel costs) for shorebirds with few options to roost elsewhere during high tide (Furness 1973; Rogers 2003; Rogers *et al.* 2006; Rosa *et al.* 2006; Peters & Otis 2007).

4.3.3. *Night vs. day*

Individuals' home ranges were roughly 20% smaller by night than by day. This was due to birds using fewer sites by night than those frequented during the day. Differences in species' diurnal and nocturnal site use have been observed in numerous studies (see McNeil *et al.* (1992) for review) and may be explained by several factors. Poor visibility at night may cause birds to avoid particular sites due to an increased predation risk. Sitters *et al.* (2001), studying Knot in Patagonia, reported that a mussel-bed used by large numbers of birds in the day was deserted at night and that birds instead dispersed over mudflats further from land to reduce risk of predation. Similarly, Burton and Armitage (2005) found that Redshank avoided riverine areas, possibly due to the risk of predation from owls (Mouritsen 1992) and perhaps mammalian predators, such as Red Foxes *Vulpes vulpes*. In terms of use of roosting sites, on the Yukon Delta in western Alaska, Handel & Gill (1992) felt that increased danger of predation by mammals explained their observations of Dunlin *Calidris alpina* avoiding onshore roost sites during nocturnal high tides that were used during the preceding or following daytime high tides. In our study site, Tawny Owls *Strix aluco* and foxes were often seen while conducting scans and trapping birds at Dunmore village and Kennet Pans and clearly posed a risk to shore-bound waders.

Some birds may be able to forage more efficiently in one place by day and in another by night. Certain prey species are known to become more active at the substrate surface at night (Dugan 1981; Robert & McNeil, 1989); however birds are able to detect visual cues less effectively under reduced light levels (Sitters 2000). For example, Goss-Custard (1969) found a diet switch in that Redshank mainly took *Corophium* by day and less profitable *Hydrobia* by night possibly because birds were not able to detect the presence of their main and most profitable prey visually. The relatively poor quality of these upriver sites on the Forth (chapter 2; McLusky 1987) and the low background light levels may make it unprofitable for birds to feed in such areas by night.

Finally, a larger diurnal range may also be a result of increased movements both between and within intertidal areas in response to human presence. Burger and Gochfeld (1991) found that at night, Sanderling ran less, flew less and generally devoted less time to avoiding people than in the day. Similarly, Sitters (2000) found that Oystercatcher on the Exe estuary performed fewer movements between mussel beds by night, possibly as a result of the reduced disturbance levels during this period. In our study, disturbances from recreational and industrial disturbance episodes were considerably fewer at night compared to day. The smaller nocturnal range observed on the Forth estuary may therefore be a result of reduced behavioural response to human disturbance episodes.

4.4. CONCLUSIONS

Our study found that space use of Redshank on the Forth estuary varied according to the time of day, the stage of the season and both the shape of the intertidal flat and its proximity to high tide roosting sites. It is therefore important that information on whole season and nocturnal distributions should be available to inform decisions on site management and protection. Other factors being equal, a bird occupying a larger home range will be more likely to overlap with zones of disturbance or habitat loss. The strong site fidelity, limited movements and small home range size of Redshank also emphasize the potential for exposure to long term disturbance. This is particularly true for individuals at the end of the winter when their ranges have contracted due to increased metabolic costs. If individuals are forced to compete for fewer habitats due to continuing disturbance of tidal flats, survival of Redshank wintering within this region could decline.

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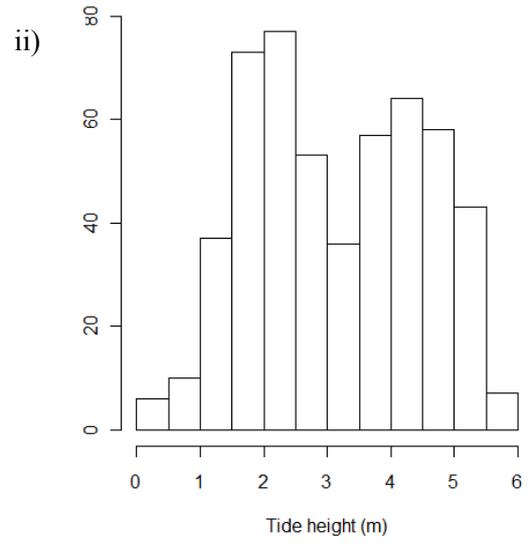
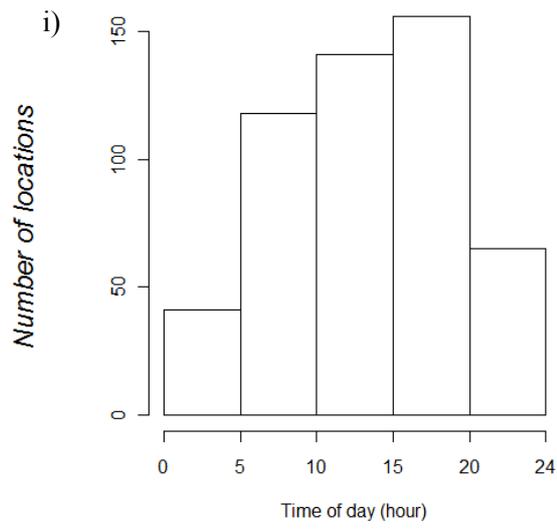
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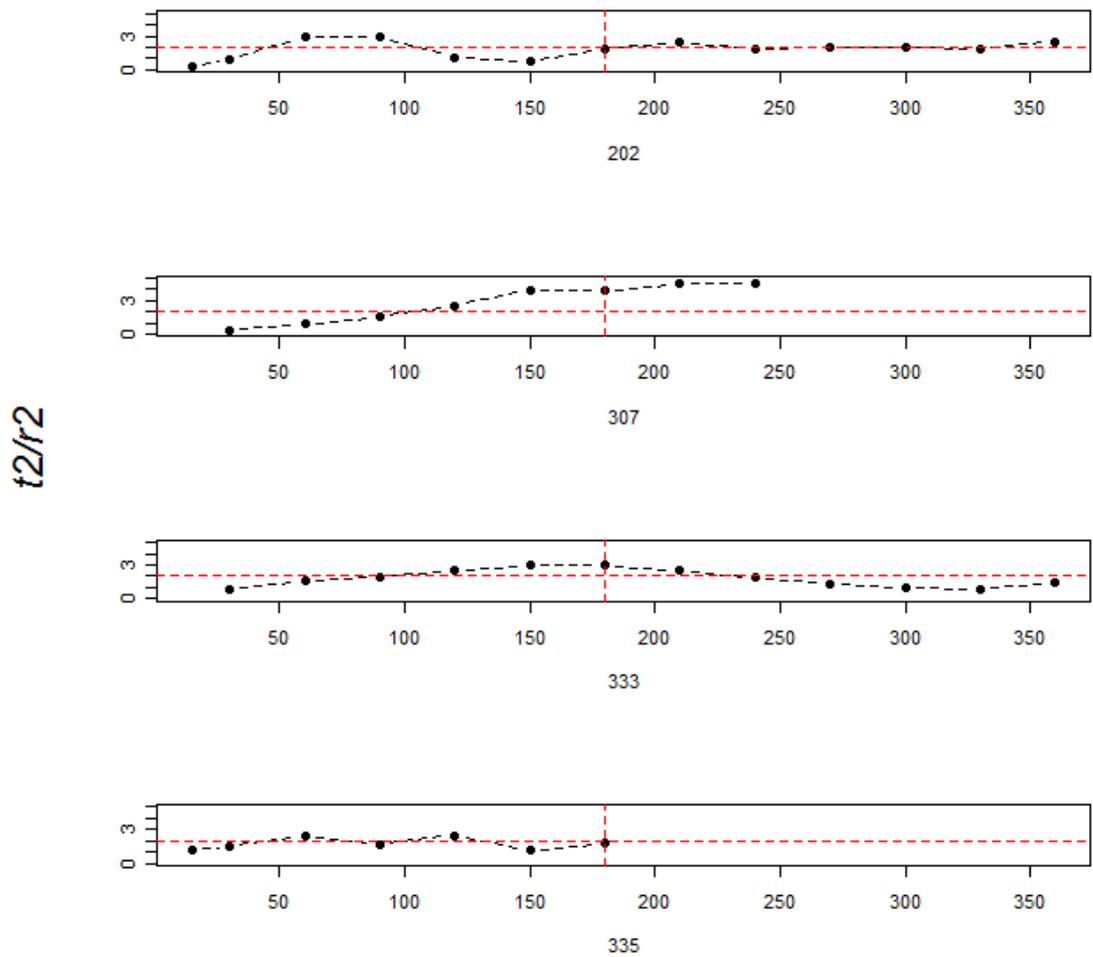
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Appendix 4.1: Habitat and location data for tagged Redshank with core area and home range estimates.

ID	Location	Catching site	Locat. day ⁻¹	No. location estimates			μ interval (hr)	UD (ha)	
				day	night	total		50%	95%
202	Upriver	Airth	0.6	21	10	31	39.11	68.96	275.08
333	Upriver	Airth	0.5	16	8	24	57.68	35.59	204.66
335	Upriver	Airth	0.5	18	12	30	53.65	83.47	341.83
744	Upriver	Kennet Pans	0.6	20	10	30	42.82	52.61	246.87
958	Upriver	Kennet Pans	0.5	33	10	43	45.00	25.75	207.85
861	Upriver	Kennet Pans	0.4	18	12	30	61.38	33.18	177.42
307	Upriver	Kennet Pans	0.4	20	12	32	57.42	32.89	143.46
274	Downriver	Kinneil lagoon	0.5	20	18	38	49.15	31.02	266.62
913	Downriver	Kinneil lagoon	0.7	28	19	47	35.99	66.91	386.04
905	Downriver	S. Skinflats	0.5	16	14	30	42.78	114.9	419.89
243	Downriver	S. Skinflats	0.6	21	14	35	42.12	100.2	342.10
708	Downriver	N. Skinflats	0.9	17	4	21	26.28	27.68	231.86
950	Downriver	N. Skinflats	0.5	19	8	27	47.93	61.28	242.62
984	Downriver	N. Skinflats	0.6	12	8	20	40.63	51.97	220.63

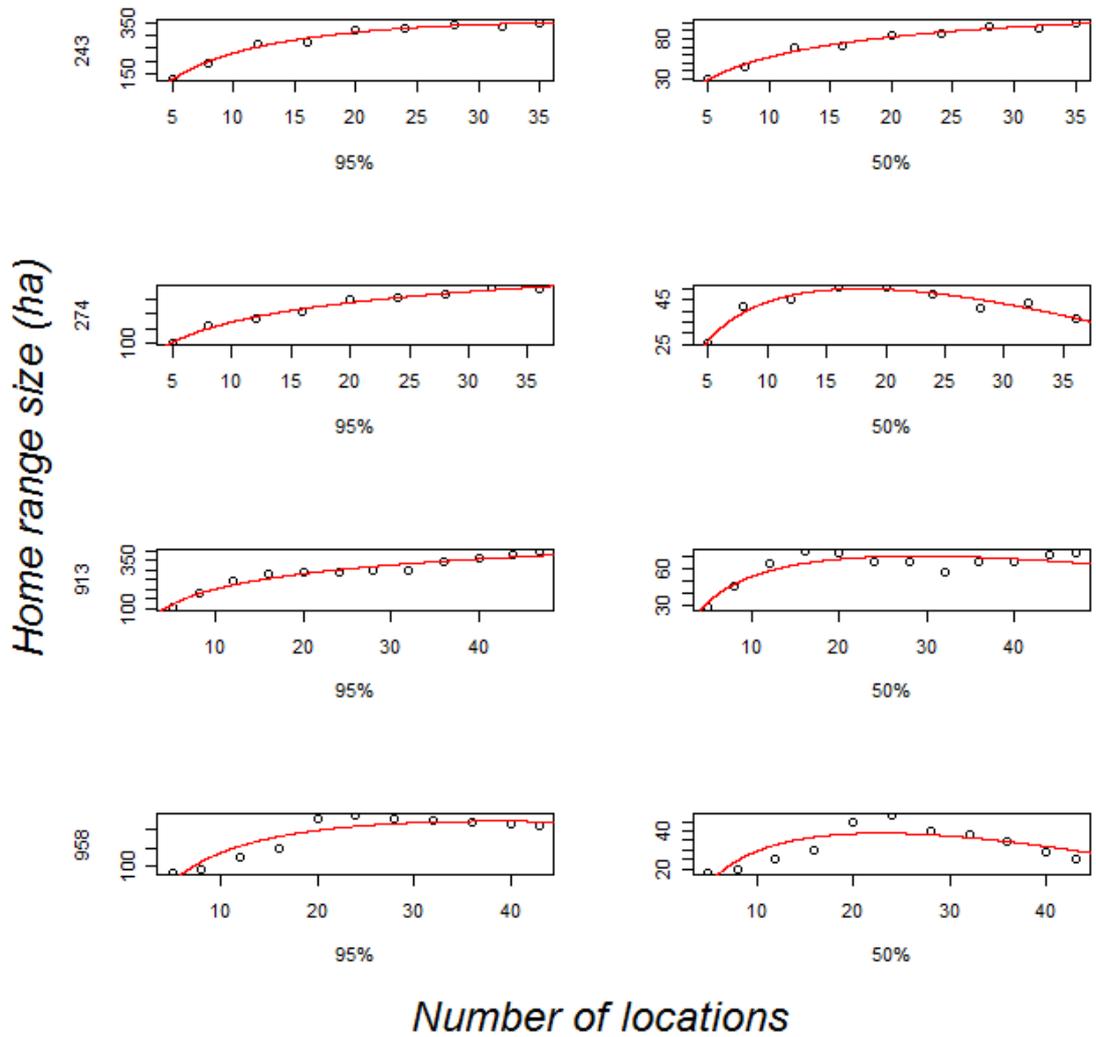


Appendix 4.2: Distribution of point locations taken of radio-tagged Redshank throughout the day (i) and throughout the tide (ii).



Interval between consecutive locations (mins)

Appendix 4.3: Values of the t^2/r^2 ratio (Swihart and Slade 1985). Data are taken from four individuals (ID 202, ID 307, ID 333, ID 335) monitored for 6 hours, 4 hours, 6 hours and 3 hours respectively. Probability levels refer to a one-tailed test of the null hypothesis that the locations were statistically dependent.



Appendix 4.4: Observation-area asymptotes for discontinuous radiotracking locations for wintering Redshank. Asymptotes were constructed using the 95% and 50% utilisation distributions for 4 individuals (ID 243, ID 274, ID 913, ID 958) tracked throughout the estuary in winter 2007/08 and in winter 2008/09.

Chapter 5
Nocturnal foraging in the Common Redshank

5. Nocturnal foraging in the Common Redshank

Many animals experience predictable diel fluctuations in food availability and/or predation risk. They are potentially faced therefore, with decisions of when is the optimal time to feed throughout each diel cycle. In this study posture-sensitive radio transmitters were used to collect quantitative measurements of nocturnal behaviour and habitat use of thirteen individually marked Common Redshank *Tringa totanus*. The degrees to which nocturnal foraging behaviour and habitat use differ from diurnal patterns and the response to moonlight and to artificial light emissions were examined.

Over the course of a winter, Redshank elicited no preference towards foraging by day or by night. Ambient light levels, however, were highly important to nocturnally foraging Redshank. In the absence of cloud cover, a greater proportion of Redshank fed on moonlit nights and fed less on moonless nights. Similarly, a greater proportion of Redshank fed in artificially-lit areas at night than birds occupying areas with little artificial illumination. Our results also suggest that when light levels are adequate, Redshank prefer to forage visually rather than by touch.

Most studies illustrate the generally negative effect of artificial lighting; however our study has shown that certain lit areas may provide benefits to birds such as improved prey and predator detection. The evidence presented in this chapter suggests that in estuaries close to major urban and industrialised regions, artificial illumination should be considered as an important environmental factor driving nocturnal habitat selection in foraging shorebirds.

5.1. INTRODUCTION

The majority of animal species have evolved to be active by day or by night; however it is often difficult to establish the primary cause for their diel activity pattern (Metcalfé *et al.* 1999). Many animals experience predictable diel fluctuations in food availability and/or predation risk, therefore they are potentially faced with decisions about when is the optimal time to feed throughout each 24 hour cycle (Alarna *et al.* 2001; Pizzatto *et al.* 2008). For shorebirds overwintering in temperate regions, diurnal feeding alone is reported to be insufficient to balance energy budgets (Goss-Custard 1969; Pienkowski *et al.* 1984; Turpie & Hockey 1993; González *et al.* 1996; Zwarts *et al.* 1996). This is not only due to increased metabolic demands during cold periods but also because foraging time is restricted by short day-length and fluctuating tides (Goss-Custard *et al.* 1977; Evans 1988; McNeil *et al.* 1992; Mouritsen 1994). For example, Goss-Custard (1969) found while Redshank *Tringa totanus* on the Ythan estuary normally roosted over high tides in autumn and spring, birds supplemented their energy reserves by foraging in nearby fields during the winter. Although diurnal prey consumption during October, equated approximately with the daily food requirement for that period, in mid-winter birds acquired less than 50% of their daily food requirements from foraging diurnally. Similar values of winter nocturnal requirements were also found in Oystercatcher *Haematopus ostralegus* (Zwarts *et al.* 1996), Red Knot *Calidris canutus* (González *et al.* 1996) and Ringed Plover *Charadrius hiaticula* (Pienkowski *et al.* 1984)

Although the improved visibility associated with diurnal foraging usually enables animals to locate, identify and handle prey more effectively (Sutherland 1982; Turpie & Hockey 1993; Sitters *et al.* 2001), studies involving behavioural observations of intertidal invertebrates have shown some prey species become more active in the substratum surface at night (e.g. *Nereis diversicolor*, *Nereis virens*, *Corophium volutator*, *Mytilus edulus*, *Carcinus maenas*; Dugan 1981; Ameyaw-Akumfi & Naylor 1987; Evans 1987; Robert & McNeil 1989). These changes in prey activity may determine foraging behaviour and availability of target prey species of shorebirds, often leading to variations in diurnal and nocturnal habitat use (Goss-Custard 1969; Dugan 1981; Mouritsen 1994).

Other advantages of shorebird nocturnality include reduced anthropogenic disturbances (Burger & Gochfeld 1991), and safety from diurnal predators (McNeil *et al.* 1992). For example, Burton & Armitage (2005) found that Redshank avoided a foraging site located adjacent to a busy heliport by day, but it was used regularly by the majority of individuals at night. In the Chacopata lagoon, Venezuela, Wilson's Plover *Charadrius wilsonia* have shown a strong tendency to do most of their feeding at night in those months when Peregrines *Falco peregrines* are present (Morrier & McNeil 1991). Although the avoidance of raptors may be an additional benefit of nocturnality in some species, night-feeding is not necessarily safe. While shorebirds are predated by raptors by day, at night, owls and mammalian carnivores (including foxes) can

pose a serious threat (Page & Whitacre 1975; Dugan 1981; Whitfield *et al.* 1988). Red Knot *Calidris canutus* avoid feeding on Delaware beaches at night because the high-tide line (where crab eggs are laid), is close to habitat that might harbour predators, and Dunlin *Calidris alpina* on the Danish Wadden Sea depress vocalisations at night and take flight less often, to escape detection by owls (Mouritsen 1992).

It may be that birds prefer to feed nocturnally, however, whenever ambient light levels are sufficiently high to permit detection of surface activity (Pienkowski 1983; Evans 1987). Both Eurasian Oystercatcher *Haematopus ostralegus* and Northern Lapwing *Vanellus vanellus* have been shown to display strong lunar periodicity in their choice of foraging strategy (Heppleston 1971; Milsom 1984; Sitters 2000). Lapwing were shown to roost more during the day and feed to a greater extent at night when the moon is full and skies held little or no cloud cover (Milsom *et al.* 1990). This interaction with cloud cover suggests that the reversal of the bird's activity cycle around full moon was opportunist and contingent upon moonlight levels, rather than a "manifestation of an endogenous circa-lunar rhythm" (Milsom *et al.* 1990).

Whereas plovers (*Charadriidae*) rely almost entirely on sight foraging to detect prey, some shorebirds are known to switch foraging strategy from visual feeding during the day, to tactile feeding by night. Oystercatcher (Hulscher 1982; Sutherland 1982; Sitters 2000), Semipalmated Sandpiper *Calidris pusilla* (Evans 1979; Schneider 1983), *Tringa* species (Goss-Custard 1969; 1970; McNeil & Robert 1988; Robert & McNeil 1989; Santos *et al.* 2010) and Dunlin (Mouritsen 1994) have all been observed feeding in this way. The main adaptation for tactile feeding in sandpipers (*Scolopacidae*) is the presence of numerous touch-sensitive nerve endings ('Herbst corpuscles') located in the tip of the bill. These organs detect pressure differences under the surface of the mud, enabling the bird to determine the location of prey items, even when they are buried beyond the reach of their bills (Piersma *et al.* 1998; Ens *et al.* 2004). The arrangement of these organs in the bill-tip of knots enables this species to detect prey more effectively than other shorebirds such as Oystercatcher, which have to touch their prey in order to find them (Hulscher 1982; Piersma *et al.* 1995)

Advances in technology have prompted scientists to incorporate investigations of nocturnal behaviours into research. Methods have ranged from the indirect (using footprints, droppings and regurgitates to assess habitat use and prey choice (Ens *et al.* 2004); to more direct methods, including artificial 'spot' lighting, surveillance radar, infrared thermal imaging and image enhancing equipment (Cooper *et al.* 1991; Burger 2001; Kuwae 2007; Santos *et al.* 2008). However, these more direct methods can be disruptive, have a short visual-range or work poorly under inclement weather (McNeil *et al.* 1995; Dodd & Colwell 1996; Cooper *et al.* 2001). These methods are also limited to tracking behaviour on accessible intertidal flats: whereas it is often impossible to follow individual birds for an entire low water period over extensive tidal

flats (Croon *et al.* 1968; Garner *et al.* 1995; Exo *et al.* 1996; Haroldson *et al.* 2003). The present study uses posture-sensitive radio transmitters to collect quantitative measurements of behaviour and habitat use of individual birds. Studies by Stock *et al.* (1992), Whittingham (1996) and Exo *et al.* (1996) have described how this method can be used to differentiate between foraging and non-foraging in Brant *Branta bernicla*, Golden Plover *Pluvialis apricaria* and Eurasian Oystercatcher, respectively. None of these studies however, has gone on to investigate the effect of biotic and abiotic processes on nocturnal foraging.

