ASSESSING THE IMPACTS OF HUMAN DISTURBANCE ON WILDLIFE: INSIGHTS FROM WILDFOWL ON THE EXE ESTUARY

By Lindsay Katherine Biermann

A thesis submitted in partial fulfilment of the requirements of
Bournemouth University for the degree of Doctor of Philosophy

May 2020

Bournemouth University
in collaboration with
British Association for Shooting and Conservation

COPYRIGHT STATEMENT

DECLARATION

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

Chapter 3 and **Chapter 5** equation derivations (Appendix 1; Appendix 2) were generated by Richard Stillman (Bournemouth University)

In **Chapter 4** archived data sets on wildfowling on Crown Foreshore on the Exe Estuary were provided by the British Association for Shooting and Conservation (BASC) with the permission of the Devon Wildfowling Club. Matt Ellis, Heather Warrender, Shane Robinson, and James Green, along with the Devon Wildfowling Club helped organize and facilitate wildfowling data collection.

Lindsay K. Biermann

ACKNOWLEDGEMENTS

This work could not have been completed without the help of my primary advisors Richard Stillman, Amanda Korstjens, and Kathy Hodder. Their patience in meeting with me weekly and continuous reassurance was an integral part to the completion of this thesis. Furthermore, their commitment to reading the endless supply of drafts to this thesis was a feat that deserves an award. A further thanks goes out to my external advisors: John Goss-Custard, Matt Ellis, and Richard Caldow, who were able to bring new perspectives and support to what often felt like an overwhelming amount of work. I also owe a thank you to my viva examiners Roger Herbert and Jennifer Gill for their constructive input that added to the finishing touches of this Thesis.

In addition to the work of my advisors, I owe a large thank you to BASC, not only for their funding support, but also for their help in organising fieldwork, as well as, providing opportunities for me to share my work with wildfowling members across the country. A particular thank you goes to the Devon Wildfowling Club members, and their representative Scott Harding who organized all of the winter wildfowling trips that I was graciously allowed to tag along for. Additional BASC staff I wish to thank are: Matt Ellis, Heather Warrender, James Green, and Shane Robinson, who personally accompanied me on wildfowling trips in both the early hours of the morning and late hours of the evening, no matter the weather.

Lastly, I owe large thank you to my friends and family who helped me maintain my work life balance throughout this entire process. To the Davis Family, thank you for opening your home to me and providing me with much needed support in a stressful time. George, your understanding and unyielding patience with me during this journey has been something I could not have managed without. To Mom and Dad, I would never have made it this far if it had not been for your unceasing support and encouragement.

ABSTRACT

Assessing the impacts of human disturbance on wildlife: Insights from wildfowl on the Exe Estuary

Lindsay Biermann

In the subject area of conservation and ecology, human disturbance is classified as any anthropogenic activity that elicits a response in an animal that would otherwise not occur under non-human related conditions. When this change in behaviour negatively impacts an animal's energy budget it has the potential to reduce reproductive output and survival, and so ultimately, human disturbance may affect animal populations. Therefore, understanding mechanisms that lead to human disturbance and its energetic cost are vital in understanding if human disturbance may affect animal populations in the present and the future. To investigate these topics, this study looked at different aspects of human disturbance relative to two species of wildfowl, Brent goose (*Branta bernicla,* L.) and wigeon (*Mareca penelope,* L.), on the Exe Estuary, during the winters of 2017-2018 and 2018-2019. This included: identifying environmental variables that lead to overlaps in space and time between wildfowl and humans, assessing the disturbance cost within those overlaps, differentiating costs of disturbance relative to human disturbance types, understanding the compensation ability of wildfowl to deal with human disturbance, and identifying the thresholds of human disturbance wildfowl are capable of experiencing without negative impacts. Primary findings indicated that conditions associated with overlaps between wildfowl and humans were predominantly associated with food availability for wildfowl and site accessibility conditions for humans. Within these overlaps, wildfowl were found to be disturbed for a minority of the time, with Brent goose being disturbed approximately 6% of the time, and wigeon being disturbed approximately 5% of the time. Costs associated with these disturbances were found to increase if wildfowl were feeding when disturbed compared to resting. Additionally, overlaps and disturbances from different human activity types were found to vary, indicating that some human activity types may be more threatening, in terms of disturbance than others. An investigation of the literature identified that animals use their 'spare-rest' time to compensate for the time and energy costs associated with human disturbance. This finding, along with a calculation of energetic costs relative to energetic needs of wildfowl on the Exe Estuary, identified that time and energy costs due to human disturbance, at the time of this study, were well below any thresholds for compensation. Projections of human disturbance using an individual-based model (IBM) validated that Brent goose

would need to be disturbed at least 7 times per hour and wigeon would need to be disturbed at minimum of 12 times per hour before they would be unable to compensate. These results indicate that Brent goose and wigeon populations on the Exe Estuary are currently under no immediate threat from human disturbance. Furthermore, this study has identified more widely applicable variables that lead to human disturbance in general, and mechanisms for determining if and when it is causing a problem for wildlife populations. Understanding and predicting these types of impacts will then help preserve animal populations and biodiversity richness throughout a wide variety of ecosystems.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

LIST OF ABBREVIATIONS AND ACRONYMS

ABM	Agent-based model
AEWA	Agreement on the Conservation of African-Eurasian Migratory Waterbirds
AIC	Akaike Information Criterion
BASC	British Association for Shooting and Conservation
BG	Brent goose
BMR	Basal Metabolic Rate
BOP	Birds Overlapping with People
BTO	British Trust for Ornithology
COD	Cost of Disturbance
DEE	Daily Energy Expenditure
DME	Daily Metabolized Energy Intake
FID	Flight Initiation Distance
FS	Focal Scan
IBM	Individual-based model
ISS	Interval Scan Sample
JNCC	Joint Nature Conservation Committee
LCT	Lower Critical Temperature
LNR	Local Nature Reserve
NNR	National Nature Reserves
SAC	Special Area of Conservation
SPA	Special Protection Area
SSSI	Site of Special Scientific Interest
UN	United Nations
W	Wigeon
WeBS	Wetland Bird Survey

1. CHAPTER 1: INTRODUCTION

1.1. WHAT IS HUMAN DISTURBANCE AND WHY IS IT IMPORTANT?

The influence of humans on wildlife has long been a topic of interest. One of the first documented works alluding to the effect of humans on nature dates back to 1864, in a book titled “Man and Nature” by George Marsh. In the book, Marsh discusses the consequences of humans not being aware of their influence on the environment, and the adverse effects it can have. Since Marsh's revelations in 1864, there have been many papers published detailing the impact of human presence on wildlife.

According to Goudie (2013), the research surrounding these documented effects of human presence on wildlife fits into five main categories: domestication, dispersal and invasion, extinction, expansion, and contraction (Goudie 2013). Each of these categories is unique in its method of influence on wildlife. However, a common thread between them is that they have the potential to alter biodiversity and the natural ecosystem (Marzluff & Rodewald 2008; McKinney 2008). These changes can sometimes be beneficial; for example, the introduction of alien species by humans can increase biodiversity through the production of novel habitat (Schlaepfer 2011). In another case, a non-native species of plant, *Casuarina stricta, A.*, in Japan, provides greater protection for native snails from rats than the native vegetation (Chiba 2010). Furthermore, human presence may actually benefit populations under some circumstances by increasing public awareness and appreciation for wildlife (Krüger 2005). This appreciation can then lead to reduced habitat destruction and increased protection which in the right circumstances can help to prevent population declines. However, in many cases, human manipulation harms natural biodiversity, through habitat destruction, land-use changes, overharvesting of species, and pollution (Sala et al. 2000).

Biodiversity in ecosystems has been shown to increase the productivity of an area and ultimately enrich the value of a region to humans (Díaz et al. 2006; Duffy 2009; Cardinale et al. 2012), which means that preserving biodiversity is directly beneficial to humans. Therefore, being able to identify specific aspects of human presence that connect to biodiversity loss is fundamental for maintaining an ecosystem that is favourable to humans.

Human disturbance is one part of human presence implicated in biodiversity loss. Human disturbance, in this context, is classified as any human-related activity that elicits a response in an animal that would otherwise not occur under non-human related conditions. Within the five categories provided by Goudie (2013), human disturbance would best fall into expansion and contraction of animal ranges. For example, a study on wild boars (*Sus scrofa,* L.) showed evidence of boars changing their activity levels and area use with human activities (Ohashi et al. 2013). Human activity correlated with a reduction in boar activity and area use (Ohashi et al. 2013). However, not all human disturbance results in expansion and contraction of the range of an animal species. For example, human disturbance and road proximity correlate with reduced Amur tiger (*Panthera tigris altaica,* T.) food consumption (Kerley et al. 2002). Reduced food consumption could indirectly result in contraction by forcing animals out of disturbed regions due to lack of food. For example, bottlenose dolphins avoid foraging areas when there is high boat traffic (Allen & Read 2000). However, if food sources are inadequate in other areas, the result could also be habituation, which may be a form of domestication. Burger & Gochfeld (1999) recorded that Layson albatross (*Diomedea immutabilis*, R.), reduce their reactions to disturbance with increasing levels of exposure to humans. Another possibility is that the lack of food availability could reduce reproduction and cause death, which could lead to extinction. Several studies report reduced reproductive success in Adelie penguins (*Pygoscelis adeliae*,H. & J.) with human and helicopter presence (Giese 1996; Culik et al. 1990). Therefore, human disturbance ultimately has the potential to influence wildlife in many ways.

1.2. TRANSLATING HUMAN DISTURBANCE EFFECTS TO POPULATION LEVEL IMPACTS

Because human disturbance has the potential to affect animals in a variety of ways, understanding how it can translate into population-level impacts is complicated (Boyle & Samson 1985; Cole 1991; Knight & Cole 1995; Gill et al. 1996; West et al. 2002; Liley & Sutherland 2007; Pirotta et al. 2018). Human disturbance can cause direct mortalities, diet changes, physiological changes, behavioural changes, changes in reproductive output, and changes in distribution (Table 1.1). However, these changes on their own don't necessarily translate to population-level impacts. Human disturbance events must first result in either direct mortalities or a reduced ability to meet energetic demands (Figure 1.1; Frid & Dill 2002; Pirotta et al. 2018). After this, disturbance-related mortality must be additive to natural population mortality or additive to decreasing population fecundity, in order to cause changes local population levels (Figure 1.1; Knight & Cole 1995; Pirotta et al. 2018). However, natural population mortality can fluctuate greatly from year to year and site to site and is greatly influenced by seasonality (Sedinger & Alisauskas 2014). Therefore, determining whether mortality associated with disturbance-related events is either additive or within natural boundaries is difficult to determine.

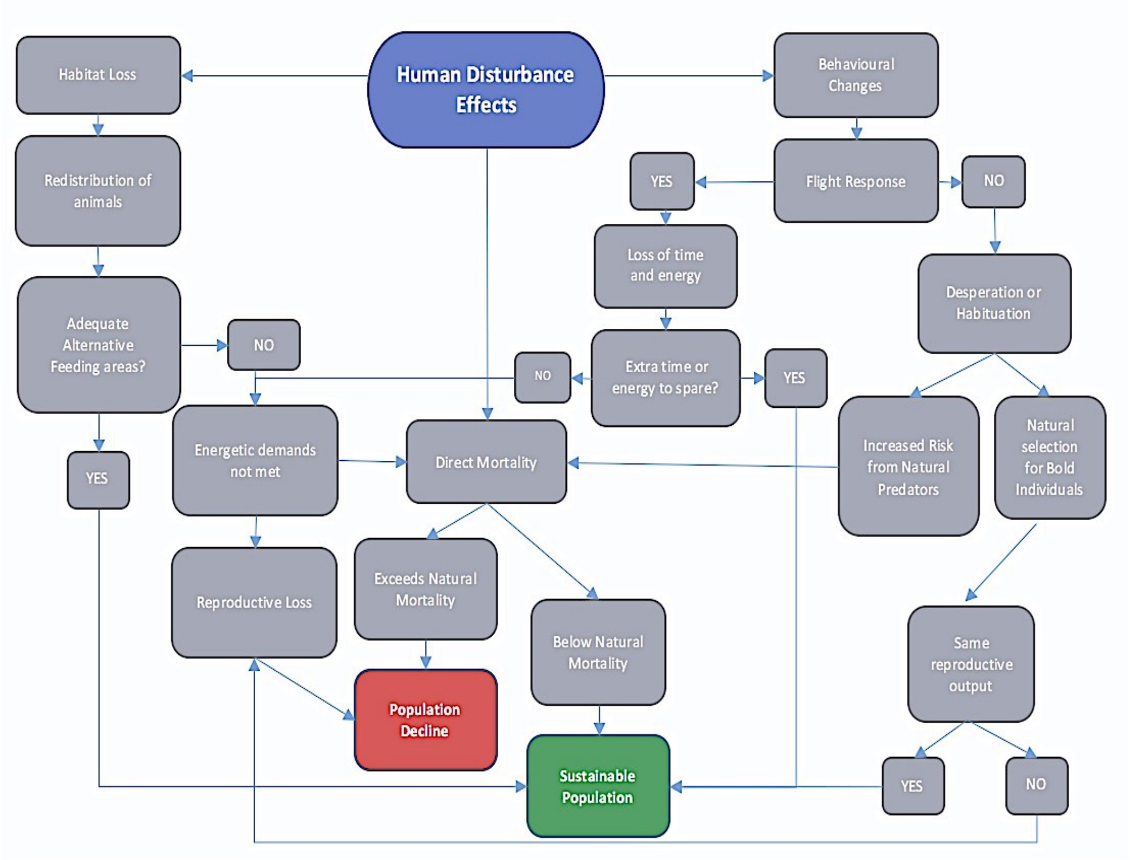


Figure 1.1 Conceptual diagrams of how human disturbance events may or may not lead to local population-level changes.

Direct mortality is the most obvious source of population level effect from human disturbance. In a study by O'Shea (1995), population declines in manatees correlated with boater recreation (*Sirenia*, I.) due to manatee deaths caused by boat collisions. Other studies indicate that direct mortalities due to road collisions also play a role in population declines of amphibians (Hels & Buchwald 2001).

Energetic demands can result in population declines in many different ways. For example, a study by Stalmaster & Gessaman (1984) showed reduced survival and reproduction in bald eagles (*Haliaeetus leucocephalus*, L.) due to increased energetic demands caused by increased flight associated with human disturbance. An energy deficit occurs when an animal's behaviours or movements associated with response to a disturbance increase to such a degree that the animal is incapable of compensating. Chronic exposure to disturbance of this level can result in reduced reproductive output or death which can cause population-level declines (Schulz and Stock 1993, Gill et al. 1996, Frid and Dill 2002, Gill 2007).

Table 1.1 Example of the methods used to measure human disturbance in the literature.

Method of Measure	**Disturbance Species**	**Disturbance Source**	**Results**	**Sources**
Food Consumption	Pink footed geese (*Anser brachyrhynchus*, B.)	Farming, birdwatchers, aircraft, hunting, cyclist, horse-riding, birds	The proportion of food consumed decreased with increasing disturbance	Gill et al. 1996
	Caribbean reef sharks (*Carcharhinus perezi*, P.)	Feeding/baiting	Shifts in food sources; change in nitrogen content	Maljković & Côté 2011
	Odontocetes, F.	Human activity	Reduced foraging	Christiansen et al. 2013
Physiology	Adelie Penguin (Pygoscelis adeliae)	Human approach	Increased heart rates	Culik et al. 1990
	Gentoo Penguin (*Pygoscelis papua*, F.)	Human approach	Increased heart rates	Nimon et al. 1996
	Odontocetes	Marine vessel traffic	Change in respiration rate	Kastelein et al. 2006
Behaviour	Adelie Penguin (Pygoscelis adeliae)	Human approach	Increased foraging trips, increased comfort behaviours,	Wilson et al. 1989; Fraser & Patterson 1997

Method of Measure	**Disturbance Species**	**Disturbance Source**	**Results**	**Sources**
			reduced responsiveness to a disturbance with regular exposure	
	Layson Albatross (Diomedea immutabilis)	Human approach	Reduced responsiveness to a disturbance with regular exposure	Burger and Gochfeld 1999
	Mixed colonies of wading birds	Human approach	Flushing distance of 30-50m	Erwin 1989
	Ungulates	Human activities	Increased group sizes; increased response to humans on foot; hunted species responded greater than non-hunted species; reduced wariness in higher traffic regions	Stankowich 2008
	King penguins (Aptenodytes patagonicus, M.)	Helicopter flights	Short term behaviour changes	Hughes et al. 2008
	Southern stingray (*Dasyatis americana,* R.)	Feeding/baiting	Increased risk of injury	Semeniuk & Rothley 2008
Reproductive success	Adelie Penguin (Pygoscelis adeliae)	Human approach,	Lower reproductive, Increased	Giese 1996; Culik et al. 1990

Method of Measure	**Disturbance Species**	**Disturbance Source**	**Results**	**Sources**
		helicopters and aeroplanes	desertion of nests	
	Wedge-tailed Shearwater (*Puffinus pacificus*, L.)	Human development	No differences in burrow density	Hill & Barnes 1989
	Norther Fulmar (*Fulmaris glacialis*, B.)	Human capture	Lower breeding success	Ollason & Dunnet 1978
	Brown pelicans (Pelecanus occidentalis, L.)	Human approach and aircraft	Nest abandonment and reduced reproductive success	Anderson & Keith 1980
	Bald eagles (Haliaeetus leucocephaus)	Human activity	Increased energetic demand and reduced survival and reproductive output	Stalmaster & Gessaman 1984
	Double-crested Cormorant (*Phalacrocorax auritus,* L.)	Human presence	Increased nest predation; population increases	DesGranges & Reed 1981; Henny et al. 1989
	Great Blue Heron (*Ardea herodias*, L.)	Logging operations	Changes in colony size, and rate of nesting; dependent on the type of intruder (land sourced activity resulted in highest nest abandonment)	Vos et al. 1985
Distribution	Great white sharks (*Carcharodon carcharias*, L.)	Baiting/feeding	Reduced horizontal activity	Huveneers et al. 2013

Method of Measure	**Disturbance Species**	**Disturbance Source**	**Results**	**Sources**
	Southern stingray (*Dasyatis americana)*	Baiting/feeding	Reduced space use	Corcoran et al. 2013
	Bull shark (*Carcharhinus leucas*, M. & H.)	Baiting/feeding	Increased residency	Brunnschweiler & Baensch 2011
	Red-footed and blue-footed boobies (*Sula dactylatra,* L.*, Sula sula*, L. *& Sula nebouxii*, M-E.*)*	Tourist trails	Nesting sites, approach to and from nest differed with distance from trails	Burger & Gochfeld 1993
	Bottlenose dolphin (*Tursiops truncatus,* M.)	Motorboat traffic	Avoidance of foraging area	Allen & Read 2000

Redistribution of animals due to disturbance avoidance can also result in energy deficits if animals move to less valuable habitat (Battin 2004; Liley & Sutherland 2007). Disturbance may cause animal species to avoid more valuable food habitat in favour of less disturbed areas, causing a shift in density (Battin 2004; Liley & Sutherland 2007). Density increases on less productive sites mean that animals may struggle to obtain adequate energy from a site, either due to increased competition, or insufficient food resources. Inability to meet energy demands again may result in either reproductive loss or death.

The indirect effects of human disturbance associated with wildlife are subtler. Such indirect effects include changes in predator risk assessment behaviour, resulting in animals that are less likely to flee from predators. Some studies have shown that if birds are either habituated to the presence of humans or desperate, they have a higher likelihood of being captured and eaten by a predator due to using habitats of higher predation risk (McNamara & Houston 1987; Geffroy et al. 2015). Another indirect effect is population selection for bolder individuals in high disturbance areas. Animals that take more risks may benefit and be more reproductively successful in high disturbance areas than non-bold individuals. Increased reproductive success of some personality types could affect population diversity in the long-term that may reduce fitness and reproductive success and thus could result in population declines in the future (Evans et al. 2010).

Because human disturbance has the potential to translate to population-level effects, and ultimately affect ecosystems and biodiversity, it has garnered the attention of many conservation government agencies. For example, in the UK, the Wildlife and Countryside Act, 1981, was developed to protect wildlife and wild places from disturbance. This act includes protection of plants and animals from disruption, as well as rules regarding conservation and parks, and public right of ways. Furthermore, the UK law for 'disturbance offence' of marine European protected species, which was based on the European Commission’s (2007) Habitats Directive, Article 12, indicates that it is an offence to:

> “deliberately disturb wild animals of any such species [i.e. a European Protected Species] in such a way as to be likely significantly to affect – i) the ability of any significant group of animals of that species to survive, breed, or rear or nurture their young; or ii) the local distribution or abundance of that species (JNCC 2011).”

Similarly, from the Agreement on the Conservation of African-Eurasian Migratory Waterbirds (AEWA 2016):

> “Disturbance should be judged as significant if an action (alone or in combination with other effects) impacts on (water)birds in such a way as to be likely to cause impacts on populations of a species through either i) changed local distribution on a continuing basis; and/or ii) changed local abundance on a sustained basis; and/or iii) the reduction of the ability of any significant group of birds to survive breed, or rear their young.”

Based on these regulations, it is clear that there is a need for evidence to advise policy makers, as well as managers, on how disturbance, that may result in population-level impacts, can be recognised.

1.2.1. MODELLING HUMAN DISTURBANCE

Within the literature, two primary methods have been used to translate human disturbance effects into quantifiable population-level impacts (Pirotta et al. 2018). These two methods are population models and individual-based models which can be empirically based or behaviour based.

Empirical models, also known as mathematical models, can take many different forms but all of them are numerically based and use observational data. Some are population based and use observed data such as distribution or abundance to generate predictions of the longer-term consequences in the form of life-history or demographic models for specific species (De Roos 2008; Pirotta et al. 2018). For example, Gill et al. (1996) predicted threshold biomass values that can support populations of pink-footed geese based the relationship between field use and disturbance rates (*Anser brachyrhynchus*). Similarly, Sutherland et al. (1998) produced a regression equation based on changes in the site area and observed energy budget costs, and then predicted the resulting change in population size.

Other mathematical models, such as the one developed by Houston et al. (2012), are more general and individual-based. Houston et al. (2012) use time and energy budgets to understand the effects of changing environments. The use of time and energy budgets means the equations can be applied across species to follow animal responses to disturbance. Disadvantages of these types of models are that they assume all individuals of a population respond equally and as such, incur the same costs and can fail to account for changes in conditions or reactions over time. These variables mean that mathematical models can be useful in understanding human disturbance but may leave out key components.

With the increase in storage space and processing speeds, more recent studies have turned to computer-based models to tackle the complexity of human disturbance. These computer models are referred to as Individual-Based Models (IBMs) or Agent-Based Models (ABMs). These models apply adaptive behaviour and decision making, to the participating individuals within a simulated population (Grimm & Railsback 2013; DeAngelis 2018). Therefore, individuals realistically react to user implemented changes, and observed patterns of population behaviour that emerge are more representative because they account for environments that vary. For example, a study conducted by West et al. (2002) using an IBM, indicated that various factors such as disturbance type, and time of year played a role in whether oystercatcher (*Haematopus ostralegus,* L.) populations were affected by human disturbance.

Furthermore, IBMs have shown that they can be generalized and adjusted to a variety of situations regarding human disturbance (Stillman et al. 2002; Goss-Custard et al. 2006; Stillman et al. 2007). For example, the MORPH model developed by Stillman

(2008), has been used to investigate human disturbances on multiple different species and locations. Additionally, the SODA model developed by Bennett et al. (2009), was used in several case studies of different species to evaluate human disturbance patterns in space and time.

It is evident that individual-based models are well suited for simulating the complexity of human disturbance which is apparent in the success of both the MORPH and SODA models. However, IBMs have fallen under criticism because they can be challenging to understand (Grimm & Railsback 2013, Wood et al. 2015). Fortunately, recent advancements in standardized reporting procedure and the development of the Overview, Design concepts and Details (ODD) protocol have helped to remedy this situation (DeAngelis & Grimm 2014). Furthermore, software platforms, such as Netlogo, have been developed to help provide the building blocks for ecological IBMs, which simplifies the modelling process (Tisue & Wilensky 2004). With these protocols and advancements in individual-based modelling there is scope for the future production of both easy to understand and easy to implement IBMs to examine the population-level effects of human disturbance.

1.3. AN ESTUARY AS A STUDY SITE

To investigate human disturbance, humans must be present, and animals must be present. Estuaries are spaces commonly used for a range of social and recreational activities, and are also important for wildlife. Estuarine environments within the UK, in particular, are areas that are frequently subject to the high intensity of human visitation, while also providing critical habitat for migratory wildfowl (Davidson & Rothwell 1993, Kennish 2002, Liley et al. 2011). Consequently, UK estuaries offer the ideal location to evaluate disturbance between humans and animals.

The Exe Estuary, the study site selected for this thesis, is located in Devon, southwest England. Three rivers feed into the estuary; including the River Exe, River Clyst and River Kenn. The Estuary is eight miles in length and varies in width from 0.25 to 1.5 miles. The Estuary is tidally influenced and leaves vast expanses of mudflats and seagrass exposed at low tide. The Estuary, qualifies under Article 4.2 of the Birds Directive: it supports 10,000 migratory wintering wildfowl and 20,000 migratory wintering waders. In conjunction with this, the estuary has regions that have been designated as Local Nature Reserves (LNR), National Nature Reserves (NNR), Special Area of Conservation (SAC), Special Protection Area (SPA), Wetlands of International

Importance (Ramsar site), and Sites of Special Scientific Interest (SSSI) (Liley et al. 2011). The surrounding region has seven towns located directly along the perimeter of the Estuary; Exmouth, Lympstone, Exton, Topsham, Starcross, Cockwood and Dawlish Warren. There are train tracks around the entire edge of the Estuary with trains running continuously from 6 am to 12 am. Furthermore, the Exe Estuary Trail is a footpath and cycling trail that extends along the coast of much of the estuary. Four primary mooring sites are present on the estuary near Topsham, Exmouth, Starcross and Exeter Canal. As such, the region is potentially subject to high degrees and variations of human disturbance sources. Furthermore, during the winter months, low water spring tides take place at midday and at midnight, meaning that one of the most prolonged exposures of the Estuary's flats takes place during daylight hours. This increased daytime exposure period potentially means that wildfowl on the Exe estuary may face greater degrees of human activity related disturbance during foraging periods, compared to that of other local estuaries and harbours. For example, in contrast to the Exe estuary, high water springs coincide with midday on the Solent and Poole harbour (Tides4fishing.com 2019). These conditions, in conjunction with the high population of wintering wildfowl, make this location an ideal spot for investigating human disturbance.

1.4. WILDFOWL AS A STUDY SPECIES

Birds, and wildfowl in particular, have been documented to be sensitive to habitat changes. Therefore, they are considered to be useful gauges of ecosystem pressures and may even be regarded as 'indicator species' (Savard et al. 2000; Mallory et al. 2006; Parsons et al. 2008; Gregory & Strien 2010). According to the McDonough in the Encyclopaedia of Life (2012) 'indicator species can signal a change in the biological condition of a particular ecosystem, and thus may be used as a proxy to diagnose the health of an ecosystem'. Furthermore, there is a strong publication background for natural history and population status for wildfowl, meaning that primary parameters, such as energetics requirements and natural mortality rates, necessary for models, are easier to access (Ganter 2000; Arzel et al. 2006; Clausen et al. 2013). Moreover, wildfowl are potentially subject to a large variety of disturbance types. These disturbance types include but are not limited to, hunting, intentional disturbance, commercial and recreational activities (Korschgen & Dahlgren 1992; Davidson & Rothwell 1993), indicating that disturbance can be investigated based on a large variety of factors. As a result, wildfowl are a valuable study subject for investigating the population-level effects of human disturbances on wildlife.

On the Exe Estuary, two wildfowl species that are abundant in high numbers are dark-bellied Brent goose (*Branta bernicla*) and Eurasian wigeon (*Mareca penelope*), henceforth referred to as Brent goose and wigeon respectively. These species begin to appear on UK estuaries from September and October, and steadily increase in numbers, to peak in November through February (Figure 1.2;Figure 1.3).

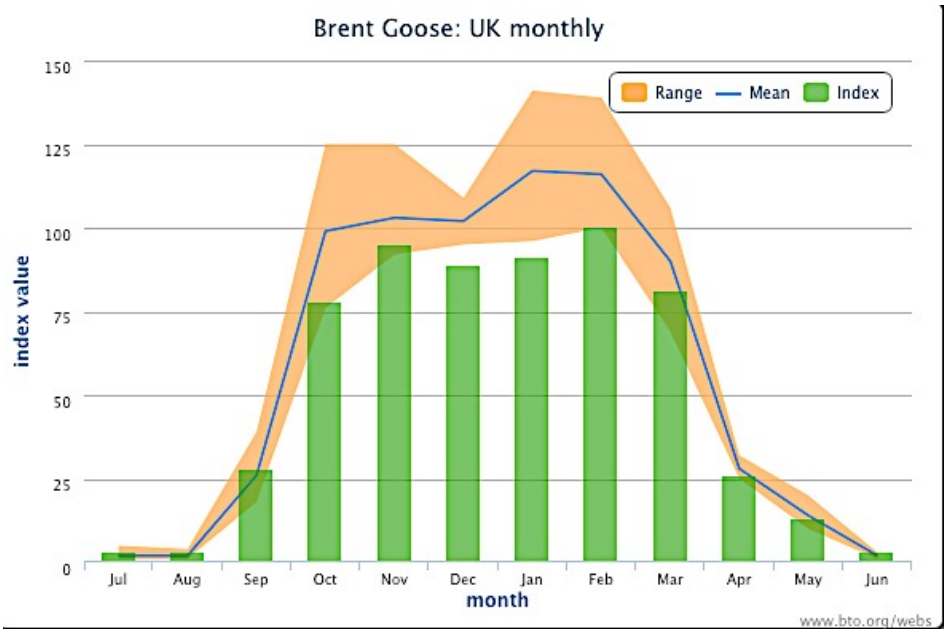


Figure 1.2 Figure taken from Frost et al. (2019) showing changes in brent goose abundance relative to the month of the year in the UK; Contains Wetland Bird Survey (WeBS) data from Waterbirds in the UK 2017/18 ©copyright and database right 2019.

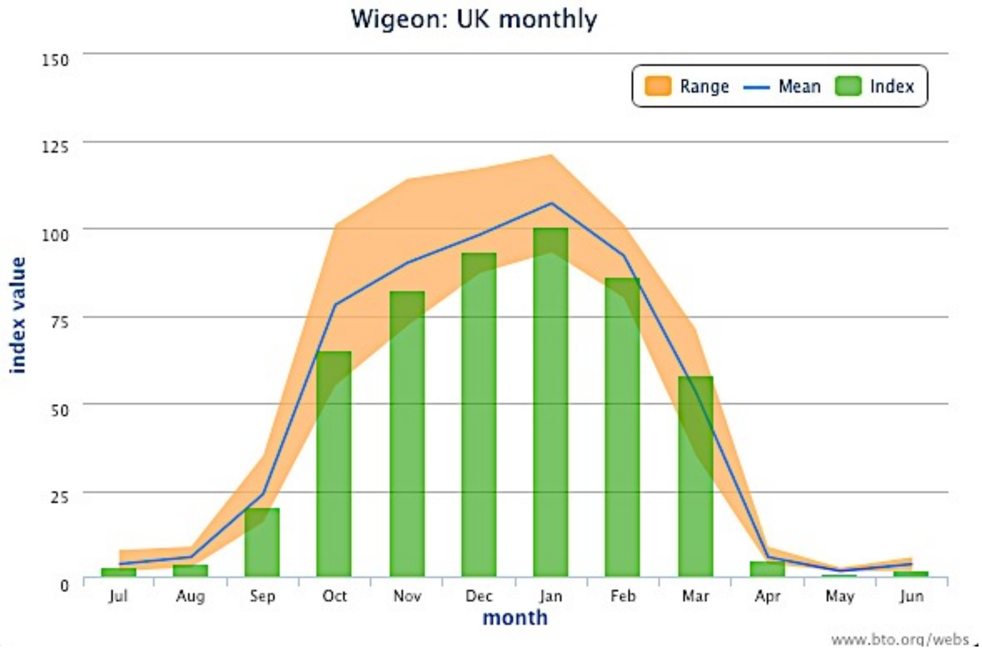


Figure 1.3 Figure taken from Frost et al. (2019) showing changes in wigeon abundance relative to the month of the year in the UK; Contains Wetland Bird Survey (WeBS) data from Waterbirds in the UK 2017/18 ©copyright and database right 2019.

Dark-bellied Brent goose are a relatively small goose species weighing in at approximately 1.5kg with an average adult wingspan of 115cm (Robinson 2017). Males and females are not sexually dimorphic, and both have a black head and neck accompanied by a white ring around the neck, followed by a grey and main black body with white tail feathers. The average lifespan for a brent goose is 11 years (Robinson 2017). The food source for Brent goose is restricted to vegetation, primarily consisting of *Zostera* spp. in early winter and field grasses in late winter. Brent goose have a reach of approximately 40cm of water depth which might extend slightly if seagrass blades are elongated and suspended. Therefore, out of a typical 24-hour day, food resources on an estuary are limited to mid to low tide times and must cease during high tide regardless of satiation (Evans 1976; Lindström 1991).

In the 1950s the Brent goose population numbers were at an all-time low. At the time it was believed that this was potentially due to the *Zostera*, L., parasite in the 1930s which nearly wiped out all *Zostera* populations, the primary food source of Brent goose, in Europe. Some studies suggested the decline in Brent goose was the result of other sources, including war-time disturbance on estuaries and wildfowling disturbance. To conserve the species, the Netherlands (in 1950), Great Britain (in 1954), and France (in 1966) granted protection status to Brent goose (Ogilvie & St Joseph 1976). Following this protection status, Brent goose population numbers began to rise. The most persuasive evidence to support the theory of wildfowling disturbance being the primary cause of Brent goose declines, occurred in the Netherlands, which showed a dramatic increase in Brent goose populations following the implementation of protection status. However, the pattern of the rise was not as evident when UK and France gave Brent goose protection. It was in fact, only after Brent goose had several successful breeding seasons that numbers began to improve (Ogilvie & St Joseph 1976). As of November 2017, approximately ninety-five thousand Brent goose use the United Kingdom for wintering grounds each year (Figure 1.4; Robinson 2017). Brent goose currently hold an amber conservation status within the UK due to recent breeding and wintering population declines, along with breeding and wintering range declines (Robinson 2017). However, their populations have a conservation status of ‘Least Concern’(LC) within Europe and worldwide (Robinson 2017). Brent goose are a non-quarry species in all European countries except for Denmark and Germany (European Parliament 2009).

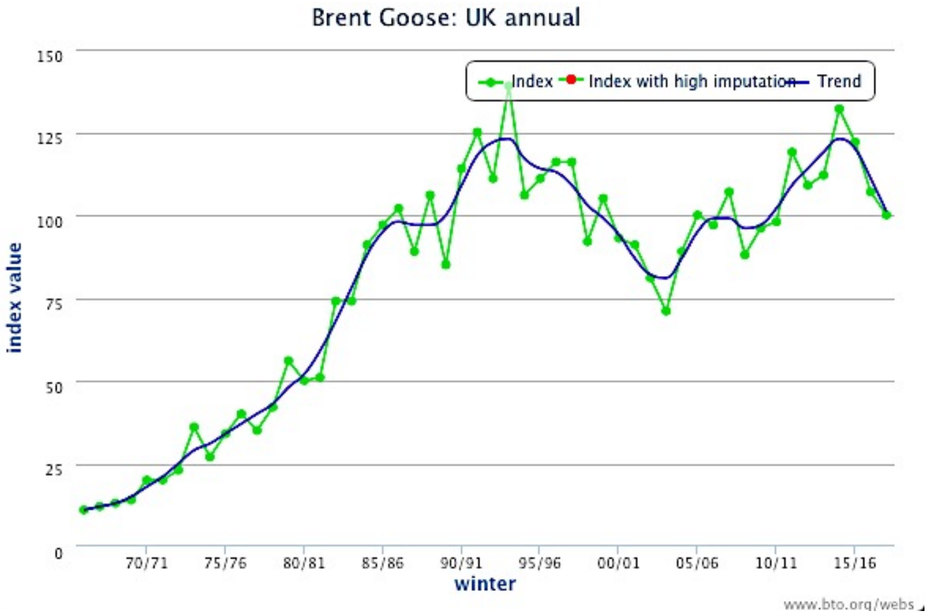


Figure 1.4 Figure taken from Frost et al. (2019) showing annual brent goose population trends in the UK from 1960 to 2015. Contains Wetland Bird Survey (WeBS) data from Waterbirds in the UK 2017/18 ©copyright and database right 2019.

Eurasian wigeon are a dabbling duck species that, like Brent goose, feed exclusively on vegetation. Wigeon, being a smaller species, have a feeding depth reach limited to approximately 30cm. Wigeon are sexually dimorphic during the breeding season (September to July), with males being larger and more colourful than females. Males generally weigh around 800g and exhibit a yellow streak along the nose bridge with a rusty brown colouration on the cheeks and neck. Other colourful aspects of the male Eurasian wigeon include grey and black wing feathers that have white marginal covert feathers and white with black-tipped secondary coverts, and bright green speculum, followed by a white underbelly and black tail feathers. Females being smaller, generally, weigh closer to 650g and are rusty brown over the whole body except for several white secondary coverts. The average lifespan for most Eurasian wigeon is three years (Robinson 2017). However, it is important to consider that much of the aging data for wigeon is accrued from wildfowling records, which is a sampling technique that may be biased to younger age classes. A study by Fox et al. (2016) indicated that wildfowling submitted kills contained 9% more young than other forms of sampling. Furthermore, species that are hunted will also have younger ages simply because a proportion of the populations is removed before they can reach maximum ages. Therefore, the actual life span for this species is likely longer. According to Robinson 2017, there are about four-hundred and forty thousand wigeon that visit the UK each winter. A number that has steadily increased from the 1950s (Figure 1.5; Atkinson-Willes & Frith 1965). Similar to Brent goose, wigeon have a conservation status listed as amber within the UK due to breeding and wintering population declines in conjunction with recent breeding and wintering range declines. Additionally, Eurasian wigeon, like Brent goose, are listed as 'Least Concern' (LC) in Europe and worldwide (Robinson 2017). Eurasian wigeon are considered a quarry species in the UK and are hunted from September 1st to February 20th (BASC 2018).

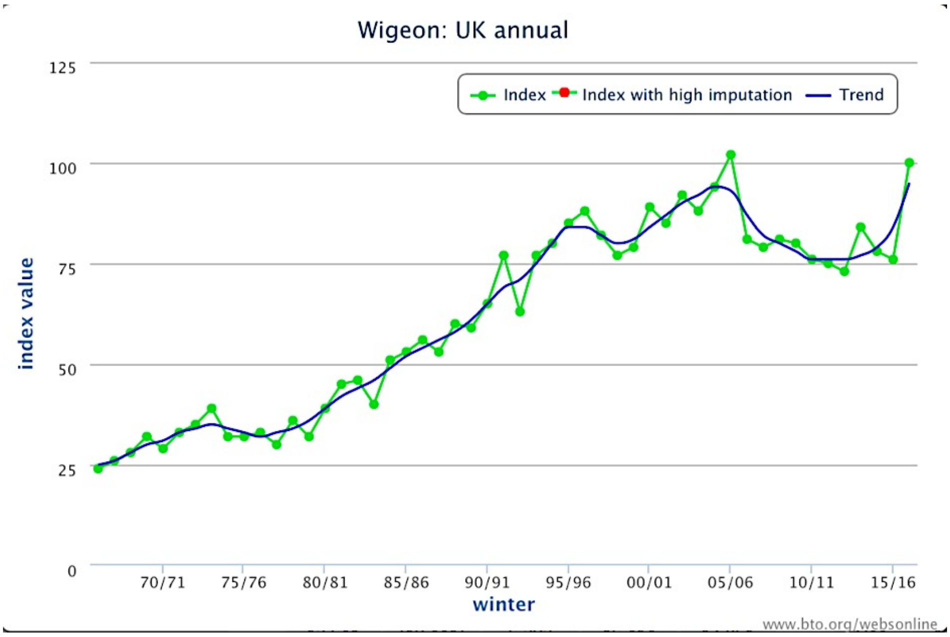


Figure 1.5 Figure taken from Frost et al. (2019) showing annual population trends of wigeon in the UK since 1960. Contains Wetland Bird Survey (WeBS) data from Waterbirds in the UK 2017/18 ©copyright and database right 2019.

Based on the abundance of Brent goose and wigeon on UK estuaries in the winter, and due to the importance of the wintering season for successful breeding and migration, this study took place over the wintering months (September to February). Ankney & MacInnis (1978) alluded to the significance of the wintering season for providing the necessary nutrients for successful hatches in lesser snow geese (*Chen caerulescens caerulescens*, L.). The importance of winter-months is further validated by more recent studies, which have connected events in the wintering months to population numbers in several migratory wildfowl (Davies & Cook 1983; Ebbinge 1992; Rappole & McDonald 1994; Scott et al. 1994; Sedinger & Alisauskas 2014). During winter months, birds have greater difficulty in meeting energetic demands and are, therefore, potentially more sensitive to effects from human disturbance than during the breeding season itself. During these months, their primary food source is *Zostera* and *Ulva,* L., species. Both of these food resources have limited availability depending on the water depth and tide state. Additionally, *Zostera* and *Ulva* species senesce over the wintering season, meaning that estuarine food resources deplete as the season progresses. Understanding how disturbance influences animals during these critical times, grants greater insight into the impacts of disturbance on wildlife populations.

1.5. AIMS AND OBJECTIVES

This project aims to increase the understanding of human disturbance and its impact on wildlife populations by using wildfowl as model species. Within the context of this goal, there are five primary project questions:

1) When and where do human activity types and wildfowl overlap in space and time?
2) How much disturbance are wildfowl experiencing within the spatiotemporal overlap?
3) How do wildfowl compensate?
4) What are the thresholds of human disturbance that wildfowl can suffer before there are impacts?
5) How can the knowledge of human disturbance impacts help inform conservation management?

1.5.1. OBJECTIVE 1. (CHAPTERS 2 & 4)

Identify and quantify spatiotemporal overlaps between human activity and wildfowl by observing the wildfowl and humans in the wild.

a) Establish types of human activity and their frequency of occurrence in space and time
b) Establish bird distribution and activity in space and time
c) Evaluate the variation in environmental factors relative to human and bird overlaps in space and time
d) Identify the environmental factors such as tide, temperature, wind, and geography that may correlate with spatiotemporal overlaps

1.5.2. OBJECTIVE 2. (CHAPTERS 2, 3 & 4)

Evaluate and quantify disturbance that takes place within spatiotemporal overlaps between humans and wildfowl.

a) Investigate trends in wildfowl disturbance rates and magnitude associated with space and time
b) Determine the energetic cost to wildfowl related to a disturbance in space and time

1.5.3. OBJECTIVE 3. (CHAPTER 3, 4 & 5)

Establish compensatory action relative to disturbance types by observing how wildfowl change their behaviour under varying degrees of disturbance in space and time.

a) Establish time budgeting bird behaviour within the context of space in the presence and absence of disturbance
b) Determine variation in time budgeting bird behaviour relative to varying environmental conditions
c) Evaluate what these variations mean for bird ability to compensate for disturbance

1.5.4. OBJECTIVE 4. (CHAPTER 6)

Develop an individual-based model that can identify thresholds of disturbance that wildfowl can experience before having an impact.

a) Establish primary factors for parameterization of an individual-based model
b) Identify impacts from various levels of human disturbance by using an IBM

1.6. A CONCEPTUAL FRAMEWORK FOR THE THESIS

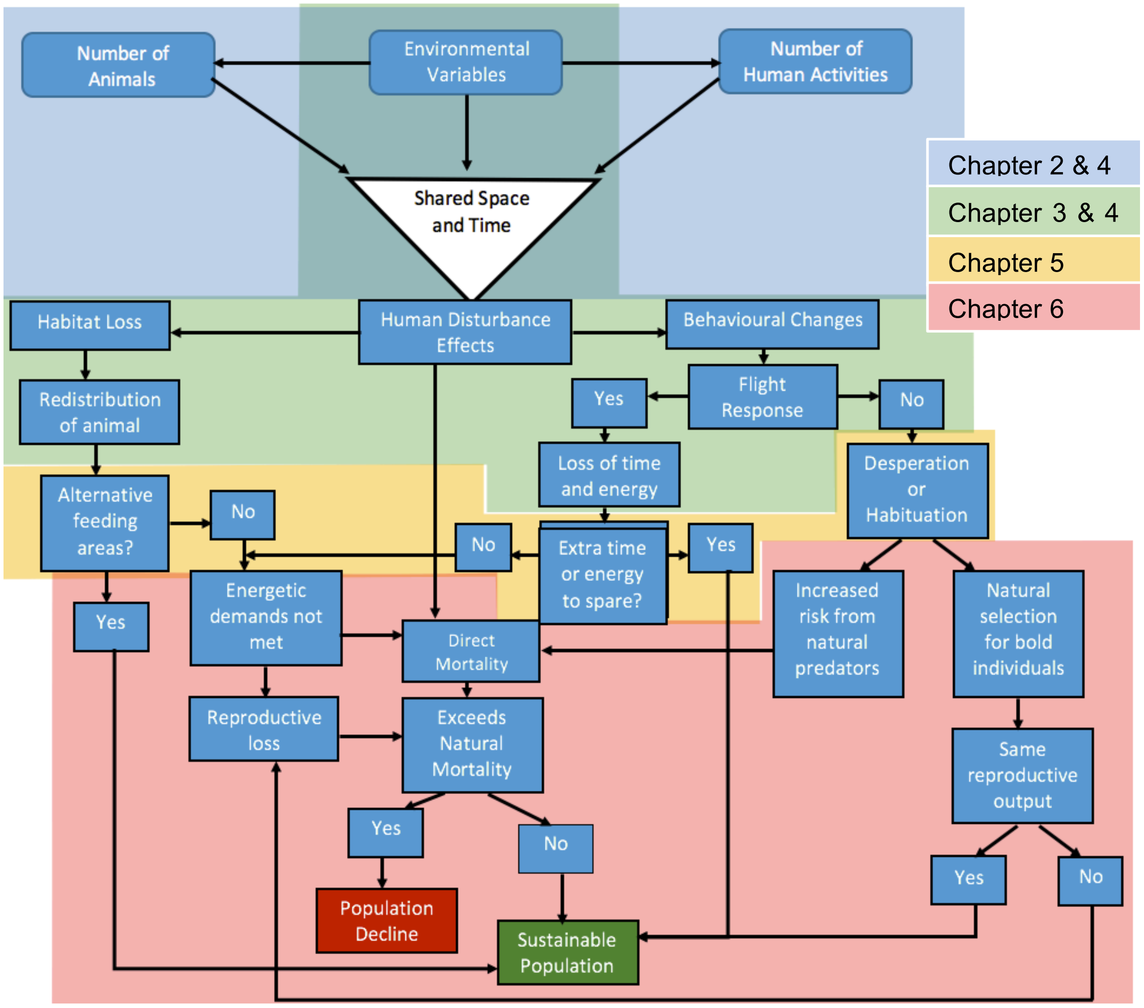


Figure 1.6 Detailed Conceptual Outline

1.7. OVERVIEW OF THESIS

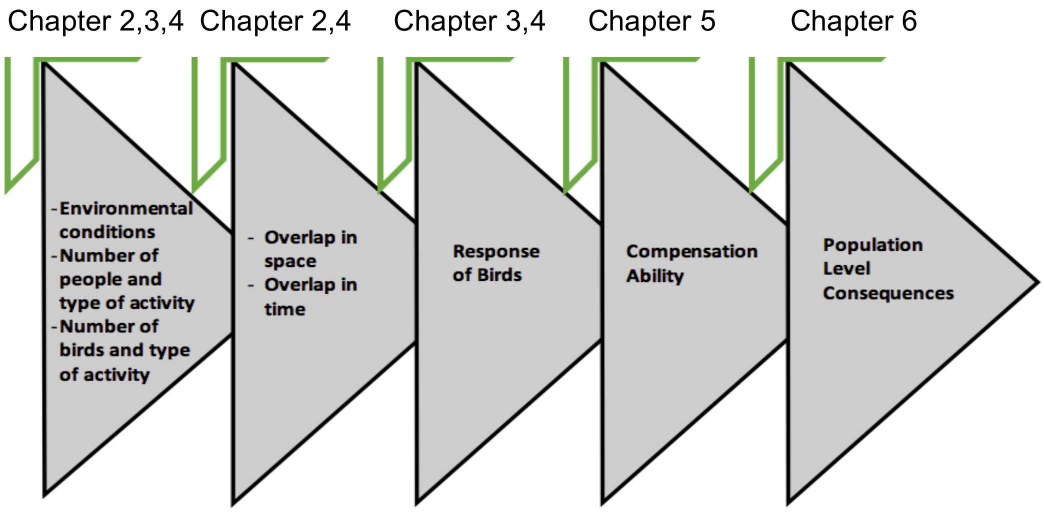


Figure 1.7 General Concept Outline of the Thesis.

Table 1.2 Thesis Summary

1. Introduction chapter Human disturbance is not a new topic of study, but the translation of human disturbance to the population level still needs further understanding. This chapter explains what human disturbance is and the necessary background information about it. It also explains what information is lacking and where more information is still needed and how this study aims to address the gaps in the research. This chapter also gives an introduction to the study species and the study site.
2. Overlaps between people and wildlife in space and time: Insights from wintering wildfowl on the Exe Estuary For human disturbance to occur, animals and humans must share both time and space. Characteristics of this shared time and space can offer insight into variables that result in human and wildlife interactions. This chapter evaluates shared time and space between birds and people to determine if environmental factors can predict overlaps. Data were collected on two wintering wildfowl species, Brent goose (*Branta bernicla,* L.) and wigeon (*Mareca penelope,* L.), wintering on the Exe estuary during the winter months from September to February of 2017-2018 and 2018-2019. Multivariate analysis of human and bird activity identified significant variation explained by several environmental variables. These variables were associated with food accessibility for birds, and human accessibility, which indicates that identifying

environmental variables that make sites desirable for both humans and animals are useful in predicting when and where disturbance is most likely to occur.

3. The response of wildlife when overlap with humans occurs: Insights from wintering wildfowl on the Exe Estuary

The degree of spatiotemporal overlap between humans and animals plays a significant role in how much disturbance animals experience. This chapter took the spatiotemporal information gathered from Chapter 2, along with observational records of disturbance events to determine the rate of disturbance within those overlaps. With this information, this chapter also analysed the actual energetic costs associated with a disturbance during these overlaps by using a modified time-energy budget equation. On the Exe Estuary, Brent goose (*Branta bernicla*, L.) experienced approximately one disturbance per hour, while wigeon (*Mareca penelope*, L.) experienced around 0.7 disturbances per hour. Disturbance thresholds were calculated to vary depending on whether birds were disturbed more when resting or feeding. By extrapolating the current rates of feeding and resting disturbance, the predicted maximum disturbances per hour that Brent goose could experience was 24 per hour and for wigeon was 34 per hour before they ran out of time to compensate. Overall disturbance costs experienced by Brent goose and wigeon on the Exe Estuary during the winter of 2017 and 2018 were below these calculated thresholds of compensation.

4. Variation in disturbance response to different human activity types: insights from wildfowl on the Exe Estuary

As different human activities have distinct characteristics, it would be expected that animals will respond in different ways to contrasting types of human activity. This chapter investigated changes in response to different types of human activity by Brent goose (*Branta bernicla,* L.) and wigeon (*Mareca penelope,* L.) on the Exe Estuary. A combination of scan-sampling and continuous-sampling were used to collect data during the winter months of 2017-2018 and 2018-2019. There were significant differences in how these species responded to the various forms of human activity, with some types of activity resulting in higher energetic and time costs to the birds. This chapter ranks different activity types in terms of their time and energy costs to the birds. Pedestrians caused the greatest time and energy costs for both species. Wildfowling was amongst the least disturbing activities, as it occurred relatively infrequently and when occurring did not incur a high time or energy cost to the birds. The current overall rates of disturbance experienced by brent goose and wigeon on the Exe Estuary are well below thresholds at which birds would fail to meet their energy requirements.

5. Time budgets: How animals can use the time to compensate for human disturbance

Time budgets can assess animal behaviour and can evaluate energetic needs. Therefore, time budgets may be able to help us understand how capable animals are of coping with energetically costly events, such as human disturbance. This chapter reviews published data on the time budgets of wildfowl to determine how they change relative to disturbance related activities, as well as body mass and environmental variables. Findings indicate that there is little association between wildfowl mass and the time allocated to feeding. However, differences in feeding time were significantly related to environmental variables that affected food availability and energetic costs. Furthermore, time feeding increased, and resting time decreased with increased time being alert, indicating a possible trade-off mechanism. This trade-off suggests that resting time in animals may be a measure of how capable animals are of compensating for disturbance events. By understanding which species-specific and environmental variables are associated with lower resting time, it may be possible to identify when animal species may be most susceptible to disturbance effects before they translate to population-level impacts.

6. Predicting consequences of disturbance on wildlife using an Individual-Based Model: Insights from wintering wildfowl on the Exe Estuary

Determining if human disturbance has an impact on wildlife populations is a pressing question faced by ecologists. Many studies have shown that human interference can cause short term effects on wildlife, but few studies have been able to translate what these effects mean for wildlife populations. This chapter uses data on distribution, behavioural responses and fitness costs of two wildfowl species, Brent goose (*Branta bernicla*, L.) and wigeon (*Mareca penelope*, L.), on the Exe Estuary during the winters of 2017-2018 and 2018-2019 to evaluate human disturbance impacts on wildfowl populations. Population effects were assessed by parameterising an individual-based model that combined the data collected, along with fitness maximising decision-making, to create a validated model environment similar to that observed on the Exe Estuary. Birds in the model environment had similar time budgets, distributions and disturbance rates to those seen on the Exe Estuary. Humans within the model environment also displayed a similar distribution behaviour to those observed on the Exe Estuary. Significant differences in model bird energy levels, behaviour and distribution were detected when human activity levels in the model increased beyond what was witnessed on the Exe Estuary. Brent goose within the model had bird threshold rates of 7 disturbances per hour, while wigeon had bird threshold rates of 12 disturbances per hour before being unable to compensate through increased feeding. To reach these disturbance rates, over 100 people needed to be on the model environment for 24 hours. These bird threshold rates were lower than those predicted by mathematical models in Chapters 3 and 4, where Brent goose could withstand up to 24 disturbances per hour, and wigeon could withstand up to 34 disturbances per hour. Both the individual-based model and mathematical model results indicate that current levels of human disturbance experienced by wildfowl populations on the Exe estuary are well below bird thresholds. Although the individual-based model is parameterized for Brent goose and wigeon on the Exe Estuary, its design and implementation allow flexibility and broader applicability. Thus, this model is also a useful tool for ecologists in understanding human disturbance in many contexts with a variety of animals.

7. Discussion Chapter

This chapter summarized findings and discussed how the results of this study relate and add to the current literature. This chapter also identifies the shortcomings of this study and makes suggestions for where further work is needed.

2. CHAPTER 2: OVERLAPS BETWEEN PEOPLE AND WILDLIFE IN SPACE AND TIME: INSIGHTS FROM WINTERING WILDFOWL ON THE EXE ESTUARY

2.1. ABSTRACT

For human disturbance to occur, animals and humans must share both time and space. Characteristics of this shared time and space can offer insight into variables that result in human and wildlife interactions. This chapter evaluates shared time and space between birds and people to determine if environmental factors can predict overlaps. Data were collected on two wintering wildfowl species, Brent goose (*Branta bernicla,* L.) and wigeon (*Mareca penelope,* L.), wintering on the Exe estuary during the winter months from September to February of 2017-2018 and 2018-2019. Multivariate analysis of human and bird activity identified significant variation explained by several environmental variables. These variables were associated with food accessibility for birds, and human accessibility, which indicates that identifying environmental variables that make sites desirable for both humans and animals are useful in predicting when and where disturbance is most likely to occur.

2.2. INTRODUCTION

2.2.1. THE IMPORTANCE OF SPATIOTEMPORAL OVERLAP IN UNDERSTANDING HUMAN DISTURBANCE

The world population is projected to increase by 2 billion people by 2030 (United Nations 2019). With this population increase, the expectation is that every year, the interaction between wildlife and humans will also become more frequent. Logically, more space is required to support larger numbers of people, which leads to increasing development and use of wild habitat. Additionally, with advances in technology, previously unreachable wild habitats are becoming more accessible. These developments indicate that in the future, shared space between humans and wildlife is likely to increase.

Shared space between humans and wildlife can result in disturbance to wildlife. Disturbance, for the context of this chapter, is any human-related activity that elicits a response in wildlife that would otherwise not occur. These interactions become an issue when an animal's behaviours or movements associated with response to a disturbance, increase to such a degree that the animal is incapable of compensating. Several studies have suggested that chronic exposure to disruption of this level has the potential to lead to reduced reproductive output or death in wildlife (Schulz & Stock 1993, Gill et al. 1996, Frid & Dill 2002, Gill 2007). Disturbance of this level, therefore, has the potential to lead to population level declines. For example, a study by Liley & Sutherland (2007) predicted that if human activity doubled on the eastern shore of the Wash, Norfolk, then local Ring Plover (*Charadrius hiaticula*, L.) populations would decrease by 23%.

By the very nature of its definition, for human disturbance to take place, it requires overlap between both humans and wild animals. Overlap, in this situation, is considered to be the zone of shared space and time around an animal in which particular human activity can cause a disturbance (Figure 2.1). Therefore, for different species of animals and different human activity types, the term 'overlap' can be defined differently. Furthermore, if an animal overlaps spatially with humans, but changes its distribution temporally, a simple spatial analysis will not be sufficient to understand the level of disturbance potentially experienced by the animals. Firstly, the animal will not be encountering human activity to the same extent as would be predicted from spatial analysis alone. Secondly, if the animal would not naturally change location, the temporal pattern change itself is a form of response to disturbance. Thus, spatiotemporal analysis is essential to understand disturbance impacts fully.

The necessity for understanding spatiotemporal overlaps between animals and humans as a method for evaluating disturbance impacts is evident within the literature. For example, a study conducted by Martin et al. (2010) on the distribution and movements of the brown bear (*Ursus arctos*, L.), showed that, although bears and humans shared the same space, bears avoided certain areas at certain times that were associated with high human activity (Martin et al. 2010). Another similar study, conducted on tigers (*Panthera tigris,* L.) in a densely populated region of Nepal, revealed that human overlap with tigers was smaller than expected, due to differences in the temporal use of areas by tigers compared to that of humans (Carter et al. 2012). African elephants (*Loxodonta africana*, B.) have also increased their movements at night in areas with increased levels of poaching (Ihwagi 2018). These studies illustrate the importance of both the space and time component in understanding human disturbance.

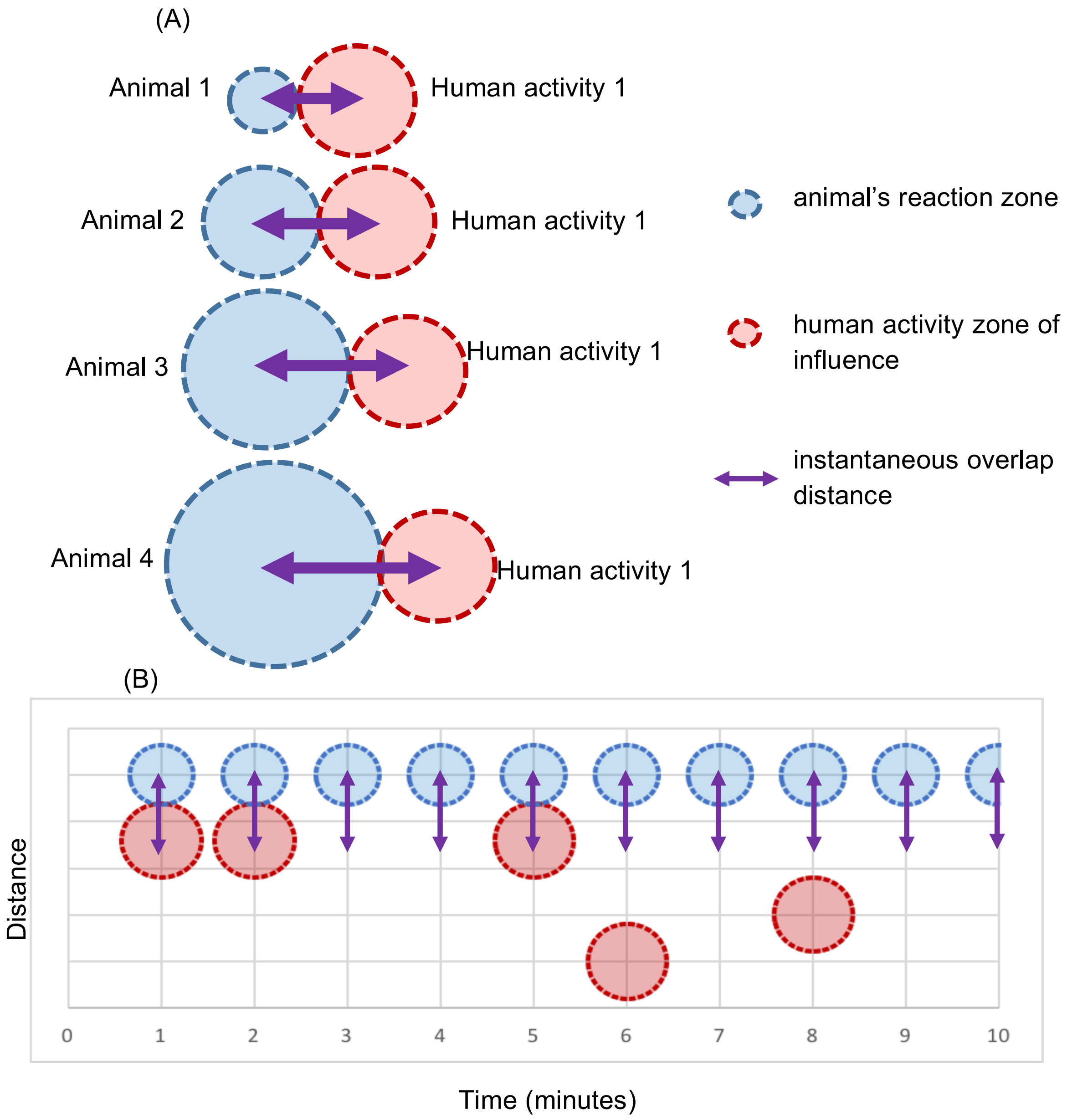


Figure 2.1(A) Graphical representation of how the definition of instantaneous overlap distance in space (purple line) might change relative to different animal types (Blue) and the same human activity type (Red). The instantaneous overlap distance is determined by the combined radius of an animal's reaction zone and a human activity zone of influence. (B) When animals and humans are within the ‘instantaneous overlap distance’, at the same time (at minutes 1, 2, and 5 in this figure) is there an overlap.

2.2.2. WHERE MORE WORK IS NEEDED

Although many studies have acknowledged the necessity of evaluating both space and time as a component of understanding human disturbance, many of these spatiotemporal studies overlook the mechanisms leading to the overlaps in the first place. As overlaps are necessary for a disturbance to occur, identifying mechanisms leading to overlaps can be very useful in the understanding of disturbance. Studies conducted in several areas around the world have shown the value in identifying variables that often lead to human-wildlife conflicts. For instance, research on brown bears in Montana indicated that variables associated with landscape conditions could be a means for determining high probability regions for bear-human conflicts and thus be used to inform management of top priority areas (Wilson et al. 2006). In Africa, studies attempted to use land-use mosaics as a way of understanding mechanisms leading to crop-damage from elephants (Hoare 1999). These studies highlight the usefulness of having a means for determining where and when humans and animals are most likely to create interactions and help provide a focus for management decisions. However, these studies tend to primarily evaluate instances where animals are considered nuisances rather than the victims of an incursion. Therefore, there is a need for more studies assessing overlaps in the context of passive overlap before disturbance.

Numerous ecological studies already exist that evaluate the environmental mechanisms for animal or plant distribution and abundance in space and time. There are also many socio-economic studies on the influence of environmental variables on human movements in space and time. Therefore, a logical method of identifying variables that lead to overlap, before disturbance, would be to merge these two topics. However, a search failed to find any examples of this methodology being used to evaluate human disturbance in the literature. As a result, this chapter assesses the differences in environmental factors that were associated with the variation in spatiotemporal overlaps between wildfowl and humans on estuaries.

With the information gained from this chapter, the conditions under which overlaps, between wildfowl and human activities on the Exe estuary, are occurring and have the highest probabilities of future occurrence, can be determined. This data can then help inform management of spaces and times with the highest recorded overlap measures between wildfowl and human activities, and thus provide direction for where and when management can be most effective. Additionally, this research could give awareness into conditions most likely to lead to overlaps between wildfowl and human activities in the future, and potentially prevent disturbance situations before they arise. Finally, because the underlying influences of environmental variables on fitness maximising decisions can apply to other species, this chapter can also give insight into variables and mechanisms that can lead human and wildlife interactions more generally.

2.2.3. AIMS AND OBJECTIVES

This chapter aims to evaluate the spatiotemporal overlaps between humans and wildlife, while simultaneously assessing correlations of these overlaps with environmental factors. By establishing environmental factors that are associated with higher degrees of bird and human overlap, when and where effects and impacts of disturbance are most likely to occur can be more effectively and efficiently evaluated.

This chapter has the following objectives:

- Establish spatiotemporal patterns of Brent goose, wigeon, and human activity and overlap therein
- Investigate the effects of various environmental factors on spatiotemporal patterns of Brent goose, wigeon, and human activity
- Evaluate the impact of human activity level and activity type on spatiotemporal patterns of Brent goose and wigeon
- Evaluate how the results can further our understanding of the effects of human disturbance

2.3. METHODS

2.3.1. STUDY SITE

Fieldwork was conducted on the Exe Estuary during the winter months (September, October, November, December, January, February) from September 2017 to February of 2019. Initial surveys took place from access points located around the estuary to establish the primary observation sites, which offered the best perspective of the estuary with the smallest amount of obstruction. Enough primary sites were ultimately selected so that the entire intertidal estuary could be surveyed (Figure 2.2).

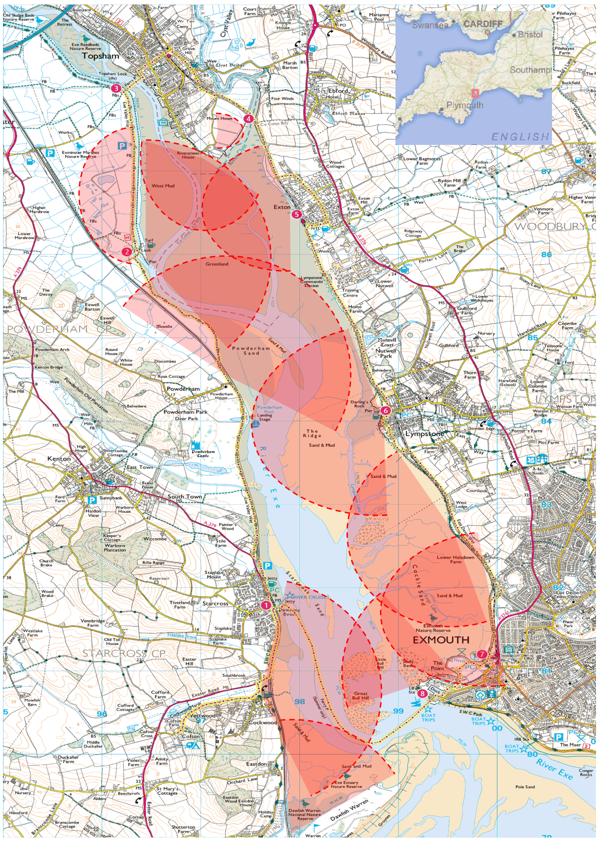


Figure 2.2 Observation sites on the Exe Estuary with view radius (shaded red); Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018.

After observation locations were selected, sections of the estuary were defined to best capture bird distributions and habitat by using habitat variation to divide existing Wetland Bird Survey (WeBs) sectors (Frost et al. 2019; Figure 2.3). Arc GIS overlays of seagrass coverage that was obtained from the Environment Agency 2017 showed variation in *Zostera* spp. distribution (Figure 2.4). Furthermore, substrate layer data collected from © Crown Copyright Ordnance survey Limited 2018, of the Exe Estuary from 2013, revealed a variety of different substrates throughout the Estuary. 'Sandy' and 'rocky' substrates dominated Southeast sites labelled 'BR' and 'CS'. Northern sites were almost exclusively soft-mud (Figure 2.5). Places that had the highest percentage of seagrass cover were primarily in the East, Southeast and Southwest estuary, where sand and 'sandy-mud' substrates also dominated (Figure 2.4; Figure 2.5). Initial observations indicated bird distribution was still variable within these subsections. Therefore, further descriptive divisions showed where the birds were residing within the subsections. These descriptions were based on compass direction and labelled as N, S, E, W, NE, NW, SE, SW, and MID (Figure 2.3).

Study sites were mapped in ArcGIS 10.1 using polygon shapefile layers that were self-drawn as well as obtained from © Crown Copyright Ordnance Survey Limited, Natural England, and the Environment Agency. Self-drawn layers were those of study sites and sections. Layers from the Ordnance Survey were from 2014 and included, county boundary lines, substrate coverage, elevation, and roads. Layers from the Environment agency were seagrass coverage collected in 2017 and sublittoral surveys collected with Natural England in 2013. All layers used the projections: Transverse Mercator to the British National Grid coordinate system, which has minimal area distortion. Polygon layers for seagrass and substrate areas were overlaid on the polygon shapefile of sub-regions to analyse percentage cover of seagrass and substrate in sub-regions. After overlaying the layers, the 'Tabulate Intersection' statistics tool in ArcGIS software measured the square meters within each subsite polygon that was occupied by seagrass and substrate polygons.