5.1.1. Aims

In this study, the occurrence and role of night feeding in shorebirds will be investigated by means of radiotelemetry. The relative contribution of environmental variables to diurnal and nocturnal foraging in wintering Common Redshank *Tringa totanus* will be analysed using a mixed model approach. The degree to which nocturnal foraging behaviour and habitat use differ from diurnal patterns and the response of Redshank to moonlight and to industrial engineering works will also be examined. If night foraging was contingent on moonlight levels rather than the influence of the lunar cycle on prey behaviour, we predict that shorebirds only capitalise on moonlight when there is little cloud cover. Finally we determine how foraging behaviour varies under various light regimes and discuss its importance in formulating management decisions of non-breeding shorebirds.

5.2. METHODS

5.2.1. Capture and transmitter attachment

This study was carried during the winters of 2007/08 and 2008/09 on the Forth estuary, Scotland, and utilised the radio-tagged birds referred to in chapter 4. Each individual was classified as an adult or juvenile according to its plumage characteristics (Prater *et al.* 1977) but was not sexed. Biometric data, including body mass, were recorded and a colour-ringing scheme was provided by the Wader Study Group Colour-marking Register. The scheme identifier was a white Darvic ring on the right tibia, above a blue ring on the right tarsus. Each individual was also given a unique combination of colour rings on the left tibia, using the colours: black (N), orange (O), blue (P), white (W), and yellow (Y). Details of all the individuals ringed during this study are presented in Appendix 5.1.

5.2.2. Posture sensors

Each transmitter was fitted with a tilt-switch posture sensor designed to alter the transmitter-pulse rate (hereafter referred to as 'pulse rate') when the bird tilted its body when feeding. As the bird changes from a standing (head up) to a feeding (head down) position, the pulse rate should instantaneously switch from a slow pulse rate of 45 pulses per minute (ppm), to a fast pulse rate of up to 65ppm. Transmitters were fixed to a small section of surgical gauze before attachment to trimmed contour feathers between the shoulders using Loctite superglue (Henkel Consumer

Adhesives, Cheshire, UK). The angle of the tilt-switch was pre-set at 0° to the longitudinal axis of the bird's back (i.e. parallel to the transmitter). This angle was chosen based on discussion with Biotrack technicians, from measurements taken from taxidermic mounts and from field trials conducted between December 2007 and February 2008. In these trials, transmitters were attached to five birds where the switch was positioned at 5° intervals between 350°-10° to establish the optimum transmitter-angle in order to collect information of feeding activities. The pulse rate was recorded manually by counting the number of pulses over a one-minute period.

Between November 2008 and March 2009, calibrations of individual bird behaviour with transmitter pulse rate were collected concurrently with tracking data collection, however it was only possible to conduct these tests during daylight hours and whenever a tagged individual was in close proximity to the shoreline. The inferred behaviour based on pulse rate, was calibrated for each bird (as recommended by *Exo et al.* 1992) using cumulative instantaneous behaviour sampling (Martin & Bateson 1993). Over a 2-minute recording session, the behaviour of the bird was recorded at 5-second sample intervals, timed using a Korg MA-30 handheld metronome (Korg UK Ltd). Individuals were identified in the field by their colour ring combinations, and their behaviours scored as *walking*, *pecking*, *resting*, *vigilant*, *preening*, *agonistic* and *flying*. Behaviours were grouped according to whether the bird was '*roosting*' (*resting and preening*) or '*feeding*' (*walking and pecking*). The pulse rate was then compared with the proportion of all sample points on which the behaviour pattern was occurring (Figures 5.1i, ii, iii). As instantaneous sampling is not suitable for recoding discrete events of short duration (Martin & Bateson 1993), *vigilant* and *agonistic* behaviours were excluded from these analyses.

5.2.1. Data collection

All tracking of Redshank behaviour was done with a Televilt model RX-81 receiver (Televilt/TVP Positioning AB, Lindesberg, Sweden) at the 173.000–173.999 MHz range with a hand-held three-element Yagi antenna. In order to fix behaviour to a location on the estuary, Redshank were located via triangulation (Heezen & Tester 1967; White & Garrott 1990), by taking 2-3 bearings obtained as quickly as possible to reduce the probability that a focal bird moved (White & Garrott 1990). When birds were not observed visually, positions were evaluated using the LOAS positioning software (Ecological Software Solutions, Sacramento, CA, USA) to estimate the locations of individuals (Taft *et al.* 2008). A single transmitter-pulse rate was recorded when taking each bearing, the first of which was used for estimating the individual's behaviour for that location.

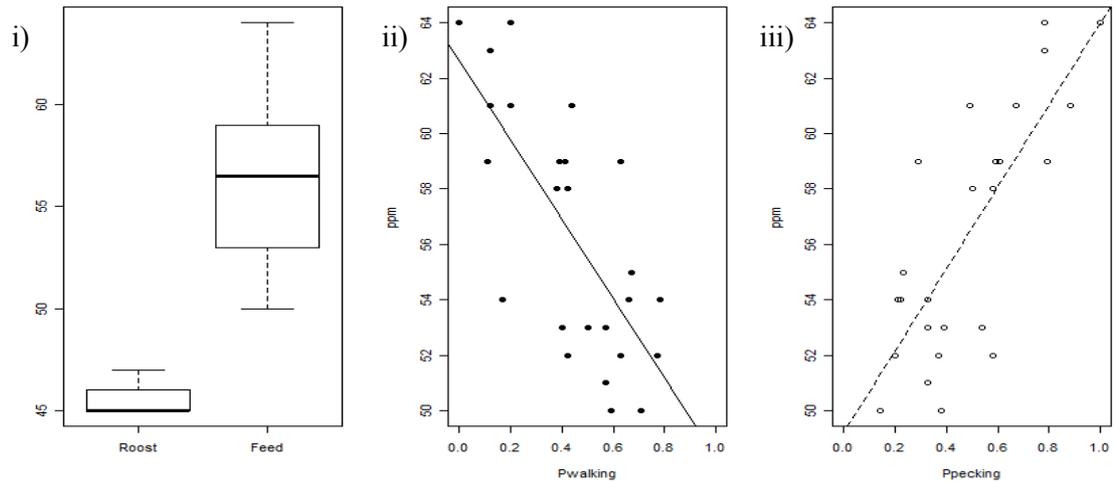


Figure 5.1: i) Distribution of transmitter-pulse rate for roosting and feeding birds. Boxes bound the 25th and 75th percentiles of the pulse rate, solid line within the box indicates the median and the whiskers indicate the range of the data. ii) Plots of pulse rate (ppm) collected from feeding birds over the proportion of time spent walking (Pwalking) and iii) the proportion of time spent pecking (Ppecking). The fitted lines in 1ii and 1iii show relationships fitted using linear regression.

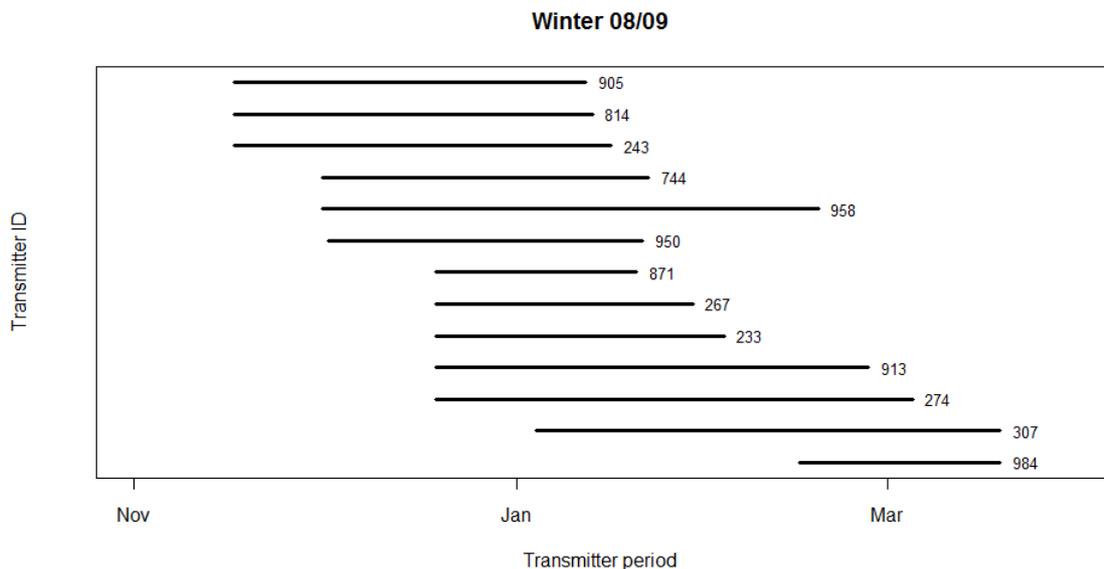


Figure 5.2: Radio-tagged Redshank present between November 2008 and March 2009.

Scans were conducted on six days per week and divided into two morning (0600-1200), two afternoon (1400-2000) and two night searches (2100-0300) per week. The order in which sites were visited within the specified times was alternated to provide a representative sample of Redshank movements throughout the tidal cycle and across spring and neap tides. Tracking

commenced on the day following release and terminated when the transmitter's signal was no longer detected after several intensive large scale searches of the estuary (Figure 5.2).

Tidal data were obtained later from the British Oceanographic Data Centre (BODC) collected by the tidal gauge site located at Leith docks, Edinburgh (NT 263781). Meteorological data (temperature, rainfall and wind speed) were supplied by the Meteorological Office from the weather station at Edinburgh Gogarbank (55.93° N, 03.34° W), and nautical day|night dawn and dusk times were obtained from the Astronomical Applications Department, U.S. Naval Observatory. Nautical twilight begins or ends when the sun's centre is 12° below the horizon. This marks the time when it is, to all intents, completely dark (Milsom *et al.* 1990). Anthropogenic light imaging data were collected by the U.S. Air Force Defense Meteorological Satellite Program (DMSP; National Geophysical Data Center of the National Oceanographic and Atmospheric Administration, Boulder, Colorado, USA). Cinzano, Falchi and Elvidge (2001) transcribed imaging data into a World Atlas of artificial night sky brightness, and detailed maps of the UK were supplied by the Campaign to Protect Rural England (CPRE). Artificial light values were calculated in ArcView 9.2 (ESRI 2009) by extracting the red, green and blue values from the artificial night sky brightness raster layer in order to estimate light levels using the following equation:

$$\textit{Artificial light intensity} = \textit{Red} - \textit{Green} - \textit{Blue} \quad (1)$$

To ensure this formula was accurate in describing ambient light values, our light intensity values were then calibrated by visually scoring raster squares on a scale of 0-20 for light score (low light intensity: dark blue = 0; high light intensity: red = 20; Figure 5.3). Artificial light intensity (Eq 1.) was found to accurately describe visually scored raster squares ($R^2=0.38$, $F_{1,519}=315.82$, $p<0.001$). For the purpose of this study, artificial light intensity score was chosen over visually scored squares in order to maintain repeatability in the experimental design. This did not affect the outcome of any of the analyses.

5.2.2. *Inferring behaviour through radio telemetry*

In our calibration tests, transmitter-pulse rate proved very effective at discriminating between roosting and feeding birds (Figure 5.1i; $F_{1,32}=47.959$, $p<0.001$). There was a positive linear relationship with regards to pulse rate and the proportion of time spent pecking (Figure 5.1ii; $F_{1,25}= 37.560$, $p<0.001$), and a negative linear relationship with respect to pulse rate and time spent walking (Figure 5.1iii; $F_{1,25}=26.887$, $p<0.001$). Based on these calibration measurements, birds in which pulse rate were below 49ppm were classed as 'roosting' and those between 49 and 65ppm were classified as 'feeding'.

5.2.3. Data analysis

Generalised linear mixed-effect models (*GLMMs*) with binomial errors were used to investigate roosting *vs.* non-roosting behaviour, while foraging-only data were analysed using general linear mixed-effect models using the original pulse rate data. *Day|night* (day *vs.* night), *moon phase* (new (=waning crescent-waxing crescent) *vs.* full (=waxing gibbous-waning gibbous)), *cloud cover* (clear (0-3 oktas) *vs.* cloudy (4-8 oktas)), *artificial light intensity* (Eq 1.), *tide height* (m), *tide period* (spring *vs.* neap), *season* (early (17/11/08-11/01/09) *vs.* late (12/01/09-19/03/09)), *day length* (hours) and *temperature* (°C) were included in our models as fixed effects (Appendices 5.1 and 5.2). Statistical analysis of telemetry data can be problematic as successive behaviours from the same individuals may lead to data points that are non-independent. Because behaviours were repeated measures from the same individuals, *Bird ID* was included within our models as random effects. Unimportant variables were removed from the *GLMMs* by stepwise deletion, until only those variables that were significant at the 5% level were retained in the final model. *GLMMs* were constructed using the ‘lme4’ package (Bates & Maechler 2009) and all analysis was conducted in the R programming language (R Development Core Team 2009).

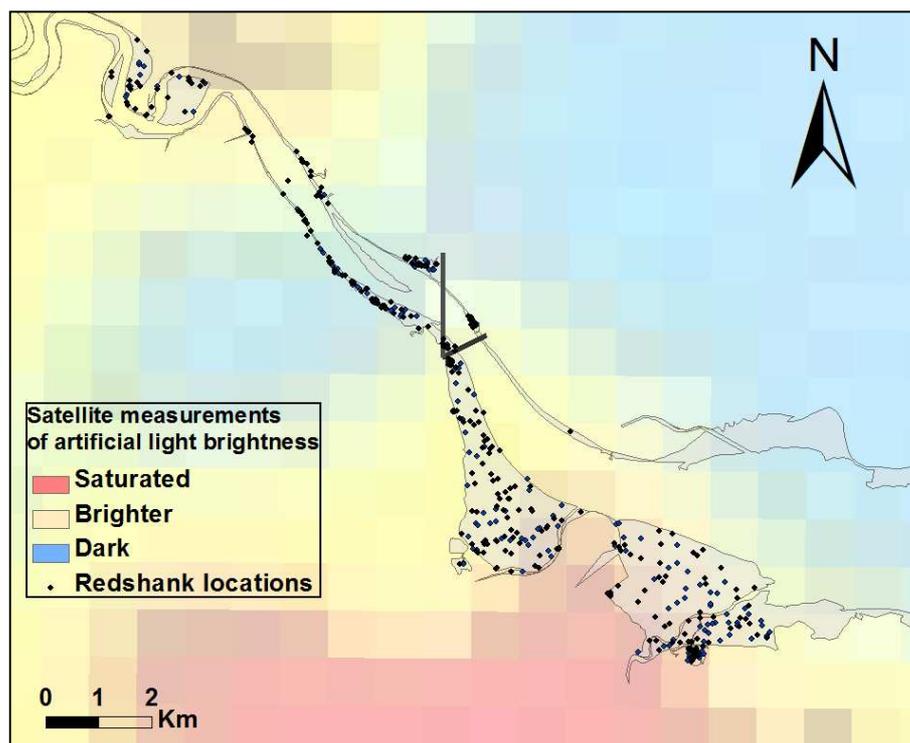


Figure 5.3: Locations of all 13 birds in study calculated by triangulation using LOAS software (points). Light intensity layer is composed of 1 km² pixels and is a colour representation of satellite measurements of artificial light taken at night by the U.S. Air Force DMSP in 2000. Each pixel represents an artificial light intensity score for that area on the Forth estuary. The light is measured on a range from -200 to 200; -200 (blue) means the satellite is detecting little light in that pixel and 200 (red) means that the satellite’s detector is saturated with light.

5.3.RESULTS

5.3.1. Effect of environmental factors and ambient light levels on day vs. night feeding

Of the 20 transmitters despatched on Redshank in winter 2008/09, accurate tracking and behaviour data were obtained from 13 individuals covering 724 bird-radio-days (Figure 5.2; Appendix 5.1). Of the 239 behavioural fixes that were obtained during the period of study, 136 of these (43%) were taken by night. There was little evidence that birds preferred to feed by day rather than by night (mean day: 0.46 ± 0.19 ; mean night: 0.28 ± 0.27), however significant interactions were found for *day|night x season* ($X^2_1=12.06$, $p<0.001$; Appendix 5.2) and *day|night x tide period* ($X^2_1=4.69$, $p=0.030$). Birds dedicated a greater proportion of time to foraging at night and less to foraging by day in the early half of the winter (Figure 5.4i). In the latter half of the winter, birds dedicated a smaller proportion of time to foraging nocturnally and dedicated a greater proportion to foraging diurnally. Birds fed for similar proportions of time during night and day on spring tides, but on neap tides, individuals increased the proportion of time spent foraging during the day (Figure 5.4ii). Day-length had no significant effect on the proportion of time spent feeding by day or by night ($p>0.05$).

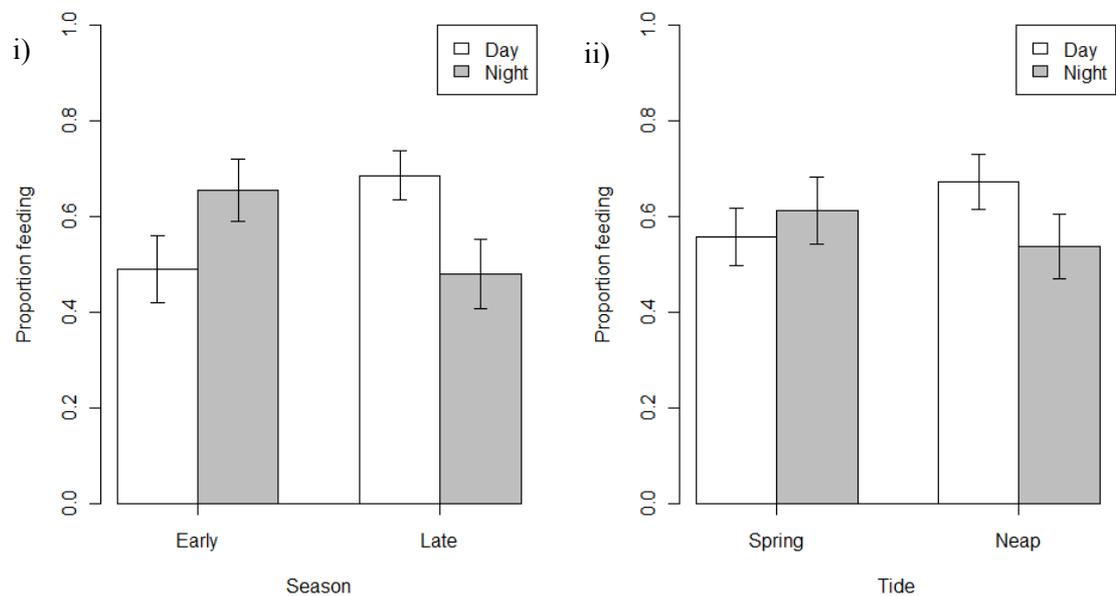


Figure 5.4: i) The proportion of Redshank feeding diurnally and nocturnally by season (\pm 1SE).
ii) The proportion of Redshank feeding diurnally and nocturnally by tidal regime (\pm 1SE).

The three-way interaction between *day|night x moon phase x cloud cover* was significant in predicting the propensity to forage ($X^2_1=7.882$, $p=0.005$). As expected, there was no effect of *moon phase* and *cloud cover* on diurnal feeding behaviour (Figure 5.5i). At night, the proportion of Redshank foraging on cloudy nights was similar to daytime numbers; however the moon appeared to influence behaviour on clear nights as a lesser proportion of birds fed on nights when there was a new moon, and greater proportion fed on brighter nights when there was a full moon (Figure 5.5ii). By selecting data for only those locations taken from darker areas of the estuary (*artificial light intensity*<0), the effect of moonlight on the proportion of birds feeding nocturnally became more pronounced (clear, new moon: 0.33 ± 0.14 ; clear, full moon: 0.83 ± 0.11). The proportion of birds feeding was also fewer on cloudy nights in these darker regions (cloudy, new moon: 0.50 ± 0.08 ; cloudy, full moon: 0.46 ± 0.14).

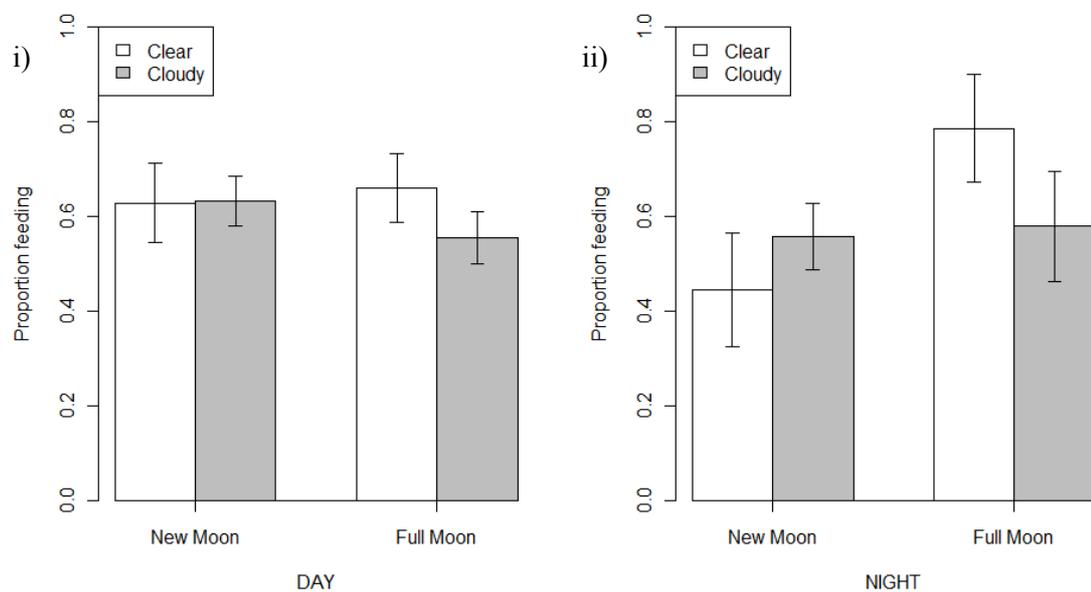


Figure 5.5: The mean proportion (\pm SE) of radio-tagged Redshank feeding in the study area by day (i) and by night (ii) and the interaction between moonlight and cloud cover.

In the GLMM, a significant two-way interaction was also found between *day|night x artificial light* ($X^2_1=12.208$, $p<0.001$). Individuals occupying dark areas of the Forth at night spent less time feeding at night and individuals occupying lit areas spent more time foraging at night (Appendix 5.3). There was also a weak negative relationship between light intensity and the proportion of birds feeding by day. Birds inhabiting less artificially-lit areas such as Kennet Pans, Airth and Dunmore, spent a greater proportion of time foraging by day (Figure 5.6i) and a smaller proportion of time foraging in these areas at night (Figure 5.6ii). Conversely, Redshank inhabiting the more artificially-lit areas around Grangemouth docks spent a greater proportion of time foraging in these areas at night than they did by day.

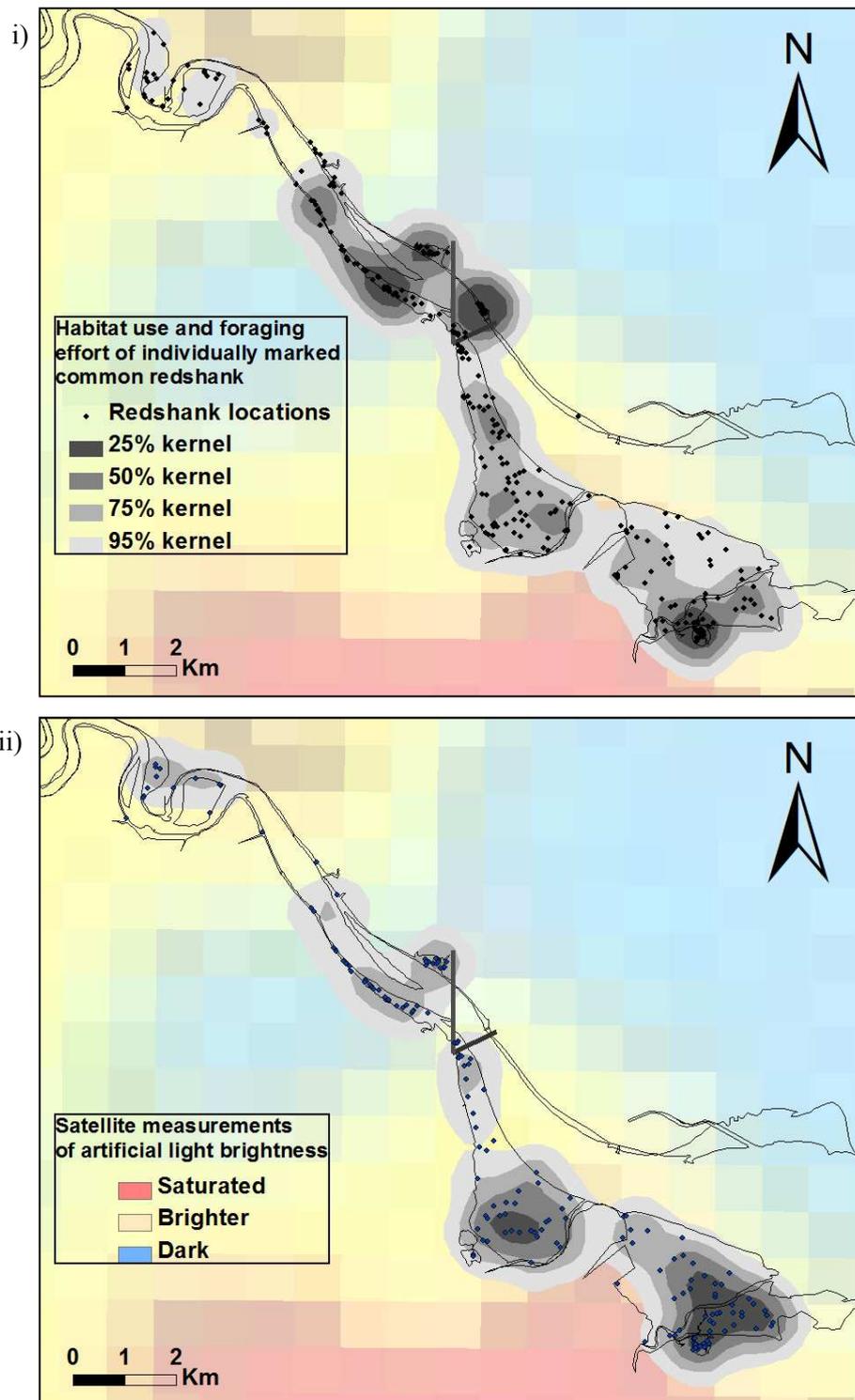


Figure 5.6: Map of diurnal (i) and nocturnal (ii) Redshank habitat use on the Forth estuary. Points represent fixes of individual Redshank during the day (i) and at night (ii). Kernels represent areas where birds are concentrating foraging effort by day (i) and by night (ii). Kernel density estimates of the animal's utilisation distribution were created using the 'adehabitat' library of functions written by Calenge (2006) in the R programming language (R Development Core Team 2009). Locations and kernels are mapped onto a map of artificial night sky brightness of the Forth estuary (Cinzano *et al.* 2001).

5.3.2. Effect of ambient light levels on day vs. night foraging strategy

Birds foraging at night had a transmitter-pulse rate which was on average 5.28 ± 1.86 pulses faster than those foraging by day (Figure 5.7). This shows that while feeding by night, birds spent approximately 16% less time walking and 18% more time pecking than when foraging during the day. As with the foraging vs. roosting data, there was a significant 3-way interaction between *day|night x moon phase x cloud cover* (Figures 5.8i, ii; $X^2_1=9.353$, $p=0.002$; Appendix 5.4). Those birds foraging on dark, clear nights had the fastest pulse rate (59.89 ± 1.52), implying that Redshank switched to tactile feeding only on the darkest nights. By selecting only those locations taken at night from darker areas of the estuary (*artificial light intensity* <0), the effect of moonlight on the transmitter pulse rate became more pronounced (clear, new moon: 62.94 ± 2.05). *Artificial light* score had no significant effect on pulse rate and no interactions were found between *artificial light x day|night* ($p>0.05$). There was, however, some evidence that pulse rate was influenced by artificial light: three out of four of the birds which showed little change (or a slight decrease) in transmitter-pulse rate between day and night (ID 274, ID 913, ID 905; Figure 5.7) occupied lit areas in and around Grangemouth docks (Appendices 5.5ii, iii, iv) a key source of artificial light. The fourth (ID 958; Appendix 5.5i) fed only at Kincardine shore by day and moved close to the Kincardine Bridge, a relatively well lit area by night (chapter 4). The significant interaction between *Bird ID x day|night* confirms that different birds often behave differently by day and by night ($X^2_1=30.425$, $p=0.002$).

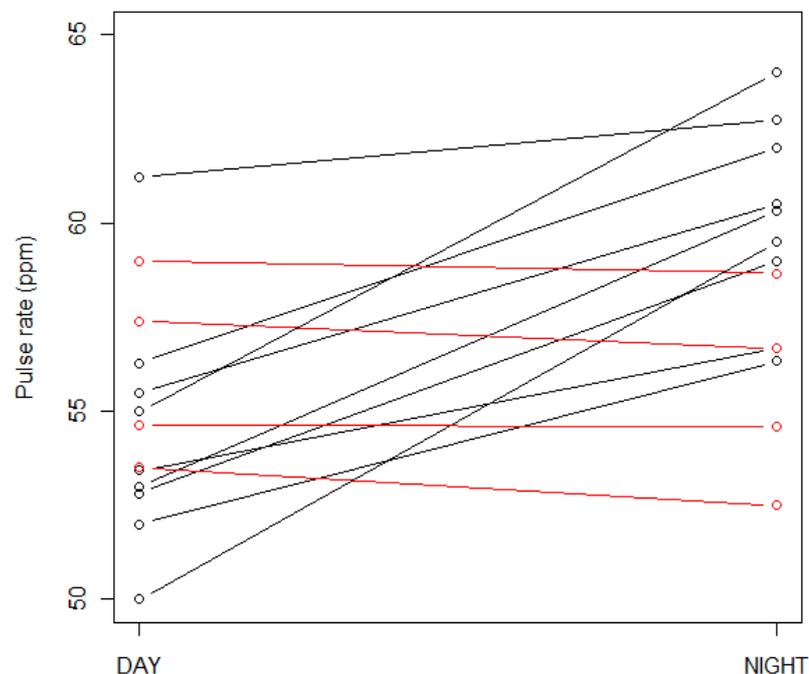


Figure 5.7: Comparison of mean pulse rate for individual birds by day and by night. Black lines represent an increase in mean transmitter-pulse rate from day to night for each individual, red lines represent Redshank ID 274, ID 913, ID 905 and ID 958 which showed little change (or a slight decrease) in mean transmitter-pulse rate between day and night.

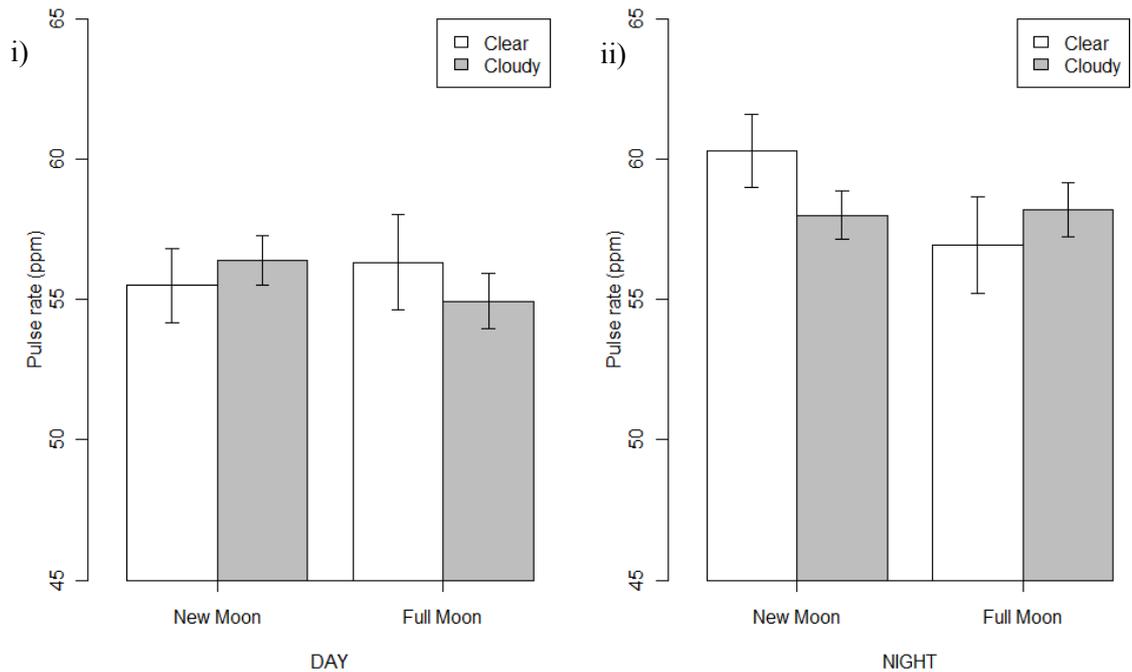


Figure 5.8: Mean transmitter-pulse rate (\pm SE) for birds feeding during the day (i) and during the night (ii) and the interaction between moonlight and cloud cover.

5.4. DISCUSSION

5.4.1. Effect of ambient light levels on feeding behaviour

Ambient light levels were highly important to nocturnally foraging Redshank. In the absence of cloud cover, a greater proportion of Redshank fed on moonlit nights and fed less on moonless nights. Similarly, our study showed that a greater proportion of Redshank fed in artificially-lit areas at night than birds occupying areas with little artificial illumination. Our findings are consistent with observational studies on shorebirds (e.g. Heppleston 1971, Pienkowski 1982; 1983, Milsom 1984, McNeil & Robert 1988; Robert *et al.* 1989, McNeil *et al.* 1992, Sitters 2000) and wildfowl (Ydenberg *et al.* 1984; Giroux 1991; Tinkler *et al.* 2009), which have also documented birds taking advantage of moonlight in order to increase foraging opportunities. None of these studies however accounted for tidal regimes and the interaction between cloud cover and lunar cycle in their analyses. Essentially it is this interaction that illustrates that this effect was opportunist and contingent upon moonlight levels, rather than the influence of the lunar cycle on benthic invertebrate behaviour (Milsom *et al.* 1990).

Studies into the effects of artificial lighting on bird behaviour are not common (Jones & Francis 2003; Miller 2006; Molenaar *et al.* 2006) and often document negative effects: such as reducing the attractiveness of nesting sites (Molenaar *et al.* 2000), and interfering with migration routes

resulting in direct mortality through collisions (Longcore & Rich 2004). For example, smokestacks, lighthouses (Squires & Hanson 1918; Wiese *et al.* 2001), broadcast towers (Ogden 1996), boats (Dick & Donaldson 1978), greenhouses and oil platforms (Wiese *et al.* 2001) have been documented as attracting large numbers of birds in this way. Such studies clearly illustrate the generally negative effect of artificial lighting; however our study has shown that certain lit areas may provide benefits to birds. We argue that the increased artificial illumination from areas around Grangemouth docks creates, in effect, a perpetual full moon effect, allowing birds to extend diurnal or crepuscular behaviours into the nocturnal environment (Rich & Longcore 2006). Diurnal species such as Lesser Kestrels *Falco naumanni*, Coots *Fulica atra*, Ruby-throated Hummingbirds *Archilochus colubris* and European Robins *Erithacus rubecula* have been sighted foraging after dusk under artificial lighting (see review by Rich & Longcore 2006). In a recent study on the Tagus estuary, Portugal, Santos *et al.* (2010) demonstrated that Dunlin, Ringed Plover *Charadrius hiaticula*, Kentish Plover *Charadrius alexandrinus*, and Grey Plover *Pluvialis squatarola* used areas illuminated by streetlights more during the night than non-illuminated areas. This is consistent with our findings that artificial lighting influences foraging site selection in shorebirds. While Santos *et al.* implemented a site-based study with control and experimentally manipulated illuminated sites, we used an individual-based approach, controlling for confounding effects such as temperature, tidal regime, date or proximity to predator concealing cover. The evidence presented in these two studies suggests that in estuaries close to major urban and industrialised regions, artificial illumination should be considered as an important environmental factor driving nocturnal habitat selection in foraging shorebirds.

Few studies have shown that shorebirds will alter their feeding method at night according to ambient light levels (McNeil & Robert 1988; Robert *et al.* 1989; Santos *et al.* 2010). The present study is the first to use an individual-based approach across large areas of mudflats to document this change in foraging behaviour. Our results suggest that when light levels are adequate, Redshank prefer to forage visually rather than by touch. This difference was present despite of the fact that most birds on the Forth rarely experience absolute darkness at night, since the principal feeding areas flank the main light sources. Although our analysis showed that transmitter-pulse rate in foraging birds was not influenced by artificial light levels, there was evidence of reduced tactile feeding in lit areas (Appendix 5.5i-iv). We argue that moonlight and anthropogenic light offer benefits to foraging Redshank, allowing them to employ some visual cues rather than using tactile methods to locate prey. In a study of Bar-tailed Godwits on the Lindisfarne NNR, Smith (1975) suggested that foraging by touch may be less profitable than sight location in daylight when the birds are able to detect the presence of their main and most profitable prey (*Arenicola*) visually by looking for casts. Night observations indicated that *Arenicola* were not taken in darkness (Smith 1975). Similarly, Sutherland (1982) discovered that Oystercatcher were less successful at locating large cockles in the dark as a result of being

unable to utilise visual cues. Although it is possible for predators feeding visually to scan for prey while handling prey at the same time, those feeding by touch cannot (Evans 1976). We would therefore expect individuals to capitalise on ambient illumination from lunar and anthropogenic sources in order to feed by sight and improve individual foraging efficiency.

A change in prey availability may influence the way in which birds maximise their habitat use. van Gils *et al.* (2000), for example, reported that, during the day, Knot *Calidris canutus* foraged in an area rich in shore crabs and shrimp, probably using visual cues. At night, however, when they could not use such cues, they foraged instead by touch in an area rich in bivalves. Similarly, Goss-Custard (1969) found a diet switch in Redshank, which mainly took *Corophium* by day and less profitable *Hydrobia* by night, possibly because birds were not able to detect the presence of their main and most profitable prey visually.

In addition to reduced foraging efficiency, low visibility could act as an obstacle to visual detection of shorebird predators. Darkness certainly decreases predator visibility (Ferguson *et al.* 1988) and poor visibility has been linked to higher levels of vigilance in diurnal species foraging in the presence of visual obstacles (Metcalf 1984; Burger & Gochfeld 1991; Mouritsen 1992; Burger 2001; Guillemain *et al.* 2001). Gorenzel and Salmon (1995) found that American Crows *Corvus brachyrhynchos* in urban areas were more likely to roost in areas of high night-time illumination, possibly to reduce their risk of predation risk from owls. Redshank in our study may have used the high luminescence around Grangemouth docks to increase visibility and therefore the detectability of stalking nocturnal predators. Redshank are also known to avoid riverine areas at night (Burton & Armitage 2005), preferring to feed on estuarine flats; possibly in an attempt to reduce the predation risk from owls (Mouritsen 1992) and perhaps mammalian predators, such as foxes. Tawny Owls *Strix aluco*, Eared-owls (genus *Asio*) and Red Foxes *Vulpes vulpes* are all present on the Forth, and were regularly observed hunting in areas frequently used, though generally avoided at night, by tagged Redshank during the period of study (chapter 4).

5.4.2. Temporal changes in foraging behaviour

This study has shown that over the course of a winter, Redshank elicited no preference towards foraging by day or by night. This is consistent with a study by Goss-Custard (1969) who found that Redshank on the Ythan estuary obtained less than 50% of their daily food requirements from daytime intertidal foraging. If birds were to balance their energy budgets, the remainder had to be collected at night or from fields at high water during the day. Although supratidal foraging is well documented in Redshank on several British and European estuaries (Goss-Custard 1969; Evans 1978-79; Velasquez & Hockey 1992; Mitchell *et al.* 2000; Masero & Perez-Hurtado 2001), there was no evidence of tagged birds feeding on fields away from the estuary. Similarly, very few observations were made of non-tagged Redshank feeding in fields

at high water during the period of study (chapter 3). It is possible the winter of 2008/09, although generally cold, was not severe enough to force Redshank off their high tide roosts into fields to supplement daily energy intake. Low prey availability (Edwards & Lofty 1977) and high risk from predators and parasites (Goss-Custard *et al.* 1996) may also have reduced the attractiveness of fields to foraging Redshank.

In our study, Redshank showed a preference for foraging nocturnally during the early half of the winter but switched to predominantly diurnal foraging in the latter half of the winter. This effect remained significant despite day-length being added to our model as a covariate, so was unlikely to be a consequence of seasonal changes in the availability of daytime feeding opportunities. With the onset of winter, declining temperatures normally increase the energy requirement of shorebirds, and at the same time, invertebrate abundance (chapter 2) and flesh content of prey declines (Speakman 1984; Zwarts 1991). In response to this decline, Redshank are thought to dedicate more time to foraging during diurnal low water periods in the latter half of the winter (Goss-Custard 1977; Zwarts *et al.* 1996). While individuals in our study increased diurnal foraging in late winter, the proportion of time allocated to foraging nocturnally was reduced. Previous studies have failed to consider the interaction between increased energy requirements and the costs of nocturnal foraging at reduced prey densities. As the density and flesh content of prey is reduced across the estuary, it becomes less productive for shorebirds to forage by touch at night and so effort is concentrated on foraging by day. Feeding by touch is thought to be effective only if prey is uniformly dispersed and the density of available prey was high (Evans 1976). This is because the area that birds can search thoroughly is much smaller than can be searched by sight in the same time. We would therefore expect that as foraging areas are depleted, it gradually becomes less advantageous for birds to forage nocturnally. Equally, daytime foraging may offer more opportunities to be selective, with regard to species, size, quality, or palatability of prey, and this would bring rewards in terms of net energy or nutrient gain rates.

The apparent bias towards captures of juveniles rather than adults in our study, a bias common amongst shorebird studies, meant that only individuals in their first winter were used in this study. Juvenile birds are thought to be less efficient foragers than adult birds: Goss-Custard (1969) found that Redshank only fed supra-tidally during times of high energy demand, such as winter, and amongst individuals, particularly immatures that are less successful feeders. Both supratidal and nocturnal foraging are suggested as mechanisms to make up for deficiencies in their diurnal food intake (Heppleston 1971; McNeil *et al.* 1992; Beauchamp 2003). If less successful foragers are more likely to forage at night, then our estimates of nocturnal foraging would overestimate the importance of nocturnal foraging among overwintering adults or wintering populations as a whole. However, our focus on juvenile birds, allowed us to maximise our sample size within an age class and include all individuals in our comparisons.

5.4.3. *Foraging and tidal regime*

Our results show that Redshank increased the proportion of time spent foraging diurnally during neap tides. This is consistent with studies by Davidson & Evans (1986), who found that because tidal exposure of assumed richer feeding areas is least on neaps, birds fed for a greater proportion of time in order to meet their food requirements. As neap tides fail to inundate some high level flats, these areas dry out progressively during a period of about a week causing some prey species to bury deeper into the sediment becoming unavailable or less available to birds. Since many shorebirds, especially sandpipers *Scolopacie*, forage preferentially close to or at the edge of the tide, the profitability of foraging during neap tides may be considerably less (Davidson & Evans 1986). Alternatively, during spring tides, the mudflats around the Forth estuary are often entirely covered by the incoming tide. Birds are therefore forced to roost on a spring tide, or feed supratidally, whereas on a neap there are always some upper intertidal areas available for foraging. Essentially, foraging time is less constrained during high neap tides, so increased foraging opportunities during high tide may explain the increased proportion of feeding birds observed on neaps in our study.

5.5. CONCLUSIONS

Research on nocturnal activity amongst birds is an unfamiliar discipline. However, it is integral to a full understanding of the ecology of virtually all wildlife. We have presented a novel and unbiased technique for collecting behavioural information on shorebirds. Our study has illustrated the importance of nocturnal feeding to a wintering shorebird and discussed the influence of prey abundance and ambient illumination on promoting this behaviour. We have shown that contrary to previous understanding, artificial light may offer benefits to shorebirds; in effect, acting as a perpetual full moon to assist birds in foraging and predator detection. However the findings of this study illustrate only the benefits to a shorebird species able to switch foraging strategy depending on ambient light levels. There may be further impacts at a community level: for example increased predation pressure by shorebirds on intertidal invertebrates in lit areas, increased competition with traditionally nocturnal foragers and reduced hunting efficiency in Redshank predators. With rapidly increasing development of terrestrial, estuarine and marine ecosystems for industry and housing, conflict between human and wildlife as a result of human disturbance, is set to increase. More study is required into the effects of artificial lighting on terrestrial, and marine ecosystems; and over a broader suite of species at different trophic levels to assess its effect on the structuring of animal communities.