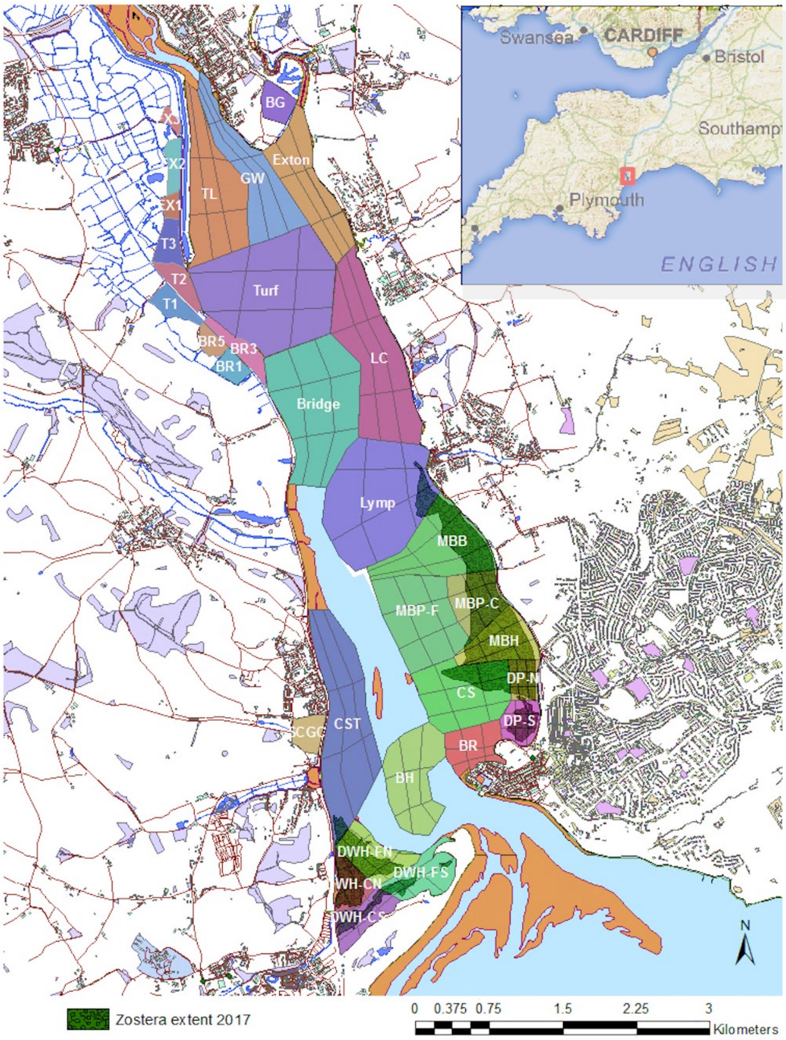
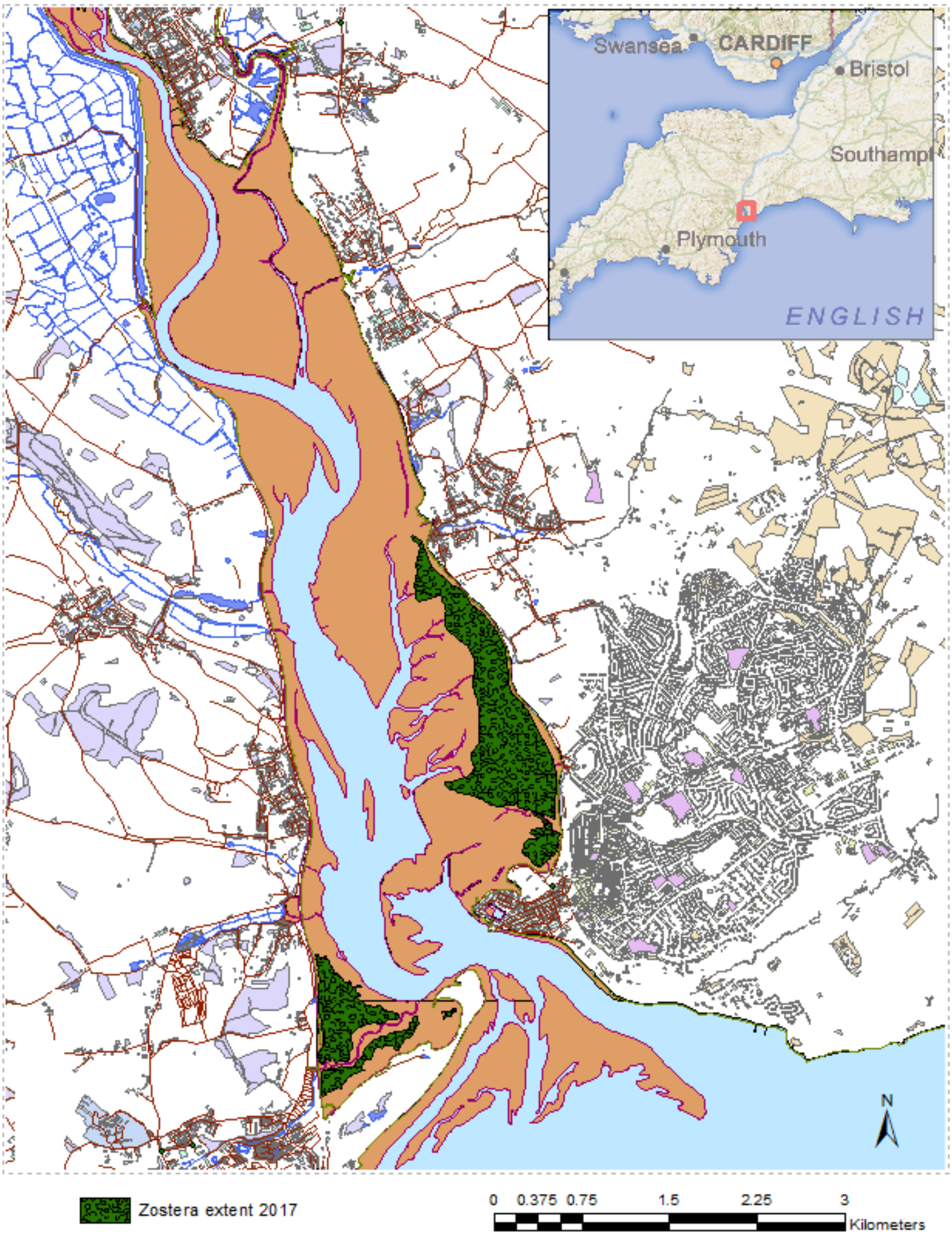


Figure 2.3 Habitat-adjusted sections with names and regional division lines for the Exe Estuary; Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, and Environment Agency 2017.



Service Layer Credits: Ordnance Survey Limited; Explorer House; Environment Agency

Figure 2.4 The 2017 Zostera spp. extent on the Exe Estuary relative to observation site designations. Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, and Environment Agency 2017.

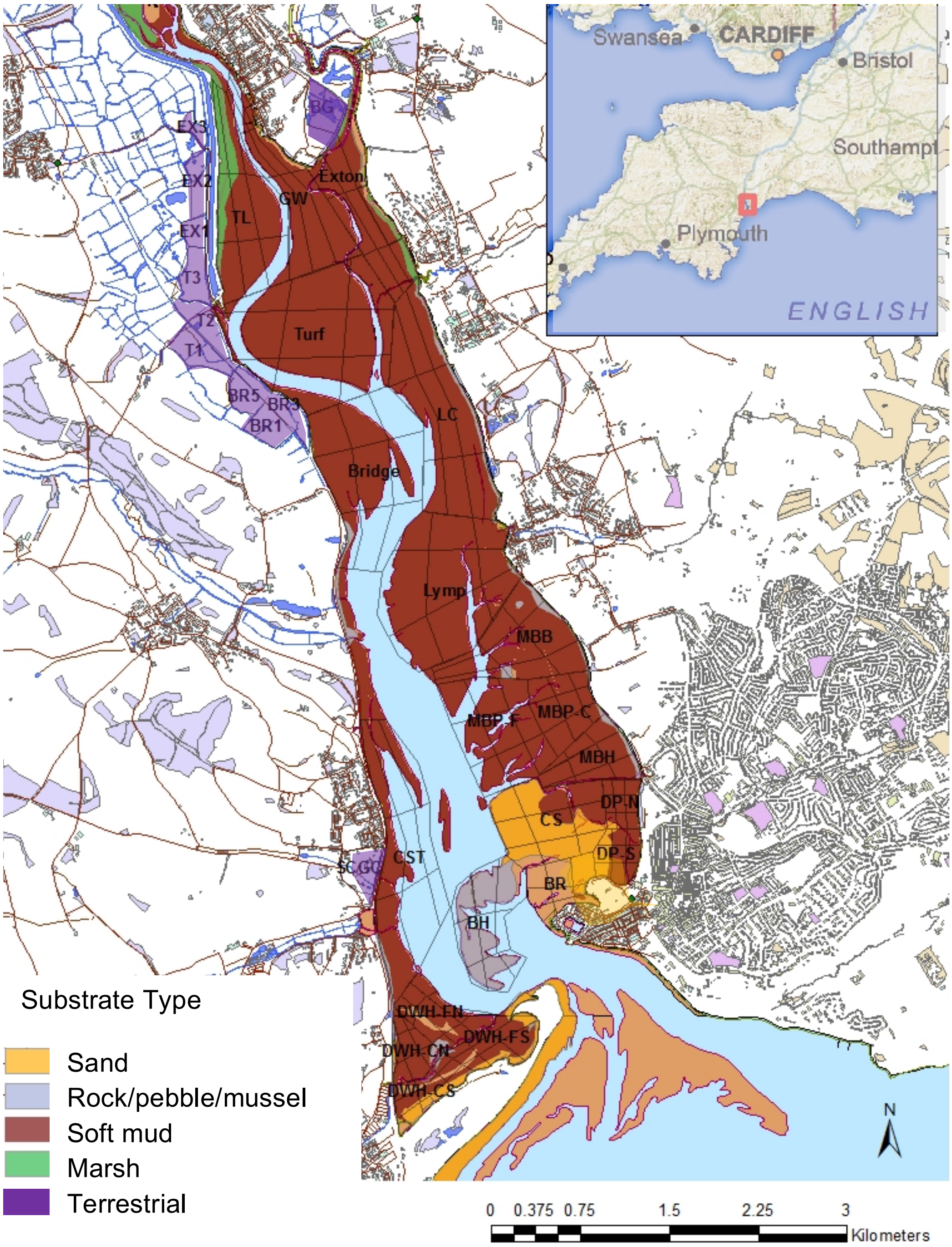


Figure 2.5 The 2013 Substrate extent on the Exe Estuary relative to observation site designations. Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, and Natural England & Environment Agency 2013.

2.3.2. OBSERVATION TECHNIQUES

Human activities were categorized according to a general group (Table 2.1) and after an initial exploratory survey around the estuary, some sites held a much higher degree of human visitation as well as more variable human activity types than other places (Figure 2.6). Therefore, to maximise efficiency, it was decided to weight surveys; with a higher proportion of time dedicated to sites that had higher numbers of visitation and higher variation in human activity type, than those sites that rarely had visitors or differentiation in those visitor types. The ending ratio was approximately 3:1, with three days spent on high activity, high variation sites for every, one day spent on a low activity and low variation sites.

Table 2.1 General category assignments of specific human activities and other disturbance sources.

General Category	Specific Human Activity
Wind-water sport	Kite Surfers Wind Surfers Sailboats
Non-wind-water sport	Canoe Kayak Paddleboard
Motorized-land	Car Lorry Train Tractor Motorbike Trolley
Noise	Non-wildfowling gunfire Unidentified noise Fireworks
People	Walker Dog walker (excl. dog) Golfer Birdwatcher
Animals	Dog Horse
Predator	Peregrine Fox
Harvester	Fisher

General Category	Specific Human Activity
	Crab-tiler
	Bait-digger
Air	Plane
	Helicopter
	Paraglider
Fast-land	Cycle
	Jog
Other	Smoke
Wildfowler	Wildfowler
	Wildfowler shots
	Wildfowler dog
Motorized-water	Motorboat
	Jet-ski
	Tour-boat

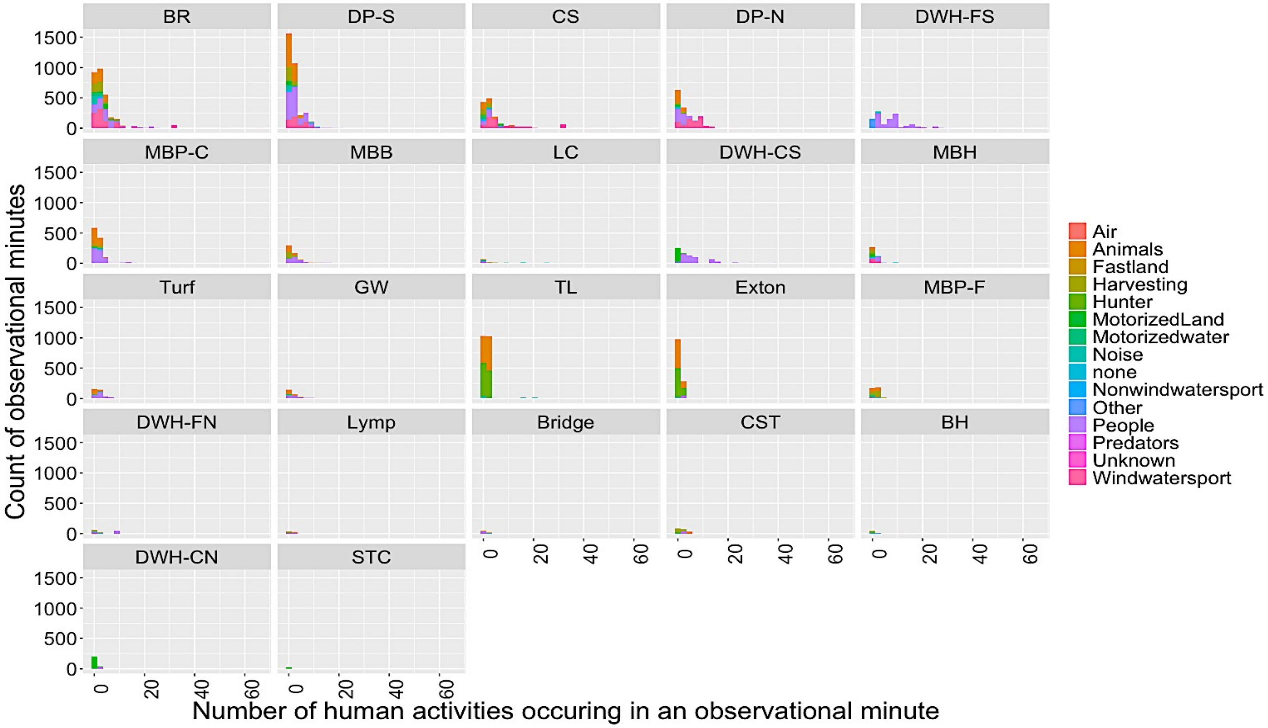


Figure 2.6 How each estuarine sites varied in terms of number of human activities, how often they were present the type of human activity types. Colours represent different types of human activity.

After several test surveys, two hours was the optimal length of a survey before data quality began to suffer, due to observer fatigue. Therefore, to optimise data quality, the day length was broken up into two-hour segments with one-hour breaks between each. The result was approximately 6 to 8 hours of observation for each day.

By using Microsoft Excel, order of survey site observations was randomised. Randomisation was accomplished by creating a column of two-hour sections per day of possible days of observation and then listing the observation sites in repeating the order to fill up the days. To weight the more variable observation sites, they were listed three times for every one time the less variable sites were listed. Then randomised numbers were assigned to the observation sites, which, when reordered, produced a randomised list of observation sites per observation period per day.

During each two-hour observation period, five scan samples were taken on Brent goose and wigeon for all visible subsections of the estuary. Several test scan samples indicated that performing scans every 30-minutes maintained independence between samples and allowed the observer to record other activities simultaneously. Therefore, five scan samples were taken over two hours, with one scan at the beginning of observation and a concluding scan performed at the end. Scan sampling parameters included total bird counts for each visible subsection. Bird counts were still recorded as zero if no birds were present in a section. In the event of a large disturbance event, or large change in bird behaviour, in which birds were redistributed, then a new scan sample was taken directly after the change disturbance and the scan interval time was restarted, so that the next scan sample took place 30 minutes from this new scan interval.

Continuous sampling methods recorded all observed human activities within the visible subsections (Martin et al. 1993). Parameters collected from continuous sampling included human activity type, the number of individuals, start time and end time of presence, to the minute, within the defined subsection, as well as closest observed proximity to any birds within the same location.

When any human activity was within the overlap distance, described in Figure 2.1, for Brent goose or Wigeon, then the event was considered an overlap. When this occurred, the time that the overlap started and ended (minutes), proximity of the human activity to the birds, and the number of birds within the overlap distance was recorded.

2.3.3. ENVIRONMENTAL VARIABLES

Environmental variables were recorded in conjunction with all observational variables. These variables included: date (dd/mm/yyyy), time (hh:mm), minutes from high tide (min), wind speed (kph), wind direction (N,E,S,W,NE,SE,NW,SW), temperature (^{o}C), precipitation (y/n), fog (y/n), site exposure (okta), cloud cover (okta), site accessibility (high/medium/low), site elevation (m) and moon phase. These environmental variables were recorded at 30-minute intervals during the 2-hour observations. Weather conditions measured without hindering data quality were recorded in real-time. Other conditions, such as temperature and tide time, were measured via metoffice.gov.uk. As wind speed and temperature are often correlated, the two variables were combined to create a wind-chill index using the following formula taken from weather.gov (2019). Site accessibility was graded based on access points and distances from a car park. Those sites that were less than a mile from a car park and also had easily accessible paths were given a value of high. Those sites that were less than a mile from a car park but had no path or were greater than one mile and had a path were given a value of medium. Those sites with no path and greater than a mile were given a value of low accessibility. Site elevation was based on elevation charts obtained from © Crown Copyright Ordnance Survey Limited layers from 2014.

$$
\begin{aligned}
&Wind\ Chill\ Index \\
&\qquad = (13.12\ +\ (0.6215 * (temperature(\ ^{o}C)) - (11.37 \\
&\qquad * (wind\ speed(kph))^{\wedge}0.16)\ +\ (0.3965 * (temperature(\ ^{o}C)) \\
&\qquad +\ ((wind\ speed\ (kph))^{\wedge}0.16))
\end{aligned}
$$

2.3.4. EQUIPMENT

The author conducted all observational surveys with a Swarovski STS 80 High Definition (HD) Straight Spotting Scope and accompanying tripod.

2.3.5. ANALYSIS

All statistical analyses used RStudio statistical software Version 1.0.136 (© 2009-2016 RStudio Inc.) with R version 3.3.3 (© 2017-03-06 R Inc.).

2.3.5.1. DATA COMPILATION

R packages lubridate and dplyr were used to merge the bird activity and human activity data sets to generate a minute by minute dataset of all observations. Bird data was collected on 30-minute scan intervals, therefore, in order to generate a minute-by-minute data set of bird data, all bird counts were assumed to remain constant in minutes leading up to the next scan sample. This was a fairly accurate representation of bird distribution because rarely were there large changes in bird counts and distribution in the minutes between scan samples. Human activity was recorded continuously and already represented a minute-by-minute interval. Merging the scan data with the continuous data provided both the human activity and the bird distribution on the site for every minute of observation. This collated data was necessary to calculate overlap between birds and people for each minute of observation.

However, because bird data were assumed to remain constant in the minutes between scan samples, they could be considered non-independent for those minutes between scan samples. To address this, using the dplyr package in R, and the fuction 'sample_n', one data point was randomly subsampled from each scan-sampling observation segment, to produce a reduced dataset. This reduced dataset allowed for a better estimation of standard errors and reduce the chance of Type 1 error. Nonetheless, this chapter has run analysis on both the full dataset and reduced dataset to avoid excluding data that may have been critical. However, because of this, significance values resulting from the full dataset should be interpreted with care.

2.3.5.1. VARIABLE SELECTION AND MULTI-MODEL INFERENCING

All variables were assessed for biological relevance and plausibility by combining observational assessments and literature evidence (Table 2.2). Final model selection was determined through multi-model inference selection using R package MuMIn Version 1.41.1 (Barton & Barton 2015). This package allowed for selecting top models that best described the data according to the lowest AIC values. If any top models had delta values less than 4, and were, therefore, not considered significantly different, they were combined, and variables that did not appear in both models were averaged for relevance to describing the variation. This process produced final models that had both the best fit and the most relevant variables. Environmental variables within the models that provided significant estimate values were considered to significantly explain the variation of the dependent variable around its mean. Whether the estimate is positive or negative, defined the direction of the variation around the mean.

Table 2.2 Rationale for selection of variables to test for variation with birds, humans and therefore, their overlap.

Index	Environmental Variable	Personal Observation	Literature Evidence
Birds	Minutes from high tide (minutes)	Birds moving up and down the estuary as the tide falls and rises	Shelduck use tides to passively move on estuaries (Bryant & Leng 1975); Eider counts changed relative to tide state (Campbell 1978); Brent goose and wigeon distribution changed over a falling tide (Fox 1996)
	Percentage cover of seagrass (%)	Birds congregating in locations where seagrass was present and feeding	Brent goose and wigeon actively redistribute relative to food availability (Fox 1996); Wildfowl wetland use is affected by the density of food available (Hagy et al. 2014)
	Wind chill Index	Birds less active at lower temperatures and wind speed pushed birds into some areas of the estuary	Shorebirds feed in sheltered areas when winds are high, and temperatures are low (Evans 1976)
	Substrate type (mud, sand, rock, mixed)	Substrate type determines food resources	*Zostera marina* (L.) growth is dependent on substrate type and favoured silt and clay for root anchorage (Nishijima et al. 2015)
	Human presence/density	If humans are disturbing birds it might cause them to leave or avoid a site if humans are present, and even more so if humans are in higher densities	Declined habitat quality in the presence of human activity reduces bird use of regions (Madsen 1995)

Index	Environmental Variable	Personal Observation	Literature Evidence
	Site depth (m) (based on tide state and site elevation relative to lowest tide)	The depth of a site determined whether birds could feed	Wildfowl occupy different regions based on the accessibility of food resources which are affected by the depth of the area (White & James 1978); Brent goose and wigeon follow the exposure of seagrass (Fox 1996)
Humans	Minutes from high tide (minutes)	Human activities were restricted based on the time of the tide in relation to the depth of the site and whether a site is underwater or exposed	
	Time of day (hh:mm)	Off work hours influenced recreational activities for those individuals that were of working age	Number of daylight hours directly affects the convenience and attractiveness of humans partaking in recreational activities (de Freitas 2003)
	Day of week	Similar to off-work hours the day of the week determines if people are available to engage in extracurricular activities	
	Substrate type	Restrictions apply to certain activities on certain substrate types, such as walking on sand or bait digging in mud/sand	Bait digging occurs where the bait of choice is most abundant, which is typically lower down the shore and in sandy substrates (Blake 1979)
	Site depth (m) (based on tide state and site	The depth of the site determined whether a site was exposed	

Index	Environmental Variable	Personal Observation	Literature Evidence
	elevation relative to lowest tide)	or underwater at different tidal states which either made the site inaccessible to water sports (if low tide) or walkers (if high tide)	
	Wind chill Index	Some activities are dependent on wind presence, and human activity, in general, seemed to drop off when the temperature was lower	The climate of a region, including temperature and wind speed, influence human recreational activities and tourism (de Freitas 2003; Richardson and Loomis 2006); Wind water sports rely on minimum wind speeds for taking place (SurferToday.com 2019)
	Site Accessibility (high, medium, low)	Places that were more difficult to reach appeared to have fewer visitations from human activities	Local sites are preferentially used more frequently in high population zones to fulfil recreation needs due to their ease of accessibility (Neuvonen et al. 2010)

2.3.5.2. PRESENCE AND ABSENCE (BINOMIAL REGRESSION)

Initial analysis was performed on binomial presence and absence of birds, humans, and overlaps between the two. Bird presence was given a value of 1 if there were more than zero birds on an observation site during an observation minute. Human presence was given a value of 1 if there were more than zero human on an observation site during an observation minute. When any human activity was within the overlap distance, described in Figure 2.1, for Brent goose or Wigeon, then the event was considered an overlap. Overlap was therefore given a value of 1 only if bird presence and human presence was equal to 1 and proximity between birds and humans was within the overlap distance. After applying the values, presence and absences were evaluated relative to environmental variables (Table 2.3). These binomial assignments provided the basis for a binomial regression which was run in R using a glm regression analysis, link = logit. Binomial regression analysis examined bird species presence as the dependent variable and human presence as the independent variable to evaluate if human activity presence influences bird presence and thus, itself, potentially causing changes in the occurrence of an overlap (Table 2.4).

Table 2.3 How binomial number assignments for bird and human presence, and overlap events were determined based on the number of humans and birds and proximity.

Number of birds	**Number of humans**	**Bird presence**	**Human presence**	**Proximity within overlap distance?**	**Overlap value assignment**
0	0	0	0	No	0
0	> 0	0	1	No	0
> 0	0	1	0	No	0
> 0	> 0	1	1	No	0
0	0	0	0	No	0
0	> 0	0	1	No	0
> 0	0	1	0	No	0
> 0	> 0	1	1	Yes	1

Table 2.4 Model structure for glm analysis on Brent goose presence, wigeon presence, human presence, and overlap presence

Dependent variable	Independent variables full dataset	Sample size full dataset	Independent variables reduced dataset	Sample size reduced dataset
Brent goose presence	tidestate + windchillindex + percentseagrass + month + humanactivitypresence + sitesubstrate + siteelevation	601171	tidestate + windchillindex + percentseagrass + month + humanactivitypresence + sitesubstrate + siteelevation	20039
Wigeon presence	tidestate + windchillindex + percentseagrass + month + humanactivitypresence + sitesubstrate + siteelevation	599978	tidestate + windchillindex + percentseagrass + month + humanactivitypresence + sitesubstrate + siteelevation	19999
Human presence	tidestate + windchillindex + siteaccessibility + dayofweek + sitesubstrate + siteelevation + hourofday	600574	tidestate + windchillindex + siteaccessibility + dayofweek + sitesubstrate + siteelevation + hourofday	20019

2.3.5.3. INDEX VARIABLES

In order to help avoid overgeneralizations of birds, humans and overlap events by only referring to them as 1 or 0, an index was created to represent a range of bird and human presence and overlap levels when they were equal to 1 (Table 2.5). This index was calculated by first determining the maximum observed density of people per 100m^2 observed. After establishing the maximum observed human density, the density of individuals per 100m^2 during a given observation minute was divided by that maximum observed density per 100m^2. This calculation provides a measure of the percentage of human presence out of the maximum observed human presence on an observation site for a single minute in time (Human Density Index; Pi,t). This process was then repeated for bird density per species to create a measure of the percentage of bird species presence out of the maximum observed bird species present on a site per minute (Bird Density Index; Bi,t). After these two measures are determined, the Human Density Index and Bird Density Index were multiplied to produce an initial measure of overlap between birds and people. This measure was divided by its maximum value recorded to give a percentage of the maximum observed overlap per observation minute called the Birds Overlap People Index (BOP index).

Table 2.5 Calculation of Index variables used to understand the magnitude of overlap events.

Index	**Equation for Calculation**	**Variable Definitions**
Bird Density Index	$B_{i,t} = \frac{b_{i,t}}{b_{max}}$	$B_{i,t}$ = bird index for 100m^2 patch i at time t $b_{i,t}$ = number of birds in 100m^2 patch i at time t b_{max} = maximum number of birds observed in any 100m^2 patch at any time t
Human Density Index	$P_{i,t} = \frac{p_{i,t}}{p_{max}}$	$P_{i,t}$ = people index for 100m^2 patch i at time t $p_{i,t}$ = number of people in 100m^2 patch i at time t p_{max} = maximum number of people observed in any 100m^2 patch at any time t

Index	**Equation for Calculation**	**Variable Definitions**
BOP Index	$BOP_{i,t} = \frac{B_{i,t} \times P_{i,t}}{BOP_{max}}$	$BOP_{i,t}$ = Birds Overlap People index for 100m^2 patch *i* at time *t* $B_{i,t}$ = bird index for 100m^2 patch *i* at time *t* $P_{i,t}$ = people index for 100m^2 patch *i* at time *t* BOP_{max} = maximum observed value of Birds Overlap People index any 100m^2 patch at any time *t*

2.3.5.4. DEGREE OF OVERLAP WHEN PRESENT (BETA-REGRESSION)

The BOP index represents the magnitude of an overlap when it is present (overlap = 1). Therefore, its values were bounded by 0 and 1. Beta regression accounts for non-linearity and variable dispersion that is associated with proportional data while maintaining the ability to interpret parameters relative to the original response (Ferrari & Cribari-Neto 2004; Ospina and Ferrari 2010). Therefore, for the analysis of the BOP index, beta regression was employed using the R-package 'betareg' version 3.1-1. The following function is the basis for Beta regressions:

$$\text{logit}(y_i) = \beta_0 + \sum_{i=1}^{p} \beta_i$$

Interpretation of all coefficients derived from the beta regression is as follows:

$$\text{logit}(y_i) = \beta_0 + \sum_{i=1}^{p} \beta_i \Rightarrow y_i = \frac{e^{\beta_0 + \sum_{i=1}^{p} \beta_i}}{1 + e^{\beta_0 + \sum_{i=1}^{p} \beta_i}}$$

Beta regression evaluated the environmental variables that influenced the degree of density of birds and humans in space and time (the indexes of bird density and human density separately) as well as the BOP index.

Evaluation of these variables was performed by using five separate models. With bird density, human density and BOP index as dependent variables and environmental variables as the independent variables (Table 2.6).

Table 2.6 Model structure for beta regression analysis on Brent goose density index, wigeon density index, human density index, and BOP index.

Dependent variable	Independent variables full dataset	Sample size full dataset	Independent variables reduced dataset	Sample size reduced dataset
Brent goose density index	humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchillindex	61033	humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchillindex	1616
Wigeon density index	humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchillindex	56097	humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchillindex	1407
Human activity index	dayofweek + hourofday + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill	23120	dayofweek + hourofday + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill	771

BOP index (with Brent goose)	dayofweek + hourofday + wintermonth + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchillindex	61033	Wintermonth + siteaccessiblity + siteelevation + sitesubstrate + windchillindex	334
BOP index (with wigeon)	dayofweek + hourofday + wintermonth + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchillindex	56097	dayofweek + wintermonth + siteelevation + sitesubstrate + tidestate + windchillindex	226

2.3.5.5. DEALING WITH SPATIAL-TEMPORAL AUTOCORRELATION

Spatial-temporal autocorrelation was inevitable due to the nature of the data collected for this chapter. However, this does not necessarily have negative implications. According to Pawley & McArdle (2018), when applying analysis to describe a particular place and time that does not attempt to predict outside of the boundaries of that place and time "it (spatial-temporal autocorrelation) can improve the precision and power of (their) analysis". The basis of this chapter is to analyse a set of data on the Exe Estuary to see if particular environmental variables can be associated with overlap events within that space and time. As such, findings within this chapter will provide the basis for future research into predicting conditions, but will not be performing any actual predictions beyond the space and times of the observations. Therefore, to most accurately identify variables associated with overlaps in this chapter, rather than accounting for spatial-temporal autocorrelation, it is retained as part of the analysis.

2.4. RESULTS

2.4.1. BIRDS AND HUMANS IN SPACE AND TIME

A total of 657 hours of data were spent collecting data on human activity and bird distribution and abundance on the whole of the Exe Estuary, between September and February 2017-2018 and 2018-2019. Out of these hours, the total number of observations recorded was 1,231,366. Each observation represented a recording session, date, time of day (in minutes), site, region, primary site substrate, bird species, bird count, bird activity-budget, primary bird substrate, human activity count, human activity type, primary human activity substrate, proximity, temperature, windspeed, wind direction, day of week, tide state, percent seagrass, site elevation, bird density, human activity density, bird density index, human density index, and BOP index. These observations were then divided between Brent goose and wigeon to represent each species separately (Table 2.7). From these observations, a total of 41,045 subsamples were taken and used for reduced model analysis. Like the full model these subsamples consisted of individual bird and human data and overlap data (Table 2.7). These observations revealed that birds and humans had different distributions and abundance in space and time that varied significantly with several of the environmental variables. There were no significant correlations between the environmental variables used in final models (Figure 2.7).

Table 2.7 Sample sizes associated with the dependent variables tested in this chapter

Dependent Variable	Full dataset (N)	Reduced dataset (N)
Brent goose presence/absence	601171	20039
Wigeon presence/absence	599978	19999
Human activity presence/absence	600574	20019
Brent goose and human activity overlap presence/absence	601171	20039
Wigeon and human activity overlap presence/absence	599978	19999
Brent goose density	61033	1616
Wigeon density	56097	1407
Human activity density	23120	771
Brent goose and human activity overlap density	61033	334
Wigeon and human activity overlap density	56097	226

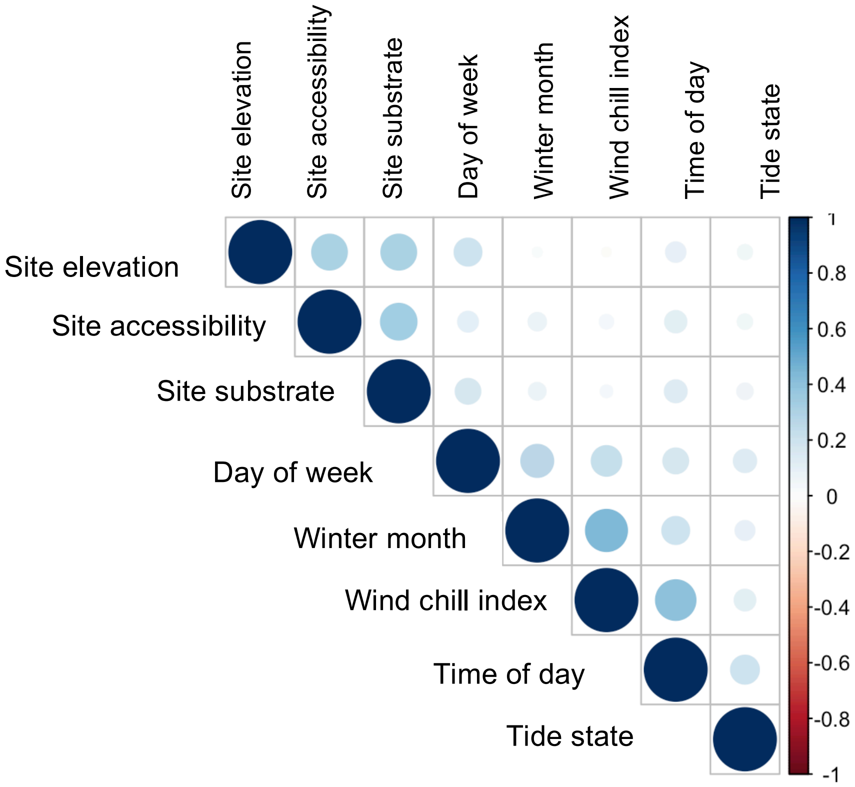


Figure 2.7 A visualization of correlations between variables used in the binomial regression equation. Colour indicates whether the correlation is positive or negative and size of the dot represents the correlation coefficient. All correlation values were considered to be non-significant with p-values > 0.05.

2.4.1.1. BIRD PRESENCE AND ABSENCE (0, 1)

Numerous environmental variables were significantly relevant in explaining the variation of presence and absence of both Brent goose and wigeon in both the full dataset and reduced dataset. These variables included human activity presence, winter month, site elevation, site substrate, tide state and wind chill index (Table 2.8).

Human activity presence was significantly positively associated with the presence of Brent goose in space and time, which means that there was a higher probability of Brent goose being present when human activities were also present. Out of the winter months, Brent goose presence had the highest significant positive association with November. Site elevation had a significantly negative association with Brent goose, which suggests that Brent goose were less likely to be found at sites with increasing elevation. Both mud and sand had significantly positive associations with Brent goose presence, however, muddy substrates produced the larger estimate indicating that out of the two, Brent goose are more likely to be found on muddy substrates, followed by sand. Out of all the tide states, high, low and rising, produced significantly negative associations with the presence of Brent goose, and no significance for falling tides. The most significant negative association was with low tide followed by high tide and then rising tide. Indicating that the least likely of the three tides for Brent goose to be present is over low tide. Lastly, Brent goose had an overall negative association with increasing wind chill index, indicating that as wind chill increases, there is a lower probability of Brent goose being present (Table 2.8; Table 2.9; Figure 2.8).