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Appendix 5.1: Trapping and location details of individuals radio-tagged and used in analyses.

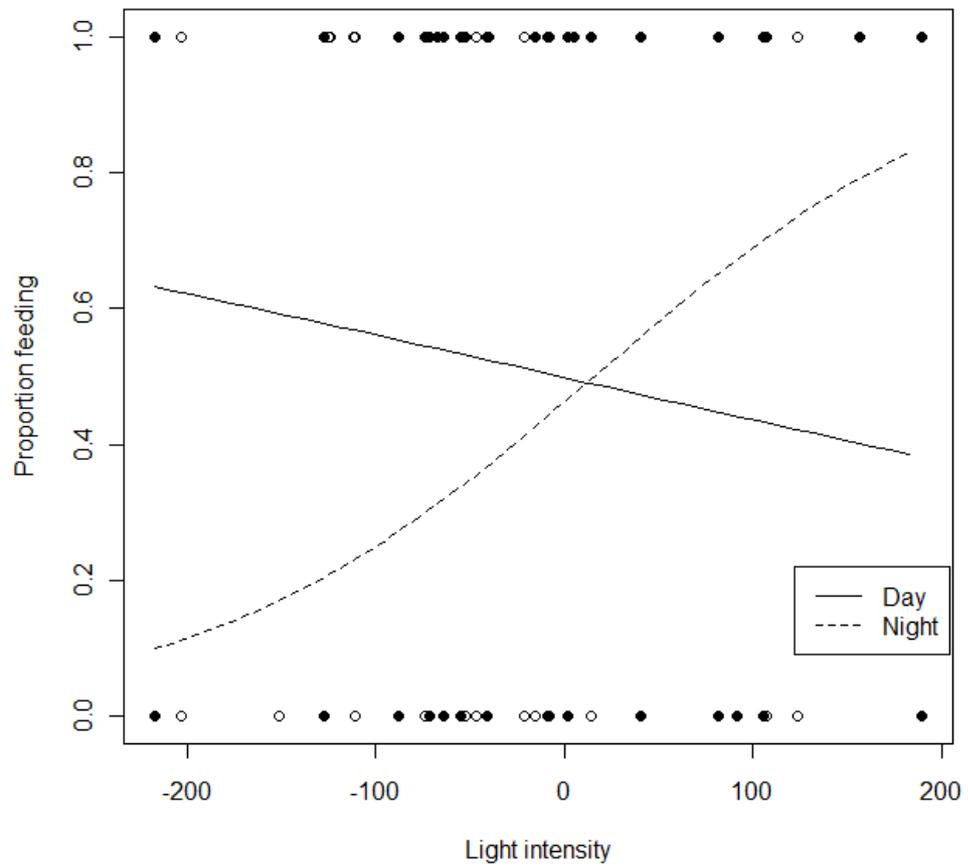
ID	Colour-ring combination*	Date captured	Catching Site	Duration (days)	No. location estimates		
					day	night	total
905	N/W; W//P	17/11/2008	S. Skinflats	56	8	2	10
814	N/O; W//P	17/11/2008	S. Skinflats	57	2	2	4
243	N/Y; W//P	17/11/2008	S. Skinflats	60	14	10	24
744	W/N; W//P	01/12/2008	Kennet Pans	52	11	7	18
958	W/W; W//P	01/12/2008	Kennet Pans	79	16	8	24
950	W/O; W//P	02/12/2008	N. Skinflats	50	11	6	17
871	Y/P; W//P	19/12/2008	Kinneil lagoon	32	5	5	10
267	W/P; W//P	19/12/2008	Kinneil lagoon	41	5	7	12
233	O/N; W//P	19/12/2008	Kinneil lagoon	46	3	7	10
913	Y/Y; W//P	19/12/2008	Kinneil lagoon	69	23	16	39
274	Y/N; W//P	19/12/2008	Kinneil lagoon	76	15	15	30
307	O/O; W//P	04/01/2009	Kennet Pans	74	20	11	31
984	P/W; W//P	15/02/2009	N. Skinflats	32	9	8	17

* Colour-ringing scheme provided by the Wader Study Group Colour-marking Register. The scheme identifier was a white Darvic ring on the right tibia, above a blue ring on the right tarsus. Each individual was also given a unique combination of colour rings on the left tibia, using the colours: black (N), orange (O), blue (P), white (W), and yellow (Y).

Appendix 5.2: Results of a GLMM to test the effects of ambient light levels on the proportion of time spent feeding, controlling for temperature and seasonal effects. Those parameters retained in the model are highlighted in **bold**.

	<i>d.f.</i>	X^2	<i>P</i>	<i>B</i>
<i>Intercept</i>				0.97 ± 0.71
<i>Day length</i>	20	0.004	0.948	
<i>Day night x temperature</i>	19	0.055	0.814	
<i>Temperature</i>	18	0.695	0.404	
<i>Day night x cloud cover x artificial light</i>	17	1.512	0.219	
<i>Cloud cover x artificial light</i>	16	0.771	0.380	
<i>Day night x season</i>	15	12.059	<0.001	-0.91 ± 0.66
<i>Day night x artificial light</i>	15	12.208	<0.001	0.50 ± 0.50
<i>Day night x cloud cover x moon phase</i>	15	7.882	0.005	-0.99 ± 0.84
<i>Day night x tide period</i>	15	4.693	0.030	0.81 ± 0.66
<i>Tide height</i>	15	41.305	<0.001	-0.69 ± 0.54

B is the model parameter estimate.

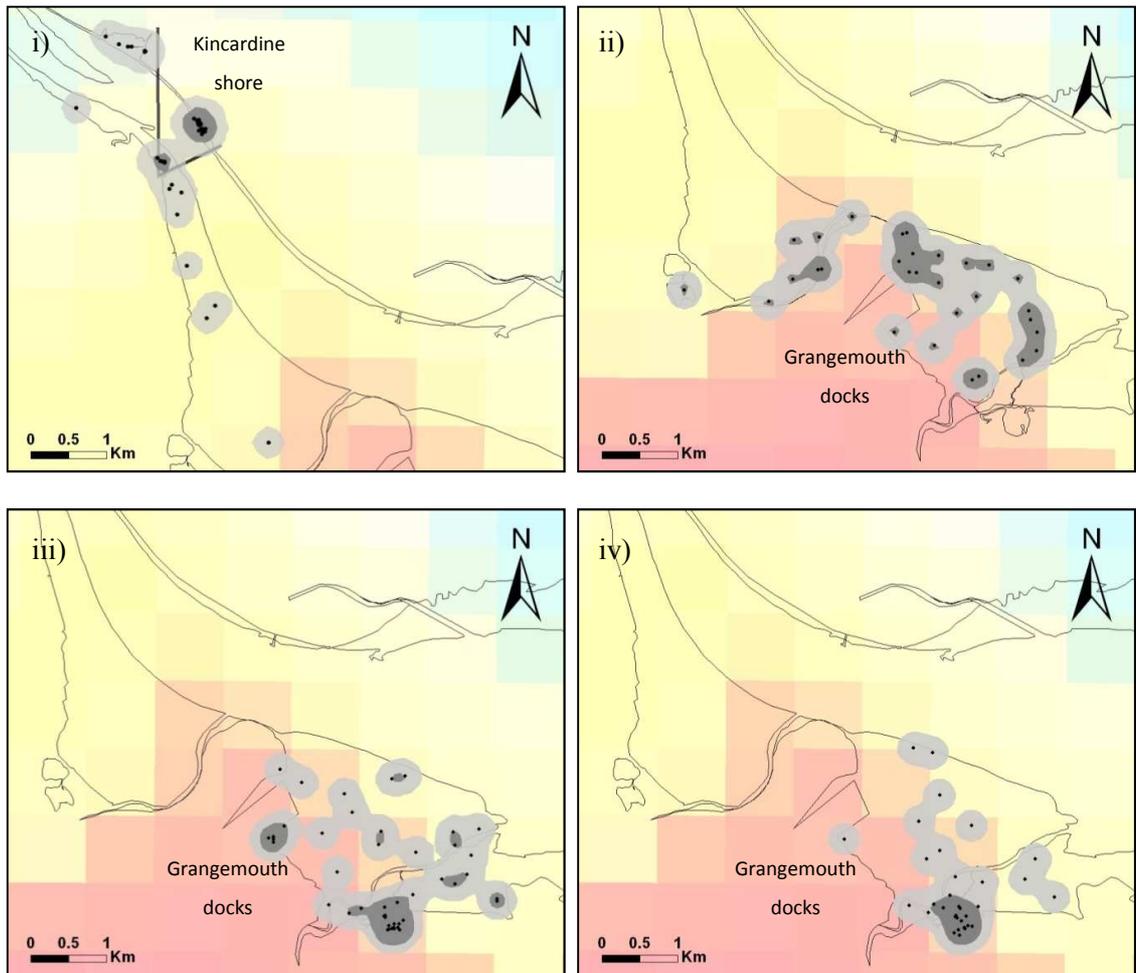


Appendix 5.3: Comparison of day and night GLMM fits for artificial light intensity and the proportion of radio-tagged Redshank feeding in the study area ($GLMM: X^2_{15}=12.208, P<0.001$). Solid dots represent whether or not an individual was foraging by day, empty dots represent whether or not an individual was foraging at night. Fitted lines added for visual comparison only.

Appendix 5.4: Results of a GLMM to test the effects of ambient light levels on transmitter pulse rate (ppm), controlling for temperature and seasonal effects. Those parameters retained in the model are highlighted in **bold**.

	<i>d.f.</i>	<i>AIC</i>	<i>L Ratio</i>	<i>P</i>	<i>B</i>	
<i>Intercept</i>	39	764			54.61	± 1.31
<i>Day night x cloud cover x artificial light</i>	39	763	0.658	0.417		
<i>Day night x artificial light</i>	38	761	0.530	0.467		
<i>Cloud cover x artificial light</i>	37	762	2.834	0.092		
<i>Artificial light</i>	36	761	0.948	0.330		
<i>Temperature</i>	35	761	2.263	0.133		
<i>Day night x cloud cover x moon phase</i>	34	761	9.353	0.002	7.89	± 3.36
<i>Bird ID x day night</i>	34	761	30.425	0.002	-3.77	± 2.31

B is the model parameter estimate.



Appendix 5.5: The radio-locations and estimated ranges of (i) Redshank ID 958, captured at Kennet Pans on 01/12/2008; (ii) Redshank ID 905, captured at Skinflats lagoon on 17/11/08; (iii) Redshank ID 913, captured at Kinneil lagoon on 19/12/2008; (iv) Redshank ID 274, captured at Kinneil lagoon on 19/12/08. Light shading indicates the extent of the 95% home range and the dark area represents the 50% core area.

Chapter 6

Does previous exposure to human disturbance influence flight response in wintering waterbirds?

6. Does previous exposure to human disturbance influence flight response in wintering waterbirds?

The flight response of animals to a standardised disturbance (i.e. an approaching human) has historically been used by wildlife managers for the creation of buffer zones. In this framework, those species which show the greatest response are those generally considered to be those most vulnerable to human disturbances. In this study, Redshank *Tringa totanus*, Curlew *Numenius arquata*, Oystercatcher *Haematopus ostralegus* and Shelduck *Tadorna tadorna* showed fewer visible behavioural responses to human disturbance during periods when they may have been a significant energetic or fitness cost (i.e. under low temperatures and poorer feeding conditions). In Redshank and Shelduck, temperature had a greater effect on flight decisions in highly disturbed localities. If individuals occupying disturbed areas have greater metabolic demands, one would expect a reduction in temperature to impact more on behavioural decisions in these areas. As tolerance depends greatly on foraging conditions, prior experience and metabolic demands, we suggest that wildlife managers move away from traditional interpretations of using a singular species-specific behavioural response distance and recognise, and seek to allow for, the seasonal and spatial variations in sensitivity to human disturbance.

6.1. INTRODUCTION

Animal populations inhabiting coastal and inland waters are suffering increasing exposure to humans, due to growing development and urbanisation of these areas (Burger 1991; Burton *et al.* 2006; Burton 2007). Such expanding anthropogenic activity has raised concern over its ecological impacts on wildlife populations (Sutherland *et al.* 2006). Considerable attention has recently focused on the ways in which human disturbance alters the behaviour of wildlife (see review in Frid & Dill 2002). Studies on organisms as diverse as marine mammals (Constantine *et al.* 2004; King & Heinen 2004), large terrestrial game species (Stockwell *et al.* 1991; Stankowich 2008), reptiles (Vega *et al.* 2000; Moore & Seigel 2006) and birds (Gill *et al.* 1996; Beale & Monaghan 2005) have indicated that human disturbance can significantly alter feeding schedules, habitat use and parental care.

When disturbed by predators or by people engaged in various commercial and recreational activities, birds will leave their chosen feeding areas. In doing so, they will consume considerable energy fleeing from the disturbance (Nudds & Bryant 2000) whilst sacrificing valuable feeding time moving to alternative areas (Quinn 1997). In order to optimise these trade-offs, individuals should vary their response dynamically so as to minimize the costs of disturbance while maximizing their chance of survival (Bonenfant & Kramer 1996; Frid & Dill 2002). By studying behaviour, it may be possible to infer the selection pressures imposed on behavioural strategies by measuring the response of individuals to various disturbance stimuli (Klein *et al.* 1995; Madsen 1998; Fernandez-Juricic & Telleria 2000; Fernandez-Juricic *et al.* 2005; Finney *et al.* 2005; Arlettaz *et al.* 2007). Some studies have demonstrated that birds react more to a disturbance when the perceived threat is greater (Madsen 1998; Delaney *et al.* 1999; Lafferty 2001; Frid & Dill 2002). If this threat is repetitive and non-lethal, however, animals can be expected to become habituated in order to reduce fitness costs (Deniz *et al.* 2003; Sutherland 2007). Those unable/unwilling to habituate to disturbance could be forced from preferred foraging areas or suffer the costs of remaining. As species are thought to differ greatly in their rates of habituation (Ikuta & Blumstein 2003; Blumstein *et al.* 2005), habituation may therefore be a key factor in determining whether species are lost from areas frequented by humans (Rees *et al.* 2005; Sutherland 2007).

Experimental flushing methods are often used to investigate and quantify the short-term effects of human activities on wildlife (Blumstein 2003). Species are known to vary in their sensitivity to humans (Blumstein *et al.* 2005) and wildlife managers and conservation biologists often use these measures to grade species by their susceptibility to disturbance (Buehler *et al.* 1991; Carney & Sydeman 1999). These data are used to provide baseline information on disturbance tolerance levels, which aid in the creation of management tools such as buffer zones (Rodgers & Smith 1995; Fernandez-Juricic *et al.* 2005). However fixed set-back distances, as recommended in the literature, may be too simplistic, (even damaging) if the flight response is related to

previous exposure, habitat conditions or fitness costs (Gill 2007). For example, if birds were able to habituate to humans, one would expect a negative relationship between flight response and previous exposure to non-lethal anthropogenic activities (Smit & Visser 1993; Lord *et al.* 2001; Ikuta & Blumstein 2003, Rees *et al.* 2005). Similarly, individuals may be forced to take greater risks later in the winter in order to compensate for increased metabolic demands and the deterioration of feeding grounds (McGowan *et al.* 2002; Stillman & Goss-Custard 2002; Yasue *et al.* 2003; Beale & Monaghan 2004). In this study we aimed to test the effect of previous exposure to humans and metabolic demands on behavioural decisions of overwintering waterbirds. Thermoregulatory demands were considered along with prey depletion to ascertain whether individuals respond less when they were indeed most vulnerable. In order to test the generality of these assumptions, several species of waterbirds were selected and routinely disturbed over a number of sites and under a range of environmental conditions. Mechanisms whereby disturbance influences behavioural response and the extent to which the costs of disturbance may be reduced by the modification of behaviour through habituation will also be discussed.

6.2.METHODS

6.2.1. *Study area*

This study was conducted between October 2008 and March 2009 over intertidal mudflats located on the Forth estuary, Scotland (56°04'N 3°42'W). Five sites were selected for disturbance experiments: Airth, Kennet Pans, Skinflats, Torry Bay and Blackness Bay (Figure 6.1). Sites were chosen for their relatively firm sediment (allowing safe access on foot), for their broad heterogeneity in human exposure, and the presence of relatively high densities of wader and duck species (hereafter referred to collectively as 'waterbirds'). During each experiment, the number of people and dogs observed within 1000m of birds were recorded over a 1 hour period and sites were scored on their ambient level of human use (*low*: <0.5 disturbances/hour and *high*: >0.5 disturbances/hour; Table 6.1).

Table 6.1: Number of visits, observed recreational disturbances at each site and disturbance scoring classification for each site.

	Airth	Kennet Pans	Skinflats	Torry Bay	Blackness Bay
Number of visits	10	8	9	8	9
Number of humans	2	0	0	16	27
Number of dogs	0	0	0	7	14
Disturbances/hr	0.2	0	0	2.88	4
Ambient disturbance score	low	low	low	high	high

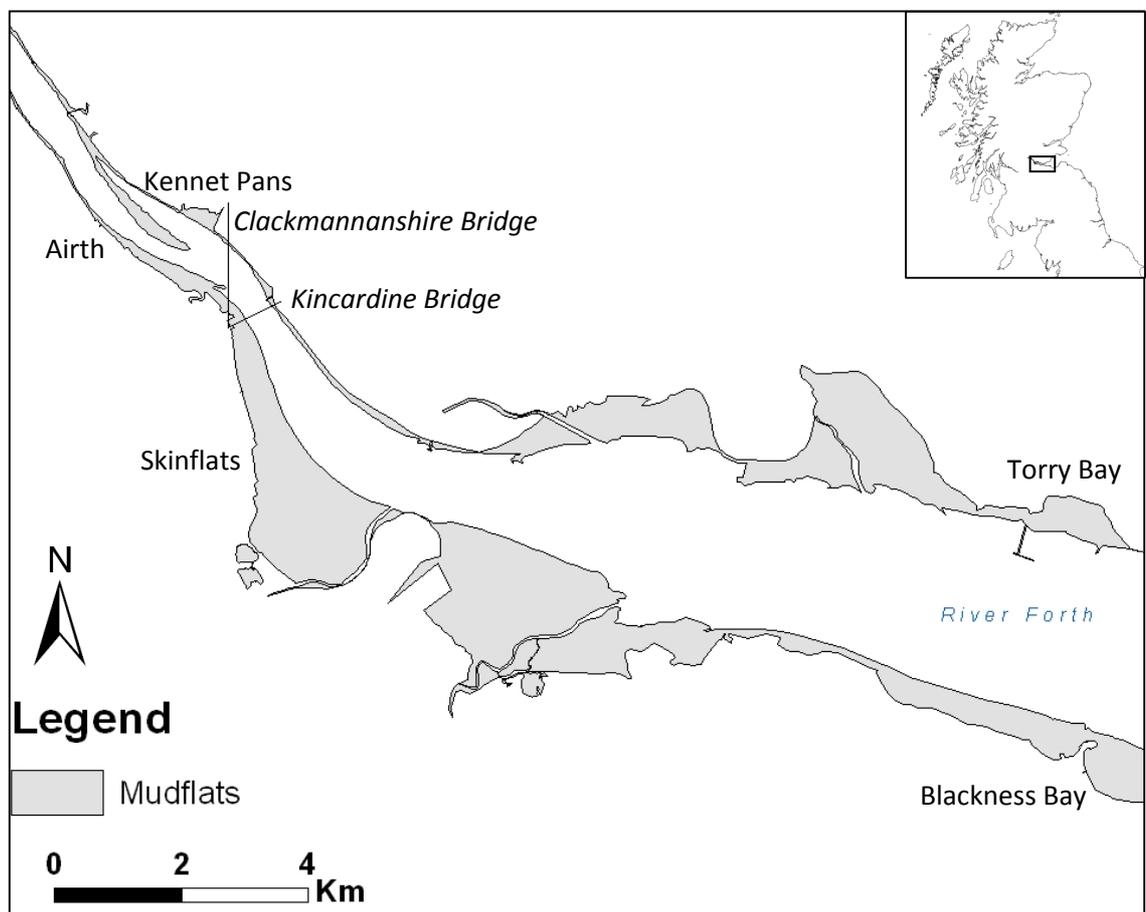


Figure 6.1: The Forth estuary study area, showing tidal mudflats (light shading), road bridges and the five sites selected for disturbance experiments.

6.2.2. Disturbance methods

To investigate habituation, the behavioural response of several species of waterbirds towards a human intruder was compared over the five sites. Alert distance (AD), flight-initiation distance (FID) and the fly-away distance (FAD) were used to explore interspecific variation in tolerance to human disturbance. As it was often difficult to observe small changes in behaviour and the location of disturbed birds whilst maintaining a constant approach, two persons were required: an *observer* and an *intruder*. Firstly, the *observer* positioned on a high vantage point and using binoculars (10x42) and a spotting scope (20x60), noted by eye the position and behaviour of a flock of birds. This information was then transcribed onto 1:10 000 OS maps in the field, in addition to the time of day, wind speed (Beaufort scale) and wind-direction. Under the *observer's* direction, a second person (hereafter referred to as 'the *intruder*') walked directly toward the flock at a constant pace of 0.5–1.0m/s. At the point where the first bird elicited an obvious change in behaviour in response to the approach, a command was given by the *observer* via a two-way radio and a marker cane was placed in the sediment (C_{AD}). The *intruder* continued the approach until the first bird of each species exhibited a flight response to the disturbance stimulus (e.g. taking flight, walking away from/towards the intruder; C_{FID}). A marker cane was positioned for a response from each species present until all species responded to the approach. The observer recorded the new position of the disturbed birds onto the OS map in order to measure the distance flown (C_{FAD}) (Fernandez-Juricic *et al.* 2005). After the disturbance, the *intruder* first walked towards the position at which each species took flight to collect the GPS position of the flock before retreating to the starting point while taking GPS coordinates of each marker and removing the canes from the sediment. Euclidean distances between original position of the flock and the C_{AD} , C_{FID} and C_{FAD} markers were measured using the distance matrix computation in R (R Development Core Team 2009) to calculate alert distance (AD), flight-initiation distance (FID) and the fly-away distances (FAD), respectively.