Under the following spatiotemporal conditions there is a higher probability of a Brent goose being present in one of the regions on the Exe estuary if: humans are present, during November and December, at low site elevation, on a muddy substrate, tides other than low, and little wind chill.

Associations of environmental variables with wigeon presence were similar to those of Brent goose and corresponded. The conditions associated with a higher probability of wigeon presence on the Exe estuary are: humans are present, during October, November, or December, high site elevation, on a muddy substrate, tides other than low or rising, and the wind chill is low (Table 2.8; Table 2.9; Figure 2.9).

When running the reduced dataset, all variable associations were the same with exception of the variables October and December for Brent goose and February and

September for wigeon become non-significant. Indicating that these variables potentially explain less variation within bird presence and absence than the other variables.

Table 2.8 Results from full dataset binomial regression of presence and absence of: Brent goose (n = 601171; AIC: 386906). Model glm(formula = brentgoosepresence ~ humanactivitypresent + wintermonth + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)); Wigeon (n = 599978; AIC: 32856). Model glm(formula = wigeonpresence ~ humanactivitypresent + wintermonth + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)).

	Brent goose		**Wigeon**	
Parameter	Estimate*	Pr (>|z|)	Estimate*	Pr (>|z|)
Presence of human activity	1.673106	< 2e-16 ***	1.3725553	< 2e-16 ***
Winter month: February	-1.282985	< 2e-16 ***	-1.2462993	< 2e-16 ***
Winter month: September	-3.120490	< 2e-16 ***	-0.3571334	6.01e-06 ***
Winter month: October	-0.529258	< 2e-16 ***	1.4390925	< 2e-16 ***
Winter month: November	0.253845	0.0327 ***	2.3071970	< 2e-16 ***
Winter month: December	0.083940	< 2e-16 ***	1.4664975	< 2e-16 ***
Site elevation	-0.083366	< 2e-16 ***	0.2606784	< 2e-16 ***
Substrate type: Mud	0.513562	< 2e-16 ***	1.1127564	< 2e-16 ***
Substrate type: Sand	0.287555	< 2e-16 ***	-1.1996405	< 2e-16 ***
Tide state: High	-0.281241	< 2e-16 ***	-0.5494640	< 2e-16 ***
Tide State: Low	-0.634912	< 2e-16 ***	-0.8336800	< 2e-16 ***
Tide State: Rising	-0.239275	< 2e-16 ***	-0.7065368	< 2e-16 ***
Wind chill index	-0.041365	< 2e-16 ***	-0.0393282	< 2e-16 ***

* Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

Table 2.9 Results from reduced dataset binomial regression of presence and absence of: Brent goose (n = 20039; AIC: 12791). Model glm(formula = brentgoosepresence ~ humanactivitypresent + wintermonth + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)); Wigeon (n = 19999; AIC: 11052). Model glm(formula = wigeonpresence ~ humanactivitypresent + wintermonth + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)).

	Brent goose		**Wigeon**	
Parameter	Estimate*	Pr (>|z|)	Estimate*	Pr (>|z|)
Presence of human activity	1.703871	< 2e-16 ***	1.28057	< 2e-16 ***
Winter month: February	-0.843709	0.013 ***	-2.12980	0.052
Winter month: September	-3.076098	< 2e-16 ***	-0.51002	0.281
Winter month: October	-0.359680	0.119	1.60614	0.0002 ***
Winter month: November	0.588388	0.01 ***	2.33385	5.52e-08 ***
Winter month: December	0.351440	0.126	1.55344	0.0003 ***
Site elevation	-0.141103	0.002 ***	0.27947	3.78e-11 ***
Substrate type: Mud	0.494765	1.5e-08 ***	1.14261	< 2e-16 ***
Substrate type: Sand	0.265957	0.006 ***	-1.13500	2.81e-13 ***
Tide state: High	-0.228117	0.0005 ***	-0.59685	< 2e-16 ***
Tide State: Low	-0.662046	< 2e-16 ***	-0.83780	< 2e-16 ***
Tide State: Rising	-0.245099	0.0001 ***	-0.71599	< 2e-16 ***
Wind chill index	-0.034947	< 2e-16 ***	-0.04197	< 2e-16 ***

* Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

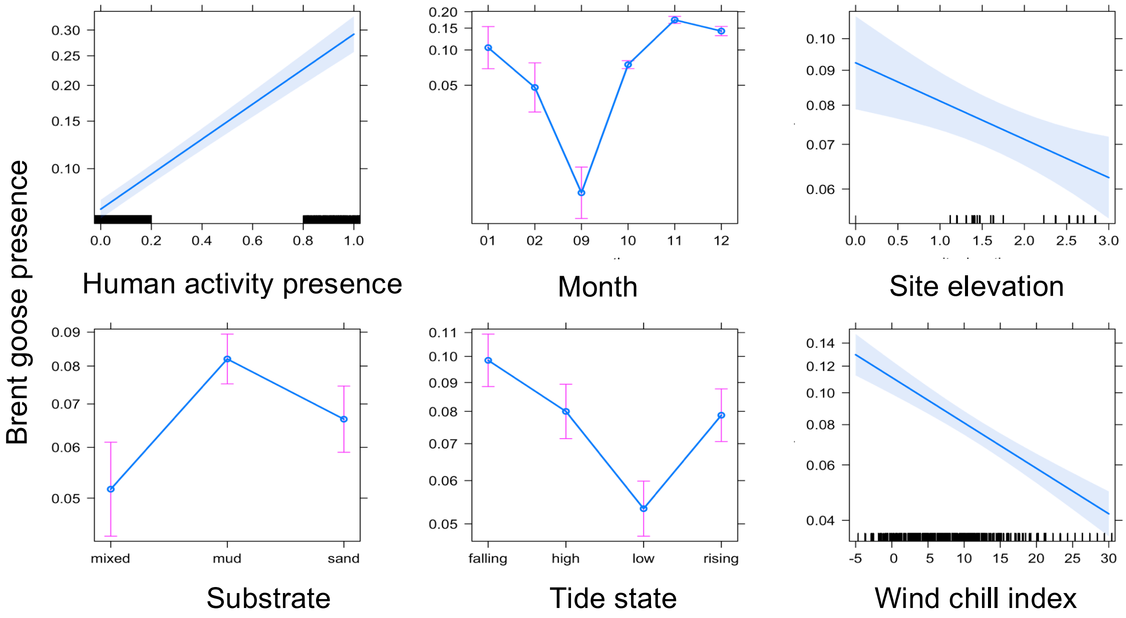


Figure 2.8 Plot of the effects of the different environmental variables used in the binomial regression model from reduced dataset for Brent goose presence (n = 20039). Shaded regions and pink lines represent confidence intervals.

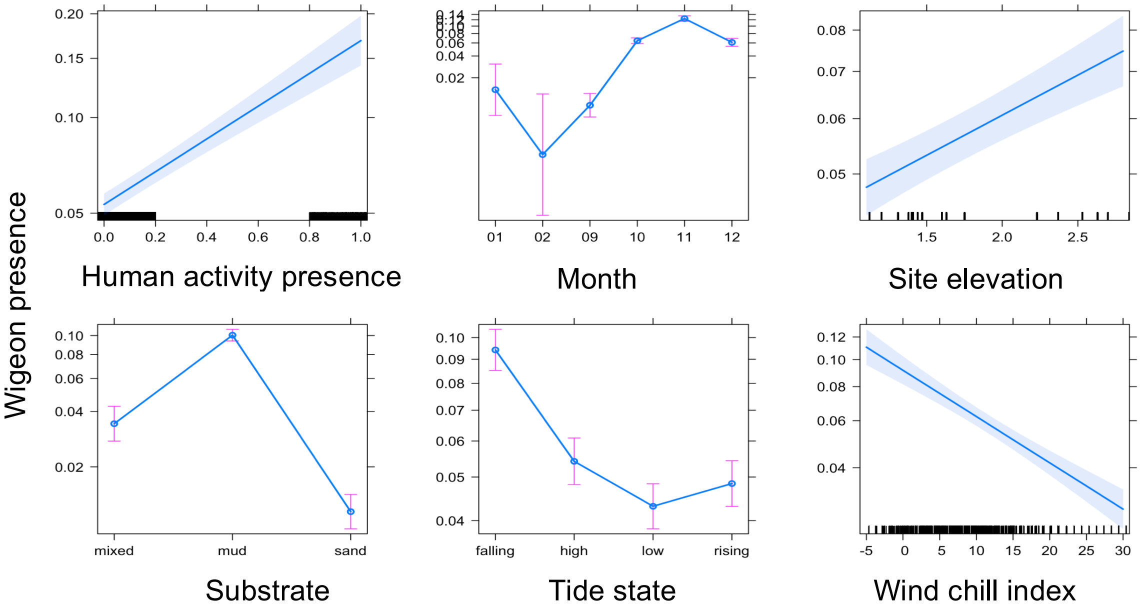


Figure 2.9 Plot of the effects of the different environmental variables used in the binomial regression model from reduced dataset for wigeon presence (n = 19999). Shaded regions and pink lines represent confidence intervals.

2.4.1.2. BIRD DENSITY INDEX ($B_{i,t}$)

Many of the environmental variables that were considered explanatory for variation in Brent goose presence were also explanatory for variation in Brent goose density. The presence of human activity again was considered a significant variable in both the full and reduced datasets, however, in this case, it had a negative relationship, and therefore Brent goose density was significantly lower when human activity was present. The full dataset indicated a potential contradiction by indicating brent goose density increased with increasing human density, however, this was no longer significant in the reduced data-set, indicating a possible sampling bias. Brent goose density measures in the full dataset were all positively associated with winter month with the strongest positive association being with September, which remained the case with the reduced dataset, with the exception of February no longer being significant. This result indicates that bird density is highest at the beginning of the season. Increasing site elevation, muddy substrates, high and rising tide, were all positively associated with Brent goose density in the full dataset. Only site elevation, high and rising tide remain significant in the reduced dataset. Sandy substrates and low tide were negatively associated with Brent goose density in the full dataset but this significance is lost in the reduced dataset. The culmination of these results is that Brent goose density is significantly higher when human activity is not present, during September, high site elevations, on a high or rising tide, and with increasing wind chill (Table 2.11; Figure 2.10).

Wigeon density, like Brent goose density, was also negatively associated with the presence of human activity but also increased with increasing density of human activity in the full dataset. In the reduced dataset the significant association of bird density with human density disappears. Additionally, similarly to Brent goose density, wigeon density was most positively associated with the earlier months of the winter season in the full dataset. However, all winter months stop being significant in the reduced dataset. Furthermore, there was a significantly positive association of wigeon density relative to increasing site elevation, muddy substrates, high tide and increasing wind chill. This is consistent in the reduced dataset. Lastly there was significantly negative association of wigeon with a low and rising tide in the full dataset, however this is lost in the reduced dataset. The combination of these results suggests that wigeon have the highest density when human activity is not present, at increasing site elevations, over muddy substrates, at high tide and with rising wind chill.

Table 2.10 Results from full dataset Beta Regression Analysis of Bird Index of Density for: Brent goose (model: betareg(formula = brentgoosedensity ~ humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchill); n = 61033; pseudo R^2 = 0.156); Wigeon (model: betareg(formula = wigeondensity ~ humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchill); n = 56097; pseudo R2 = 0.21)

Brent goose			**Wigeon**			
Parameter	**Coefficient***	**P-Value**	**Corresponding Brent goose density (per 100m^2)**	**Coefficient***	**P-Value**	**Corresponding wigeon density (per 100m^2)**
Presence of humans	-0.2874345	< 2e-16 ***	116.2450146	-0.5795640	< 2e-16 ***	535.3180888
Density of humans	0.9471239	1.49e-05 ***	195.4094726	1.8204421	1.38e-13 ***	1283.183178
Winter month: February	0.1040640	0.04737 ***	142.6491789	-0.7850873	2.87e-11 ***	467.0177198
Winter month: September	1.1870280	< 2e-16 ***	207.7959088	0.0513227	0.479451	764.6263383
Winter month: October	0.6684855	< 2e-16 ***	179.3076644	0.2186984	0.000955 ***	826.6964576
Winter month: November	0.5357263	< 2e-16 ***	171.0777568	0.0355302	0.590697	758.742489
Winter month: December	0.3446425	< 2e-16 ***	158.7381871	-0.3771641	1.49e-08 ***	606.5552954
Site elevation	0.2757832	< 2e-16 ***	154.1804863	0.0340460	7.42e-07 ***	758.1894208
Substrate type: Mud	0.1435292	< 2e-16 ***	145.3146082	0.5936833	< 2e-16 ***	960.5168398
Substrate type: Sand	-0.0266480	0.14114	133.7933725	0.0146311	0.600360	750.9536452

Tide state: High	0.1388988	< 2e-16 ***	145.0022272	0.0960526	< 2e-16 ***	781.2761047
Tide State: Low	-0.0438267	0.00034 ***	132.6290253	-0.0622236	1.94e-08 ***	722.3136337
Tide State: Rising	0.0827878	< 2e-16 ***	141.2098092	-0.0805061	2.27e-13 ***	715.5075485
Wind chill index	0.0190936	< 2e-16 ***	136.8945068	0.0135336	< 2e-16 ***	750.5445724

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

Table 2.11 Results from reduced dataset Beta Regression Analysis of Bird Index of Density for: Brent goose (model: betareg(formula = brentgoosedensity ~ humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchill); n = 1616; pseudo R^2 = 0.166); Wigeon (model: betareg(formula = wigeondensity ~ humanactivitypresent + densityhumanactivity + wintermonth + siteelevation + sitesubstrate + tidestate + windchill); n = 1407; pseudo R^2 = 0.196).

	Brent goose			**Wigeon**		
Parameter	**Coefficient***	**P-Value**	**Corresponding Brent goose density (per 100m^2)**	**Coefficient***	**P-Value**	**Corresponding wigeon density (per 100m^2)**
Presence of humans	-0.27500	2.83e-05 ***	117.0716205	-0.562296	< 2e-16 ***	541.257417
Density of humans	0.28646	0.713	154.8902559	0.581496	0.600	956.3446408
Winter month: February	0.42773	0.131	164.1658983	NA	NA	NA
Winter month: September	1.01309	0.018 ***	198.9589495	0.046371	0.937	762.7816937
Winter month: October	0.72605	9.54e-05 ***	182.7719516	0.438543	0.434	906.3964969
Winter month: November	0.58966	0.001 ***	174.4594697	0.219108	0.695	826.8473214
Winter month: December	0.43102	0.019 ***	164.1658983	-0.180827	0.748	678.2798021
Site elevation	0.28294	< 2e-16 ***	154.6563714	0.088742	0.017 ***	778.5568894
Substrate type: Mud	0.13373	0.148	144.6534056	0.657480	< 2e-16 ***	982.1128709
Substrate type: Sand	-0.06615	0.509	131.1166647	0.108010	0.490	785.7216324

	Brent goose			**Wigeon**		
Parameter	**Coefficient***	**P-Value**	**Corresponding Brent goose density (per 100m^2)**	**Coefficient***	**P-Value**	**Corresponding wigeon density (per 100m^2)**
Tide state: High	0.20190	0.001 ***	149.2425083	0.151563	0.007 ***	801.8872087
Tide State: Low	-0.00768	0.912	135.0792986	-0.041359	0.487	730.08563
Tide State: Rising	0.11846	0.05 ***	143.622209	-0.010164	0.864	741.7114016
Wind chill index	0.02136	2e-07 ***	137.0481529	0.015785	2.72e-05 ***	751.3837366

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

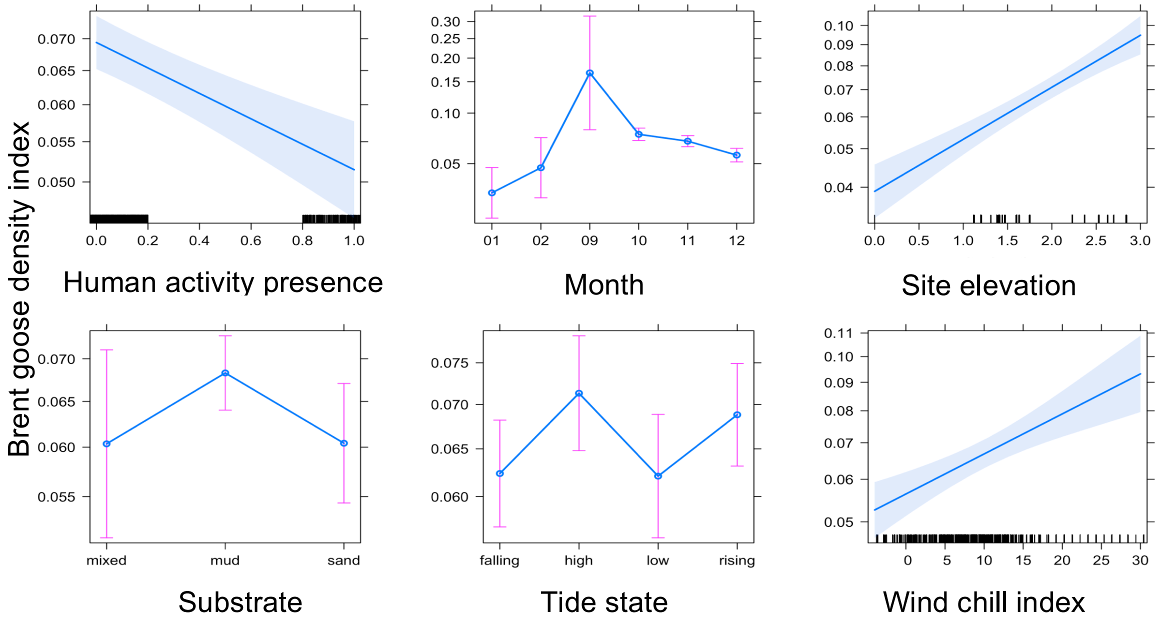


Figure 2.10 Plot of the effects of the different environmental variables used in the beta regression model from the reduced dataset for Brent goose density index (n = 1616). Shaded regions and pink lines represent confidence intervals.

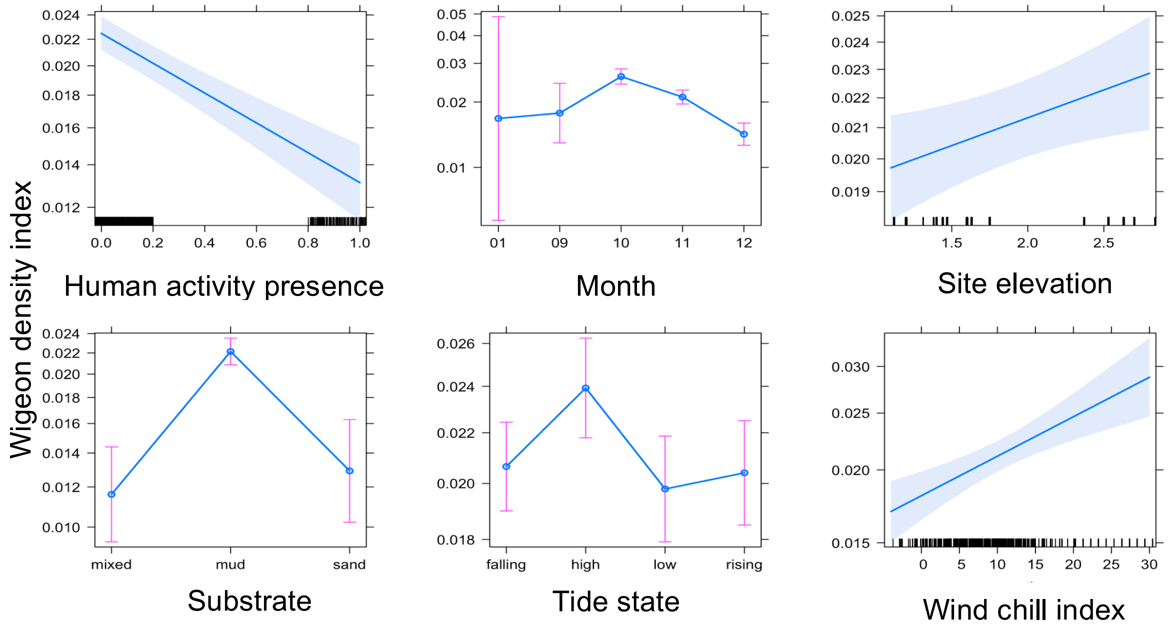


Figure 2.11 Plot of the effects of the different environmental variables used in the beta regression model from the reduced dataset for wigeon density index (n = 1407). Shaded regions and pink lines represent confidence intervals.

The Southeast regions recorded the highest density of Brent goose on the estuary. These were regions that also corresponded with the presence of seagrass, increased elevation, and muddy substrates (Figure 2.4; Figure 2.5; Figure 2.12). Wigeon density did not have as strong associations with specific areas on the estuary as Brent goose. However, there was still evidence of the wigeon preference for south-eastern and southwestern regions of the estuary (Figure 2.13).

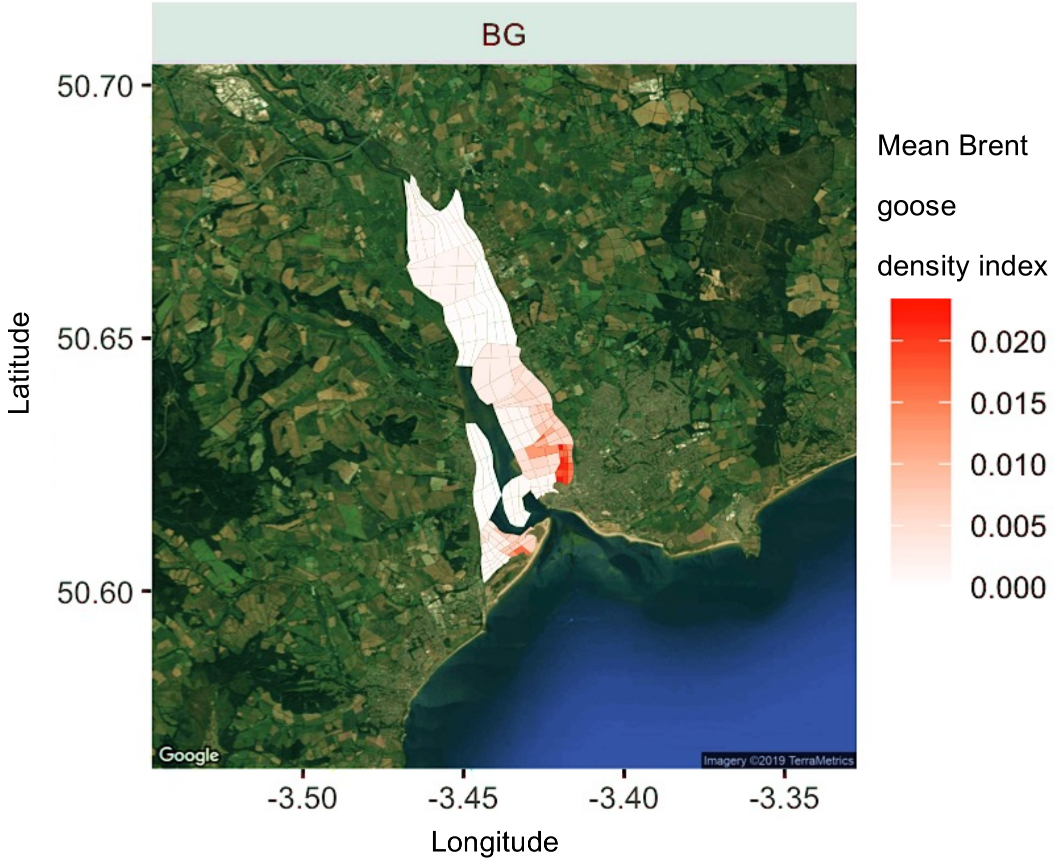


Figure 2.12 A map of Bird Density Index values of the possible presence of Brent goose per 100m^2. Reds indicate higher index values, while white indicates lower index values. Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, Map data ©2018 Google.

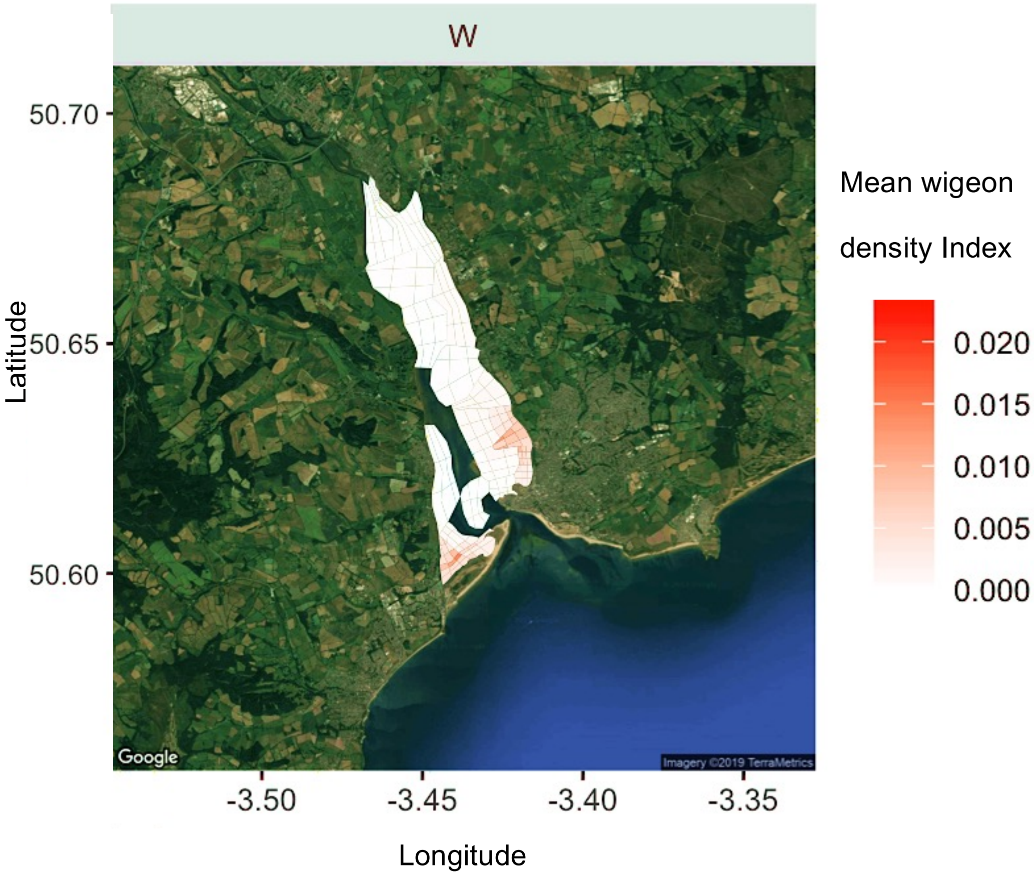


Figure 2.13 A map of Bird Density Index values of the possible presence of wigeon per 100m^2. Reds indicate higher index values, while white indicates lower index values. Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, Map data ©2018 Google.

2.4.1.3. *HUMAN ACTIVITY PRESENCE AND ABSENCE (0, 1)*

Several environmental variables significantly explained the variation in human activity presence in both the full and reduced datasets. These variables were the day of the week, the hour of the day (6:00 to 20:00), site accessibility, site elevation, site substrate, tide state and wind chill. Of these variables, Saturday, Sunday, Tuesday, Wednesday, and Thursday, were all considered to have a significant positive association with human activity presence in both the full and reduced datasets. Indicating that human activity was more likely to be present on one of these days. Both datasets revealed that time of day was not significantly associated with human activity presence, suggesting that human activities had an equal chance of occurring regardless of the time of day. Low and medium site accessibilities were negatively associated with human activity presence as were muddy substrates and rising tide and increasing wind chill in the full dataset. However, rising tide is considered non-significant in the reduced dataset. Whereas, sandy substrates, high tide, and low tide all had positive associations with human presence in the full and reduced dataset, with the exception of sand being non-signifcant in the reduced dataset. Overall, the data indicates that human activity is most likely to be present on the estuary when: it is Saturday, Sunday, Wednesday or Thursday, site elevation is high, the substrate is not mud, and the tide is high or low (Table 2.12;Table 2.13; Figure 2.14).

.

Table 2.12 Results from full dataset binomial regression of presence and absence of human activity (n=600574; AIC: 173546). Model: glm(formula = humanactivitypresent ~ day + hour + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)).

Parameter	**Estimate***	**Pr (>|z|)**
Day of week: Monday	-0.326409	< 2e-16 ***
Day of week: Saturday	0.721179	< 2e-16 ***
Day of week: Sunday	0.948682	< 2e-16 ***
Day of week: Thursday	0.803929	< 2e-16 ***
Day of week: Tuesday	0.587409	< 2e-16 ***
Day of week: Wednesday	1.344963	< 2e-16 ***
Time of day: 06:00	10.581902	0.768
Time of day: 07:00	11.822516	0.742
Time of day: 08:00	11.932464	0.740
Time of day: 09:00	12.218729	0.734
Time of day: 10:00	12.548142	0.727
Time of day: 11:00	12.435941	0.729
Time of day: 12:00	12.965501	0.718
Time of day: 13:00	12.901848	0.719
Time of day: 14:00	12.647055	0.725
Time of day: 15:00	12.684006	0.724
Time of day: 16:00	12.523618	0.727
Time of day: 17:00	12.205784	0.734
Time of day: 18:00	12.216263	0.734
Time of day: 19:00	11.249364	0.754
Time of day: 20:00	8.288918	0.817
Site accessibility: low	-1.003416	< 2e-16 ***
Site accessibility: medium	-0.608576	< 2e-16 ***
Site accessibility: mixed	-13.050854	0.784
Site elevation	0.798681	< 2e-16 ***
Substrate type: mud	-0.175458	1.49e-14 ***

Parameter	**Estimate***	**Pr (>|z|)**
Substrate type: sand	0.222763	< 2e-16 ***
Tide State: high	0.265074	< 2e-16 ***
Tide State: low	0.136270	< 2e-16 ***
Tide State: rising	-0.357031	< 2e-16 ***
Wind chill index	-0.088243	< 2e-16 ***

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant
*** Statistically significant

Table 2.13 Results from reduced dataset binomial regression of presence and absence of human activity (n=20019; AIC: 6041). Model: glm(formula = humanactivitypresent ~ day + hour + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill + 1, family = binomial(link = logit)).

Parameter	**Estimate***	**Pr (>|z|)**
Day of week: Monday	0.02670	0.908
Day of week: Saturday	0.98384	8.24e-06 ***
Day of week: Sunday	1.24430	9.55e-09 ***
Day of week: Thursday	1.04159	5.88e-06 ***
Day of week: Tuesday	0.81479	0.0003 ***
Day of week: Wednesday	1.51745	1.77e-12 ***
Time of day: 06:00	11.31508	0.970
Time of day: 07:00	11.78663	0.968
Time of day: 08:00	12.03768	0.968
Time of day: 09:00	12.52027	0.966
Time of day: 10:00	12.58414	0.966
Time of day: 11:00	12.70278	0.966
Time of day: 12:00	13.03485	0.965
Time of day: 13:00	13.04972	0.965
Time of day: 14:00	12.86413	0.966
Time of day: 15:00	12.88345	0.966
Time of day: 16:00	12.37880	0.967
Time of day: 17:00	12.23962	0.967
Time of day: 18:00	12.66176	0.966
Time of day: 19:00	11.30484	0.970
Time of day: 20:00	-0.13204	0.9997
Site accessibility: low	-0.90727	4.09e-12 ***
Site accessibility: medium	-0.49114	1.84e-08***
Site accessibility: mixed	-13.38881	0.968
Site elevation	0.76512	< 2e-16 ***
Substrate type: mud	-0.45479	0.004 ***
Substrate type: sand	-0.14407	0.364
Tide State: high	0.39545	0.0002 ***
Tide State: low	0.26768	0.009 ***

Parameter	**Estimate***	**Pr (>|z|)**
Tide State: rising	-0.22946	0.06
Wind chill index	-0.08840	< 2e-16 ***

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

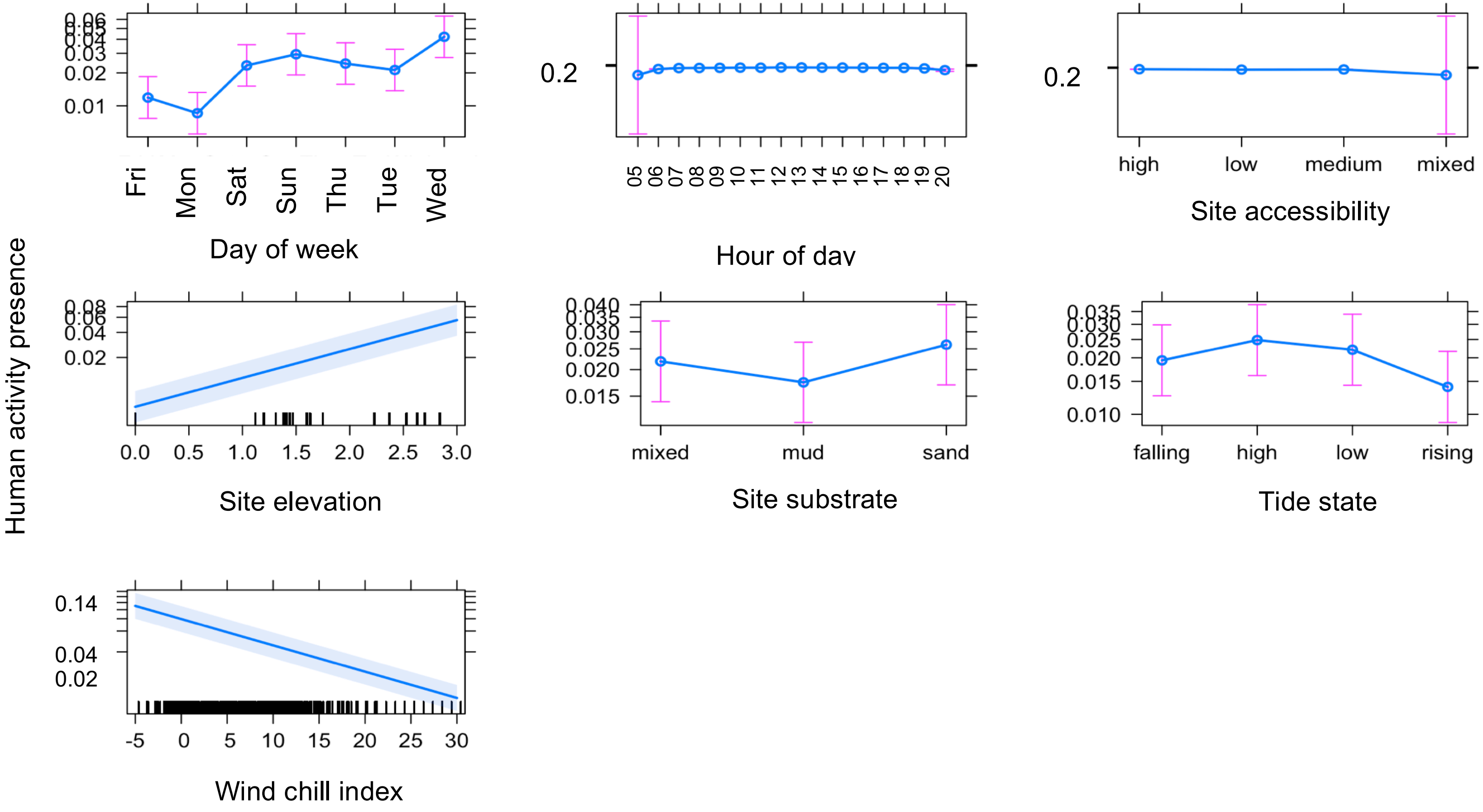


Figure 2.14 Plot of the effects of environmental variables used in the binomial regression from the reduced dataset of human activity presence (n = 20019). Shaded regions and pink lines represent confidence intervals.