Experiments were performed at two different sites each day. The combinations in which the five sites were used were randomised and at least three days were allowed to pass before a site was used again in the experiment. These measures were taken in order to avoid problems of bias and autocorrelation in the response of birds. To reduce the effect of autocorrelation between the first bird flushed and subsequent flushing events, and to minimize observer-effects on avian activities, we limited the number of controlled disturbances to a maximum of two approaches at each site per test day. Implicit in this protocol is the assumption that no habituation would occur after a single disturbance event, but it may after two or more disturbances. Flush distance for an individual bird or flock was measured only once. Because of these restrictions, sample sizes often were unbalanced (i.e. not all species were represented by equal sample sizes) in terms of species, and site-variable classes (e.g. level of disturbance, location). Experiments were conducted in early-winter (Oct 2008-Nov 2008) and late-winter (Feb 2009-Mar 2009) to

investigate if the behavioural response varies temporally. Tidal data were obtained later from the British Oceanographic Data Centre (BODC) collected by the tidal gauge site located at Leith docks, Edinburgh (55.99°N, 03.18°W). Temperature data were supplied by the Meteorological Office from the weather station at Edinburgh Gogarbank (55.93°N, 03.34°W).

6.2.1. Statistical analysis

For those species with $n > 20$ flushes (Table 6.2), General Linear Mixed Models (GLMMs) were used to investigate factors influencing *AD*, *FID* and *FAD* for each individual species. Response variables were \log_{10} -transformed prior to analysis to meet model assumptions of normality and homoscedasticity. *Ambient disturbance score* (Table 6.1), *flock-size*, *tide height* (m), *temperature* (°C), *mixed-flock* (i.e. whether the flock contained a single or multiple species) and *season* (i.e. whether the treatment took place in early or late winter) were included in our models as fixed effects. The total *approach distance* (i.e. the distance between the intruder's starting point and the position of the flock) was added to our model as a fixed effect in an attempt to control for this startling component (Blumstein 2003). Because disturbances were repeated measures from the same intertidal mudflats, *site* was included within our models as a random effect. Unimportant variables were removed from the GLMMs by stepwise deletion, until only those variables that were significant at the 5% level at explaining variation in behavioural responses were retained in the final model. Despite the log-transformation of *FID* and *AD* values for Shelduck, the residual spread of *season* remained unequal, violating the homogeneity of variance assumption. To incorporate this pattern into the model, the *varIdent* function in R (Pinheiro *et al.* 2009) was used to fit a model incorporating different variances for early and for late winter. GLMMs were constructed using the 'nlme' package (Pinheiro *et al.* 2009) and all analysis was conducted in the R programming language (R Development Core Team 2009).

6.3. RESULTS

Between October 2007 and April 2009 we exposed 16 species of waterbirds (*Charadriiformes* (e.g. plovers and sandpipers), *Anseriformes* (e.g. ducks) and *Ciconiiformes* (herons)) to experimental disturbance using a direct human approach ($n=158$ flushes; Appendix 6.1). Sample size per species varied from 1 to 43 flushes. Whilst we attempted to control for weather conditions on test days by the paired nature of the experimental procedures, this was not always achieved. For this reason, data on windy days (Beaufort 3+) were removed from the analyses as strong winds were seen to affect the flight response (McGowan *et al.* 2002). The flock size at each site varied from 2 to 168 individuals, however no consistent difference was found in the number of birds in relation to either site (*Anova*, $F_{4,39}=0.86$, $p=0.487$) or treatment (*Anova*, $F_{1,43}=1.47$, $p=0.233$). The number of people observed visiting each site was significantly different (*Anova*, $F_{4,40}=5.33$, $p=0.002$) with visitor numbers significantly greater at Blackness Bay and Torry Bay than at the other three study sites (Table 6.1). For this reason, Torry Bay and

Blackness were classed as ‘high’ disturbance sites, with Airth, Kennet Pans and Skinflats: ‘low’ disturbance sites (Table 6.1). Numbers of visitors in early and late winter were similar ($F_{1,39}=0.38$, $p=0.539$).

Table 6.2: The number of flushes for each species at each site ($n \geq 7$) and their respective mean flight-initiation distance (*FID*) score.

Species	Airth	Kennet Pans	Skinflats	Torry Bay	Blackness Bay	Total	<i>FID</i> (meters)	\pm SE
<i>Shelduck</i>	4	4	9	2	3	22	178.39	38.79
<i>Wigeon</i>	2	0	0	2	3	7	151.38	62.90
<i>Mallard</i>	4	1	0	2	0	7	162.52	61.26
<i>Oystercatcher</i>	0	1	3	12	6	22	137.61	40.53
<i>Curlew</i>	8	7	6	9	6	36	235.16	63.09
<i>Redshank</i>	14	7	7	8	7	43	149.90	37.92

Within sites, there was considerable variation in *FID* among species ($X^2_5=20.841$, $p<0.001$), however alert distances (*AD*) were similar ($X^2_5=5.002$, $p=0.416$). Curlew *Numenius arquata* had the longest *FID* (i.e. were most sensitive to an approaching intruder), while Oystercatcher *Haematopus ostralegus* appeared least sensitive to our approach.

Within each species, the behavioural responses of birds to our approach appeared less extreme at sites with high ambient levels of recreational disturbance (i.e. Torry Bay and Blackness bay; Appendices 6.2, 6.3, 6.4). To investigate the role of prior disturbance and environmental effects on *AD*, *FID* and *FAD*, Redshank *Tringa totanus*, Curlew, Shelduck *Tadorna tadorna* and Oystercatcher were selected (based on their high flush frequency, $n>20$) for multiple regression analysis using a mixed-model approach (GLMMs).

Redshank

Disturbance score and the distance at which the approach was initiated was a significant predictor of *AD* in Redshank ($X^2_1=7.40$, $p=0.007$; $X^2_1=22.20$, $p<0.001$). Redshank occupying disturbed areas allowed the intruder to approach closer before eliciting an alert response. However, the greater the distance an intruder started his approach, the greater the distance at which birds reacted. Significant two-way interactions were found between *disturbance score* \times *season* and *disturbance score* \times *temperature* for Redshank *FID* ($X^2_1=7.58$, $p=0.006$; $X^2_1=5.37$, $p=0.020$). Those birds occupying sites with a high ambient disturbance score (i.e. Torry Bay and

Blackness Bay) allowed the closest approach, especially later in the winter (Figure 6.2i). *Disturbance score* and *season* negatively affected *FAD* in Redshank ($X^2_1=4.65$, $p=0.031$; $X^2_1=10.73$, $p=0.001$). Redshank made shorter escape flights in heavily disturbed areas and later in the winter. *Tide height*, *flock size*, and *mixed flock* did not influence Redshank *AD*, *FID* or *FAD* ($p>0.05$).

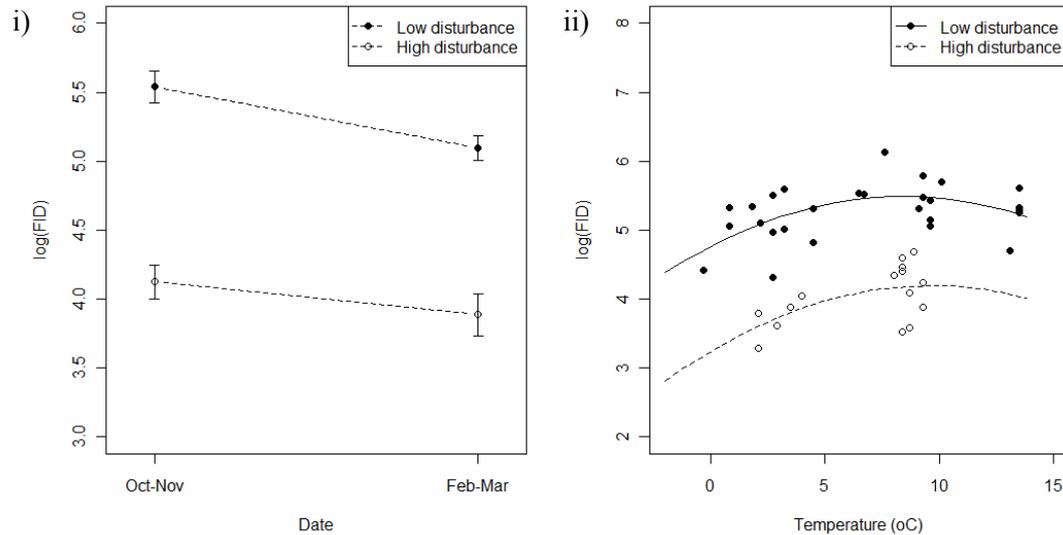


Figure 6.2: Relationship between Redshank log-transformed flight-initiation distances (*FID*) and (i) *site-disturbance score* and *season*; and (ii) *site-disturbance score* and *temperature*. High and low site-disturbance scores were generated from their ambient disturbance level (Table 6.1). Error bars (± 1 SE) taken from predicted standard error in GLMM; regression lines in (ii) represent predicted values from the GLMM ($X^2_1=5.37$, $p=0.020$).

Curlew

Disturbance score and *approach distance* were the only important factors affecting Curlew *AD* ($X^2_1=11.45$, $p=0.001$; $X^2_1=16.53$, $p<0.001$) and *FID* ($X^2_1=15.90$, $p<0.001$; $X^2_1=6.75$, $p=0.009$) and). As with Redshank, birds occupying heavily disturbed areas allowed an intruder to approach closer before becoming alert and taking flight. Similarly, birds became visibly alert and flushed at greater distances when the intruder began his approach from further away. *Tide height*, *temperature*, *flock size*, *season* and *mixed flock* (i.e. whether or not the flock contained multiple species) had no significant effect on the *FID* or *AD* of Curlew ($p>0.05$). No pattern was found for fly-away distances in Curlew ($p>0.05$).

Oystercatcher

Disturbance score negatively affected Oystercatcher *AD* ($X^2_1=6.53$, $p=0.023$), *FID* ($X^2_1=10.10$, $p=0.002$) and *FAD* ($X^2_1=9.26$, $p=0.002$). Birds in more disturbed areas allowed an intruder to approach closer before becoming vigilant and moving away. Birds then flushed shorter

distances in these disturbed areas than in areas of low human disturbance. *Season* and *approach distance* had no significant effect on Oystercatcher *FID*, however they were significant in predicting *AD* ($X^2_1=5.14$, $p=0.023$; $X^2_1=12.62$, $p<0.001$) and *FAD* ($X^2_1=6.09$, $p=0.014$; $X^2_1=17.49$, $p<0.001$). Although there was no evidence that *AD* or *FID* were negatively affected by *temperature*, birds flew shorter distances when it was colder ($X^2_1=4.60$, $p=0.032$). Similarly, Oystercatcher flew shorter distances at higher tides ($X^2_1=12.05$, $p=0.001$), in smaller flocks ($X^2_1=11.89$, $p=0.001$) and when the flock contained multiple species ($X^2_1=5.36$, $p=0.021$).

Shelduck

Shelduck in undisturbed areas became visibly alert at greater distances than birds in disturbed areas ($X^2_1=18.06$, $p<0.001$). A significant two-way interaction was also found between *disturbance score* \times *temperature* for *FID* in Shelduck ($X^2_1=18.76$, $p<0.001$). The distance at which birds flushed increased with temperature in disturbed areas, however little change in *FID* was observed with temperature in undisturbed localities (Figure 6.3i). As with Redshank, Oystercatcher and Curlew, the distance at which the intruder began his approach positively influenced alert distance ($X^2_1=4.34$, $p=0.037$). Birds in mixed-species flocks became alert at greater distances than flocks containing only conspecifics ($X^2_1=7.68$, $p=0.006$). *Season* was the only important factor affecting *FAD* with Shelduck flying shorter distances in response to an intruder in late winter than they did early in the winter (Figure 6.3ii, $X^2_1=6.02$, $p=0.014$).

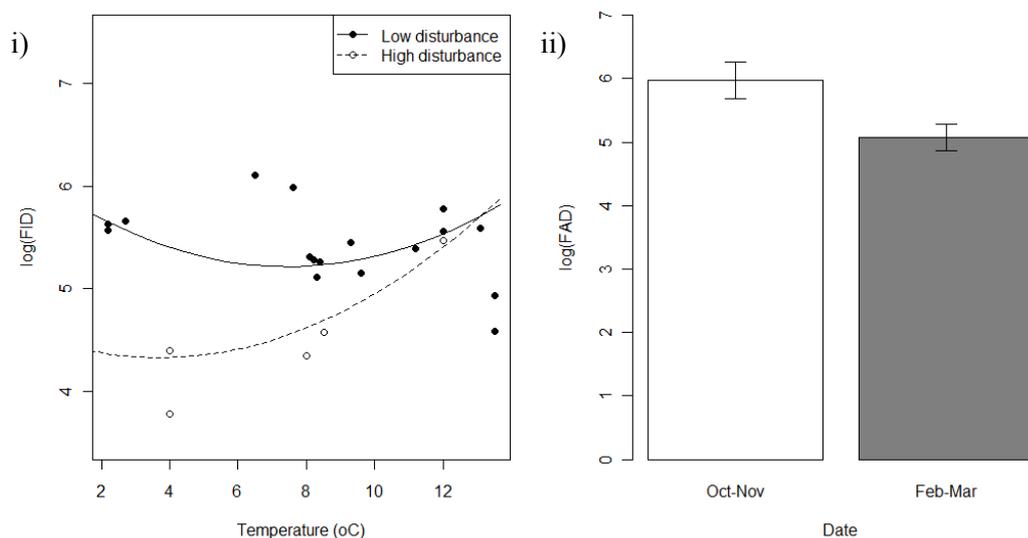


Figure 6.3: (i) Relationship between Shelduck log-transformed *FAD* and *disturbance score* and *temperature*. ii) Mean log-transformed fly-away distances (*FAD*) for Shelduck by *season*. Regression lines in i) represent predicted values from the GLMM. Error bars (± 1 SE) in ii) taken from predicted standard error in GLMM estimates.

6.4. DISCUSSION

6.4.1. *Previous exposure to humans*

In this study, we have shown that variation in habituation occurred at relatively large scales on the Forth estuary. All four species selected for species-specific analysis allowed a closer human approach in heavily disturbed areas before becoming alert and moving away, than did individuals of the same species within the less disturbed areas. Redshank and Oystercatcher also flew shorter distances in response to an intruder at sites with a low frequency of human disturbance. Our findings support those of previous studies indicating that habituation is likely to occur with repeated non-lethal exposure to humans (Deniz *et al.* 2003; Sutherland 2007). For example, Urfi *et al.* (1996) found Oystercatchers occupying quieter areas of Exe estuary show greater flushing distances than those in areas with a high frequency of recreational use. Likewise, Ikuta and Blumstein (2003) found that in disturbed sites, Black-necked Stilts *Himantopus mexicanus*, Great Blue Herons *Ardea herodias*, Great Egrets *Ardea alba*, Snowy Egrets *Egretta thula*, and Willets *Catoptrophorus semipalmatus* all showed greater *FID* values than in undisturbed sites and fenced-off areas. Such habituation permits birds to ameliorate some negative impacts of disturbance by maximising foraging time and reducing energy expenditure (Whittaker & Knight 1998; Fernandez-Juricic & Telleria 2000). Due to concerns about personal safety on the soft mud and spatial autocorrelation between closely connected foraging sites, only five sites (three low disturbance sites and two high disturbance sites) were selected on the Forth for disturbance experiments. Although this may place some constraints on our ability to conclude human exposure as the true cause of behavioural differences, we argue that as all species in our study consistently showed a reduced behavioural response in the disturbed habitat (Appendices 6.2, 6.3, 6.4), this low number of sites is likely not to be a problem in our study. On a local scale, authors have shown the intensity of a behavioural response may be influenced by some other site-level factor such as prey availability, distance to forest cover and proximity to alternative feeding areas (Gill *et al.* 2001; Yasue 2006; Gill 2007). In this study, experiments were only performed on calm, clear days and over a range of sites and locations within each site, in an attempt to control for this variability in perceived habitat quality.

6.4.2. *Seasonal effects and physiological stress*

During periods when they may have been a significant energetic or fitness cost, Redshank, Oystercatcher and Shelduck appear to moderate their responses to human disturbance. All three species flew shorter distances in response to a disturbance later in the winter, and Redshank allowed the intruder to approach closer before eliciting a response. Similarly when the temperature was colder, Redshank and Shelduck allowed a closer approach before flushing while Oystercatcher flew shorter distances. Our findings supported previous studies indicating that birds show fewer visible behavioural responses to human disturbance (Ydenberg & Dill

1986; Yasue 2006) or natural predators (Lima 1998) when there is a significant energetic or fitness cost (Delaney *et al.* 1999; McGowan *et al.* 2002). In Redshank and Shelduck, our study found temperature had a greater effect on *FID* decisions in highly disturbed localities. If individuals occupying disturbed areas have greater metabolic demands, one would expect a reduction in temperature to impact more on behavioural decisions in these areas. Essentially, the fitness cost of responding to a disturbance during extreme periods will be greater for disturbed birds; these 'habituated' individuals may already be compensating for a negative energy balance, and so will have less opportunity to compensate for any further deficiencies in energy requirements. As the preferred prey of Redshank and Shelduck feeding on intertidal mud-flats consists mainly of small items, namely *Corophium*, *Hydrobia* and smaller sizes of worms (Bryant & Leng 1975; Goss-Custard *et al.* 1977; Evans *et al.* 1979), severe weather may be more likely to lead to a negative energy balance in these species; which have less scope to increase their energy budget than those species feeding on larger prey items (Mitchell *et al.* 2000). By selecting small prey, Redshank achieve a much lower rate of net energy intake than the larger shorebird species and require longer periods of feeding to meet their daily energy requirements. This may explain why an interaction was not found in Oystercatcher or Curlew, which feed mainly on larger prey consisting of large polychaetes and bivalves such as *Macoma* and *Mytillus* (Goss-Custard *et al.* 1977; Evans *et al.* 1979). Although Shelduck take 'bill-fulls' rather than single prey items as is the case in most shorebirds, their relatively energy poor hard-shelled *Hydrobia* prey and their inability to capitalise on larger soft bodied prey below the mud-surface (Buxton 1975; Buxton & Young 1981), may make Shelduck more susceptible to energy deficiencies than other larger-bodied shorebirds.

If those birds occupying disturbed sites are under more energetic stress, one would expect a reduced behavioural response later in the winter when foraging grounds are depleted. Contrary to this prediction, *season* had a greater effect on the flight distance of undisturbed Redshank than those occupying disturbed areas (Figure 6.2i). The rate of prey depletion is known to vary spatially across the Forth (chapter 2), and human disturbance has previously been shown to reduce waterbird predation pressure on prey densities (Gill *et al.* 1996). A high prey depletion rate at low disturbance sites would result in a greater temporal change in flight response than sites with little seasonal variation in prey densities. A comparison of seasonal variation in prey densities and flight decisions at disturbed and undisturbed sites would provide a greater insight into this resource-risk trade-off.

6.4.3. *Distance of approach*

In all four species, the distance at which individuals became vigilant was positively affected by the distance at which the intruder began his approach. The openness of a landscape is well known to be an important factor for waterbirds safety (Cresswell 1994), as high visibility can increase the distance at which threats are detected (Metcalf 1984; Whittingham *et al.* 2004).

The fact that only alert distance was consistently affected by the approach distance suggests that although birds changed their behaviour in response to the intruder, they weren't prepared to take flight immediately. When birds are able to see the approach from further away, however, they are better able to determine whether humans pose a threat and to take evasive action under these conditions (Rees *et al.* 2005). Only in Curlew was the distance of approach significant in predicting *FID* values. In practice, Curlew often took flight immediately after becoming vigilant to the intruders approach (RD pers. obs). Due to the large body-size of Curlew, more time is required for this species to accelerate to an adequate speed in order to gain flight (Burger & Gochfeld 1991; Skagen *et al.* 1991; Fernandez-Juricic *et al.* 2001); thereby reducing the time available between risk assessment and the decision to take-off.

6.4.4. Conservation implications

Understanding how animals respond to anthropogenic activities is fundamental to resolving potential conflicts between humans and animals (Beale 2007). While conservation managers acknowledge the variability in *FID* (e.g. Carney and Sydeman, 1999), they nevertheless use estimates of a species' *FID* to create buffer zones in an attempt to minimize human impacts. The results of this study have implications for the interpretation of *FID* values and the design of these buffer areas. Many factors are known to influence *FID* and as we have shown, a given *FID* estimate can be location-specific. Species were shown to differ greatly in their level of habituation, and habituation may reduce a species *FID* by as much as 25%. Habituation to humans may permit site managers to be less conservative in the creation of these buffer areas to allow for likely habituation effects. Alternatively, if buffer areas are created using *FIDs* from habituated birds, there may still be deleterious effects on local, non-habituated, wildlife populations (Keller 1989). More study is therefore required on whether there are indeed fitness costs of habituation in wintering waterbirds.

Buffer areas commonly assume that tolerance indicators do not change in time or under various environmental conditions. However, our study has shown that flight initiation distance, alert distance and fly-away distances vary with time. This may not be a problem in cases where buffer areas are established to protect animals during a focused breeding season, but might be a problem if the goal is to reduce human disturbance throughout the year. Stillman & Goss-Custard (2002) showed that birds responded less to a disturbance when they were more energetically stressed and less able to compensate for lost feeding time. Our study took this idea further and showed this pattern varies between sites and is strongest for individuals possibly already compensating for a negative energy balance.

Management measures are essential if we are to mitigate the effects of an increasingly urbanised coastline. The information presented here may be useful in suggesting guidelines for the planning, development and improvement of mitigation measures aimed at protecting bird

species and diversity. On reflection, there appears to be at least two potential set-back distances for each species: a habituated figure and a non-habituated figure. In order to minimise the risk of hidden fitness costs associated with habituation, use of the non-habituated figure is recommended. As tolerance depends greatly on foraging conditions, prior experience and metabolic demands, wildlife managers should move away from traditional interpretations of using a singular species-specific behavioural response distance and recognise, and seek to allow for, the seasonal and spatial variations in sensitivity to human disturbance.

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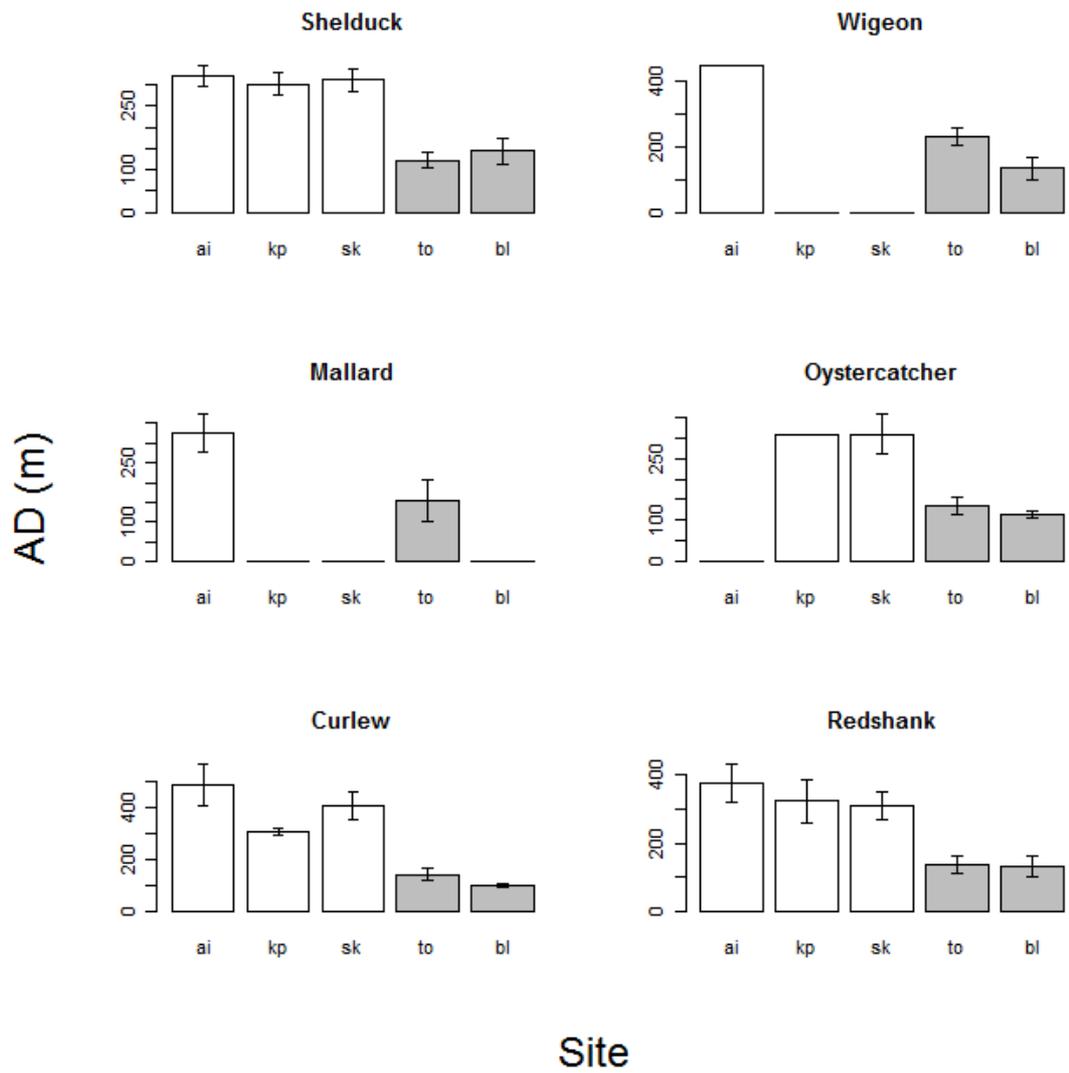
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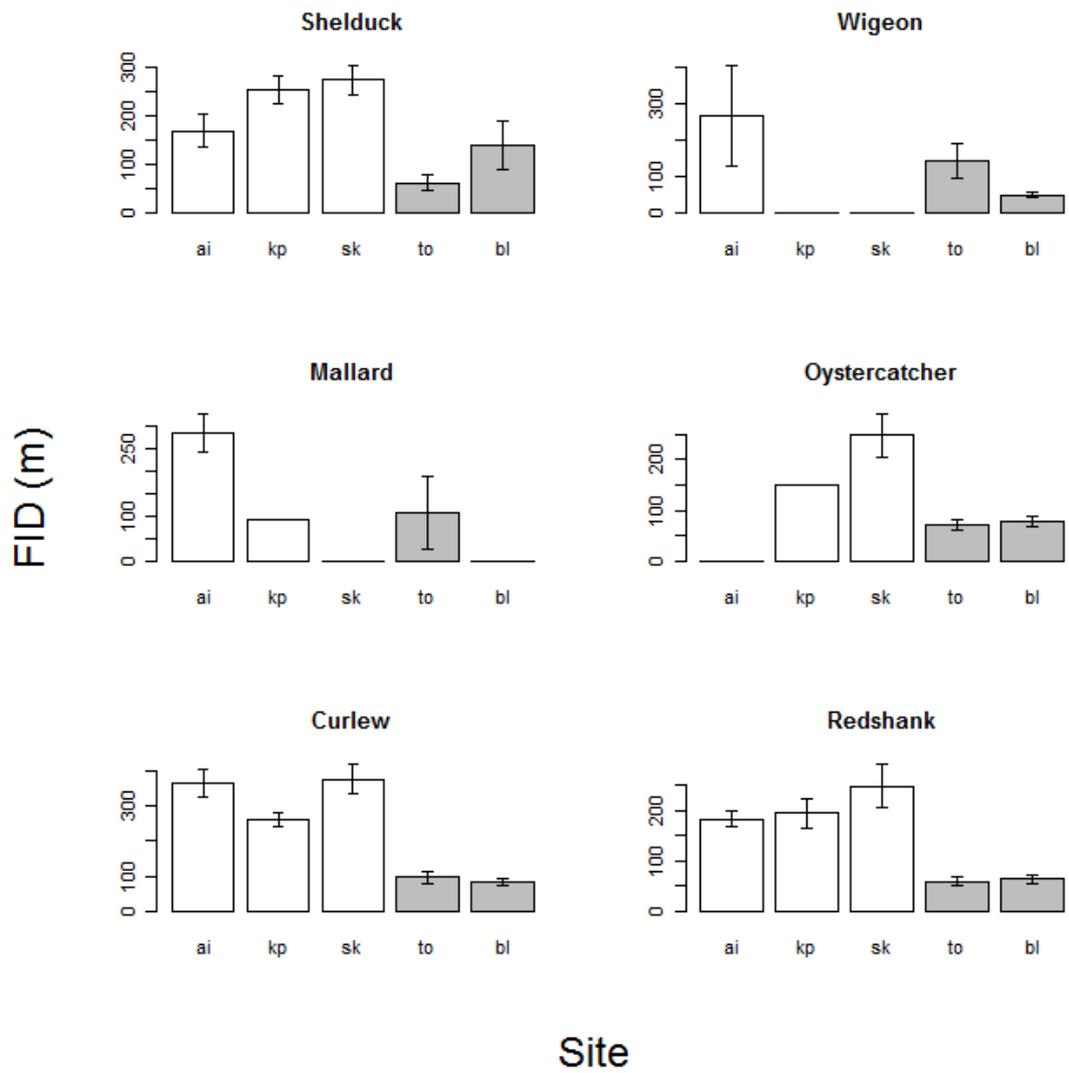
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Appendix 6.1: The number of flushes for all flushed species at each site and their respective mean flight-initiation distance (*FID*) score.

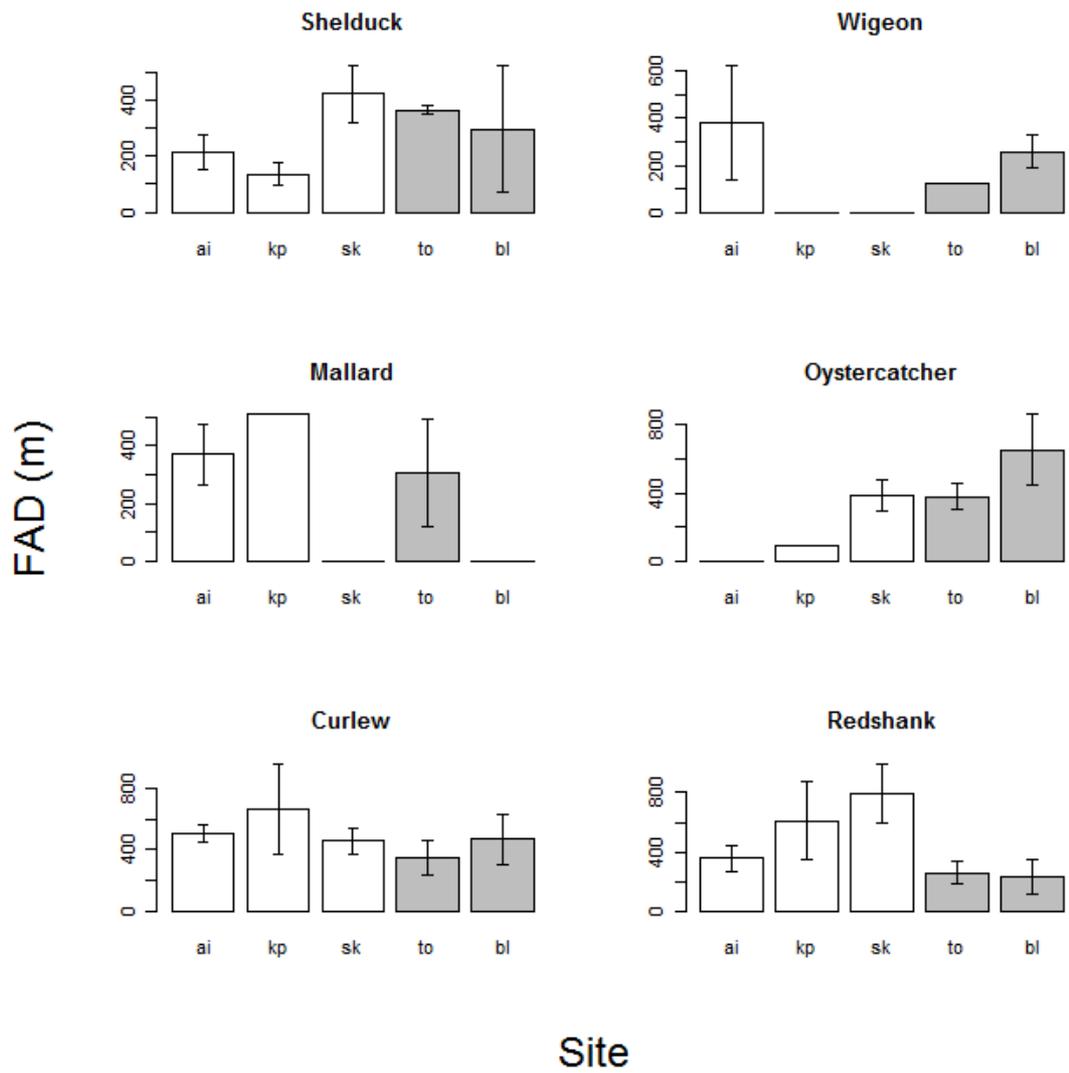
Species	Airth	Kennet Pans	Skinflats	Torry Bay	Blackness Bay	Total	<i>FID</i> (meters)	±SE
<i>Grey Heron</i>	1	0	0	0	0	1	172.04	-
<i>Shelduck</i>	4	4	9	2	3	22	178.39	38.79
<i>Wigeon</i>	2	0	0	2	3	7	151.38	62.90
<i>Teal</i>	0	3	0	0	0	3	203.96	55.18
<i>Mallard</i>	4	1	0	2	0	7	162.52	61.26
<i>Oystercatcher</i>	0	1	3	12	6	22	137.61	40.53
<i>Ringed Plover</i>	0	0	0	1	0	1	31.91	-
<i>Golden Plover</i>	0	0	1	0	1	2	280.90	212.17
<i>Lapwing</i>	1	1	0	0	2	4	235.37	78.08
<i>Knot</i>	0	0	0	0	1	1	60.01	-
<i>Dunlin</i>	0	3	0	0	1	4	163.87	61.08
<i>Bar-t Godwit</i>	0	0	0	1	2	3	96.91	13.50
<i>Curlew</i>	8	7	6	9	6	36	235.16	63.09
<i>Redshank</i>	14	7	7	8	7	43	149.90	37.92
<i>Greenshank</i>	1	0	0	0	0	1	494.17	-
<i>Turnstone</i>	0	0	0	0	1	1	43.19	-



Appendix 6.2: Average (\pm SE) alert distance (*AD*) for selected species at each location. White bars represent sites with a 'low' ambient disturbance score; grey bars represent sites with a 'high' ambient disturbance score.



Appendix 6.3: Average (\pm SE) flight-initiation distance (*FID*) for selected species at each location. White bars represent sites with a 'low' ambient disturbance score; grey bars represent sites with a 'high' ambient disturbance score.



Appendix 6.4: Average (\pm SE) fly-away distance (*FAD*) for selected species at each location. White bars represent sites with a 'low' ambient disturbance score; grey bars represent sites with a 'high' ambient disturbance score.

Appendix 6.5: Results of four GLMMs to test habituation affects on the alert distance (*AD*) of a species (\log_{10} -transformed), controlling for flock, temperature and seasonal effects.

		<i>d.f.</i>	X^2	<i>P</i>	<i>B</i>	
<i>Redshank AD</i>	<i>Intercept</i>				4.91	± 1.18
	<i>Tide height</i>	12	0.05	0.830		
	<i>mixed flock</i>	11	0.51	0.474		
	<i>Dscore x Season</i>	10	1.56	0.211		
	<i>Dscore x Temperature</i>	9	0.87	0.351		
	<i>Season</i>	8	0.83	0.362		
	<i>Temperature</i>	7	1.21	0.271		
	<i>Temperature²</i>	6	0.93	0.334		
	<i>Flock size</i>	5	3.71	0.054		
	<i>Approach distance</i>	4	22.20	<.0001	0.00	0.00
	<i>Dscore</i>	4	7.40	0.007	-0.46	± 1.00
<i>Curlew AD</i>	<i>Intercept</i>				5.34	± 1.16
	<i>Flock size</i>	12	0.02	0.020		
	<i>mixed flock</i>	11	0.06	0.814		
	<i>Dscore x Temperature</i>	10	0.11	0.736		
	<i>Tide height</i>	9	0.27	0.602		
	<i>Temperature</i>	8	2.86	0.091		
	<i>Temperature²</i>	7	1.03	0.311		
	<i>Dscore x Season</i>	6	2.99	0.084		
	<i>Season</i>	5	2.45	0.117		
	<i>Dscore</i>	4	11.45	0.001	-0.91	± 0.16
	<i>Approach distance</i>	4	16.53	<.0001	0.00	± 0.00
<i>Oystercatcher AD</i>	<i>Intercept</i>				4.67	± 0.29
	<i>Flock size</i>	12	0.07	0.785		
	<i>Temperature²</i>	11	1.07	0.301		
	<i>mixed flock</i>	10	3.15	0.076		
	<i>Dscore x Temperature</i>	9	1.23	0.268		
	<i>Temperature</i>	8	0.00	0.985		
	<i>Tide height</i>	7	1.82	0.178		
	<i>Dscore x Season</i>	6	1.83	0.176		
	<i>Dscore</i>	5	6.53	0.011	-0.46	± 0.19
	<i>Season</i>	5	5.14	0.023	0.26	± 0.12
	<i>Approach distance</i>	5	12.62	0.000	0.00	± 0.00
<i>Shelduck AD</i>	<i>Intercept</i>				5.51	± 0.14
	<i>Dscore x Season</i>	12	0.23	0.634		
	<i>Season</i>	11	0.52	0.472		
	<i>Temperature²</i>	10	1.29	0.257		
	<i>Dscore x Temperature</i>	9	2.47	0.116		
	<i>Temperature</i>	8	3.28	0.070		
	<i>Tide height</i>	7	2.61	0.106		
	<i>Flock size</i>	6	3.07	0.080		
	<i>Dscore</i>	5	18.06	<.0001	-0.69	± 0.11
	<i>Approach distance</i>	5	4.34	0.037	0.00	± 0.00
	<i>mixed flock</i>	5	7.68	0.006	-0.21	± 0.07

Appendix 6.6: Results of four GLMMs to test habituation affects on the flight initiation distance (*FID*) of a species (\log_{10} -transformed), controlling for flock, temperature and seasonal effects.

		<i>d.f.</i>	X^2	<i>P</i>	<i>B</i>	
<i>Redshank FID</i>	<i>Intercept</i>				5.30	± 0.26
	<i>Tide height</i>	13	0.00	0.980		
	<i>mixed flock</i>	12	0.04	0.833		
	<i>Dscore x Temperature²</i>	11	0.92	0.339		
	<i>Approach distance</i>	10	0.95	0.330		
	<i>Flock size</i>	9	1.70	0.193		
	<i>Dscore x Temperature</i>	8	5.37	0.020	0.13	± 0.06
	<i>Temperature²</i>	8	7.23	0.007	-0.01	± 0.00
<i>Dscore x Season</i>	8	7.58	0.006	0.94	± 0.36	
<i>Curlew FID</i>	<i>Intercept</i>				5.32	± 0.19
	<i>Dscore x Temperature</i>	12	0.00	0.958		
	<i>Tide height</i>	11	0.30	0.585		
	<i>Temperature</i>	10	0.79	0.375		
	<i>Temperature²</i>	9	0.09	0.770		
	<i>Flock size</i>	8	0.80	0.372		
	<i>Dscore x Season</i>	7	0.78	0.377		
	<i>mixed flock</i>	6	1.89	0.170		
	<i>Season</i>	5	3.40	0.065		
	<i>Dscore</i>	4	15.90	<0.001	-1.11	± 0.16
	<i>Approach distance</i>	4	6.75	0.009	0.00	± 0.00
<i>Oystercatcher FID</i>	<i>Intercept</i>				5.36	± 0.21
	<i>Temperature²</i>	12	0.01	0.920		
	<i>mixed flock</i>	11	0.20	0.654		
	<i>Dscore x Season</i>	10	0.55	0.456		
	<i>Tide height</i>	9	0.42	0.516		
	<i>Flock size</i>	8	0.39	0.530		
	<i>Season</i>	7	0.86	0.353		
	<i>Approach distance</i>	6	0.72	0.396		
	<i>Dscore x Temperature</i>	5	1.29	0.256		
	<i>Temperature</i>	4	0.11	0.738		
	<i>Dscore</i>	3	10.10	0.002	-1.13	± 0.23
	<i>Shelduck FID</i>	<i>Intercept</i>				6.08
<i>Tide height</i>		13	0.80	0.372		
<i>mixed flock</i>		12	0.80	0.372		
<i>Dscore x Season</i>		11	0.70	0.403		
<i>Season</i>		10	1.08	0.299		
<i>Flock size</i>		9	0.52	0.469		
<i>Approach distance</i>		8	2.39	0.122		
<i>Dscore x Temperature</i>		7	18.76	<.0001	0.12	± 0.02
<i>Temperature²</i>		7	13.39	<0.001	0.02	± 0.00

Appendix 6.7: Results of four GLMMs to test habituation affects on the fly-away distance (*FAD*) of a species (\log_{10} -transformed), controlling for flock, temperature and seasonal effects.

		<i>d.f.</i>	X^2	<i>P</i>	<i>B</i>		
<i>Redshank FAD</i>	<i>Intercept</i>				6.50	± 0.25	
	<i>Approach distance</i>	12	0.06	0.800			
	<i>Flock size</i>	11	0.31	0.580			
	<i>mixed flock</i>	10	0.52	0.471			
	<i>Temperature²</i>	9	0.79	0.375			
	<i>Dscore x Temperature</i>	8	1.53	0.216			
	<i>Dscore x Season</i>	7	0.28	0.594			
	<i>Tide height</i>	6	1.80	0.180			
	<i>Temperature</i>	5	2.11	0.146			
	<i>Dscore</i>	4	4.65	0.031	-0.85	± 0.32	
	<i>Season</i>	4	10.73	0.001	-0.89	± 0.26	
<i>Curlew FAD</i>	<i>Intercept</i>				5.89	± 0.18	
	<i>Dscore x Season</i>	12	0.11	0.742			
	<i>Season</i>	11	0.00	0.993			
	<i>Dscore x Temperature</i>	10	1.05	0.306			
	<i>Temperature²</i>	9	0.51	0.475			
	<i>Tide height</i>	8	0.77	0.380			
	<i>mixed flock</i>	7	1.68	0.196			
	<i>Temperature</i>	6	1.72	0.190			
	<i>Approach distance</i>	5	1.43	0.232			
	<i>Flock size</i>	4	1.19	0.276			
	<i>Dscore</i>	3	3.09	0.079			
	<i>Oystercatcher FAD</i>	<i>Intercept</i>				9.52	± 1.05
		<i>Dscore x Temperature</i>	12	0.02	0.879		
<i>Dscore x Season</i>		11	0.13	0.713			
<i>Temperature</i>		10	4.09	0.043	0.26	± 0.18	
<i>Temperature²</i>		10	4.60	0.032	-0.02	± 0.01	
<i>Dscore</i>		10	9.26	0.002	-1.19	± 0.50	
<i>Approach distance</i>		10	17.49	<.0001	-0.01	± 0.00	
<i>mixed flock</i>		10	5.36	0.021	-0.69	± 0.40	
<i>Tide height</i>		10	12.05	0.001	-1.60	± 1.16	
<i>Season</i>		10	6.09	0.014	-0.63	± 0.34	
<i>Flock size</i>		10	11.89	0.001	1.06	± 1.02	
<i>Shelduck FAD</i>		<i>Intercept</i>				5.97	± 0.35
	<i>Dscore x Season</i>	12	0.01	0.942			
	<i>Dscore x Temperature</i>	11	0.09	0.765			
	<i>Flock size</i>	10	0.05	0.823			
	<i>Tide height</i>	9	0.16	0.691			
	<i>Approach distance</i>	8	0.23	0.630			
	<i>Temperature²</i>	7	1.56	0.211			
	<i>Dscore</i>	6	1.56	0.211			
	<i>Temperature</i>	5	3.62	0.057			
	<i>mixed flock</i>	4	1.95	0.163			
	<i>Season</i>	3	6.02	0.014	-0.90	± 0.00	

Chapter 7

General Discussion

7. General Discussion

The biodiversity of many habitats is changing as a result of man-made habitat loss (Myers *et al.* 2000; McKinney 2002), the deterioration of habitat quality through human disturbance and contamination (Takekawa *et al.* 2006), and processes of global environmental change such as global warming and rising sea levels (Vitousek 1994). Pressure on coastal habitats is also expected to increase indirectly, with the recent onus on governments to increase electricity generation from renewable sources (Inger *et al.* 2009). Many of these large renewable energy projects exploit the marine environment, including fabrication yards, tidal barrages, tidal-current schemes, wave energy and offshore wind farms. Given the UK Government's commitment to the EU target, and the large numbers of wintering and breeding waterbirds present around the UK coastline, it is important that the possible impacts of these developments are investigated.