2.4.1.4. *HUMAN ACTIVITY DENSITY INDEX* $(\boldsymbol{P_{i,t}})$

Evaluation of the environmental variables related to human index of density revealed that the same variables that were considered to best explain human activity presence also significantly explained human activity density. However, unlike human activity presence, human activity density was only significantly positively associated with Sunday in the full-dataset and wasn't significantly positive for any days in the reduced dataset. Additionally, the full dataset revealed times 11:00 and 12:00 were detected as being associated with significantly greater densities of human activities, however no times were significant in the reduced dataset. Similar to human activity presence, human activity density in the full dataset also had the highest positive relationships with increasing site elevation, sandy substrates, low tide and high tide, but also had a positive association with muddy substrates, rising tide and increasing wind chill. This was consistent in the reduced dataset with the exception of high tide and mud being non-significant. Low and medium site accessibility remained negatively associated with human activity density in both the full and reduced datasets. Therefore, the variables that together are associated with high human activity density in both datasets are: high site elevation; low and rising tide; and high wind chill (Table 2.14;Table 2.15;Figure 2.15).

Table 2.14 Results from full dataset Beta Regression Analysis of Human Activity Index of Density (model: betareg(formula= Humanactivitydensity ~ day + hour + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill); n = 23120; pseudo R^2 = 0.39).

Parameter	**Coefficient**$^{\#}$	**P-Value**	**Interpreted corresponding human activity density (per 100m^2)**
Day of week: Monday	-0.1168875	1.96e-06 ***	1.365352916
Day of week: Saturday	-0.0003013	0.98927	1.449781558
Day of week: Sunday	0.1487542	1.29e-11 ***	1.557648366
Day of week: Thursday	-0.4600802	< 2e-16 ***	1.122203715
Day of week: Tuesday	-0.2130975	< 2e-16 ***	1.296086314
Day of week: Wednesday	-0.2010631	< 2e-16 ***	1.304718357
Time of day: 11:00	0.2314273	0.02258 *	1.617039922
Time of day: 12:00	0.4087946	5.51e-05 ***	1.742316553
Time of day: 19:00	-0.6952477	8.14e-08 ***	0.965313473
Site accessibility: low	-0.4553717	< 2e-16 ***	1.125444638
Site accessibility: medium	-0.2793254	< 2e-16 ***	1.248795596
Site elevation	0.4146515	< 2e-16 ***	1.746387816
Substrate type: mud	0.0578329	0.00467 **	1.49191717

Parameter	**Coefficient**#	**P-Value**	**Interpreted corresponding human activity density (per 100m^2)**
Substrate type: sand	0.1652097	2.02e-15 ***	1.569505339
Tide State: high	0.1133859	< 2e-16 ***	1.532116819
Tide State: low	0.1470981	< 2e-16 ***	1.556454238
Tide State: rising	0.0632539	1.16e-06 ***	1.495843793
Wind chill index	0.0245270	< 2e-16 ***	1.467781184

#Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

Table 2.15 Results from reduced dataset Beta Regression Analysis of Human Activity Index of Density (model: betareg(formula= Humanactivitydensity ~ day + hour + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill); n = 771; pseudo R^2 = 0.44).

Parameter	**Coefficient**#	**P-Value**	**Interpreted corresponding human activity density (per 100m^2)**
Day of week: Monday	-0.374950	0.045 ***	1.18130187
Day of week: Saturday	-0.156598	0.363	1.3366979
Day of week: Sunday	0.055525	0.741	1.49024529
Day of week: Thursday	-0.659850	0.0003 ***	0.98824259
Day of week: Tuesday	-0.347720	0.064	1.20041273
Day of week: Wednesday	-0.297407	0.077	1.23595531
Time of day: 11:00	0.140029	0.796	1.55135546
Time of day: 12:00	0.365758	0.499	1.71225734
Time of day: 19:00	-0.775274	0.317	0.91448409
Site accessibility: low	-0.583805	2.64e-06 ***	1.03836685
Site accessibility: medium	-0.307726	4.18e-06 ***	1.22864269
Site elevation	0.505430	< 2e-16 ***	1.8088302
Substrate type: mud	-0.031544	0.815	1.4271325
Substrate type: sand	0.178620	0.192	1.57915629
Tide State: high	0.118941	0.127	1.53613071
Tide State: low	0.187295	0.023 ***	1.58539331
Tide State: rising	0.257224	0.003 ***	1.63546593
Wind chill index	0.025337	3.80e-07 ***	1.46836834

#Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

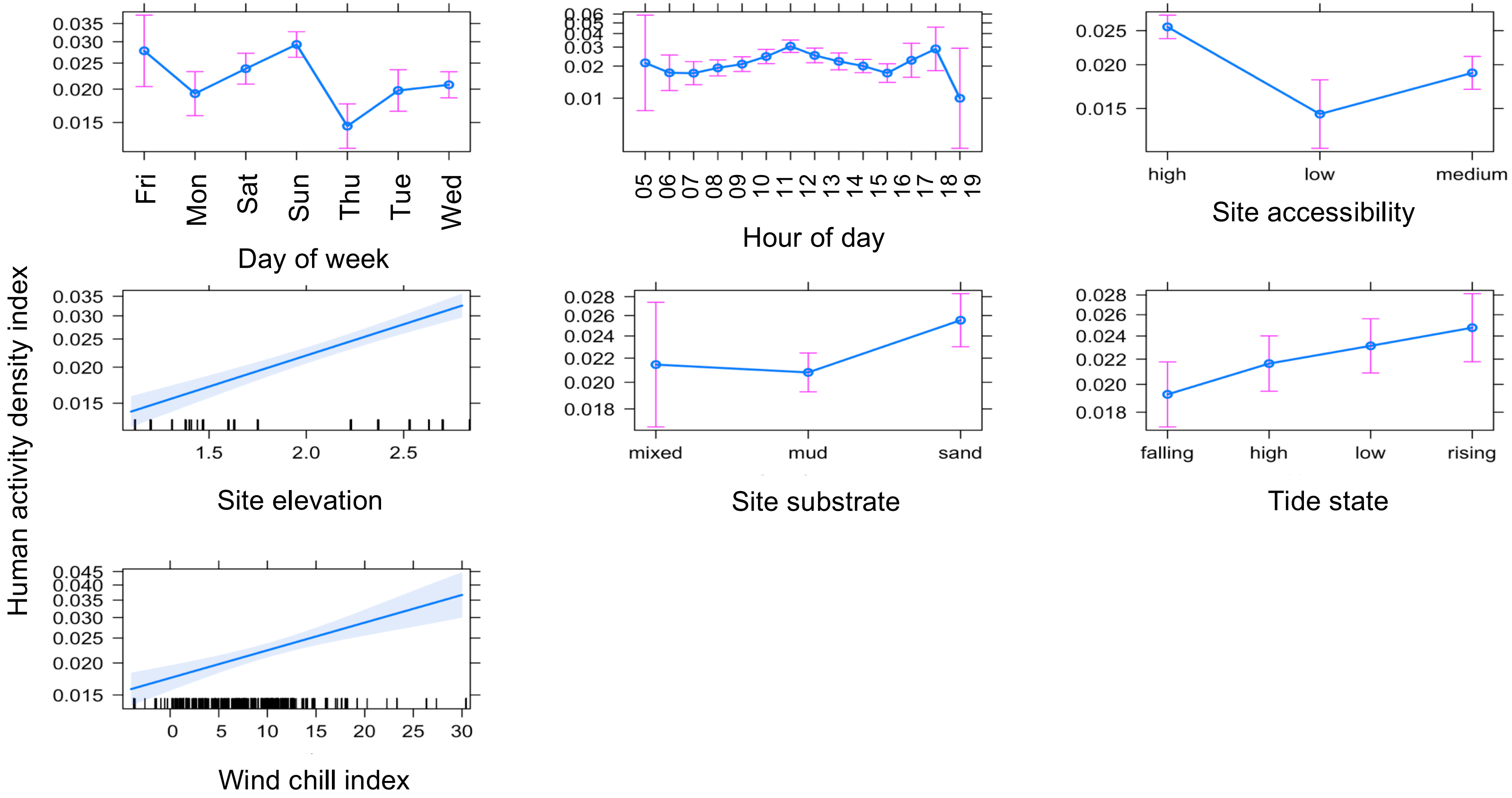


Figure 2.15 Plot of the effects of different environmental variables used in the beta regression from the reduced dataset of human activity density (n = 771). Shaded regions and pink lines represent confidence intervals.

Relative to the site geography, the highest human activity densities are in the South-eastern and western regions of the estuary (Figure 2.16). These regions correspond with high accessibility, sandy substrates and high elevations (Figure 2.3; Figure 2.5), which is consistent with the variables that were significantly associated with increases in human activity density (Table 2.14).

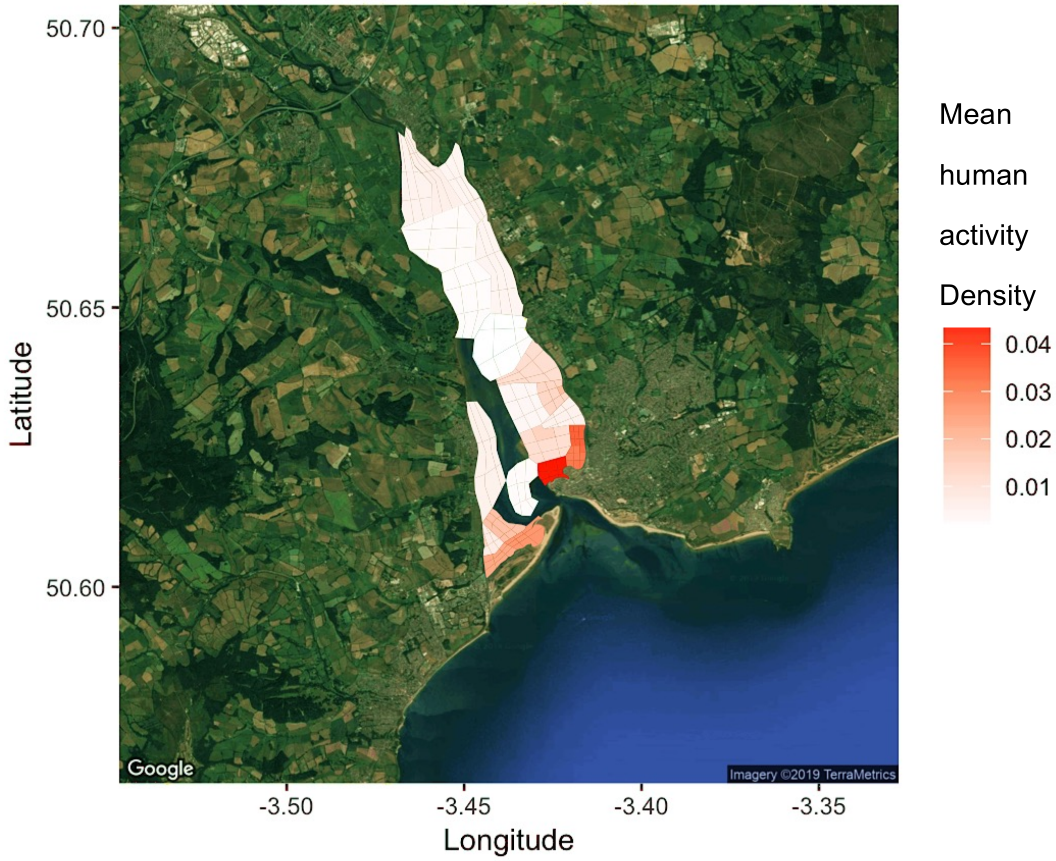


Figure 2.16 A map of human activity density index values per 100m^2. Reds indicate higher index values, while white indicates lower index values. Highest index values for human activity were in the south-eastern and southwestern regions of the Estuary; Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, Map data ©2018 Google.

2.4.2. OVERLAP AND BOP INDEX VALUES IN SPACE AND TIME

2.4.2.1. OVERLAP PRESENCE AND ABSENCE

The presence and absence of overlap in human activity relative to Brent goose revealed that the environmental variables considered to best explain the variation in overlap were: the day of the week, time of day, winter month, site accessibility, site elevation, site substrate, tide state and wind chill. These were all variables that were also relevant for explaining the variation in Brent goose presence and human activity presence independently. The variables that were significantly associated with increased probability of overlap were: Saturday, Sunday, and Tuesday, medium site accessibility, increasing site elevation, and high tide. Environmental variable values associated with decreasing probability of overlap were: Monday, Thursday, and Wednesday; February, September, October, and December; low, and mixed site accessibility; low, and rising tide; and increasing wind chill.

The results of binomial regression for evaluation of the presence and absence of overlap between human activity and wigeon revealed similar results to that of Brent goose. Day of week, hour of day, winter month, site accessibility, site elevation, site substrate, tide state and wind chill were all variables that were considered to best explain the variation in the presence of an overlap between human activity and wigeon. Sunday was the only day of the week that was significantly associated with an increase in the probability of overlap between human activity and wigeon. Other environmental variables that were significantly associated with the increasing likelihood of overlap were: the months of February, October, and November, medium site accessibility, muddy substrate, and increasing site elevation. Negative probabilities in the overlap between human activity and wigeon occurred in the following variables: the winter months of September, and December, low site accessibility, sandy substrates, low, high or rising tides, and increasing wind chill.

2.4.2.2. BOP INDEX IN SPACE AND TIME

The model formula used for the comparing the BOP index to Brent goose in the full dataset was as follows: betareg(formula = BOP index ~ day + hour + wintermonth + siteaccessibility + siteelevation + sitesubstrate + tidestate + windchill; Table 2.16). For wigeon several models were considered to adequately explain changes in BOP Index. Therefore, a conditionally - averaged model was used (Table 2.16). The following variables were used in the conditionally-averaged model: day of week (1), hour of day (2), winter month (3), site accessibility (4), site elevation (5), site substrate (6), tide state

(7), wind chill index (8). Four component models were selected from these variables to generate final model average. These models had the following variables, in the following order with the respective delta AIC values: 1234678 (AIC = -77422.14); 123467 (AIC = -77421.84); 12345678 (AIC = -77420.29); 1234567 (AIC = -77420.23).

The same environmental variables that best explained the variation in the probability of overlap between human activities and Brent goose, also best explained the change in the BOP index relative to Brent goose in the full dataset. These variables were the day of the week, time of day, winter month, site accessibility, site elevation, site substrate, tide state and wind chill. Contrary to the finding of the overlap with Brent goose, the BOP index was significantly positively associated with the day of the week Monday. In contrast, it was negatively associated with the days Thursday, Tuesday and Wednesday. Furthermore, in the full-dataset the time 17:00 was significantly associated with positive increases in the BOP index. In this analysis, there were not enough individual observations of each winter month to adequately analyse the variable at the factor level. Therefore, the variable was run as a numeric vector, which produced a significant relationship relative to increasing BOP index values. This considerable relationship indicates that as the month increases, there tend to be higher BOP index values, but it is unclear which months are the most influential. The remaining variable values had significantly positively correlated with BOP index values were: increasing site elevation; high and rising tide; and increasing wind chill. The residual environmental variable values significantly negatively associated with BOP index values were: low and medium site accessibility; sandy substrates; and low tide (Table 2.16).

The beta regression of the full dataset for BOP Index relative to wigeon indicated that more than four separate combinations of environmental variables were able to explain the variation in the BOP index equally. Therefore, model averaging was employed to produce a final model with automatically calculated weighted values applied to variables that did not show up in all models (Barton & Barton 2015). These weighted values represent the amount of consequence a variable has in describing the final model. For example, if a variable only shows up in one of the three top models, then the weight for that variable in the final averaged model is one-third. In this analysis, the final averaged model had the following variables: day of the week, the hour of the day, winter month, site accessibility, site elevation, site substrate, tide state and wind chill index. Both wind chill index and site elevation only appeared in two out of the four models and were given the weights of 0.53 and 0.30 respectively. The result is that two model options are presented; one with the values as if all variables are treated equally; and one with weighted values.

The results of the full dataset model indicate that the variables that were significantly associated with increasing BOP index values with wigeon were: Mondays and Saturdays; the months, September, October, November, and December; medium site accessibility; and sandy substrates. Those variable values associated with decreasing BOP index values with wigeon were: Thursday and Tuesday; hours of the day between 7:00 and 17:00; the month of February; low site accessibility; and low and rising tide (Table 2.16; Figure 2.17).

Table 2.16 Results from full dataset Beta Regression Analysis of BOP Index relative to Brent goose (n = 10020; pseudo-R^2 = 0.33) and wigeon (n = 6782).

	Brent goose		**Wigeon**	
Parameter	**Coefficient***	**P-Value**	**Coefficient***	**P-Value**
Day of week: Monday	0.149722	0.00362 ***	0.661737	< 2e-16 ***
Day of week: Saturday	0.016887	0.72075	0.204964	0.000965 ***
Day of week: Sunday	0.057175	0.21255	-0.107317	0.080666
Day of week: Thursday	-0.339488	1.34e-09 ***	-0.299618	2.30e-06 ***
Day of week: Tuesday	-0.139432	0.00690 ***	-0.441485	< 2e-16 ***
Day of week: Wednesday	-0.156456	0.00116 ***	0.109672	0.058215
Time of day: 07:00	NA	NA	-1.291975	1.10e-06 ***
Time of day: 08:00	0.157305	0.04942 ***	-1.318714	1.00e-07 ***
Time of day: 09:00	0.010752	0.89104	-1.259974	5.00e-07 ***
Time of day: 10:00	0.116714	0.13211	-1.107220	9.30e-06 ***
Time of day: 11:00	0.105937	0.17646	-1.176781	2.50e-06 ***
Time of day: 12:00	0.103808	0.18573	-1.205334	1.20e-06 ***
Time of day: 13:00	-0.160537	0.05178	-1.052650	2.43e-05 ***
Time of day: 14:00	-0.032121	0.70323	-1.242250	6.00e-07 ***
Time of day: 15:00	0.026364	0.74109	-1.152046	2.20e-06 ***
Time of day: 16:00	0.073038	0.40880	-1.142614	4.90e-06 ***
Time of day: 17:00	1.256706	1.22e-12 ***	-1.337774	0.000602 ***
Time of day: 18:00	NA	NA	-0.604332	0.320579
Winter month: February	NA	NA	-0.460020	0.009174 ***
Winter month: September	NA	NA	2.625633	< 2e-16 ***
Winter month: October	NA	NA	1.218827	< 2e-16 ***
Winter month: November	NA	NA	1.285340	< 2e-16 ***
Winter month: December	NA	NA	0.928764	< 2e-16 ***
Winter month: General	0.025777	9.24e-06 ***	NA	NA

	Brent goose		**Wigeon**	
Parameter	**Coefficient***	**P-Value**	**Coefficient***	**P-Value**
Site accessibility: low	-0.261945	3.31e-07 ***	-0.183321	0.000427 ***
Site accessibility: medium	-0.109876	5.75e-05 ***	0.112649	7.24e-05 ***
Substrate type: mud	0.197729	< 2e-16 ***	0.113357	0.103166
Substrate type: sand	0.040742	0.47120	0.923469	< 2e-16 ***
Tide State: high	-0.287432	5.59e-07 ***	-0.011050	0.722118
Tide State: low	0.122277	8.40e-06 ***	-0.492780	< 2e-16 ***
Tide State: rising	-0.270785	2.45e-12 ***	-0.535860	< 2e-16 ***
Wind chill index	0.067964	0.03727 ***	0.002741/ 0.005185#	0.438149/ 0.117370#
(Phi)	NA	NA	96.748186	< 2e-16 ***
Site elevation	0.011147	1.96e-07 ***	-0.004185/ -0.014165#	0.790214/ 0.591376#

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

Conditional average

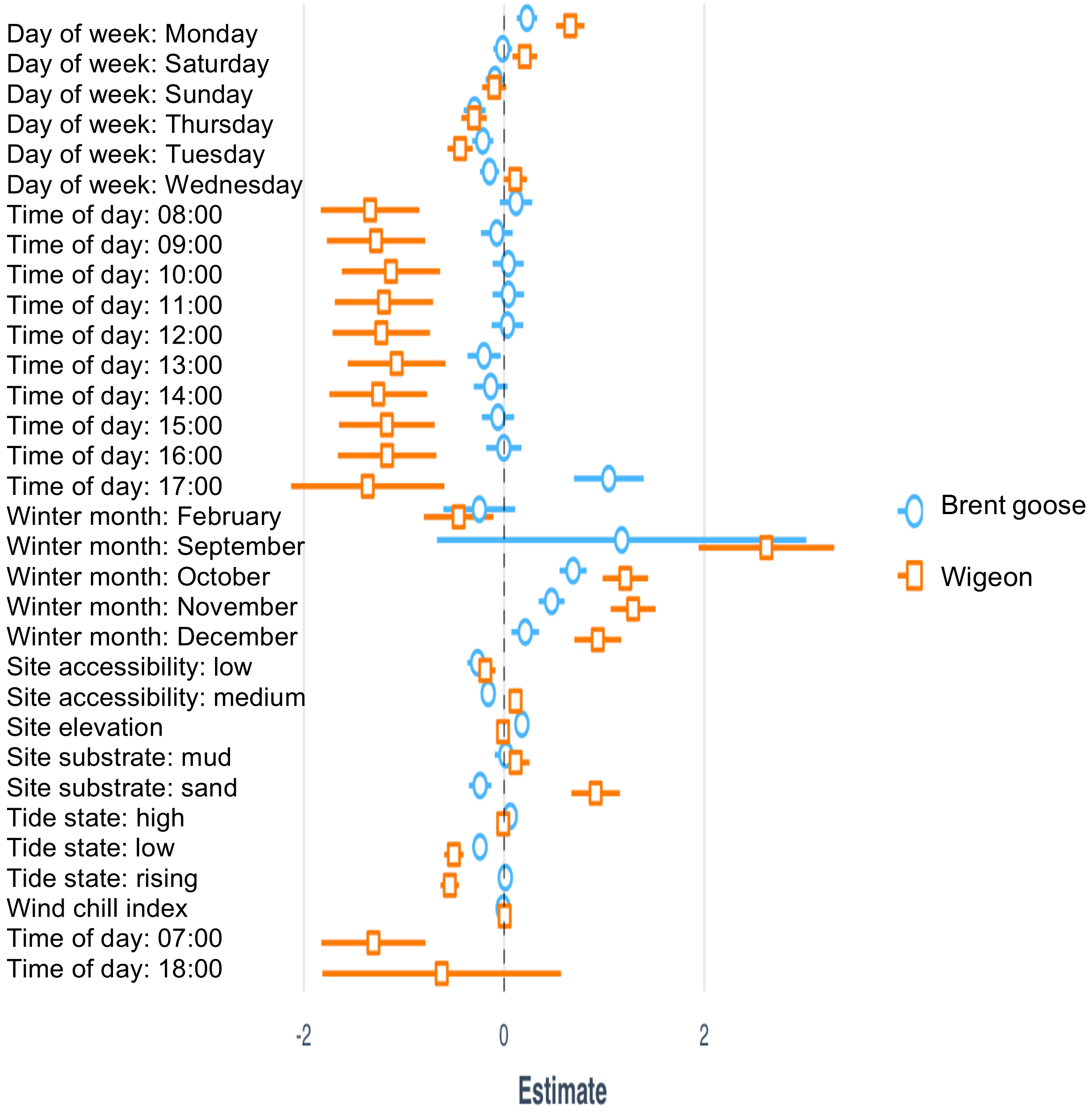


Figure 2.17 A visual representation of the coefficient estimates derived from the beta regression of BOP Index (Table 2.16) between humans and Brent goose (blue) and wigeon

Multiple models were found to be relevant to describing the BOP index in the reduced dataset. Therefore, model averaging was employed again. For the reduced-dataset models, for both Brent goose and wigeon, model structures differed from full-dataset models (Table 2.17). For Brent goose, the following variables were selected: winter month (1), site accessibility (2), site elevation (3), site substrate (4), wind chill index (5). Then three component models were selected using those five variables, for the final model average. The respective variables selected, their order in the model and their delta

AIC values are as follows: 1235 (AIC = -3100.62); 12345 (AIC = -3098.38); 123 (AIC = -3096.73. For wigeon the following variables were selected: day of week (1), winter month (2), site elevation (3), site substrate (4), tide state (5), wind chill index (6). From these variables, four component models were selected for the final model average. The respective models and the order of their variables with corresponding delta AIC values are as follows: 1245 (AIC = -2638.58); 12456 (AIC = -2637.03); 123456 (AIC = -2634.87); 12356 (AIC = -2634.80).

In the reduced dataset, the BOP index with Brent goose, day of week and tide state were eliminated during model selection and therefore were not considered to be relevant variables. Only month, site accessibility, wind chill and site elevation were considered to significantly explain BOP index variability with Brent goose. Based on the reduce dataset, highest BOP Index values were associated with October, November and December with increasing site elevation (Figure 2.18).

Concerning wigeon in the reduced dataset, site accessibility was not considered relevant for describing the BOP index. Furthermore, only day of week, month, tide state and substrate types were found to account for significant variation in the BOP index. Of these, November and sandy substrates were significantly associated with positive BOP index values with wigeon. Whereas, Thursday, Tuesday, and low tide were significantly associated with negative BOP index values (Figure 2.19).

Table 2.17 Results of reduced, conditionally - averaged models from Beta Regression Analysis of BOP Index relative to Brent goose (n = 334) and wigeon (n=226).

	Brent goose		**Wigeon**	
Parameter	**Coefficient***	**P-Value**	**Coefficient***	**P-Value**
Day of week: Monday	NA	NA	0.300454	0.411
Day of week: Saturday	NA	NA	-0.009598	0.979
Day of week: Sunday	NA	NA	-0.518538	0.120
Day of week: Thursday	NA	NA	-0.678739	0.05 ***
Day of week: Tuesday	NA	NA	-0.792868	0.02 ***
Day of week: Wednesday	NA	NA	-0.592583	0.06
Winter month: February	NA	NA	-0.909052	0.157
Winter month: October	1.33643	2.00e-06 ***	0.725275	0.103
Winter month: November	1.05062	3.94e-05***	1.109962	0.01 ***
Winter month: December	0.58520	0.032***	0.562612	0.231

	Brent goose		**Wigeon**	
Parameter	**Coefficient***	**P-Value**	**Coefficient***	**P-Value**
Site accessibility: low	-0.66628	0.004 ***	NA	NA
Site accessibility: medium	-0.38534	0.002 ***	NA	NA
Site elevation	0.30308	0.001 ***	-0.016061/ -0.092481[#]	0.817/ 0.519[#]
Tide State: high	NA	NA	-0.048091	0.76630
Tide State: low	NA	NA	-0.669960	0.003 ***
Tide State: rising	NA	NA	-0.305004	0.193
Wind chill index	-0.02747/ -0.03044[#]	0.05***/ 0.008***[#]	0.008173/ 0.018841[#]	0.594/ 0.308[#]
(Phi)	65.97665	< 2e-16 ***	144.700674	< 2e-16 ***
Substrate type: mud	0.03919/ 0.17632[#]	0.772/ 0.464[#]	0.227627/ 0.248861[#]	0.569/ 0.545[#]
Substrate type: sand	-0.01589 /-0.0715[#]	0.895/ 0.773[#]	1.075314/ 1.175627[#]	0.08/ 0.03 ***[#]

*Log odds relative to 1 unit of change in the parameter value, when all other values are held constant

*** Statistically significant

[#] Conditional average

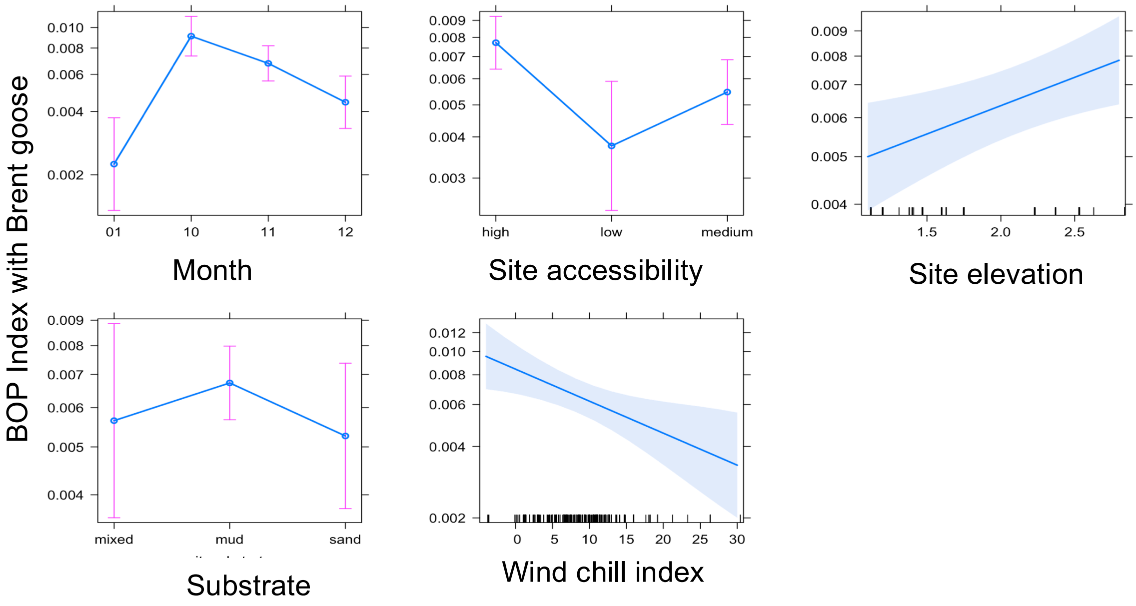


Figure 2.18 Plot of the effects of different environmental variables used in the beta regression from the reduced dataset of BOP Index with Brent goose (n = 334). . Shaded regions and pink lines represent confidence intervals.

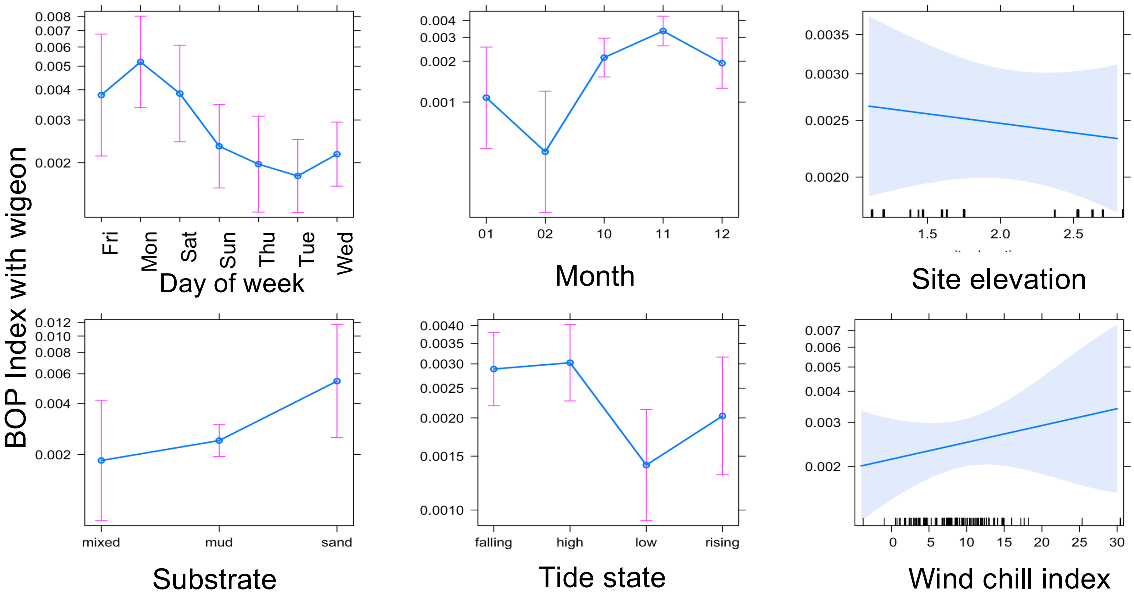


Figure 2.19 Plot of the effects of different environmental variables used in the beta regression from the reduced dataset of BOP Index with wigeon (n = 226). Shaded regions and pink lines represent confidence intervals.

The same regions of the estuary that corresponded to a high density of Brent goose (Figure 2.12) and human activities (Figure 2.16) were the regions that corresponded to high BOP index overlaps (Figure 2.20). Additionally, these regions contained values of environmental variables such as high accessibility and muddy substrates, that corresponded with the significant variables detected in the beta regression (Figure 2.5; Table 2.16; Table 2.17; Figure 2.18).

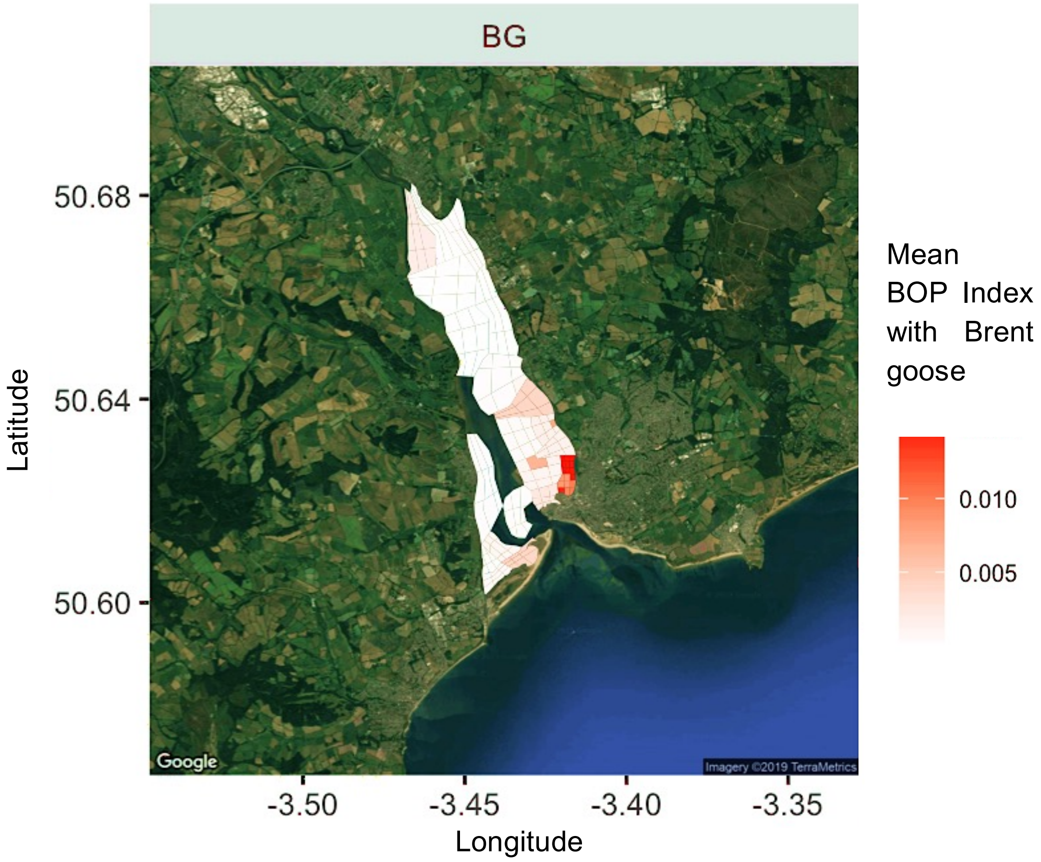


Figure 2.20 Magnitude of BOP Index values throughout the estuary relative to Brent goose. Highest values of overlap (red) were in southeast regions of the Estuary; Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, Map data ©2018 Google.

The BOP index relative to wigeon show a similar distribution in space to that of Brent goose. Highest index values were in the southeast, and southwest regions of the Estuary (Figure 2.21). Again, these were regions that have increased site elevation, site accessibility, and sandy substrates. The variable values were all listed in the model as being positively associated with BOP index values in the beta regression model (Table 2.16; Table 2.17; Figure 2.19).

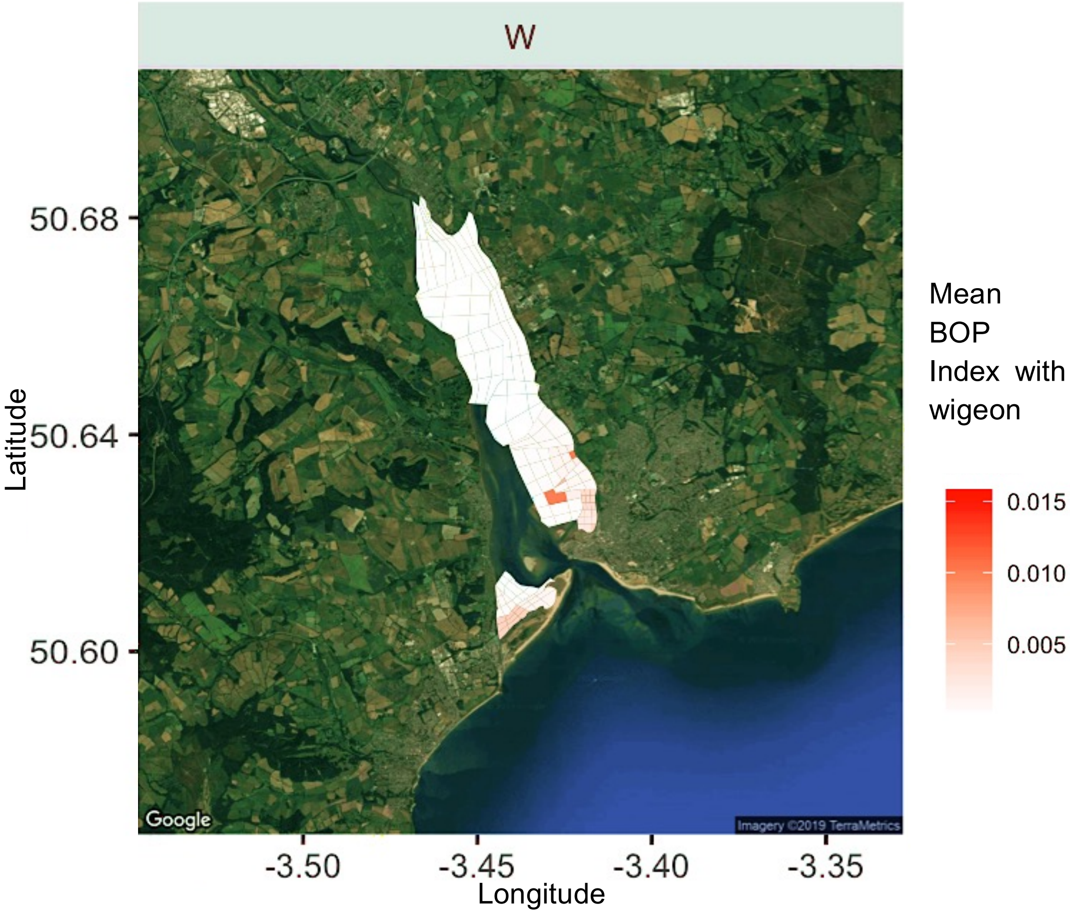


Figure 2.21 Magnitude of BOP Index values throughout the estuary relative to wigeon. Highest values of overlap (red) were in southeast regions of the estuary; Service Layer Credits: © Crown Copyright Ordnance Survey Limited 2018, Map data ©2018 Google.

The combination of human presence and bird presence appears to contribute to the presence of overlap (Table 2.18). As does the combination of human density and bird density with respect to the BOP index (Table 2.19). However, some discrepancies are apparent that are further examined in the discussion.

Table 2.18 A representation of how the combination of significant variables from the full dataset associated with human presence and bird presence can help interpret variables with significant overlap values relative to each species. (+) indicates a significantly positive variability, (-) indicates a significantly negative variability and (N/A) means that variable was not separately evaluated within the column.

Parameter	HUMAN PRESENCE	WIGEON PRESENCE	WIGEON OVERLAP PRESENCE	HUMAN PRESENCE	BG PRESENCE	BG OVERLAP PRESENCE
Day of week: Monday	-	N/A	-	-	N/A	-
Day of week: Saturday	+	N/A	+	+	N/A	+
Day of week: Sunday	+	N/A	-	+	N/A	+
Day of week: Thursday	+	N/A	-	+	N/A	-
Day of week: Tuesday	+	N/A	-	+	N/A	+
Winter month: February	N/A	-	+	N/A	-	-
Winter month: September	N/A	-	-	N/A	-	-
Winter month: October	N/A	-	+	N/A	-	-
Winter month: November	N/A	+	+	N/A	+	-
Winter month: December	N/A	+	-	N/A	+	-
Site accessibility: low	-	N/A	-	-	N/A	-
Site accessibility: medium	-	N/A	+	-	N/A	+
Substrate type: mud	-	+	+	-	+	
Substrate type: sand	+	-	-	+	+	
Tide State: high	+	-	-	+	-	+
Tide State: low	+	-	-	+	-	-
Tide State: rising	-	-	-	-	-	-
Wind chill index	-	-	-	-	-	-
Site elevation	+	+	+	+	-	+

Table 2.19 How values of human and bird density from the full dataset associated with different environmental variables can help interpret the variables that were significant relative to BOP index values. (+) indicates a significantly positive variability, (-) indicates a significantly negative variability and (N/A) means that variable was not separately evaluated within the column.

Parameter	**HUMAN DENSITY**	**WIGEON DENSITY**	**WIGEON BOP INDEX**	**HUMAN DENSITY**	**BG DENSITY**	**BG BOP INDEX**
Day of week: Monday	-	N/A	+	-	N/A	+
Day of week: Saturday		N/A	+		N/A	
Day of week: Thursday	-	N/A	-	-	N/A	-
Day of week: Tuesday	-	N/A	-	-	N/A	-
Day of week: Wednesday	-	N/A		-	N/A	-
Time of day: 07:00		N/A	-		N/A	
Time of day: 08:00		N/A	-		N/A	+
Time of day: 09:00		N/A	-		N/A	
Time of day: 10:00		N/A	-		N/A	
Time of day: 11:00	+	N/A	-	+	N/A	
Time of day: 12:00	+	N/A	-	+	N/A	
Time of day: 13:00		N/A	-		N/A	
Time of day: 14:00		N/A	-		N/A	
Time of day: 15:00		N/A	-		N/A	
Time of day: 16:00		N/A	-		N/A	
Time of day: 17:00		N/A	-		N/A	+
Winter month: February	N/A	-	-	N/A	+	
Winter month: September	N/A		+	N/A	+	

Parameter	**HUMAN DENSITY**	**WIGEON DENSITY**	**WIGEON BOP INDEX**	**HUMAN DENSITY**	**BG DENSITY**	**BG BOP INDEX**
Winter month: October	N/A	+	+	N/A	+	
Winter month: November	N/A		+	N/A	+	
Winter month: December	N/A	+	+	N/A	+	
Winter month: General	N/A	N/A	N/A	N/A	+	+
Site accessibility: low	-	N/A	-	-	N/A	-
Site accessibility: medium	-	N/A	+	-	N/A	-
Substrate type: mud	+	+		+	+	+
Substrate type: sand	+		+	+		
Tide State: high	+	+		+	+	-
Tide State: low	+	-	-	+	-	+
Tide State: rising	+	-	-	+	+	-
Wind chill index	+	+		+	+	+
Site elevation	+	+		+	+	+

2.5. DISCUSSION

Data collected between September and February 2017-2018 and 2018-2019 on human activity and wildfowl distribution and abundance on the Exe Estuary, Devon, England, detected significant variation in overlaps between birds and human activities relative to variation of several environmental variables. When evaluating bird density and human activity density separately in space and time, it was evident that measures of environmental variables that corresponded with high frequencies of both birds and humans were the same variable measures that corresponded with high spatiotemporal overlaps between birds and human activities. Additionally, based on the measures in this chapter, there is little evidence to suggest that human activities are significantly negatively impacting Brent goose and wigeon distribution in space and time.

2.5.1. BIRDS IN SPACE AND TIME

The primary environmental factors that best explained the variation of bird presence and absence, as well as the density of birds in a region, were the same for both Brent goose and wigeon. These variables were the presence and magnitude of human activity, winter month, site elevation, substrate type, tidal state, and wind chill index. These findings are mostly consistent with what the literature indicates are driving factors for wildfowl distribution and abundance in space and time.

Much of the literature surrounding wildfowl suggests that human activity can be associated with a decrease in site use for wildlife due to either degradation of the site or general human disturbance (Knight & Cole 1995; Madsen 1995). If this were taking place on the estuary, then it would be expected to find negative associations of bird presence with human presence. However, in this chapter, bird presence was positively related to human activity presence. There are several possible explanations for this observation.

Some research has shown that in particular instances, human activity can be a beacon for food resources or a source of safety and thus draw animals in (Whittaker & Knight 1998). Such examples include herring gulls (*Larus argentatus,* L.) flocking on bin collection day, or brown bears (*Ursus arctos*) raiding local rubbish heaps. There was no evidence to suggest that, the Brent goose and wigeon observed in this chapter, were actively seeking out food from humans. Although, it is plausible that these wildfowl might be using human activity as protection from birds of prey. Wigeon, in particular, are subject to predation events by peregrine falcons (*Falco peregrinus,* L.) and while conducting observations in this chapter, several predation events occurred. Furthermore, there is evidence that some birds of prey are highly deterred by human activities, with bald eagles avoiding stationary boats by up to 400 meters (McGarigal et al. 1991). Unfortunately, there were not enough established predation events witnessed in this chapter to be able to confirm or deny the wildfowl using human activities as a form of protection.

Nonetheless, the more likely explanation is that there are coinciding geographical environments that are favourable for both humans and wildfowl in the same places, at the same time. For example, many of the regions with high densities of seagrass also held high accessibility for human activities. These findings suggest that rather than wildfowl flocking to the areas because humans are there, the same sites that human activities also favour, birds' favour. This conclusion is further supported by other research conducted by Davidson & Rothwell (1993), that indicated Brent goose were found significantly closer to footpaths than other bird species. They concluded that this was likely due to food sources located within proximity to the walkways. The positive relationship between bird density and human density detected in the beta regressions also supports this theory.

Something else to consider is that the lack of redistribution can, in some cases, indicate a lack of suitable alternative habitat for birds to choose from (Gill et al. 2001). Concerning the Exe Estuary, there is no indication to suggest that birds are 'forced' to feed in high human activity regions. Throughout, and surrounding the estuary, there are several habitat reserves, with food resources that are nearly void of all human activity. These sites include the Dawlish Warren Nature Reserve and Bowling Green Marsh. Both of these habitats are tidally influenced and have high quantities of aquatic vegetation. The presence and proximity of these similarly suitable habitats suggest that birds have the option to redistribute within the estuary to non-disturbed regions, with little extra cost or loss to feeding quality if necessary.

Although both Brent goose and wigeon were considered more likely to be present when human activities were present, bird density was negatively associated with whether human activity was present or not. This association implies that although birds favour the same regions as humans, they do so at lower densities when humans are present. Reduced densities of birds may be an indication of avoidance of human activity. However, concerning this chapter, the finding of decreased bird density relative to human activity presence is contradicted by the increasing Brent goose and wigeon density with increasing human activity density. This association is not apparent in the reduced dataset indicating that perhaps sampling bias was the reason for relationship. The occurrence of this contradiction could also be an indication that there are other interacting environmental variables that are corresponding with both bird density and human activity and thus influencing the perceived related variation between the two.

There were a few regions of the estuary that supported high probabilities of the presence of human activity as well as high possibilities of the occurrence of birds but neither in high density. These regions were easily accessible but were limited to low tide for walkers, or high-tide for water activities. Both of these times coincide with lower densities of Brent goose and wigeon. As a result, high probabilities of human presence coincided with low frequencies of birds. For occurrences of high bird density and high human density, similar to presence and absence, several environmental variables corresponded to both high bird density and high human density. These samples were limited but provided a strong association, which is likely why the relationship disappeared in the reduced dataset.

There was also variation between winter months. The winter months of September and February had negative associations with bird presence and abundance, while there were positive associations with October, November and December. The most significant positive associations for bird presence relative to winter month occurred for November. This association is consistent with the British Trust for Ornithology Wetland Bird Surveys that show Brent goose and wigeon numbers gradually increase from September until November and drop off around February (Frost et al. 2018). Brent goose and wigeon are both migratory wildfowl that winter in the UK, on estuarine environments. Migration is an individually based process, such that, birds can only begin their movement when they are physically capable, and the conditions are suitable (Klaassen 1996). The state of the environment that animals are leaving dictates physiological condition (Lehikoinen & Jaatinen 2012). Therefore, arrival times within the UK are variable, and as such, maximum bird counts on the estuary change over the winter months as a product of different bird arrival times.

Interestingly, although it was most likely for birds to be present in November or later, bird density was most positively associated with September and October. This finding is likely due to the distribution and abundance of eelgrass (*Zostera noltii,* L.) and sea lettuce

(*Ulva lactuca,* L.*;* Campbell 1946; Mayhew 1985; Fox 1996; Hansen et al. 2000). This particular food source is most abundant in the early season and diminishes over the wintering months due to natural senescence, winter storms, as well as from grazing of wildfowl (Campbell 1946; Fox 1996). As a result, the quality of food resources on the estuary shrinks over the wintering months, which would logically affect when and where birds spend their time on the water and forcing them to spread out (Campbell 1946; Fox 1996). Another factor to consider is the influence of bird aggregation on counts. When birds are in high density and tightly packed, there is the possibility of reduced visibility. If this visibility reduction was consistent when birds reached a certain aggregation level, it could feasibly affect and potentially have reduced the counts of birds during the months in which their numbers were highest. Regardless, it is realistic that winter month is a factor that contributes to the variability in bird presence and absence as well as abundance.

After winter month, site elevation was the next component listed that significantly explained variability in bird presence and density. For presence and absence, site elevation had a negative relationship with Brent goose and positive relationship with wigeon. There are several possible reasons for this finding. The first and possibly most obvious is due to differences in bird size. Brent goose are near twice the size of wigeon, weighing in at an average of 1.4 kg with a body length of 58cm compared to the 0.7 kg and 48cm of average wigeon (Kear 2005). Part of fitness maximising decisions of species is related to the finding and accessing of food resources at a minimal energetic cost. As such, due to their larger size, Brent goose can access food resources at greater depths with less energy expenditure than wigeon. Therefore, the negative relationship of Brent goose presence with site elevation may be due to less influence of site elevation on whether Brent goose can access food resources at a site. Whereas, wigeon, due to smaller size, are much more restricted by the accessibility of food due to site elevation. This hypothesis is reinforced by the finding that even though Brent goose were generally present on lower elevation sites, their frequency did increase with increasing elevation. A pattern that is also evident with wigeon. These results indicate that food access was an influential component of both Brent goose and wigeon distribution and abundance.

Substrate type was also important. Both Brent goose and wigeon had the most substantial positive probabilities of occurrence relative to muddy substrates. Eelgrass and sea lettuce have optimal growing conditions based on substrate type and light attenuation, and therefore have variation in biomass depending on these variables

(Backman & Barilotti 1976; Moore & Wetzel 2000; Hansen et al. 2000). The most optimal growing conditions for eelgrass happen to be on silty or clay substrates which are descriptive characteristics for muddy substrates (Nishijima et al. 2015). As a result, the positive occurrence of these species relative to muddy substrates is consistent with the higher probability of food resources that come with them. There was also a significant positive association of brent goose presence with sand. When further evaluating the data, it becomes apparent that this is heavily influenced by just two locations on the estuary (Northwest CS and Southeast BR) that have muddy/sandy patches. These patches of mud were too small to characterise the region as mud, but that did support growth of some *Ulva* spp., and *Zostera* spp. As a result, there were often a few Brent goose present feeding, but not in high numbers. Indicating food availability is still the primary mechanism at work even though sandy substrates are not typically associated with food resources for these birds. Observed density indexes further validate this finding. Both Brent goose and wigeon showed increasing density abundance associated with muddy substrates and non-significant trends in density relative to sandy substrates.

If site elevation and substrate are serving as a proxy for food accessibility, it is consistent that the next variable in the model listed as being relevant to Brent goose and wigeon presence and density, was tide state. Yet, both Brent goose and wigeon had strong negative associations with low tide state in both presence and density. Although low tide should be when the majority of food is available, research suggests that both Brent goose and wigeon preferentially feed when *Zostera* is at least partially submerged (Fox 1996). When food is either partially or entirely submerged the feeding efficiency in both wigeon and Brent goose is increased (Fox 1996). Wigeon feeding on *Zostera* blades have an easier time acquiring the leaves when they are floating than when on top of the mud (Fox 1996). Brent goose that feed on *Zostera* blades, as well as rhizomes, have increased ease of dislodging of rhizomes when the substrate is suspended rather than exposed (Fox 1996). Therefore, birds would be less inclined to be present on sites at low tide due to reduced profitability (van Eerden 1984; Fox 1996). The density results of both Brent goose and wigeon, which were also negative at low tide, further support this.

Furthermore, there are a handful of regions on or surrounding the estuary not involved in observations. These unobserved regions included the northern reserves and mouth of the estuary. Birds may have been using these regions as resting areas and thus not included in the analysis. Furthermore, there are several deep channels in many of the patches that if viewed from the wrong angle, would make it difficult to spot birds. These hard-to-see regions could mean underestimated bird counts in those regions and thus make for lower than average densities at low tide. In this case, if birds were difficult to spot, then they were in areas that were also difficult for any humans to access and thus overlap measures would still have been accurate.

Other aspects to consider concerning the tidal influence on presence and abundance of both Brent goose and wigeon, is their relation to the energetics of movement. Tidal movements can be a way of passively navigating estuarine regions with little to no energetic cost. For example, Bryant & Leng (1975) documented observations of shelduck (*Tadorna tadorna*, L.) using tides as a way of moving to different regions within an estuarine environment. The tidal movement also provides different levels of protection from predators. When food is inaccessible, or rest is needed, often wildfowl will choose a roosting position based on the tide. When the tide is up, they will roost in large rafts in the middle of an estuary as a mechanism for spotting birds of prey as well as preventing access from land predators (Fox 2006; Bregnballe et al. 2017). When the tide is down, they will select channels with quick access to water for the same reason. Therefore, significant variation in bird presence and abundance relative to the tide in this particular chapter is likely due to combinations of these factors.

Finally, the last parameter that the model detected as significant in explaining Brent goose and wigeon variability in presence and density was wind chill index. Birds were less likely to be present as wind chill increased, but if they were present, they tended to increase in density as the wind chill index increased. The most likely rationalisation for this is the relationship between wind chill and month. As the season progresses, two things happen: the wind chill decreases and bird numbers increase as they arrive from migration. Therefore, as wind chill goes down, the probability of birds being present goes up. This is also relevant with respect to density. When birds first arrive and wind chill is high, food resources are more plentiful and therefore, even though there are fewer birds likely to be present, bird density would be expected to be higher to take advantage of the food.

2.5.2. HUMANS IN SPACE AND TIME

When evaluating human activities in space and time, the environmental variables that were significant to the presence of human activity were: day of the week, site accessibility, site elevation, site substrate, tide state and wind chill. These factors, along with the time of the day, were also significant relative to the density of human activity.

The indication that human activity presence and density are related to the day of the week is not surprising. Estuarine environments are well known as a source of recreational entertainment for people. Recreational activities are traditionally considered activities that individuals partake in during their spare time. Additionally, during the winter months, daylight hours are limited and as a result, extra time for recreational activities becomes restricted (de Freitas 2003). Therefore, it is no revelation that human activities presence and density were more likely during Saturday and Sunday, as these are traditionally days that most individuals are not working. When the day of the week is held constant, the first hours associated with significantly positive differences in human activity density were 11:00, 12:00, 13:00. These times coincide with typical lunch break times as well as spring low-tide during daylight, implying that accessibility and off-work hours and days are influential factors in determining if human activities occur on the estuary and how dense they are when they do. There were also positive relationships of human presence with Wednesday and Thursday, but this did not extend to human density. The reason for this was unclear, but could potentially be club or dog walking days, or even just the desire for individuals to get outside mid-week, increasing the overall probability of seeing someone on those days, but not necessarily the density.

Site accessibility was the next variable listed as significant in explaining the variability of human activity presence and density on the estuary. Sites categorised as low or medium accessibility had a significantly negative association of human activity presence as well as human activity density. This finding corroborates with the fact that if regions are more challenging to access, humans are more likely to be deterred due to the amount of time taken to access those sites. Consistent with other studies on the use of recreational sites by tourist, the amount of time spent in those regions is potentially less due to the time of egress. A survey conducted by Neuvonen et al. (2010) showed evidence that, in high population areas, tourists were more likely to choose local sites over distant sites to fulfil recreational needs.

Site elevation, site substrate and tide state were significantly associated with human activity presence and density, due to them improving site accessibility to humans. High elevation sites are the sites that will be accessible to human activities for the most prolonged periods. Concerning site substrate, sand is significantly positively associated with human activity presence as well as human activity density, which is also logical because sand is a better substrate for walking on than mud. Lastly, low and high tidal states had significant positive associations with human activity presence and density compared to other tidal states. This makes sense because human accessibility to the estuary is limited either to intertidal activities or water-based activities which are restricted by the tide. Accordingly, when the tide is low, human activities related to land can stretch out to the intertidal regions. And when the tide is high, water activities can spread out beyond the channels and onto the flats. Based on these results, it is evident that accessibility plays a significant role in explaining the variability in human activity presence and density.

The last variable that significantly explained the variation in human activity and density was wind chill index. Human activity presence was negatively associated with increasing wind chill, while human activity density was positively associated with the rising wind chill. It is common knowledge weather influences recreational outdoor activities (de Freitas 2003; Richardson and Loomis 2005). In general, humans tend to be deterred by colder temperatures, as it is associated with a decrease in comfort level (de Freitas 2003). This helps explain the increase in human activity density with increasing wind chill index values because this represents low winds and high temperatures. However, some activities, such as sailing, kitesurfing and windsurfing, require wind at certain speeds and directions to take place (SurferToday.com 2019). In the UK, wind direction influences the temperature (Met Office 2019). In particular, north-westerly winds that originate from the polar regions are associated with decreasing temperatures. This would mean that low temperature and high winds that are associated with low wind chill index values. Therefore, low wind chill values are best for wind water-sports and help explain why there is a higher probability of human activities being present with the low wind chill.

2.5.3. THE OVERLAP BETWEEN BIRDS AND HUMANS IN SPACE AND TIME

According to the models implemented, the primary environmental variables that significantly explain the variation in the presence of overlap were: day, hour, month, site accessibility, site elevation, site substrate, tide state and wind chill. These factors were also significant to the magnitude of overlap.

The overlap and BOP index values are a combination of both the wildfowl and human activity presence (0,1) and density data ($B_{i,t}$; $P_{i,t}$). Therefore, it is not unexpected that this chapter found similar environmental variables to be significant in explaining variations in the presence and degree of their overlap. However, although the same variables were significant for overlaps, the relationships of the overlaps to the variables are dependent on how the variables affected wildfowl and human activity independently.

For an overlap to occur, it requires both the presence of human activity and wildfowl. Therefore, when levels of environmental variables occurred that favoured either only human activity or only bird presence but not the other, overlap probability and density was generally still significantly low. For example, a 'low' tide state was significantly negatively associated with Brent goose and wigeon presence as well as density. Meaning there was a low probability of wildfowl being present over low tide. Whereas, 'low' tide state was significantly positively associated with human activity presence. Meaning there was a high probability of human activity being present over 'low' tide. Although tide state was significant for both wildfowl and human activities, the relationship was not the same for both. Therefore, because, wildfowl were unlikely to be present, the resulting overlap remained significantly negative (Table 2.16).

Variable values that produced above-average presence of overlaps with wigeon include Saturday, February, October, November, medium accessible sites, muddy substrates, and increasing site elevation. These variables were similar for Brent goose, with the addition of Sunday, Tuesday and sandy substrates. These variables make sense relative to the previous data on the individual presence of humans and birds attributed to site accessibility for humans and food availability for birds. However, on several occasions, there appears a disconnect between the presence of either birds or people and their overlap. For example, human existence is significantly negative on muddy substrates, which, based on the previous argument, should mean that conditions for overlap are also unfavourable. Interestingly, in this instance, the overlap is positive. There are several reasons for this type of result. First, is that although it is less likely for a human to be present on that substrate, it does not mean they will not ever be present. Furthermore, if wigeon are always present on that substrate, then even below the average presence of humans will still produce an overlap event, meaning there is an above-average chance for an overlap on that substrate. The same logic applies to Brent goose presence at high tide, and human presence at increasing elevations. Each of these instances is associated with such a high degree of either bird presence or human presence, which even low values of the other occurrence, result in an above-average positive overlap presence (Table 2.18).

Environmental variables that produce above-average BOP index values for wigeon are Monday, Saturday, September, October, November, December, medium site accessibility, and sandy substrates. These were slightly different for Brent goose, which had above-average BOP index values in the following variables: Monday, 8:00, 17:00, increasing winter-months, muddy substrates, low tide, increasing wind-chill and increasing site elevation. Similar to presence and absence, these results appear to follow the attributes of situations that combine site accessibility for humans and food availability for birds. However, several variables show different densities of humans and birds relative to BOP index values. This difference is evident with low tide and high tide variables between humans and Brent goose. At high tide, Brent goose have significantly above average densities, as do humans; however, the BOP index values registered as significantly negative.

Further evaluation of this outcome identified that although humans were present in higher densities at high tide, their presence was recorded primarily on the land, which would mean humans were on the edges of the estuary. At the same time, birds were mainly on the water; this would produce a lack of actual overlap. Additionally, there is positive human density and negative Brent goose density relative to low tide, which is similar to what was occurring with the presence/absence data. Human activity is so dense at low tide that even with reduced density of Brent goose, an above-average BOP index value results (Table 2.19).

Some factors, evaluated relative to human activity, were not independently assessed relative to wildfowl and vice-versa. These factors included winter month, day, and hour. The reason for this was because of applicability. The month was a relevant factor in investigating wildfowl presence due to arrival times associated with migration. The month is associated with temperature changes and may influence human activity in this way. However, this is already a variable that is tested through wind chill index. There are off-work hours related to the month in the form of Christmas Holidays. Although, this is less relevant because most birds moved to fields before this time.

Day and hour were other variables investigated relative to human activity but not wildfowl. Day and hour were relevant to human activity with off-work hours, whereas the time tide times and daylight hours illustrated time for birds. As a result of these variables only being investigated independently for wildfowl or human activity, insight as to the driving forces relative to an overlap value was only from one perspective. Nonetheless, this is still useful in understanding the effects at work. An example of this is the weekday 'Saturday' (Table 2.18). Weekday was significant relative to human activity presence, with Saturday producing a significantly positive association. This pattern was maintained when evaluating overlap. Indicating that wildfowl activity did not vary significantly relative to Saturday to affect the probability, and therefore, the increase in the likelihood of overlap is due to the relationship of human activity relative to the weekday.

2.5.4. IMPLICATIONS OF CHANGING ENVIRONMENTS

All of these results are relevant to the current state of the environment on the Exe Estuary. However, if the environment were to vary or food sources were to change, overlaps and conditions leading to those overlaps could also change. Climate change is becoming an increasingly relevant topic. With climate change, various environmental changes can be expected. These include, but are not limited to, sea level rise, warmer temperatures, and more extreme weather events (IPCC 2007; Møller et al. 2010). This could mean several things with respect to the findings in this chapter.

Sea level rise would mean changes in aquatic food distribution. If sea level rises occurred over substrates that were unfavourable for the growth of *Zostera* spp. then there could be an overall decrease in food distribution and abundance. If the distribution of the limited food resources were located in regions that were favourable for human activities, this might result in increased overlaps with human activities. However, equally, if this redistribution of food occurred in regions with lower access for human activities, the conditions for overlap may actually decrease.

In the event of increased temperatures several things can occur. First, warmer temperatures would reduce the energy demands of Brent goose and wigeon, meaning that they would need to feed less and potentially spend less time on feeding grounds (Kendeigh 1969). Furthermore, increased temperatures could mean longer growing seasons for aquatic species, and a reduction of senescence therefore increasing the amount and quality of food that would be available on an estuarine environment. However, research has shown that increases in water temperature in the early growing season can actually lead to decline in cover meaning less *Zostera* spp. grow in general (Moore et al 2014). Furthermore, increased water temperatures can also increase eutrophication, which can reduce the quality of the water which could then actually decrease growth of aquatic species such as *Zostera* (Moore & Wetzel 2000; Moore et al. 2014). Yet, eutrophication can also mean increases algal mats and species such as *Ulva* which can serve as alternative food sources for wildfowl such as wigeon and Brent goose (Campbell 1946). This indicates that temperature changes can have large implications for food, and quality of habitat, that can be beneficial and detrimental in different ways, which could lead to various changes in habitat use and ultimately affect the degree of overlap between Brent goose and wigeon with human activities.

Extreme weather events can also affect food resources. Windstorms can increase energetic needs of birds both in temperature regulation as well as cost of flight. Furthermore, strong winds can easily displace and uproot *Zostera* spp. and thus, prematurely reduce food resources in the wintering months and force birds into habitat that is more sheltered and thus potentially subject to different degrees of human activity. However, with increased extreme weather, there may be a resulting reduction in human activities which may mean that birds will not actually experience any higher degrees of overlap with human activity.

Ultimately changing weather conditions, associated with climate change, on the Exe estuary can mean many different things for the distribution and accessibility of food resources for birds as well as the desirability of a site for humans. These changes have the potential to lead to both increased as well as decreased overlap between birds and humans and thus should be considered when evaluating a site in space and time for overlaps conditions in the future.

2.6. CONCLUSION

Studies highlighting the influence of environmental factors on both wildlife abundance and distribution as well as human activity distribution and abundance are plentiful in the literature. However, few papers attempt to marry the two topics as a means for evaluating the abundance and distribution of overlap between wildlife and human activities before disturbance. This chapter has highlighted that environmental variables can potentially be a means for predicting when the highest probability of overlap may occur between human activities and wildlife. The presence of contradictions in observed overlap presence and density compared to predicted overlaps based on separate measures of human and bird presence, emphasises the complexity of overlap events themselves, and the need to include overlap measures within observations. Although this chapter focused on two wildfowl species, the variables identified as being influential in overlaps could apply to many species because of what they predominantly represent food availability, predator avoidance, and fitness maximising decisions. This generalisation is also true for the driving mechanisms in human activity, such as off-work hours, comfort level, and conditions for specific events to occur. Therefore, this information can be useful for a range of recreational and wildlife administrators in helping to identify where and when human and wildlife interactions are most likely to occur and help mitigate negative interactions before they arise.

2.7. FUTURE WORK

This chapter identified the environmental variables associated with the distribution of wildfowl and humans in space and time and was limited to estuarine environments. As a result, any applicability to other species and activities is purely theoretical. Therefore, future research could focus on examining and validating whether these same core variables do indeed apply to other species and locations. In using this research for predictive scenarios, then spatial-temporal autocorrelation would need to be taken into account. Additionally, although this chapter highlighted variables associated with overlaps between human activities and wildlife, this does not directly translate to human disturbance events. Future work could look into what level of disturbance occurs within these overlaps and examine whether environmental variables also play a role in this.

3. CHAPTER 3: THE RESPONSE OF WILDLIFE WHEN OVERLAP WITH HUMANS OCCURS: INSIGHTS FROM WINTERING WILDFOWL ON THE EXE ESTUARY

3.1. ABSTRACT

The degree of spatiotemporal overlap between humans and animals plays a significant role in how much disturbance animals experience. This chapter took the spatiotemporal information gathered from Chapter 2, along with observational records of disturbance events to determine the rate of disturbance within those overlaps. With this information, this chapter also analysed the actual energetic costs associated with a disturbance during these overlaps by using a modified time-energy budget equation. On the Exe Estuary, Brent goose experienced approximately one disturbance per hour, while wigeon experienced around 0.7 disturbances per hour. Disturbance thresholds were calculated to vary depending on whether birds were disturbed more when resting or feeding. By extrapolating the current rates of feeding and resting disturbance, the predicted maximum disturbances per hour that Brent goose could experience was 24 per hour and for wigeon was 34 per hour before they ran out of time to compensate. Overall disturbance costs experienced by Brent goose and wigeon on the Exe Estuary during the winter of 2017 and 2018 were below these calculated thresholds of compensation.

3.2. INTRODUCTION

3.2.1. FROM OVERLAP TO POPULATION-LEVEL IMPACT

For human disturbance to occur, there must be an overlap in both space and time between humans and animals. However, the simple measure of overlap does not quantify the costs and potential population-level impacts associated with human disturbance. This is because the presence of overlap does not guarantee a response in animals and because a behavioural reaction does not necessarily translate to a disturbance impact (Gill et al. 2001). Population-level impacts from disturbance are the result of cumulative individual responses of wildlife that exceed the ability of those animals to compensate. When this occurs, animals fail to reproduce or may even starve to death, leading to population impacts (Figure 3.1; Schulz & Stock 1993, Gill et al. 2001, Frid & Dill 2002, Gill 2007; Pirotta et al. 2018). Therefore, identifying the probability of a response within an overlap, and calculating the cost, are necessary to determine whether human disturbance might have a population level consequence (Figure 3.1).

By combining time loss with energetic expenditure, the overall cost of disturbance becomes quantifiable (Houston et al. 2012). The amount of time an animal loses to disturbance events is measured by the observed rate of disturbance within an overlap, combined with the length of time for which the disturbance lasts (Riddington et al. 1996; Houston et al. 2012). Depending on the activity that an animal is engaged in when disturbed, there are different energetic consequences associated with lost time. The disturbance event itself is energetically costly. Additionally, if the animal is feeding during a disturbance, further energy is lost in the form of lost feeding time. To avoid an energy deficit, animals that lose energy must regain it by increased feeding time. Based on the theory that animals strive to be in a state of energetic equilibrium, this increase in feeding time can be calculated by combining time budgets, with daily energy expenditure equations (Equation 3.1; Houston et al. 2012). Evaluating disturbance in this manner allows individual costs of disturbances to be measured in terms of an animal’s ability to compensate (Houston et al. 2012;Figure 3.1).

Several factors determine the amount of additional time an animal is capable of feeding to make up for disturbance. Every animal naturally has a maximum amount of time in which to feed within 24hrs. For some animals, this may be the full 24 hours, whereas for others, there may be additional factors that limit feeding time. For instance, estuarine waders and wildfowl can only access food resources at specific tidal states and therefore, have less than 24hrs in which to 'make up' for lost time and energy (Evans 1976; Lindström 1991). Additionally, behavioural and physiological requirements, such as rest, digestion, or socializing, might also restrict possible time for feeding (Kirkwood 1983; Sedinger & Raveling 1988; Lindström 1991). Therefore, more study is necessary to evaluate the influence of these factors and how they may affect an animal's threshold for coping with the costs of disturbance based on feeding time.