This thesis has considered the impact of industry-generated disturbance on wintering waterbirds as a focus for research. In the general introduction, I argued (1) although much research has been done on disturbance, little is known about the effect of large-scale engineering works on wildlife; (2) that a full understanding requires research into the effects at both the population level and at the individual level; and (3) the effect of disturbance may be enhanced during periods where birds are having trouble meeting their energy requirements. Throughout this thesis I have discussed specific conclusions at the end of each chapter. Here, I will focus on drawing these studies together to form a general picture of disturbance effects and discuss these effects with respect to site protection and wildlife management.

7.1. Landscape approach

In **chapter 1** I gave an overview of how disturbance can affect wildlife, and the importance of the Forth as a whole for overwintering populations of waterbirds. Numerous studies have shown how proximity to man-made landscape features such as roads, paths and engineering works can affect spatial variation in bird numbers or densities (Meire *et al.* 1989; Fernandez-Juricic & Telleria 2000; Burton *et al.* 2002). However, as estuaries are heterogeneous habitats, waterbird distributions may be due to variations in other biotic and abiotic factors such as food supply, substrate type and proximity to roosts and predation risk. By manipulating the presence of the disturbance stimuli, factors that may influence the distribution of animal populations may be accountable (Gill 2007). The construction of the Clackmannanshire Bridge provided an excellent opportunity to conduct a before-after-control-impact (BACI) study on the effects of disturbance on an estuary-wide scale.

Despite being described as having 'remarkable' long-term stability in waterbird densities (Newton & Bryant 1991), there remained significant variation in the numbers of several species over the six winters of this study (**chapter 3**). Contrary to expectations, based on the high level of anthropogenic activity inherent in bridge construction, there was a general increase in total

waterbird numbers during the two winters of bridge construction within the study area. Within this wider pattern, however, there were clear local responses to the disturbance during the bridge build. The increases mostly occurred at high tide far from the construction site, where ducks were often found in large numbers loafing next to riverine areas (**chapter 3**). For individual bird species in close proximity to the Clackmannanshire Bridge site, construction work had consequences ranging from neutral to considerably negative. During bridge construction, several species were displaced from areas adjoining the construction site to more distant count sectors. Cormorant *Phalacrocorax carbo* declined in the area, probably as a result of the disturbance of an important low tide roost, and Redshank *Tringa totanus* also suffered an overall decline, especially in areas in close proximity to the construction site (**chapter 3**). The impact of long-term disturbance on local bird populations is well known to differ between species (Gill 2007), however unless the consequences of changes in habitat-use are investigated, the true sensitivity of individuals to disturbance cannot be assessed (West *et al.* 2002).

To determine the fates of animals displaced by the construction work, it was necessary to conduct a finer scale study on environmental quality and animal behaviour. Despite the relatively close proximity of the study sectors, there was a significant heterogeneity in prey quality between intertidal areas (**chapter 2**). Neighbouring mudflats away from the construction site were found to be relatively poor in prey quality and unlikely to sustain large numbers of displaced birds. In **chapter 3**, we, like others, showed that disturbance caused a greater number of birds to use suboptimal feeding habitat (Hill *et al.* 1997; Percival *et al.* 1998). Flocks of Redshank, previously abundant in the prey-rich areas adjacent to the construction site, were displaced into poorer areas for most of the construction period (**chapters 2, 3**). If numbers extend beyond the carrying capacity of that foraging area, interference among foragers will increase, as will rates of prey depletion (Goss-Custard & Durell 1990; Goss-Custard *et al.* 1995; Goss-Custard *et al.* 1995). As more birds are forced to feed in poorer areas as a result of this disturbance, a greater proportion feed at levels below the feeding rate required to survive, leading to increased starvation mortality (Sutherland & Anderson 1993), or displacement to yet more remote sites, or even long distance emigration (Burton & Armitage 2008). This was illustrated on the Severn estuary, where the loss of intertidal feeding grounds at Cardiff Bay resulted in the displacement of all but a few roosting Redshank (Burton *et al.* 2006). Displaced Redshank were later found to be significantly lighter and suffer greater winter mortality than prior to displacement by habitat loss; presumably as a result of the increased competitor densities in recipient areas (Burton *et al.* 2006). The local increase in Redshank density shown in **chapter 3**, in particular at Kincardine shore, may have impacted directly, through starvation, or indirectly through increased predation risk (Minderman *et al.* 2006). The narrow width of the mudflat (**chapter 2**), close proximity to predator-concealing wooded cover, and high numbers of Sparrowhawks *Accipiter nisus* in the area (**chapter 3**), probably increased the likelihood that

birds may have been predated (Cresswell 1994; Goss-Custard 2003; Quinn & Cresswell 2004). Winter habitat selection may also ‘carry-over’ into the breeding season (Marra *et al.* 1998), influencing the time of arrival, condition of arrival, and fecundity at arctic breeding grounds (Ebbinge & Spaans 1995; Bearhop *et al.* 2004; Trinder *et al.* 2009). In the first winter following the completion of the bridge, Redshank numbers had recovered in the estuary, due to the increased numbers in previously-disturbed areas adjacent to the construction site (**chapter 3**).

Contrary to predictions, Oystercatcher *Haematopus ostralegus*, Teal *Anas crecca* and Curlew *Numenius arquata* numbers increased at high tide in areas adjoining the construction site. In the controlled disturbance study (**chapter 6**), Oystercatcher were found to appear most tolerant of human disturbance, requiring the smallest set-back distances. The creation of the realignment site, including a secure roost, may also benefitted Oystercatcher and Teal (**chapter 3**). The raised bank of the Canal burn between Kennet Pans and the Realignment site provided a safe high tide roost; offering greater security through greater visibility of approaching predators. In **chapter 6**, the distance at which individuals became vigilant was positively affected by the distance at which the intruder began his approach. The openness of a landscape is well known to be an important factor for waterbirds safety, as high visibility can increase the distance at which threats are detected and allow more time for them to be evaluated. The creation of the realignment site also reduced pedestrian access to the west edge of Kennet Pans. Historically, large numbers of Curlew have used the fields behind the sea wall at Kennet Pans as supratidal foraging grounds (Ader & Bryant 2003). I argue that in these areas, out of sight of construction activity, Curlew would be relatively unaffected by construction disturbance.

The impact of disturbance on the numbers of birds a whole site can support, however, depends on the availability of alternative habitat. If other neighbouring sites are below their carrying capacity (i.e. they do have surplus food supplies for displaced birds), then the overall impact on fitness is likely to be reduced. It is not clear if the declines observed in Redshank and Cormorant were a direct consequence of the loss of birds from mudflats adjacent to construction work or a result of low juvenile recruitment into the population. Comparison of our through-the-tide counts (TTTCs) with the Inner Forth WeBS counts from that period (Holt *et al.* 2009), provides some evidence of how wider-scale changes may be driving the variation observed around the bridges. Redshank (Figure 7.1i), Curlew (Figure 7.1ii) and Teal (Figure 7.1iv) populations were stable throughout the study period, with little change between winters and no obvious divergence from that of our TTTCs. Based on this evidence, I argue that the decline of Redshank observed around the Clackmannanshire Bridge was mainly due to local factors, in particular the disturbance and changes in land management related to the building of a new road bridge. Oystercatcher (Figure 7.1iii) and Shelduck *Tadorna tadorna* (Figure 7.1v), however, increased and Cormorant (Figure 7.1vi) declined in both series of counts throughout the period of study. Although this consistency suggests external causes, such as those occurring at the

breeding or staging grounds, resulted in the changes observed next to the Clackmannanshire Bridge, the loss of an important roosting site due to local disturbance may have driven the decline in Cormorant numbers seen in WeBS counts.

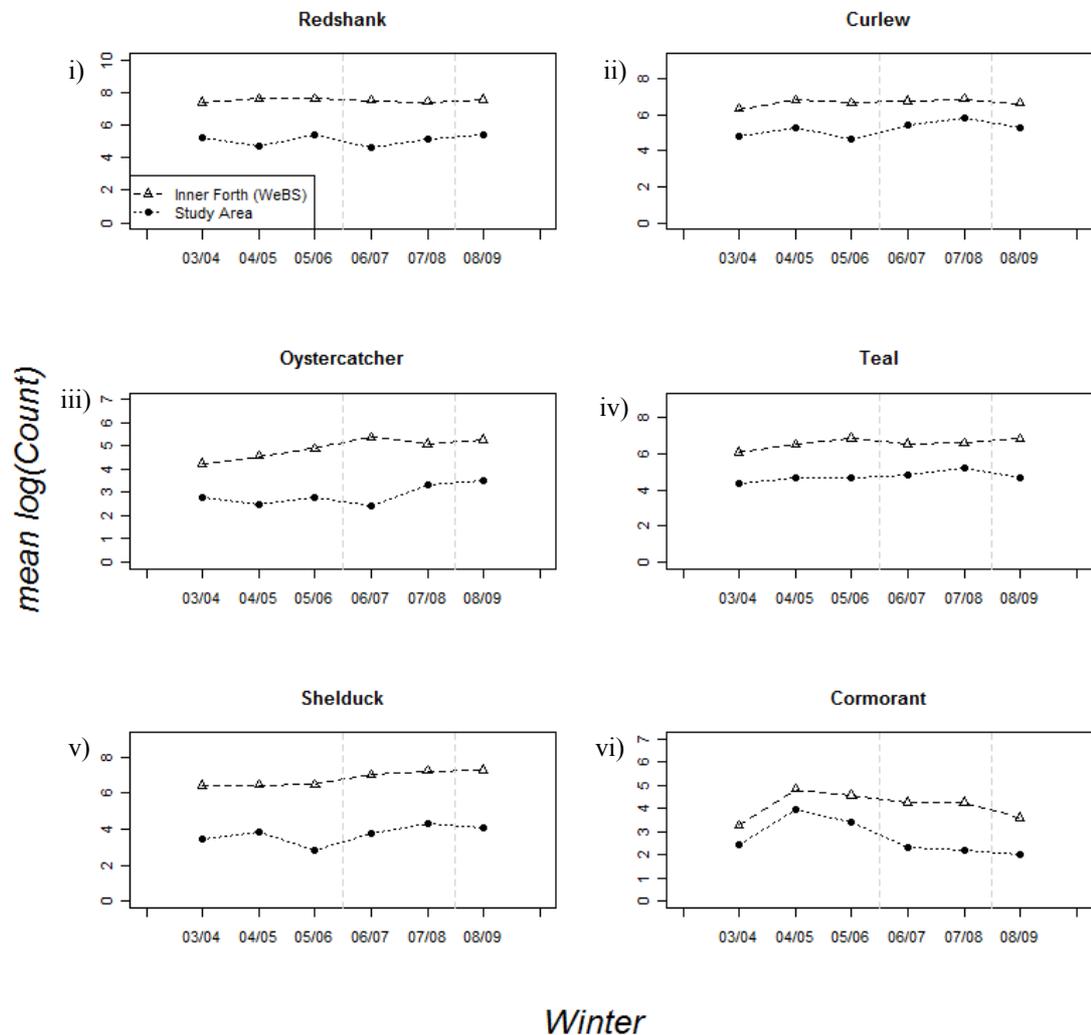


Figure 7.1: Annual indices for Redshank (i), Curlew (ii), Oystercatcher (iii), Teal (iv), Shelduck (v) and Cormorant (iv) in BTO Inner Forth WeBS counts vs. the TTTCs reported in **chapter 3**. WeBS counts conducted monthly at all wetland habitats on the Forth between Cambus ($56^{\circ}12'N$, $3^{\circ}82'W$) and Grangepans ($56^{\circ}01'N$, $3^{\circ}61'W$) and supplied by the BTO. Mean winter population data taken as geometric mean.

7.2. Behavioural studies

Much of the literature on human disturbance focuses on the effects on wildlife behaviour: animals will stop feeding temporarily or flee in response to disturbance stimuli, for example. The general theory behind this area of study is that fitness consequences are mediated by the behavioural decisions made by individual birds (Sutherland 1998a; 1998b). A number of issues

affecting our understanding of the effects of human disturbance on bird behaviour have been addressed in this thesis. In summary, I have shown that while industrial disturbance causes an increase in active (i.e. flying, running or swimming) and vigilance behaviour (**chapter 3**), birds may be able to compensate for disturbance by increasing supplementary foraging (**chapter 3**), altering feeding behaviour (**chapters 3, 5**), or by habituating to human activities (**chapter 6**).

Unless birds are able to compensate for lost foraging opportunities via decreased energy expenditure, one would expect the disturbance to have a negative effect on bird survival (Goss-Custard 1969; Belanger & Bedard 1990; Madsen 1995). To avoid this, Redshank and Shelduck on the Forth supplemented prey intake during construction by spending more time foraging during mid and low water (**chapter 3**). An increase in supratidal foraging was not observed in either species; it may be that energy requirements were not high enough to force birds into foraging over high water, where they may be subjected to an elevated predation risk, or an unprofitable level of prey availability. Shelduck were also able to adapt by spending more time feeding in the water than on land (**chapter 3**). Although Shelduck spent more time active and in the water in response to the increased perceived threat of construction disturbance, they were able to adopt an alternative feeding method (i.e. increased water-based foraging) in order to compensate for a negative energy balance. This may further explain why duck numbers increased moderately during the study in areas surrounding the bridges, especially at high tide, while those wader species, unable to take advantage of new or supratidal roosts, or find greater security on the water, declined.

In order to avoid disturbance, or to supplement prey intake, animals are known to forage by night (McNeil 1991; McNeil *et al.* 1992). Although Redshank were regularly found foraging by night (**chapter 5**), there was no evidence this was in response to human disturbance during the day (**chapter 4, 5**). Night foraging has been reported for several species of shorebirds during the winter in the tropics (Venezuela) without the influence of people (McNeil & Robert 1988, Robert & McNeil 1989, Robert *et al.* 1989). Clearly night foraging may offer other benefits to birds, such as increased prey activity (Dugan 1981) or avoidance of diurnal predators (Morrier & McNeil 1991). In this thesis, I presented evidence showing that foraging nocturnally may have presented a greater predation risk to Redshank than diurnal foraging, due to the reduced visibility of stalking predators (**chapter 4, 5**). Some positive effects of industrial development were also revealed; where Redshank were able to capitalise on the improved nocturnal visibility in areas around Grangemouth docks, allowing birds to extend diurnal or crepuscular behaviours into the nocturnal environment (Rich & Longcore 2006), while improving predator and prey detection.

As escaping from a disturbance event immediately could be costly; leading to superfluous, energetically wasteful, escape responses (Lima 1994; Lima 1995), animals are expected to

habituate to a non-lethal disturbance (Deniz *et al.* 2003). Predator density (i.e. humans) tends to be negatively associated with flight initiation distance (Stankowich & Blumstein 2005). This association has not only been found in birds (Fernandez-Juricic *et al.* 2001; Ikuta & Blumstein 2003), but also in mammals (Magle *et al.* 2005) and reptiles (Labra & Leonard 1999; Cooper *et al.* 2003). In **chapter 6**, all four waterbird species (in which habituation was investigated) allowed a closer human approach in heavily disturbed areas before becoming alert and moving away, than did individuals of the same species within the less disturbed areas. An increase in tolerance to humans would allow birds to ameliorate some negative impacts of disturbance by maximising foraging time and reducing energy expenditure. Species were shown to vary in their degree of habituation (**chapter 6**), and some have suggested that this ability to habituate is a key factor in determining if a species will be lost from areas frequented by humans (Rees *et al.* 2005; Sutherland 2007). However the reduction in flush distance could cause negative effects in wildlife populations, such as an increase in stress levels (Fowler 1999), and a reduction in the strength of the escape response to humans may increase the probability of being captured by a wild predator (Cooper & Frederick 2007; Rodriguez-Prieto *et al.* 2009).

This thesis presents evidence that construction disturbance also increased vigilance in both a wader and a wildfowl species (**chapter 3**). In areas with an elevated predation risk, such as close proximity to raptor-concealing cover, birds respond by increasing scanning and vigilance (Cresswell 1994; Cresswell & Quinn 2004). In a similar way, vigilance is known to increase and foraging rates decrease in response to an elevated human threat (Burger 1991; Goss-Custard *et al.* 2006; Yasue 2006). Increased background noise caused by construction may also compromise predator detection and vigilance may have increased to compensate for the masking of important auditory cues (Klump 1996). At one of the count sectors in **chapter 3**, the increased vigilance in response to workers and work vehicles, resulted in a 19% reduction in Redshank foraging time. Similarly, Quinn *et al.* (2006) found by exposing captive Chaffinches *Fringilla coelebs* to white noise, intake rate suffered due to a change in vigilance pattern. Unless birds were able to increase foraging efficiency at these sectors, they may be unable to acquire enough resources to maintain their energy reserves (Belanger & Bedard 1990; Burger 1997), which may reduce an individual's chances of surviving cold weather (Clark 2009).

The consequence of habitat loss/long-term disturbance is thought to vary between species due to their site faithfulness (Burton 2000). Shorebird species which move regularly between well-dispersed feeding areas, such as Sanderling *Calidris alba* or Knot *Calidris canutus*, may exhibit greater behavioural plasticity in response to the loss of any one site (Evans 1981; Myers 1984). More site-faithful species, such as Turnstone *Arenaria interpres* or Redshank, may be at greater risk (Metcalf & Furness 1985; McLusky *et al.* 1992; Burton 2000). For example, McLusky, Bryant and Elliot (1992), also in study on the Forth estuary, suggested that the effects of reclamation on a Redshank population were initially delayed, as birds remained faithful to

neighbouring (although formerly less favoured) areas. In **chapter 4**, radiotracking confirmed the high wintering site fidelity of Redshank in that area of the estuary, especially during late winter. This high degree of site fidelity, in combination with the large numbers of Redshank previously occupying the areas next to the construction site, may have made disturbance easier to detect in this species than a more vagile species such as Dunlin *Calidris alpina*, which are present at relatively low densities historically in areas adjacent to the construction site.

Burton and Armitage (2005) found that Redshank avoided sites by day but used the same sites at night when a busy heliport was inactive; this resulted in a smaller home range by day than by night. On the Forth, no evidence was found of radio-tagged birds avoiding sites due to human disturbance (**chapter 4**). However, both studies found that Redshank avoided riverine areas at night that were used frequently by day, probably in response to the increased threat from nocturnal predators (**chapter 4**; Burton & Armitage 2005). Wader densities during the day were generally greatest close to creeks and drainage channels, where birds may benefit from the higher invertebrate densities (Lourenço *et al.* 2005), more accessible prey (Kelsey & Hassall 1989), or shelter from strong winds (Ravenscroft & Beardall 2003). Creeks may also offer anti-predation benefits, offering shelter from hunting diurnal predators such as Sparrowhawks (Hilton *et al.* 1999). These riverine sites may become more dangerous by night to roosting and feeding birds, once nocturnal predators become active in these areas (**chapter 5**) and flock vigilance-benefits will be impaired due to the reduced visual abilities at night (Mouritsen 1992). This study, like many before, has shown that individuals behave differently by night than by day. Redshank show stronger site fidelity by night and the loss of important night-time roosts may put Redshank at greater risk from nocturnal predators. This stresses the importance of night monitoring to fully assess wintering behaviour and inform decisions on site protection and management.

7.3. Meeting energy requirements

During winter, birds may face particular difficulty in obtaining enough food (Goss-Custard *et al.* 1977); as a result many winter deaths are due to starvation, especially during severe weather episodes (Davidson & Evans 1982; Mitchell *et al.* 2000; Clark 2009). As others have reported before, I found that birds dedicate more time to feeding (**chapter 3**) and take greater risks (**chapters 3, 6**) when they are energetically stressed (McGowan *et al.* 2002; Yasue *et al.* 2003). Not only will extreme weather increase thermoregulatory demands, but it can also cause short-term behavioural responses in invertebrate prey (Zwarts & Wanink 1993). Individuals must therefore spend longer feeding and, as a result, have less time in which to compensate for disturbance. In **chapter 6**, I showed that when the temperature was lower, Redshank and Shelduck allowed a closer approach before flushing while Oystercatcher flew shorter distances. This effect was strongest for individuals occupying heavily disturbed areas which were possibly already compensating for lost feeding time and a negative energy balance (**chapter 6**). Our

findings provide yet more evidence in support of Gill *et al.* (2001), who hypothesised that those individuals that respond most to human disturbance were those least likely to suffer fitness consequences. This is the opposite from what is commonly assumed when behaviour is used as an index of disturbance effects, most notably in the use of flush distance in the design of wildlife buffer zones (Blumstein *et al.* 2003). If animals make state-dependent decisions about their responses to human presence, the use of behavioural responsiveness as a surrogate for fitness consequences of disturbance is potentially flawed, since the nature of the response may vary widely depending on an animal's unknown state and context. Only by quantifying the physiological state of the individual and the present energetic quality of the foraging patch can conclusions be drawn.

In **chapter 6**, this interaction between temperature and habituation was strongest for the anti-predator response of Redshank. Of all shorebird species wintering on British and European estuaries, Redshank suffer the heaviest mortality during severe weather (Pilcher *et al.* 1974; Davidson & Clark 1985; Mitchell *et al.* 2000). By selecting small prey, Redshank achieve a much lower rate of net energy intake than the larger shorebird species, thus requiring longer periods of feeding to meet their daily energy requirements. This means that they have less scope to increase their energy budget than those species feeding on larger prey items and hence severe weather is more likely to lead to a negative energy balance in this species.