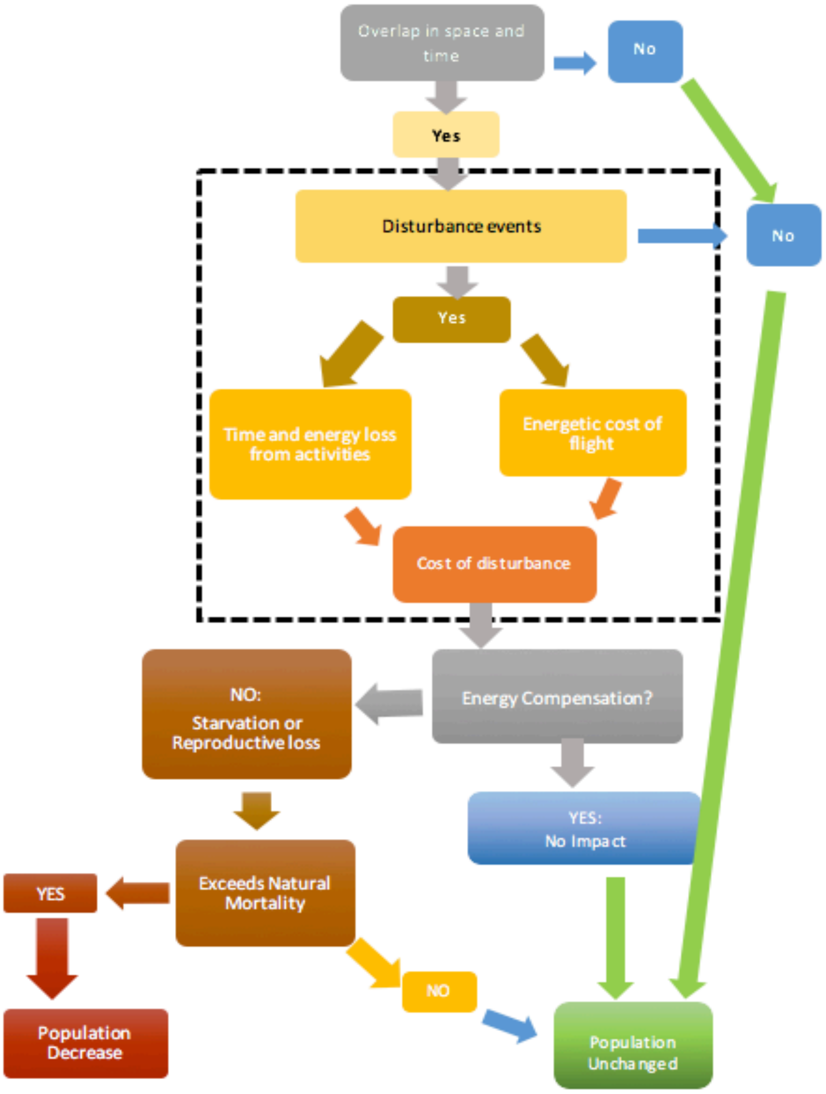


Figure 3.1 A conceptual diagram of how overlap leads to disturbance events which are a combination of both time and energetic cost (outlined by the black dashed line) and how this feeds into the larger picture of population-level impacts from disturbance.

3.2.2. AIMS AND OBJECTIVES

This chapter aims to further understand the response of animals relative to overlaps with human activity and quantify costs of these responses when feeding time is naturally restricted. This aim is addressed by modifying the Houston et al. (2012) equation and parameterising it using human disturbance of Brent goose (*Branta bernicla*) and wigeon (*Mareca penelope*) observed on the Exe Estuary.

This chapter will address the following objectives:

- Establish time budgets of Brent goose and wigeon in the presence and absence of disturbance on the Exe Estuary
- Modify the Houston et al. 2012 'Cost of Disturbance' (COD) equation to include time limitations due to environmental and behavioural conditions
- Use the modified equation to evaluate and quantify disturbance events that Brent goose and wigeon experience on the Exe Estuary
- Determine thresholds of disturbance that Brent goose and wigeon are capable of experiencing based on values derived from the modified equation

3.3. METHODS

3.3.1. STUDY SITE

The study site was the Exe Estuary located in Southwest England, divided into 21 estuary segments and 11 field/marsh segments (details in section 2.2; Figure 2.3).

3.3.2. OBSERVATIONS

Collection of data took place during the winter months of September 2017 to February 2018, and from September 2018 to February of 2019. Observation days and sites were selected using methods detailed in section 2.2 of this document. Brent goose and wigeon were the study species.

3.3.2.1. TIME BUDGETS

Observation points for sampling were randomly selected based on methods detailed in section 2.2. Two-hour observations were performed at each observation point with scan sampling every thirty minutes. This method of sampling meant that over a two-hour observation period, 5 scan samples were collected. During scan sampling, bird counts, bird activity and bird locations were recorded for any Brent goose or wigeon visible from an observation point. Bird activity encompassed four primary activities: resting, feeding, natural flight, and small locomotion (Table 3.1). If no birds were present in a subsection, that site was still recorded but with a value of zero. Between each scan sample, continuous sampling collected data on natural flight events as well as disturbance events. Natural flight events included with the number of birds, duration and distance of each flight. Disturbance events were given precedence over any other observations when they occurred. Disturbance parameters recorded included: disturbance source, the proximity of the source to birds when a disturbance occurred, number of birds disturbed, reaction type of birds, duration of disturbance, and distance of any movement. Disturbance source referred to any identifiable activity that resulted in an interruption of bird behaviour (Table 2.1). All time observations were recorded in minutes.

When it was not clear if a flight was due to natural movement or disturbance, a set of criteria were consulted based on observed behaviour. These criteria included activity of birds before a flight, time of day, tide, bird behaviour directly after a flight, and the number of birds involved in the flight. Under the majority of instances, natural flights followed a predictable pattern. Birds generally had ceased feeding; tides were changing; it was either dawn or dusk; birds settled directly after the flight; the number of birds involved was typically small groups of no more than 50. Disturbance flights, on the other hand, were generally accompanied by a direct interruption of feeding; at mid-day; at a steady tide state; with birds being agitated after the flight; and usually an entire flock of birds flying at once. In instances where the reason for a flight was still uncertain, the source of the flight was recorded as unknown (Table 3.1).

Table 3.1 Ethogram for behavioural monitoring.

Disturbance Activity	**Description**
Disturbance Flight	Active flight away from a disturbance source may accompany a direct interruption of feeding, birds agitated and vocal after the flight and usually an entire flock of birds flying at once; Recorded continuously
Disturbance Locomotion	Active swimming or walking away from a disturbance source, may accompany a direct interruption of feeding, birds agitated, and vocal after the movement and usually large portion of birds move at once; Recorded continuously
Natural Activity	
Rest	Lack of overall movement, the head may be tucked back, may be standing or sitting, includes preening activities; Recorded every 30 minutes
Small locomotion	Active swimming or walking, consistent movement in a direction for more than 5 seconds, usually only done in singles or family groups; Recorded every 30 minutes

Feed	Head up and down on feeding area, intake of visible food, maybe underwater, on the surface of the water, or a solid substrate; Recorded every 30 minutes
Natural Flight	Birds in flight, accompanied by a cessation of feeding prior and increased small locomotion, can be at dawn or dusk or during a tide change, birds settle directly after the flight, typically small groups of no more than 50 unless it is a dawn or dusk flight; Recorded continuously

3.3.2.2. OVERLAP EVENTS

Human activity was recorded with continuous sampling. When any human activity was within the overlap distance, described in Chapter 2, Figure 2.1, for Brent goose or Wigeon, then the event was considered an overlap. When this occurred, the proximity of the human activity to the birds, the duration of that proximity, the number of birds, and the primary activity of the birds, within the overlap distance was recorded. This method meant that the total number of minutes that birds were exposed to a potentially disturbing human activity were accounted for.

In order to compare overlap minutes to bird presence in general. Brent goose and wigeon scan samples were extrapolated to assume bird presence over the time in between scan samples. This generated a minute by minute dataset of bird presence. As detailed in section 2.3.2, if there were large variations in bird numbers and presence in between scan samples then new counts and activities were recorded. This helped maintain assumptions of bird activity and distribution in between samples that were as accurate as possible.

3.3.2.3. ENVIRONMENTAL VARIABLES

Details on the Environmental variables and collection guidelines are given in section 2.3.3 and followed the same directions.

3.3.2.4. EQUIPMENT

A single individual conducted all observational surveys with a Swarovski STS 80 High Definition (HD) Straight Spotting Scope and accompanying tripod.

3.3.3. ANALYSIS

All analyses used RStudio statistical software Version 1.0.136 (© 2009-2016 RStudio Inc.) with R version 3.3.3 (© 2017-03-06 R Inc.).

3.3.3.1. TIME BUDGET ANALYSIS

Time budgets were based on percentages of birds engaged in each activity type during each observation. Changes in time budgets were evaluated relative to the presence and absence of overlaps with human activities and environmental variables. A description how this thesis defines overlap presence and absence can be found in Chapter 2, 2.2 and Table 2.3. A two-sample t-test was performed using the 't.test' function in R to explore initial differences between bird time-budget activities in the presence and absence of an overlap with human activities. However, because 't.test' statistics are less applicable to percentage data and there were other environmental variables to consider. A more robust multivariate analysis was conducted using 'glm' function in R. Each activity type was tested for variation due to overlap, as well as, environmental variables identified as being influential in bird distribution from Chapter 2. Brent goose and wigeon were evaluated separately (Figure 3.2).

Figure 3.2 Model structure for multivariate analysis of time-activity budgets relative to overlap and environmental variables

Species	Dependent variable	Independent variables
Brent goose	Feeding	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
	Resting	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
	Small locomotion	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
	Natural flight	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
Wigeon	Feeding	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
	Resting	overlap + windchillindex + siteelevation + tidestate + sitesubstrate

Species	Dependent variable	Independent variables
	Small locomotion	overlap + windchillindex + siteelevation + tidestate + sitesubstrate
	Natural flight	overlap + windchillindex + siteelevation + tidestate + sitesubstrate

3.3.3.2. TIME-ENERGY COSTS OF DISTURBANCE

All disturbances recorded on the estuary during observations were used to derive total rates of disturbance on the Estuary. A modified version of the equation developed by Houston et al. (2012) calculated the amount of time needed to spend foraging to make up for time and energy losses to disturbance. As tidal influences and natural behaviours constrain Brent goose and wigeon, and because disturbance occurs during resting as well as foraging, Houston's equation was modified to reflect these conditions (Equation 3.1). The derivation of this cost of disturbance (COD) equation is in Appendix 1.

$$F = \frac{T\left(\frac{E_R + E_D t_R \lambda_R}{1 + t_R \lambda_R} + E_\Delta\right)}{g - (E_F + E_D t_F \lambda_F) + \frac{(1 + t_F \lambda_F)(E_R + E_D t_R \lambda_R)}{1 + t_R \lambda_R}} \qquad \text{Equation 3.1}$$

F : time spent foraging (hrs)

T: total amount of time (hrs)

E_R : metabolic rate while resting (kJ/hr)

t_R : average time spent (hrs) per disturbance while resting

λ_R : rate of disturbance while resting (/hr)

t_F : average time spent (hrs) per disturbance while feeding

λ_F : rate of disturbance while feeding (/hr)

E_D : metabolic rate while being disturbed (kJ/hr)

g: gross rate of energy gain while feeding (kJ/hr)

E_F : metabolic rate while foraging (kJ/hr)

E_Δ: the rate of change in metabolic gain, based on how much energy above or below equilibrium the animal is expected to be striving for (in this chapter, this parameter is equal to zero, because Brent goose and wigeon in this chapter are assumed to be aiming for equilibrium only)

The total amount of time used in this equation was 24 hours. However, both Brent goose and wigeon have less than 24 hours to feed within a daily cycle. This restriction is due to the average estimate of the time that *Zostera* beds are within the necessary feeding depths on the Exe Estuary as well as the essential rest requirements of the species (Table 3.4). Therefore, interpretation of the results of this equation was made with these time limitations in mind.

Disturbance rates were calculated based on the number of observations with a recorded disturbance divided by the total number of observations of that bird in general. This proportion of disturbances was then combined with the average amount of time a bird spent being disturbed during each recorded disturbance event. This was done for Brent goose and wigeon separately and divided between disturbance events that occurred while the majority of birds were resting vs. birds that were feeding (Equation 3.2).

$$\lambda_{R+}\lambda_F = \frac{(N_{DR}+N_{DF})}{(N_{tR}+N_{tF})} * (t_{R+}t_F)$$ Equation 3.2

N_{DR} : Number of observations of disturbance while birds were resting
N_{DF} : Number of observations of disturbance while birds were foraging
N_{tR} : Total number of observations of birds resting
N_{tF} : Total number of observations of birds foraging

Essential rest time was calculated by the average daily percent of 'rest' activities found within the literature for each species in similar regions, during winter months, while feeding on aquatic vegetation (Table 3.4). Values for metabolic rate of resting, fleeing, and foraging were calculated based on literature-based conversions (Table 3.4).
For the metabolic cost of flight (COF) events for the birds, the following equation from McWilliams et al. (2004) was used (Equation 3.3):

$$10^{1.7} * M^{0.868} * 3.6$$ Equation 3.3

M: mass (kg)

The costs of disturbance events of Brent goose and wigeon accounted for the 'primary' activity that birds were engaged in during the time of disturbance.

3.4. RESULTS

3.4.1. OVERLAPS AND DISTURBANCES

Each observational minute of Brent goose or wigeon presence represents one minute in time, on a site where at least one Brent goose or wigeon had been recorded. There were 601,171 observational minutes of Brent goose presence and 599,978 observational minutes of wigeon presence. Each observational minute of overlap represents one minute in time, on a site where at least one Brent goose or wigeon was present and also at least one human activity was present within overlap distance. There were just under 10,000 of those Brent goose observational minutes that also had an observational minute of overlap and approximately 6,500 observational minutes of wigeon presence that also had an observational overlap. These figures mean, human activities were within overlap distance in approximately 1.7% of all observational minute records of brent goose presence (10,000 observation minutes of overlap, out of 601,171 observation minutes of brent goose presence). For wigeon, only 1.2% of observational minutes of wigeon presences also had an overlap with human activities (6,500 observation minutes of overlap out of 599,978 observation minutes of wigeon presence). Out of those recorded overlaps, 6% of Brent goose overlaps with human activity resulted in a disturbance, and 5% of wigeon overlaps with human activity resulted in a disturbance (Figure 3.3). These figures amount to approximately 0.39% of all recorded presences of Brent goose and 0.28% of all recorded presences of wigeon, included a disturbance event (Table 3.2).

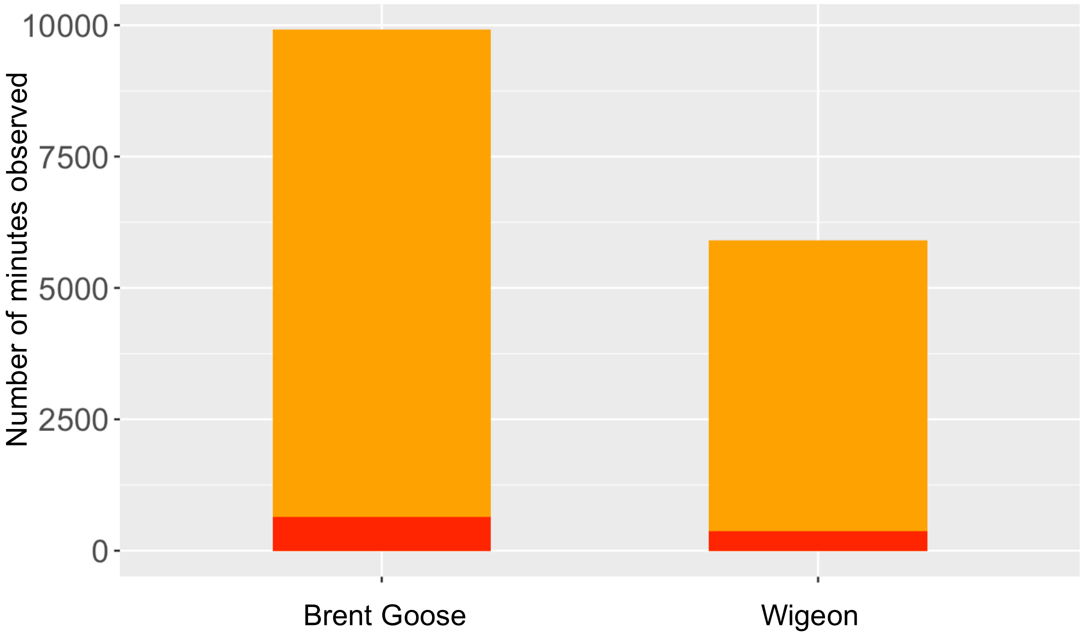


Figure 3.3 The total number of observation minutes with an overlap between human activities and Brent goose (left; orange) and wigeon (right; orange) and of those, the number of observation minutes that also recorded a disturbance (red).

Overall time budget analysis revealed that both Brent goose and wigeon spent the majority of observation hours (between 5:00 and 20:00) on the Exe Estuary, engaged in either resting or feeding (Table 3.2;Figure 3.4). Feeding and resting activities were found to mirror each other depending on the state of the tide, with feeding percentages being highest during mid-tide and resting highest during low and high tide (Figure 3.4). Small locomotion and natural flights were most common during the tide times between feeding and resting (Figure 3.4).

Table 3.2 Observed percentage of time Brent goose and wigeon spent engaged in each activity type. If disturbances are assumed to cease during non-observation hours, the projected amount of time birds will spend being disturbed is taken out of the hours observed (total disturbance percent*8hrs). If disturbances are assumed to remain constant over the entire day, then the amount of time spent being disturbed is taken out of 24hrs (total disturbance percent*24hrs).

Species	Activity type	Mean percent of birds engaged in an activity (x100)	Standard Error	95% CI	Time spent in activity per day (hh:mm) (disturbances assumed to only occur during 8hrs per day)	Time spent in activity per day (hh:mm) (disturbances are assumed to occur all 24hrs)
Brent goose	Feeding	50.7	1.2	1.8	12:11	12:10
(n=1616)	Resting	34.1	1.1	1.8	08:12	08:11
	Small locomotion	11.7	0.7	1.1	02:49	02:49
	Natural flight	2.2	0.4	0.7	00:31	00:31
	Total disturbance	0.4	0.1	0.2	00:03	00:06
Wigeon	Feeding	43.6	1.2	2.3	10:28	10:28
(n=1407)	Resting	43.6	1.2	2.2	10:28	10:28
	Small locomotion	10.4	0.7	0.9	02:30	02:30
	Natural flight	1.5	0.3	1.0	00:22	00:22
	Total disturbance	0.3	0.2	0.3	00:03	00:04

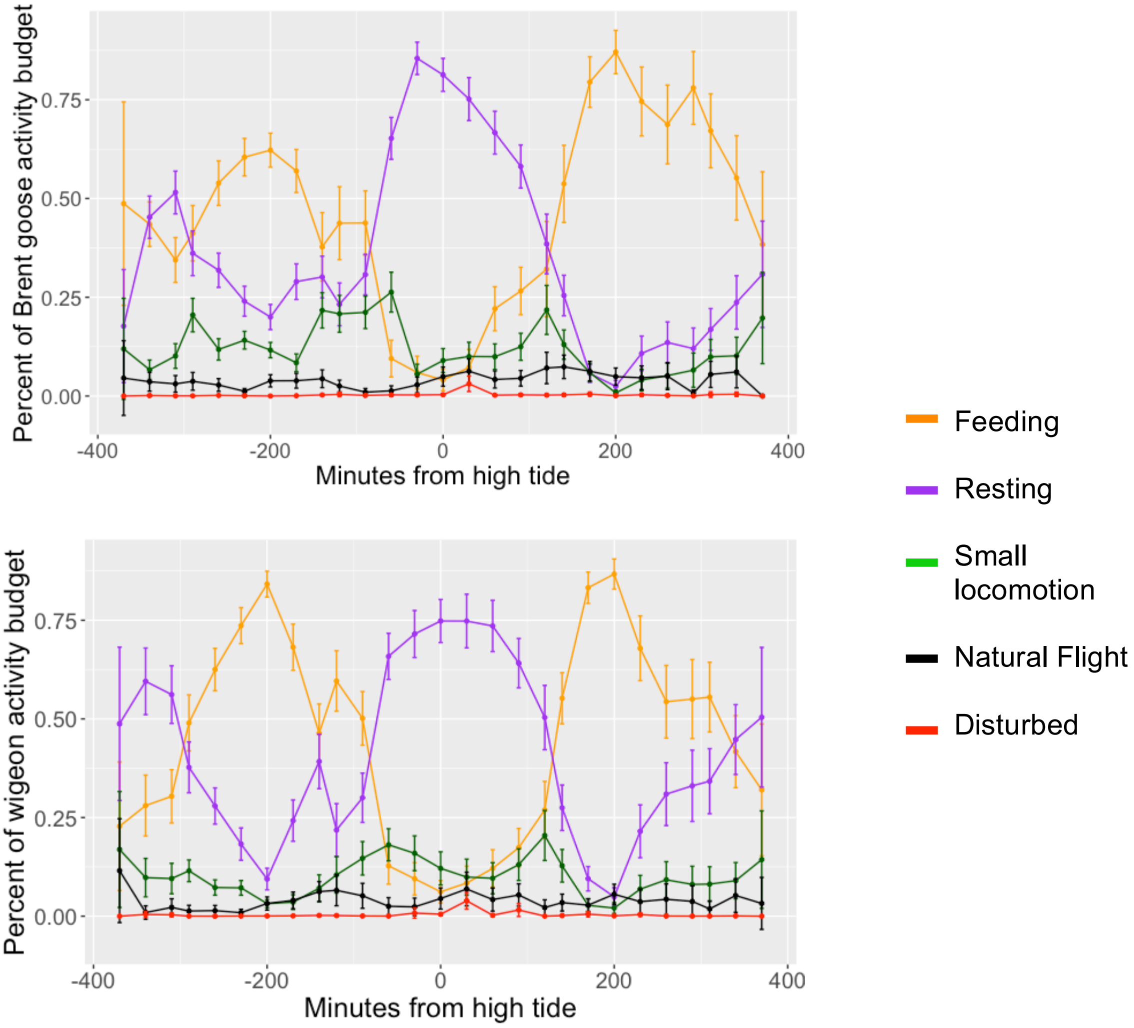


Figure 3.4 Calculated mean time budgets with 95% confidence intervals of Brent goose (top; n = 2280) and wigeon (bottom; n = 4446) relative to minutes from high-tide, on the Exe Estuary from September, October, November, December of 2017, and 2018, and January, February of 2018 and 2019. High tide is at 0 minutes from high tide, low tide is at approximately +/-360.

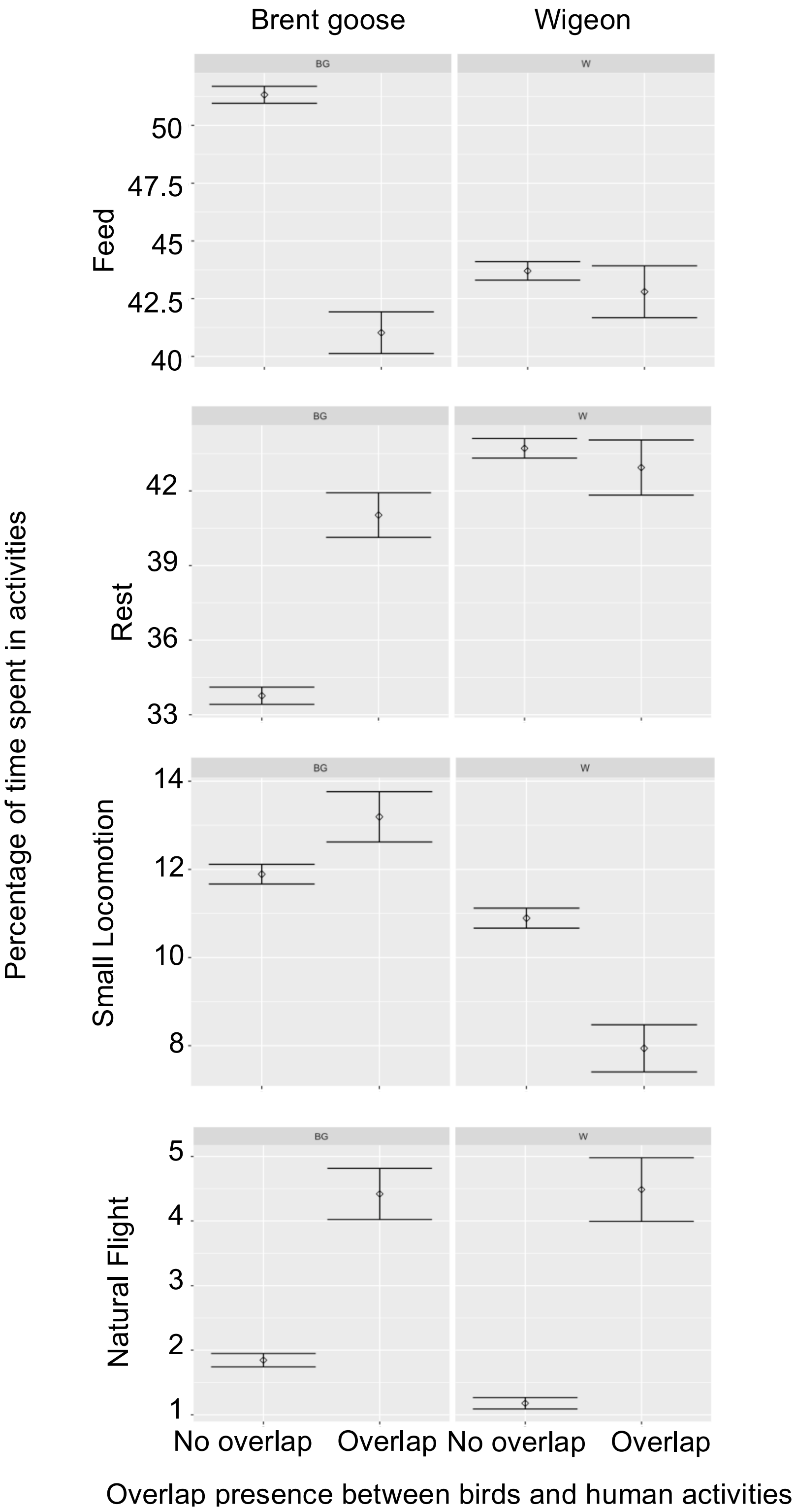


Figure 3.5 Visual differences in the percentage of time Brent goose (left) and wigeon (right) engaged in different activities (from top: feeding, resting, small locomotion, and natural flight) between instances when birds overlapped with human activities and did not overlap with human activities.

Exploratory t-tests revealed significant differences in time budgets of Brent goose and wigeon relative to the presence and absence of overlaps (Figure 3.5). When including the environmental variables, the multivariate analysis revealed that Brent goose still had significantly different feeding ($n = 2058$; $p = 0.03$), resting times ($n = 2058$; $p = 0.03$), small locomotion ($n = 2058$; $p = 0.01$) and natural flight ($n = 2058$; $p = 0.04$), relative to the presence and absence of overlaps (Table 3.3;Figure 3.6). Wigeon were found to not have significantly different rest ($n = 1502$; $p = 0.25$), but did have significantly different, feeding ($n = 1502$; $p = 0.01$), natural flights ($n = 1502$; $p < 0.001$) and small locomotion ($n = 1502$; $p < 0.001$), relative to the presence and absence of overlaps with human activity (Table 3.3;Figure 3.7). Significant interactions were also detected between several environmental variables and the presence and absence of overlaps indicating that changes in activity could be confounded by these variables (Table 3.3).

Table 3.3 Results of multivariate analysis of Brent goose and wigeon time activity budgets relative to overlap and environmental variables

Species	Dependent Variable	Independent Variable	Estimate	Standard Error	T value	Pr(>|t|)
Brent Goose	Percent feed	Overlap	-0.073	0.033	-2.183	0.029***
	(n = 2058)	Tidestate: high	-0.492	0.022	-21.979	< 2e-16***
		Tidestate: low	-0.034	0.023	-1.452	0.147
		Tidestate: rising	-0.009	0.023	-0.373	0.709
		Windchill index	0.001	0.001	0.745	0.457
		Site substrate: mixed	0.265	0.074	3.577	3e-04***
		Site substrate: mud	0.254	0.073	3.475	0.001***
		Site substrate: sand	0.272	0.073	3.709	2e-04***
		Site elevation	0.131	0.018	7.142	1e-12***
		Overlap: windchill index	0.007	0.003	2.148	0.032***
Brent goose	Percent rest	Overlap	0.108	0.048	2.25	0.025***
	(n = 2058)	Tidestate: high	0.468	0.021	22.532	< 2e-16***
		Tidestate: low	0.046	0.022	2.091	0.037***
		Tidestate: rising	0.025	0.021	1.157	0.248
		Windchill index	-0.002	0.001	-2.121	0.034***
		Site substrate: mixed	0.531	0.069	7.714	2e-14***
		Site substrate: mud	0.539	0.068	7.969	3e-15***
		Site substrate: sand	0.553	0.068	8.143	7e-16***
		Site elevation	-0.099	0.02	-5.009	6e-07***
		Overlap: site elevation	-0.066	0.033	-1.98	0.048***

Species	Dependent Variable	Independent Variable	Estimate	Standard Error	T value	Pr(>|t|)
Brent goose	Percent small locomotion (n = 2058)	Overlap	0.071	0.029	2.463	0.014***
		Tidestate: high	0.057	0.017	3.284	0.001***
		Tidestate: low	-0.013	0.018	-0.746	0.456
		Tidestate: rising	0.028	0.017	1.596	0.111
		Windchill index	0.003	0.001	3.122	0.002***
		Site substrate: mixed	0.076	0.049	1.564	0.118
		Site substrate: mud	0.119	0.048	2.493	0.013***
		Site substrate: sand	0.108	0.048	2.263	0.024***
		Site elevation	0.009	0.012	0.738	0.46
		Overlap : tide state high	-0.054	0.032	-1.664	0.096
		Overlap : tide state low	0.084	0.034	2.495	0.013***
		Overlap : tide state rising	-0.017	0.033	-0.498	0.618
		Overlap : windchill index	-0.008	0.002	-4.125	4e-05***
Brent goose	Percent natural flight (n = 2058)	Overlap	-0.043	0.021	-2.039	0.042***
		Tidestate: high	-0.03	0.009	-3.322	0.001***
		Tidestate: low	-0.031	0.01	-3.254	0.001***
		Tidestate: rising	-0.052	0.009	-5.521	4e-08***
		Windchill index	-0.002	0	-3.273	0.001***
		Site substrate: mixed	-0.854	0.03	-28.124	< 2e-16***
		Site substrate: mud	-0.881	0.03	-29.506	< 2e-16***
		Site substrate: sand	-0.907	0.03	-30.271	< 2e-16***
		Site elevation	-0.035	0.009	-4.022	6e-05***
		Overlap : site elevation	0.034	0.015	2.309	0.021***
Wigeon	Percent feed (n = 1502)	Overlap	-0.238	0.09	-2.647	0.008***
		Tidestate: high	-0.454	0.032	-14.073	< 2e-16***

Species	Dependent Variable	Independent Variable	Estimate	Standard Error	T value	Pr(>|t|)
		Tidestate: low	-0.122	0.032	-3.853	1e-04***
		Tidestate: rising	0.037	0.032	1.173	0.241
		Windchill index	-0.004	0.002	-2.472	0.014***
		Site substrate: mixed	0.536	0.153	3.501	5e-04***
		Site substrate: mud	0.503	0.152	3.3	0.001***
		Site substrate: sand	0.633	0.154	4.114	4e-05***
		Site elevation	-0.05	0.025	-2.004	0.045***
		Overlap : tide state high	0.141	0.059	2.391	0.017***
		Overlap : tide state low	0.099	0.061	1.607	0.108
		Overlap : tide state rising	0.18	0.061	2.955	0.003***
		Overlap : windchill index	0.007	0.004	1.964	0.05***
		Overlap : site elevation	0.103	0.045	2.273	0.023***
Wigeon	Percent rest (n = 1502)	Overlap	0.046	0.04	1.161	0.246
		Tidestate: high	0.459	0.031	14.6	< 2e-16***
		Tidestate: low	0.162	0.031	5.262	2e-07***
		Tidestate: rising	-0.009	0.031	-0.279	0.78
		Windchill index	0.001	0.001	0.7	0.484
		Site substrate: mixed	0.279	0.149	1.867	0.062
		Site substrate: mud	0.365	0.149	2.459	0.014***
		Site substrate: sand	0.265	0.15	1.762	0.078
		Site elevation	0.012	0.021	0.582	0.561
		Overlap : tide state high	-0.126	0.057	-2.202	0.028***
		Overlap : tide state low	-0.044	0.058	-0.754	0.451
		Overlap : tide state rising	-0.115	0.058	-1.974	0.049***

Species	Dependent Variable	Independent Variable	Estimate	Standard Error	T value	Pr(>|t|)
Wigeon	Percent small locomotion (n = 1502)	Overlap	-0.048	0.013	-3.631	3e-04***
		Tidestate: high	0.039	0.016	2.357	0.019***
		Tidestate: low	0.006	0.016	0.372	0.71
		Tidestate: rising	0.001	0.016	0.075	0.94
		Windchill index	-0.001	0.001	-0.753	0.452
		Site substrate: mixed	0.094	0.093	1.016	0.31
		Site substrate: mud	0.098	0.092	1.058	0.29
		Site substrate: sand	0.074	0.093	0.789	0.43
		Site elevation	0.016	0.013	1.236	0.217
Wigeon	Percent natural flight (n = 1502)	Overlap	0.208	0.047	4.443	1e-05***
		Tidestate: high	-0.036	0.017	-2.18	0.029***
		Tidestate: low	-0.045	0.016	-2.721	0.007***
		Tidestate: rising	-0.017	0.016	-1.034	0.301
		Windchill index	0.003	0.001	3.56	4e-04***
		Site substrate: mixed	-0.81	0.08	-10.191	< 2e-16***
		Site substrate: mud	-0.871	0.079	-11.007	< 2e-16***
		Site substrate: sand	-0.876	0.08	-10.965	< 2e-16***
		Site elevation	-0.001	0.013	-0.074	0.941
		Overlap : tide state high	-0.029	0.031	-0.934	0.35
		Overlap : tide state low	-0.051	0.032	-1.61	0.108
		Overlap : tide state rising	-0.08	0.032	-2.524	0.012***
		Overlap : windchill index	-0.011	0.002	-5.979	3e-09***
		Overlap : site elevation	-0.048	0.024	-2.024	0.043***

*** Statistically significant

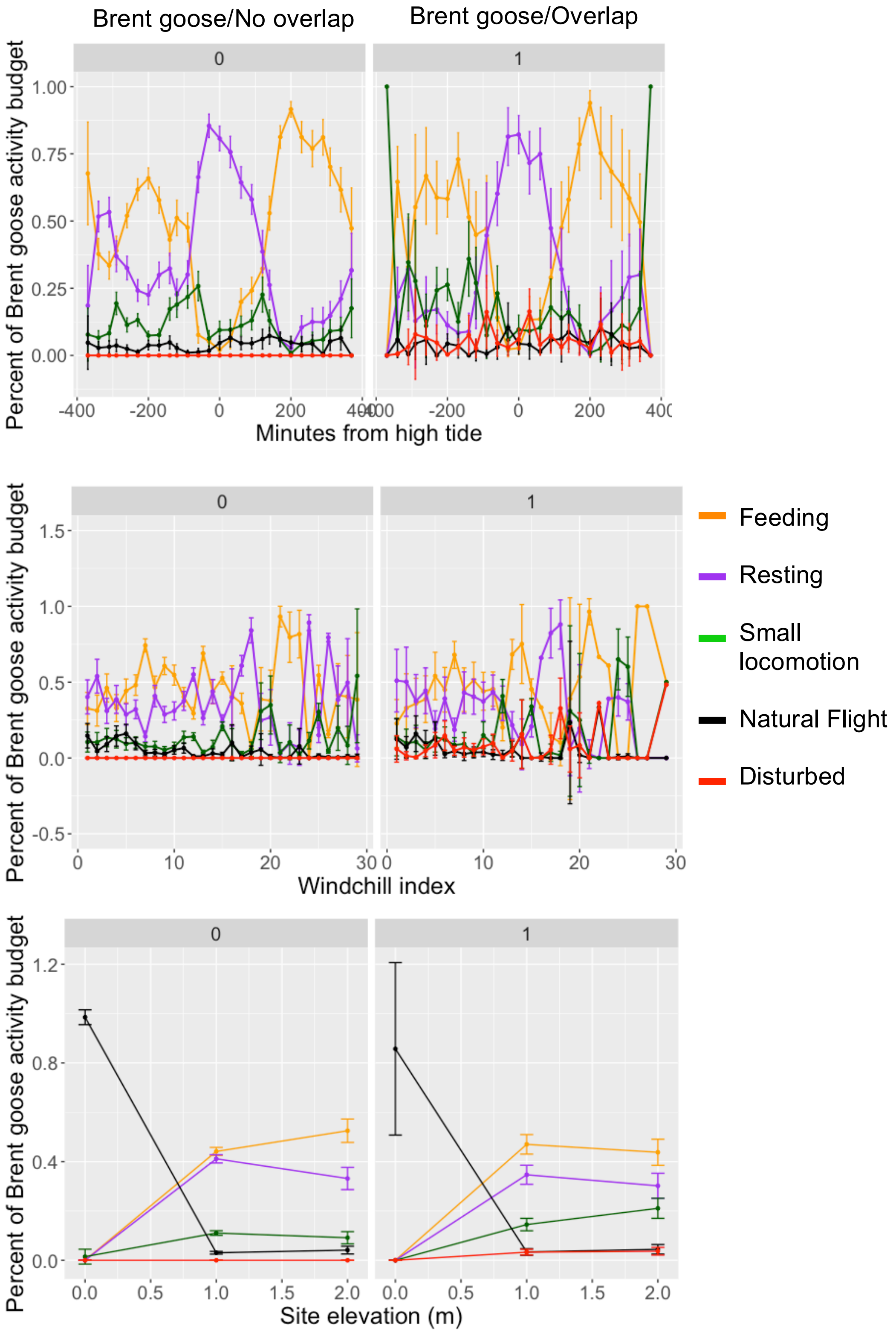


Figure 3.6 Mean measures of time budgets and corresponding 95% confidence intervals of Brent goose relative to tide (top; n = 6411), wind chill (middle; n = 4538) and site elevation (bottom; n = 4731) between instances when birds overlapped with human activities (right) and did not overlap with human activities (left).