For birds wintering in temperate intertidal habitats, food resources may change dramatically over the course of a season. In response to this decline, it is generally thought that birds are forced to dedicate more time to foraging and take greater risks later in the winter in order to meet energy requirements (Goss-Custard 1977; Zwarts *et al.* 1996). In **chapter 6**, Redshank, Oystercatcher and Shelduck were shown to fly shorter distances in response to an intruder later in the winter, while Redshank permitted a closer approach before it elicited a response. Similarly, the home range of Redshank contracted in late winter with individuals becoming more sedentary than early in the winter (**chapter 4**). If individuals were more stressed in late winter, they may be reluctant to expend extra energy, or lose foraging opportunities while travelling between patches (Bernstein *et al.* 1991; De Leeuw 1997). Such a contraction in home range size may limit the ability of Redshank to compensate for loss of habitat or long-term disturbance in late winter. If individuals are constrained to remain in a site, despite disturbance and regardless of fitness costs, an effect of the disturbance may be less detectable simply from the study of changes in bird densities.

Kincardine shore, an area of intertidal mud which was previously avoided by Redshank until later in the winter due to low prey and high predation risk (**chapter 2, 3**), was used earlier on during construction winters (**chapter 3**). These findings fit into the general framework that habitat choice amongst non-breeders is strongly dependent on the trade-off between starvation

and predation risk (Yasue *et al.* 2003). The combination of increased energy expenditure and increased competition on neighbouring mudflats may have forced Redshank to use the area at Kincardine shore earlier and in greater numbers than in winters where there was no bridge construction. In conclusion, because Redshanks do not accumulate substantial energy reserves and are always vulnerable to starvation (Mitchell *et al.* 2000), deterioration of abiotic conditions (e.g. weather and season) can readily force them to exploit less-preferred habitat (Cresswell 1994; Yasue *et al.* 2003), thus increasing their risk of predation (Minderman *et al.* 2006; Cresswell & Whitfield 2008).

7.4. Management options

Given the increasing exposure of wildlife to industrial disturbance, and the possibility of significant adverse effects on the conservation value of particular habitats for birds, the demand for research into the effects of disturbance on animal populations is increasing. During the course of this thesis, a number of management recommendations have been made; it would be useful to bring these together to build a fuller picture of the management options available. Firstly, I have demonstrated throughout this thesis that in order to gain a full understanding, the effects of disturbance must be considered throughout the wintering period. The susceptibility of birds to industrial disturbance may increase throughout the winter as food resources are gradually depleted (**chapter 2**), and in the case of Redshank, individuals become less vagile (**chapter 4**). Similarly, as severe weather increases metabolic demands and depressed prey availability, more consideration should be given to limiting heavy construction operations during prolonged cold spells when birds are most metabolically stressed (**chapters 3, 5, 6**), in the same way that hunting is already often banned and bird-ringing is halted in many places during severe weather (Goss-Custard *et al.* 2006; Stroud *et al.* 2006).

In order to develop conservation strategies for coastal wetland landscapes, attempts should be made to follow habitat-use throughout the tidal cycle (**chapter 3**), and nocturnally as well as diurnally (**chapters 4, 5**). Current population surveys of waterbirds, such as BTO high tide (WeBS) counts combine waterbird counts within sections of large estuaries to provide total bird counts. These are often used to detect changes that occur at a whole estuary scale; however these methods have limitations when used to detect an impact on a finer scale. Although counting at high tide allows for efficient counting, birds cannot be linked with feeding grounds because individuals often move great distances at high tide to roost elsewhere. Low Tide Counts (LTCs) have the advantage that they monitor the full extent of the intertidal habitat; however like WeBS counts they are not fully representative of bird usage and may miss important stages of the tide. For example, north Skinflats and upriver sites often lose birds at low tide to neighbouring mudflats (Newton & Bryant 1991) and some species feed most actively during the intermediate tidal stages (Ader & Bryant 2003). Through-the-tide counts (TTTCs; **chapter 3**), invariably conducted during daylight, are often recommended to wildlife managers of estuaries,

as they give a more accurate and ‘complete’ picture of feeding usage of diurnal site use. I have shown, however, that individuals may behave differently at night and certain habitats are avoided by night, which are commonly used by day. Here I present a map of important roosting sites on the Forth estuary for Redshank, illustrating high tide roosts (>5m) commonly used by day yet avoided by night (Figure 7.2). The created island on the Realignment site was often used by radio-tagged birds, but only at night; presumably in response to the threat from foxes and tawny owls which were observed hunting beside Canal Burn during mist netting attempts at Kennet Pans. As the predator landscape changes from day into night, birds adopt different strategies to minimise the risk from nocturnal predators. It is clearly important, therefore, that information on nocturnal distributions is available to inform decisions on site management.

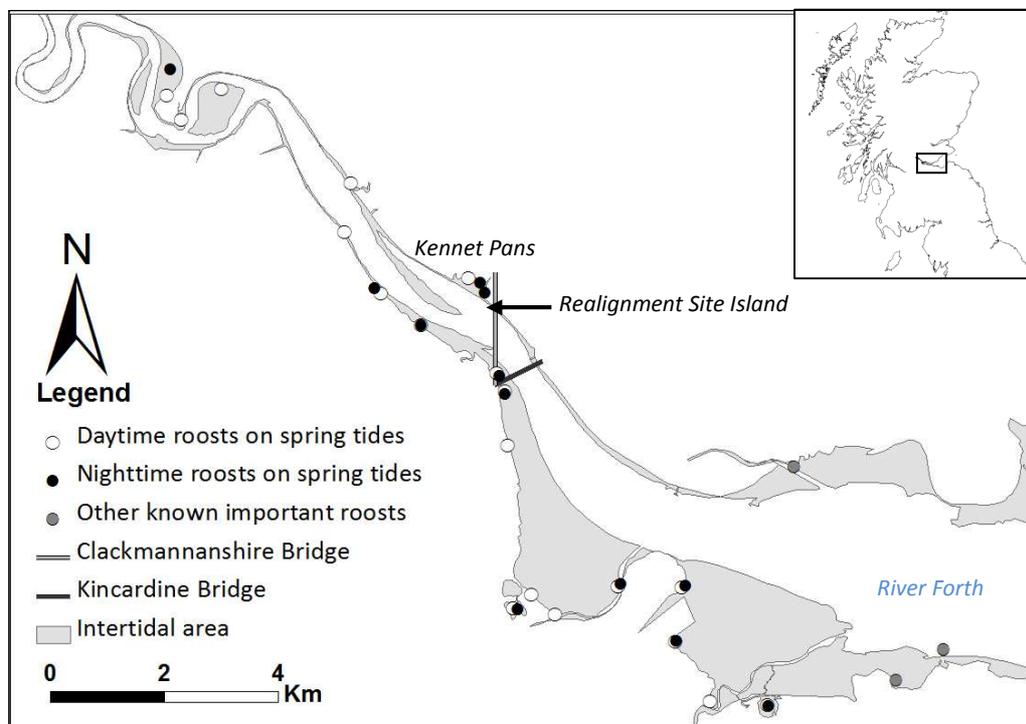


Figure 7.2: Diurnal and nocturnal spring tide (>5m) roosts used by radio-tagged Redshank. Figure also includes other daytime roosts identified in WeBS surveys (D. M. Bryant pers comm).

I have shown that contrary to previous understanding, artificial light may offer some benefits to shorebirds; acting as a ‘perpetual full moon’ to assist birds in foraging and predator detection. However, although this study described the benefits for Redshank, there may be further impacts on a community level: such as increased predation pressure by shorebirds on intertidal invertebrates in lit areas, increased competition with traditionally-nocturnal foragers, and reduced hunting efficiency handicapping Redshank predators. During the planning phase of the Clackmannanshire Bridge, efforts were made to create a bridge without up-shining street lights

to minimise this effect of light disturbance in the direct vicinity of the bridge, particularly relating to possible disorientation of geese in overcast or foggy conditions. While there is some value in this light-minimisation approach, I recommend further research at a community level to assess the wider impacts of anthropogenic light on animal and plant communities.

Prior to the development of the Clackmannanshire Bridge, the Environmental Impact Assessment (EIA) identified waterbirds were at risk of being disturbed during construction when using a 320m ‘fly-up’ or buffer zone around the construction site (Ader & Bryant 2003). This buffer was chosen over a shorter alternative due to the likely exaggerated effects of disturbance because of the elevated position of the bridge, the involvement of more than one concurrent cause (i.e. sound and movements) and the accommodation of the most ‘sensitive’ species (Davidson & Rothwell 1993; Ader & Bryant 2003). Using the data collected in **chapter 6**, the validity of this buffer zone was tested. Following methods based on Rodgers and Smith (1995; 1997) and Rodgers and Schwikert (2002), recommended set-back (*RS*) distances for individual species were created. Because controlled disturbances were repeated measures from the same intertidal mudflats, *FID* and *AD* were averaged across site (*df* = 4) before applying the appropriate formula:

$$RS = (\overline{FID} + Z_{0.95} \overline{\delta}) + \overline{AD} \quad (1)$$

where \overline{FID} and $\overline{\delta}$ are the sample mean and standard deviation for the observed values of *FID*, $Z_{0.95}$ is the 0.95 quartile of the standard normal variable (i.e. $Z_{0.95} = 1.6495$) and \overline{AD} is the mean distance that birds became alert prior to flushing.

Table 7.1: Mean flight initiation distances (*FID*) and recommended set-back distances (*RS*) between wintering waterbirds and an intruder walking directly towards the flock, for waterbirds on the Forth estuary ($n \geq 4$). Set-back distances are based on mean sector *FID* and *AD* values and rounded to the nearest 10m interval.

Species	<i>FID</i> (meters)	<i>RS</i> (meters)
<i>Shelduck</i>	180	380
<i>Wigeon</i>	150	450
<i>Teal</i>	200	420
<i>Mallard</i>	160	410
<i>Oystercatcher</i>	140	350
<i>Lapwing</i>	240	650
<i>Dunlin</i>	160	400
<i>Curlew</i>	240	520
<i>Redshank</i>	150	400

Although the flush distances (*FID*) of all nine waterbird species fell well within the 320m zone recommended by the EIA, the recommended set-back distances (*RS*) calculated using Eq. 1 were far more conservative (Table 7.1). Although Rodgers and Smith recommend a minimum of twenty flushes in order to calculate *RS*, Shelduck (n=22), Oystercatcher (n=22), Curlew (n=36) and Redshank (n=43) all required a larger buffer than the 320m recommended in the EIA. Rodgers and Schwikert (2002) and Fernández-Juricic *et al.* (2005) considered this method to provide a sufficiently conservative strategy to minimise escape responses by birds and a reasonable margin for the estimation of buffer zones for avian fauna in both wetland and grassland habitats. Although buffers based on only *FID* do not control for the effects of detection distances, I argue that in the case of the Forth, the values generated by Equation. 1 were too conservative due to the large distances at which birds were able to visually detect the disturbance stimuli on an open estuary (**chapter 6**). Viewing areas delimited by fences have previously been shown to reduce disturbance on waterbirds (e.g. Ikuta & Blumstein 2003), consequently fencing was used as a mitigation measure during the construction of the bridge to limit the visual disturbance on bird habitat (Ader & Bryant 2003). Based on this evidence, the combination of fencing and a 320m buffer around the construction site appears justified as a measure to mitigate the negative effects of construction disturbance on wintering waterbirds.

Considerable variability was found in the critical distances (i.e. the distance at which birds flushed) at which humans may cause disturbance (**chapter 6**). Behavioural decisions were shown to vary widely within a species depending on individual state, metabolic demands and previous exposure to human disturbance. Based on these findings, I argue that a reserve manager relying entirely on daytime flush distances (in order to determine which birds are at greater risk) is likely to make inappropriate decisions. Current practice involves measuring flush distances at various sites and determining in which area responses are greatest; those sites where responsiveness is high are the most sensitive areas requiring greatest protection (Madsen 1998; Evans & Day 2001). In contrast, a low level of responsiveness may be due to birds being metabolically stressed, which are actually the most vulnerable group requiring greatest protection (Gill *et al.* 2001; Beale & Monaghan 2004). Habituation to humans may sometimes permit site managers to be less conservative in the creation of these buffer areas to allow for likely habituation effects. Alternatively, if buffer areas are created using flush distances from habituated birds, there may still be deleterious effects on local, non-habituated, wildlife populations (Keller 1989).

Most buffer zones currently assume that tolerance indicators are a species-specific trait, which do not change in time or under various environmental conditions (Blumstein *et al.* 2003). I argue that animals are individuals that make context-dependent decisions, rather than being an average or 'ideal bird' which can be applied across any management scenario for species in concern. As tolerance depends greatly on foraging conditions, prior experience and metabolic

demands, I recommend that wildlife managers should move away from traditional interpretations of using a singular species-specific behavioural response distance and recognise, and seek to allow for, the seasonal and spatial variations in sensitivity to human disturbance.

7.5. Limitations of this study

My aim in this thesis was to understand the effects of industrial disturbance at both an individual and population level in non-breeding waterbirds. I made a number of assumptions which may be evaluated by further study. For example, in earlier chapters, night foraging was seen as being more dangerous due to the avoidance of particular sites thought to be occupied by nocturnal predators of Redshank. In order to justify this reasoning, this needs to be tested empirically by monitoring the movements of nocturnal predators in relation to these riverine areas and by observing attacks on shorebirds (Mouritsen 1992; Quinn & Cresswell 2004). Radiotelemetry and camera traps have been used successfully in the past to collect information on secretive nocturnal carnivores (Kucera & Barrett 1993; Redpath 1995; Lucherini *et al.* 2009). I also recommend that in future studies, image intensifiers should be used in combination with moonlight, artificial lighting, background lux (using a portable photodiode), or artificial night sky brightness maps (**chapter 5**) to investigate nocturnal vigilance, foraging behaviour and foraging efficiency in relation to ambient light levels. By documenting the presence, abundance and activity patterns of nocturnal as well as diurnal predators, a more complete assessment of habitat quality can be made by wildlife managers.

Redshank was chosen as the species best suited to investigate the effects of engineering disturbance on foraging behaviour and habitat use (**chapters 4, 5**). This choice was based on their relatively high densities on the Forth, their apparent ease of capture, their high degree of site fidelity and their sensitivity to environmental change. Population, behaviour and experimental studies throughout this thesis exposed Redshank as indeed being highly sensitive to the effects of disturbance, and therefore an excellent candidate for telemetry studies of movements and behaviour. Due to logistical problems, however, the number of transmitters dispatched in the first winter (2007/08) was inadequate to use telemetry to document the effects of bridge construction on habitat-use. Burton and Armitage (2005) found that Redshank avoided an intertidal foraging habitat by day, but used these sites at night when a busy heliport was inactive. After the impoundment of the Cardiff Bay, displaced birds later moved to this site and remained there regardless of the daytime disturbance (Burton & Armitage 2008). Future research should attempt to assess how engineering disturbance affects habitat use using marked individuals before, during and after construction. Care should be taken when assessing such changes in habitat use: an increase in the nocturnal use of mudflats around the bridge during construction may not be wholly due to disturbance avoidance, but instead the improved nocturnal visibility presented by temporary on-site floodlights (**chapter 5**).

Each telemetry chapter in this thesis focuses specifically on the habitat use of juvenile Redshank, as only a single adult bird was captured and fitted with a transmitter. For the purpose of our study, this worked to our advantage as the larger sample made it possible to include all birds confidently when comparing habitat-use and foraging behaviour without this being confounded by age effects (Goss-Custard & Durell 1983). However there are enough differences in the ecology of adults and juvenile birds to warrant more investigation. Attachment to foraging sites tends to develop from autumn into winter in an individual's first year (Metcalf & Furness 1985; Myers *et al.* 1988; Baccetti *et al.* 1995; Rehfish *et al.* 2003). As a result, juvenile Redshank are initially more likely to move between areas than adults (Rehfish *et al.* 1996; Rehfish *et al.* 2003; Burton & Armitage 2008). This was clearly shown in **chapter 4** where Redshank held a larger home range during early winter compared to later winter. Essentially, juveniles might be expected to relocate to new sites in response to long-term disturbance more readily than adult birds. As a result, the average home range may not only have been overestimated in Redshank in this study, but adult birds, which were arguably most susceptible to the negative effects of disturbance, were overlooked. The high site fidelity of adult birds may delay the initial response to disturbance and those birds which remain may suffer greater fitness consequences than juveniles which show greater plasticity in their habitat use.

Juveniles are known to be excluded frequently from favoured areas by more experienced adults (Monaghan 1980; Goss-Custard *et al.* 1982; Cresswell 1993; Sol *et al.* 2000). For example, Cresswell (1994) found that adult Redshank excluded juveniles from low risk habitat at the Tynninghame estuary, forcing them to feed in areas where they were almost five-times more likely to be killed by Sparrowhawks. As discussed previously, use of high risk/low productivity sites by Redshank increased significantly during bridge construction (**chapter 3**). During this study, no attempt was made to understand if these 'risky' sites were used primarily by juveniles, or if the increase in use later in the winter was due to an influx of adult birds abandoning their territories once these neighbouring sites became depleted. Future work should investigate the impact of disturbance on the intraspecific composition of a site and examine how construction disturbance affects habitat use by adult and juvenile birds. For example, using a larger sample of radio-tagged adult and first-year birds may reveal if this Kincardine shore site was used more by adult birds by day and juveniles by night. Image intensifiers may further be used to examine if an influx of adult birds at night resulted in an increase in agonistic interactions between conspecifics (Kuwaie 2007; Santos *et al.* 2008).

In order to investigate the effects of habituation and depletion on trade-off decisions (**chapter 6**), our study assumed that the individuals exposed to a controlled disturbance generally remained at that site for the duration of the study. Observations of colour ringed and radio-tagged individuals suggest that some species (e.g. Redshank and Oystercatcher) on the Forth

exhibit site fidelity both between and within winters (Symonds *et al.* 1984). By monitoring individual birds equipped with radio transmitters, the effect of repeated exposure on habituation rates could be investigated. Similarly, the use of transmitters fitted with posture sensors would permit investigation into trade-off decisions at night compared to at day, under moonlight and in areas of artificial light disturbance. Transmitters would allow the location and relocation of individuals before and after flushing, while posture sensors would permit detection of the moment the individual became disturbed by our presence. Future study should seek to address the effect of visibility on trade-off decisions, whilst controlling for alert distance, group size, predator pressure and other factors thought to affect responsiveness.

Fundamental in almost all disturbance-based research, is the underlying assumption that non-lethal disturbance stimuli by humans are analogous to predation risk (Frid & Dill 2002). Responses both to predation risk (Lima & Dill 1990) and to disturbance stimuli (Gutzwiller *et al.* 1994; Beale & Monaghan 2004) divert time away from other fitness enhancing activities such as feeding, mating displays or parental investment. One may argue that predation risk and disturbance stimuli are not analogous as humans do not pose a direct mortality risk and animals may habituate towards a threatening stimulus in order to optimise fitness, provided it is non-lethal (Deniz *et al.* 2003). However waterbirds are very vulnerable to hunting and in much of Europe shorebirds and wildfowl are shot as legitimate quarry species (McCullough *et al.* 1992; Barbosa 2001; Jensen *et al.* 2009); the approach on foot by humans may be therefore be indistinguishable from the animal's perspective (Frid & Dill 2002). It is possible that human disturbance is merely replacing disturbance by absent predators, such as White-tailed Eagles *Haliaeetus albicilla*, whereby birds compromise their rate of resource acquisition accordingly to reduce the probability of death (Ydenberg & Dill 1986; Lima 1998). Future studies may adopt a programme of controlled natural predator disturbances (e.g. a trained falcon) compared to that of an approaching human and a remote-controlled vehicle (e.g. Rodriguez-Prieto *et al.* 2009) to allow comparisons in risk perception to be made.

In this discussion, I have argued that disturbance has a variety of effects on birds which can have important implications on population size. However, although I have shown disturbance may affect animal behaviour, no direct effect of construction disturbance on population size was detected. In migratory animals (particularly birds) the impacts of disturbance can be difficult to identify because they may only become manifest thousands of kilometres away in the breeding areas (Monaghan 1980; Goss-Custard *et al.* 1982; Summers *et al.* 1990; Cresswell 1993). Testing the impact of a disturbance on wild populations can therefore be a major challenge even in simple ecological systems, requiring long-term ringing/ tagging studies to estimate return rates in wild bird populations (Stillman *et al.* 2007). Future studies should incorporate individual-based modelling to predict the long-term and large-scale consequences of anthropogenic disturbance. By tracking the locations of animals and their behavioural decisions,

such as prey-choice, the distance from which a bird is excluded from the disturbance source, the time taken to return after a disturbance has ceased, and the amount of time spent flying, individual-based models are able to predict over-winter mortality (Durell *et al.* 2005; Stillman *et al.* 2007). Such models have recently been applied to investigate the impact of offshore wind farm development (Kaiser *et al.* 2005), and the benefit of proposed mitigation measures (Durell *et al.* 2005) to predict the impact of construction disturbance on waterbird populations. However, this approach is still largely inaccessible to wildlife managers; therefore greater effort should be made in constructing an evaluation protocol whereby wildlife managers may test with confidence the impact of proposed development schemes without requiring a strong theoretical, modelling or statistical background.

7.6. Synopsis

Disturbance from engineering works is an increasing problem, not just on UK coastlines, but for terrestrial and marine ecosystems throughout the world. The results presented in the preceding chapters, together with earlier work, shows that assessments of human disturbance are usefully grounded within predation-risk theory. As with the response to a predation risk, disturbance will cause animals to divert large proportions of time and energy away from resource acquisition. Equally, if this threat is long term, it may also cause habitat shifts at the cost of reduced access to resources. Despite the fact that disturbance impacted negatively on animal distribution and behaviour, individuals appear capable of adjusting their behaviour in order to reduce risk and mitigate some of the impact of disturbance. When resources are abundant and conditions are benign, all of the costs of disturbance could be offset by appropriate behavioural responses. Consideration of life histories and energetic constraints on trade-off decisions can help managers predict how animals will respond, and efforts can be made to limit the impact on wildlife particularly during metabolically stressful or demanding periods. In order to understand how developments are impacting on wildlife areas, research is required on a community level and on the wider environment to predict the consequences of environmental change. Gill (2005) argued that the biggest single problem for the integration of ecology into the planning and decision process for offshore renewable energy developments is a lack of appropriate knowledge. I argue that some of this knowledge is already present under the guise of predation-risk theory. An understanding of population and behavioural processes will allow managers to predict how wildlife will respond to future developments and if necessary mitigate against any potential ecological problems during the construction and operational phases.

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