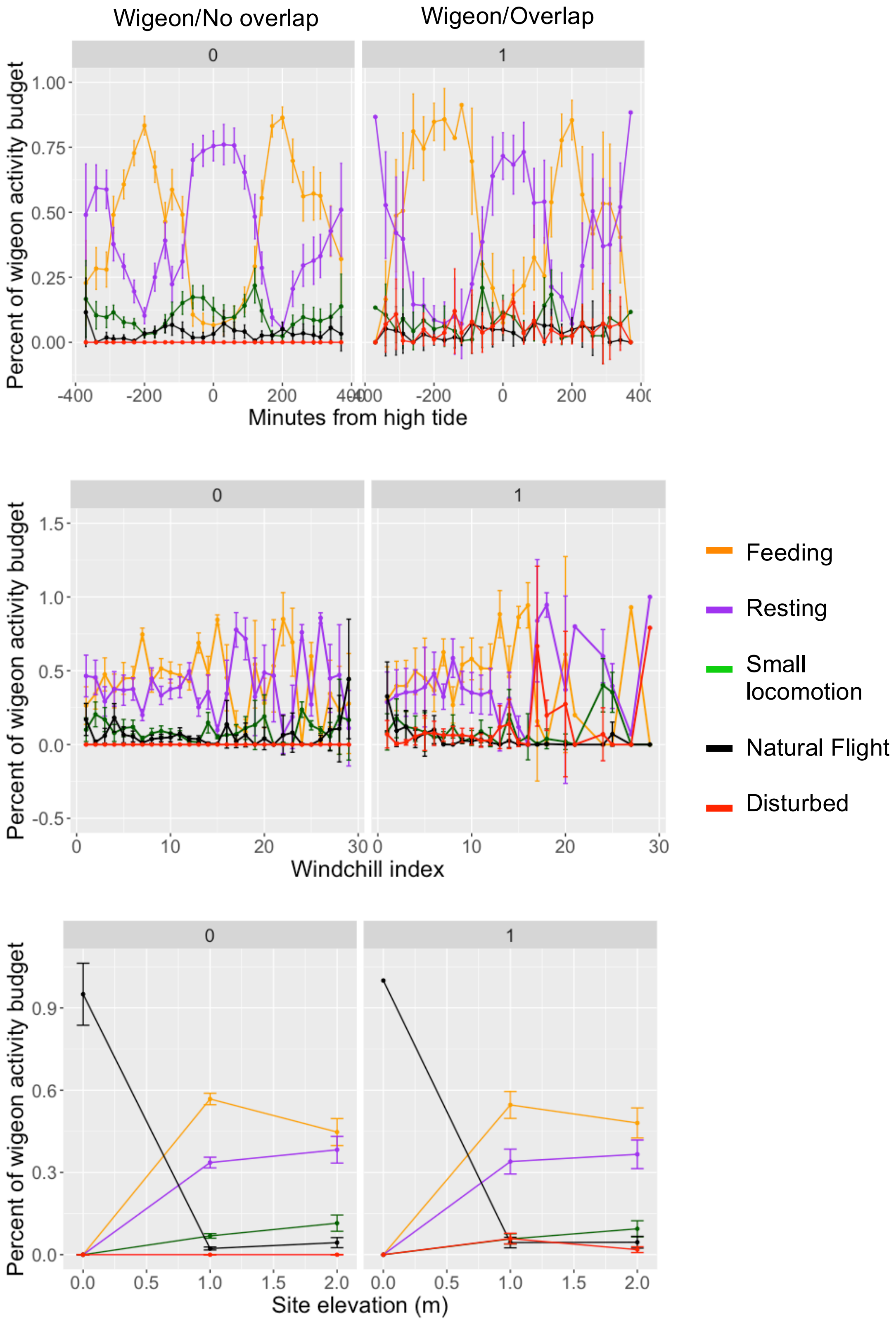


Figure 3.7 Mean measures of time budgets and corresponding 95% confidence intervals of wigeon relative to tide (top; n = 4966), wind chill (middle; n = 3425) and site elevation (bottom; n = 3553) between instances when birds overlapped with human activities (right) and did not overlap with human activities (left).

3.4.2. CALCULATED TIME-ENERGY COSTS OF DISTURBANCE

Using the COD equation (Equation 3.1) along with the observed time budgets and literature-based metabolic rates, the maximum proportion of foraging and resting Brent goose and wigeon could lose to disturbance was calculated (Table 3.2; Table 3.4).

Table 3.4 Variable values derived from equations and observational measures.

Species	Variable	Symbol	Values	Source
Brent goose	Resting metabolic rate	E_R (kJ hr^{-1})	33.23	1.6 x BMR (Clausen et al. 2012)
	Proportion of resting time lost to disturbance	$t_R \lambda_R$	.005	Percent of resting time spent being disturbed*resting time(hrs)*average flight time per disturbance(hrs)
	Metabolic rate during disturbance	E_D (kJ hr^{-1})	241.62	$10^{1.7}$*mass(kg)$^{0.868}$*3.6 (McWilliams et al. 2004)
	Energy gain on Exe Estuary	g (kJ hr^{-1})	69.45	g = (tE_r + tE_f + tE_h)/tH (Houston et al. 2012)
	Metabolic rate during feeding	E_F (kJ hr^{-1})	35.316	1.7 x BMR (Clausen et al. 2012)
	Proportion of feeding time lost to disturbance	$t_F \lambda_F$	.004	Percent of feeding time spent being disturbed*feeding time(hrs)*average flight time per disturbance(hrs)
	Essential rest time	T_{er} (hrs/24hrs)	4.9	20.43% of a 24hr budget (20% Riddington et al. 1996; 18.6% & 16.1% Ladin 2011;

Species	Variable	Symbol	Values	Source
				27% Clausen et al. 2012)
	Environmental time constraint	T_{ec} (hrs)	3	The average number of hours that water depth was more than .40cm (maximum feeding depth) on the Exe Estuary
	Average mass (kg)		1.4	Encyclopaedia of life
Brent goose	Digestive efficiency (%)		43.2	Mathers et al. 1998
	Daily energy expenditure	DEE (kJ day^{-1})	800; 986	Mathers et al. 1998; Madsen 1988
	Basal metabolic rate	BMR (kJ hr^{-1})	20.77	Clausen et al. 2012
Wigeon	Resting metabolic rate	E_R (kJ hr^{-1})	19.656	1.4 BMR (Wooley & Owen 1978)
	The proportion of resting time lost to disturbance	$t_R\lambda_R$	.005	The percentage of resting time spent being disturbed*resting time(hrs)*average flight time per disturbance(hrs)
	Metabolic rate during disturbance	E_D (kJ hr^{-1})	135.66	$10^{1.7}$*mass(kg)$^{0.868}$*3.6(McWilliams et al. 2004)
	Energy gain on Exe Estuary	g (kJ hr^{-1})	50.2922	g = (tE_r + tE_f + tE_h)/tH (Houston et al. 2012)
	Metabolic rate during feeding	E_F (kJ hr^{-1})	23.868	1.7 BMR (Wooley & Owen 1978)
	The proportion of feeding time lost to disturbance	$t_F\lambda_F$	.002	The percentage of feeding time spent being disturbed*feeding

Species	Variable	Symbol	Values	Source
				time(hrs)*average flight time per disturbance(hrs)
	Essential rest time	T_{er} (hrs/24hr)	6.84	28.5% of 24hr budget (29% Paulus 1988; 28% Houhamdi & Samraoui 2013)
	Environmental time constraint	T_{ec} (hrs)	3.5	The average number of hours that water depth was more than .30cm (maximum feeding depth)
Wigeon	Average mass (kg)		0.720	Encyclopaedia of life
	Digestive efficiency (%)		28.8	Mayhew 1988
	Daily energy expenditure	DEE (kJ day^{-1})	592	Madsen 1988 (wigeon feeding on *Zostera noltii*)
	Basal metabolic rate	BMR (kJ hr^{-1})	14.04	Wooley & Owen 1978

In this chapter, Brent goose were limited to less than 24hrs to feed for several reasons. Due to tidal depth, food was only accessible to Brent goose on the Exe estuary for 21hrs per day (Table 3.4). Furthermore, the literature indicates that Brent goose on average spend at least 20.43% of a 24hr time budget (4.9hrs) resting (Table 3.4). This finding suggests that even with 3 hours of enforced rest due to inaccessible food, Brent goose still, on average, require an additional 1.9 hours more of rest, which means, that on the Exe estuary, Brent goose would only be able to feed for a maximum of 19.10hrs out of 24hrs.

Brent goose on the whole Exe Estuary during this investigation lost a combined 0.9% of feeding and resting time; 55% of that 0.9% was lost resting time (0.5%), and 45% of that 0.9% was lost feeding time (0.4%). This lost time amounted to approximately 0.98 disturbances per hour (Figure 3.8). Based on energy equilibrium, to make up for this disturbance time, Brent goose had to feed an additional 15 minutes and 37 seconds per day, more, than in the absence of disturbance. Based on projections of the COD equation (Equation 3.1), if disturbance on the Exe Estuary were to increase and affect a similar portion of feeding and resting time, the average brent goose could experience 24 times more disturbance before they would run out of time to compensate for it (Figure 3.8).

However, if disturbance increased unevenly and affected different proportions of feeding and resting time, the rate of reaching the thresholds changes. For example, if disturbance occurred only during feeding times when the energetic cost is highest, Brent goose could only sustain 12.28% of foraging time loss (12 times the current amount) before they would run out of time to make up for it. Conversely, if disturbance only occurred during resting, Brent goose would be able to sustain 92% loss of that rest time (92 times the current amount) before they would no longer have enough time to feed to compensate (Figure 3.9).

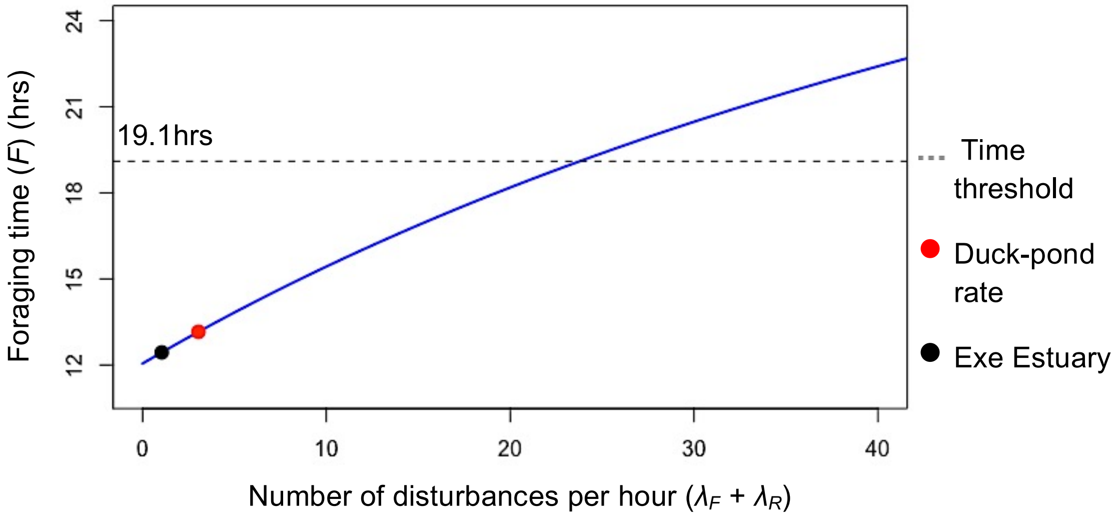


Figure 3.8 Projected total foraging time needed for Brent goose to make up for disturbances per hour based on current disturbance rates on the Exe Estuary. Rates of disturbance on the Exe Estuary at the time of this study were 0.98 disturbances per hour (black dot) and 2.85 disturbances per hour in the most disturbed region of the estuary (the Duck-pond; red dot). Based on projections of the COD equation (Equation 3.1), the maximum number of disturbances Brent goose could experience on the Estuary before running out of time (19.1hrs; grey dotted line) was 24 disturbances per hour.

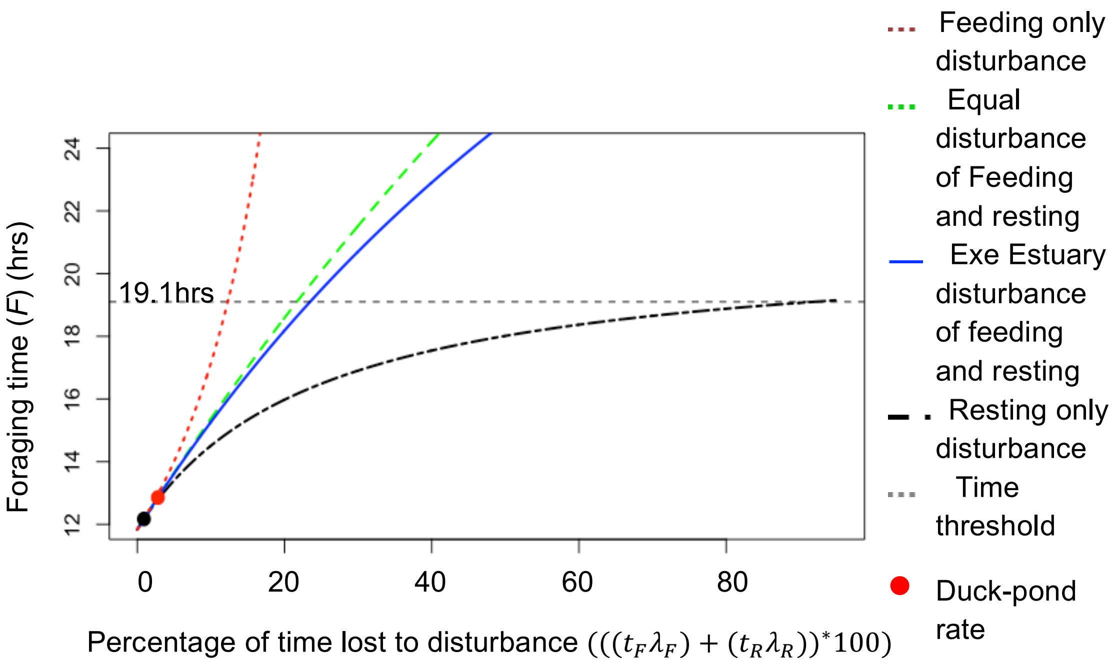


Figure 3.9 The amount of total time Brent goose need to feed to balance energy as disturbance increases from low to high (left to right). If a brent goose is disturbed more during feeding (red dotted line), it takes less disturbance to reach the thresholds of time (19.1hrs; grey dotted line) than if disturbed more during rest (black dotted line). Brent goose on the Exe Estuary are disturbed slightly more while resting than while feeding (solid blue line). Percentage of time Brent goose lost to disturbances on the Exe estuary in this study was 0.9% (black dot). In the most disturbed region of the Exe estuary, the Duck-pond, the percentage of time lost was 2.8% (red dot).

Wigeon were similarly limited to less than 24hrs to feed due to tidal restrictions and necessary rest time. Due to wigeon having less reach than Brent goose, they are only able to access food 20.5hrs out of 24hrs. Additionally, the average literature resting percentage for wigeon was 28.5% out of 24 hours (6.84hrs; Table 3.4). Therefore, the maximum feeding time for wigeon on the estuary was 17.16hrs.

When performing the same calculations on as those for Brent goose, approximately 0.2% of wigeon foraging time and 0.5% of wigeon resting time on the Exe Estuary was spent being disturbed, which means that the total combined loss of time to disturbance was

0.7%. Wigeon are currently feeding an additional 15 minutes and 16 seconds a day to account for this energetic loss (Figure 3.10). Based on projection from the COD equation (Equation 3.1), if wigeon are disturbed and the same ratio of resting and foraging time as in this study, the maximum percent of combined foraging and resting time that wigeon would be capable of losing to disturbance was 34.7% (Figure 3.10). However, if wigeon are only disturbed during feeding, the maximum amount of foraging time they can lose, before they run out of time to compensate, becomes 15.9%. On the other hand, if wigeon are only disturbed while resting, wigeon can sustain up to 65.4% of their resting time disturbed before they can no longer have time to compensate (Figure 3.11).

When further evaluating one of the most disturbed regions of the Exe Estuary, the Duck Pond (see Chapter 2), the combined loss of feeding and resting time amounted to 2.8% for Brent goose and 1.6% for wigeon. This amount of disturbance is still well below the threshold values calculated for these birds (Figure 3.8; Figure 3.9; Figure 3.10; Figure 3.11).

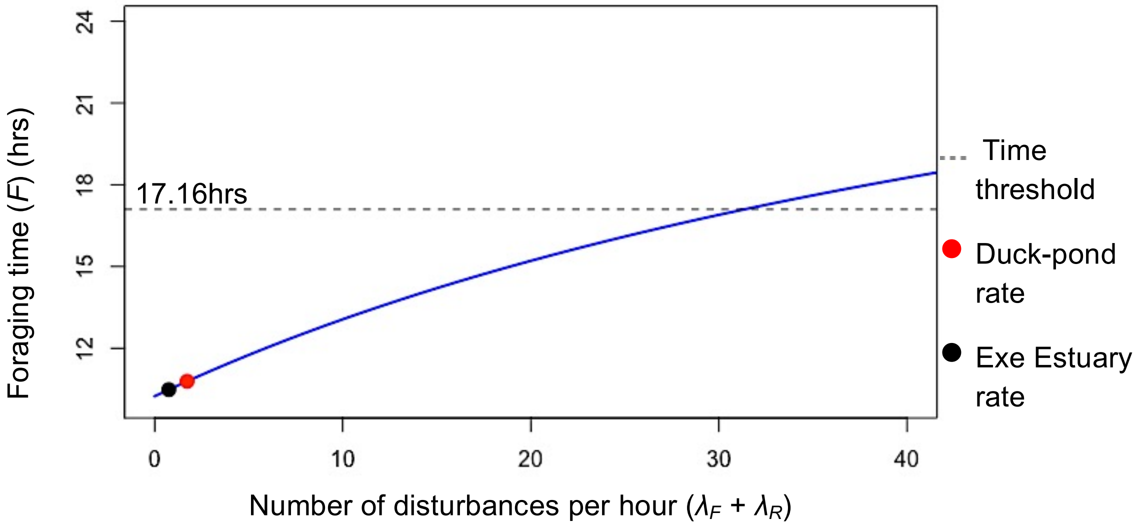


Figure 3.10 Projected total foraging time needed for wigeon to make up for disturbances per hour based on current disturbance rates on the Exe Estuary. Rates of disturbance on the Exe Estuary at the time of this study were 0.68 disturbances per hour (black dot) and 1.56 disturbances per hour in the most disturbed region of the estuary (the Duck-pond; red dot). Based on projections of the COD equation (Equation 3.1), the maximum number of disturbances wigeon could experience on the Estuary before running out of time (17.16hrs; grey dotted line) was 33.87 disturbances per hour.

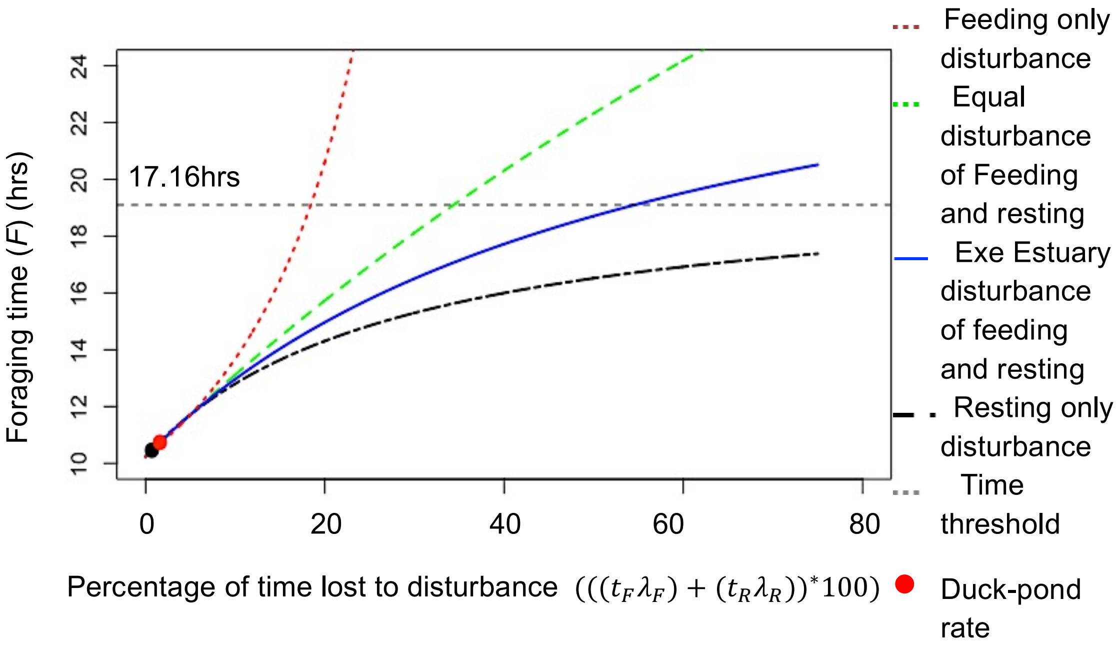


Figure 3.11 The amount of total time wigeon would need to forage to balance energy as disturbance increases from low to high (left to right). If wigeon are disturbed more during feeding (red dotted line), it takes less disturbance to reach the thresholds of time (17.16hrs; grey dotted line) than if disturbed more during rest (black dotted line). The percentage of time lost to disturbance by wigeon on the Exe Estuary, in this study, was 0.7% (black dot). In the most disturbed region of the Estuary (the Duck Pond) the percentage of time lost was 1.6% (red dot).

3.5. DISCUSSION

This chapter investigated the responses of wildfowl on the Exe Estuary when there was an overlap in space and time between wildfowl and human activities. These responses were translated into the time and energy costs to the animals involved.

3.5.1. TIME BUDGET VARIATION

The time budgets of both Brent goose and wigeon on the Exe Estuary were significantly different in the presence and absence of human activity. Brent goose and wigeon both had lower feeding time, higher resting time and more natural flights when overlapping with human activities. While Brent goose had higher small locomotion and wigeon had less small locomotion. These changes in time budgets could be directly linked to the reallocating of time to different activities to deal with disturbances that occurred during overlaps. The lower feeding time in overlap zones could be due to the simple loss of feeding opportunities when disturbances occur, and the higher resting may be a method for conservation of energy to counteract higher energy expenditure associated with disturbance. The higher degree of locomotive activity may be a pure reflection of more movement often associated with disturbance. Many animal species change time budgets as a mechanism for dealing with disturbance activity. For example, the American coot (*Fulica americana*, L.) has higher locomotive movements relative to the presence of human activity and lower feeding (Schummer & Eddelman 2003). The white-headed langur (*Trachypithecus leucocephalus,* L.) in China sacrifices socialization time and has higher feeding time in areas with high disturbance (Li & Rogers 2004).

However, there are also other factors potentially influencing Brent goose and wigeon time budgets relative to the presence and absence of overlap with human activity. The differences detected in bird activities associated with overlaps in this chapter may be a product of the difference in conditions related to overlap events, rather than the result of the overlap itself. Based on the findings in Chapter 2, there is evidence that there are specific environmental conditions that lead to higher chances of overlap with human activities. Furthermore, multivariate analysis of time budgets relative to overlaps and environmental variables had significant interactions relative to bird activities. This interaction indicates that it is the combination of overlaps and the different environmental variables that are leading to the changes in time budgets relative to overlap events.

Differences in an animal’s time budget could simply mean that the animal has the capacity to change its behaviour (Gill et al. 2001). If an animal does not change its behaviour or feeding time, it either is not being energetically affected by the disturbance, or it is incapable of feeding any more than it already is. Therefore, to fully understand what effect disturbances within overlaps are causing, it is essential to be able to identify the energetic requirements as well as the time constraints that animals have and whether disturbance events are exceeding the ability of the animals to compensate.

Standard error and confidence intervals of daily time budgets of both Brent goose and wigeon revealed relatively little variation. According to Houston et al. (2012), time budgets are primarily a reflection of energy budgets. Based on the measures of environmental variables and disturbance levels on the Exe estuary, it is apparent that Brent goose and wigeon are having little difficulty meeting their energetic needs.

Therefore, it is not surprising that their time budgets varied very little. However, under conditions where birds are struggling to meet energy needs, where an environment is more varied, or where human activity is creating greater degrees of disturbance, we might expect to see greater variation reflected within daily time budgets.

3.5.2. COST OF DISTURBANCE

The current rate of disturbance experienced by Brent goose and wigeon on the Exe Estuary amounts to approximately 0.9 % and 0.7% of combined feeding and resting time, respectively. These values are both below the calculated thresholds for time and energy. For instance, if Brent goose were disturbed at the same rates during feeding and resting as they were in this chapter, it would require, at least 23 times more disturbance per day, before Brent goose would run out of foraging time to make up for the losses. Concerning wigeon, it would take 34 times more disturbance. From a more conservative perspective, if disturbances are isolated to only feeding time, it would still take 12 times and 15 times the current disturbance rate for Brent goose and wigeon respectively. From this, it is apparent that Brent goose and wigeon on the Exe Estuary are experiencing non-threatening levels of disturbance.

Although constraints have been placed on these birds based on estuarine conditions and the availability of food within them due to tide states, there are often instances when both Brent goose and wigeon still have access to food resources that are not on the estuary. This access includes resources such as field grasses and pond networks. In these instances, any time constraints on feeding would be isolated to necessary rest time for digestion.

In a study conducted by Ross et al. (2015 unpublished), the Exe Estuary was listed as the fourth most at-risk estuary in the UK for potential impacts of human disturbance. This ranking was based on the natural geography of the site, the surrounding urbanization, human access, and presence of water-sports. As such, understanding how birds are energetically coping with disturbances on this site, offers insight into how animals, in general, are dealing with disturbance in regions that experience high human activity. Calculations of energetic losses, associated with disturbances recorded on the Exe Estuary, indicated that both Brent goose and wigeon were well suited to be able to compensate for the degree of the disturbance they were experiencing during this study.

3.5.3. THRESHOLDS FOR DISTURBANCE

Although Brent goose and wigeon on the Exe estuary are not currently within danger of reaching energetic thresholds for disturbance, it is important to consider potential situations where these thresholds might be reached. Based on evidence in this chapter, when Brent goose and wigeon are disturbed while feeding, thresholds are reached more swiftly. Therefore, if human activities were suddenly to increase during time periods when birds are feeding, then Brent goose and wigeon would not be able to tolerate as high of a degree of disturbance. Furthermore, as environmental conditions also affect the ability of birds to be able to reach their energetic needs, if environmental conditions were to suddenly shift then bird time budgets would also likely change. If the time budgets shift to higher degrees of feeding then threshold for disturbance would be lower, because the birds would have less time to compensate.

3.6. CONCLUSION

The purpose of this chapter was to investigate the responses of animals when overlaps with human activities occur. This purpose was achieved through the combination of time budget analysis and energetics balancing equations. The principles within these analyses are based on daily activities and concept that if animals are to survive, they must be able to gain back the energy they have lost participating in those activities. Therefore, the methods in this research can be applied to many different types of animals in many different situations. The results of using these principles to Brent goose and wigeon on the Exe Estuary indicate that currently, these birds are not having any difficulty reaching necessary energetic requirements for survival in the presence of current disturbance rates. Additionally, based on energetic calculations, Brent goose and wigeon are both capable of tolerating a minimum of 12 and 15 times more disturbance than they are currently experiencing on the estuary before they are constrained by feeding time. This result is positive news for an estuary that is considered to be one of the most disturbed estuaries in the United Kingdom.

3.7. FUTURE WORK

Expansion upon the work in this chapter could include the implementation of these methods on other species and sites to determine the thresholds for other animals in different situations. Additionally, there is scope within the equation provided in this chapter, for application to animals that require more than just energy equilibrium, such as animals preparing for reproduction or migration. There is also scope to account for either habituation or sensitization within the equation. Being able to isolate and account for such behavioural changes can influence how much disturbance will cost animals in future projections. Future work could include an integrated example of how these additional variables might be useful. Furthermore, this chapter has not investigated the costs of disturbance from different individual sources of human activities. By identifying and investigating the effects of different types of disturbance, those activities that are potentially the costliest for animals can be identified, which can help inform management decision making.

4. CHAPTER 4: VARIATION IN DISTURBANCE RESPONSE TO DIFFERENT HUMAN ACTIVITY TYPES: INSIGHTS FROM WILDFOWL ON THE EXE ESTUARY

4.1. ABSTRACT

As different human activities have distinct characteristics, it would be expected that animals will respond in different ways to contrasting types of human activity. This chapter investigated changes in response to different types of human activity by Brent goose (*Branta bernicla*) and wigeon (*Mareca penelope*) on the Exe Estuary. A combination of scan-sampling and continuous-sampling were used to collect data during the winter months of 2017-2018 and 2018-2019. There were significant differences in how these species responded to the various forms of human activity, with some types of activity resulting in higher energetic and time costs to the birds. This chapter ranks different activity types in terms of their time and energy costs to the birds. Pedestrians caused the greatest time and energy costs for both species. Wildfowling was amongst the least disturbing activities, as it occurred relatively infrequently and when occurring did not incur a high time or energy cost to the birds. The current overall rates of disturbance experienced by brent goose and wigeon on the Exe Estuary are well below thresholds at which birds would fail to meet their energy requirements.

4.2. INTRODUCTION

4.2.1. BACKGROUND

Different human activity types have inherently unique characteristics. Some are fast-moving, some are slow-moving, some are in the air, and some are on the water. These diverse characteristics mean that individual human activities are likely to be interacted with and to be perceived differently by animals. For example, a person walking on a coastal path is expected to only come into contact with animals that are near the top of the shore. In contrast, an individual in a motorboat will only come into contact with animals on or near the water. Furthermore, a reaction from an animal to a walking activity would require a much slower response than to a fast-moving speed boat. Therefore, if there are differences in the overlap between animals and human activity (see Chapter 2) and perception of distinctive human activities by animals, there are likely disparities in the level and cost of disturbances associated with diverse human activities.

Four main variables determine how an animal responds to a recreational activity: location, frequency, predictability and characteristics of the animal (Cole 1991). For example, bighorn sheep (*Ovis canadensis canadensis*, L., in Turner Valley, Alberta) show changes in heart rate with the location of approach from a human as well as whether the activity was consistent and predictable (MacArthur et al. 1982). In addition, heart rates of bighorn sheep were higher if a human approached from over a ridge compared to approaching from open land (MacArthur et al. 1982). Furthermore, there was low heart rate elevation with road traffic which could be considered frequent and predictable (MacArthur et al. 1982).

Wildfowling is a particularly unique form of human activity. Not only is shooting associated with a potential direct mortality event, but it also represents an indirect noise disturbance (Knight & Cole 1995). Mortality events are exceptionally well known for deterring animals and, so much so, that they are often used as scare tactics to keep birds from feeding on crops (Bishop et al. 2003). Additionally, hunters deliberately overlap their activity and location with those of the target species. Therefore, by combining a mortality event with a noise event and an active, rather than passive, overlap, it might be expected that disturbance effects due to wildfowling are higher than other forms of disturbance.

The literature indicates that wildfowling disturbance causes changes in behaviour, redistributions, as well as, increased escape distances in wildfowl (Owen 1993; Madsen & Fox 1995; Madsen 1998a & 1998b; Sokos et al. 2013). Based on these effects, wildfowling-related activities rank as the most disturbing activity to wildfowl during autumn staging in Nibe-GjØl, Bredning (Madsen 1998a & 1998b). However, Gill et al. (2001) indicated that redistributions and responses might not necessarily be an indication of a negative impact, but rather an indication of the adequate alternative resources. Consistent with Gill et al. (2001), a review paper by Sokos et al. (2013) revealed that, although wildfowling disturbance affects bird behaviour and distribution, the literature has failed to detect associated increases in non-wildfowling mortality. Furthermore, Sokos et al. (2013) discovered that there were no differences in feeding rates, body condition, breeding success, or population numbers concerning the presence and absence of wildfowling disturbance.

Moreover, Collop (2017) showed that although wildfowling disturbance, on average, produced a greater magnitude of response in wading birds than other forms of human activity, the frequency of occurrence was much less than that of other human activity sources. Collop (2017), therefore, concluded that wildfowling activities were a lower source of energetic cost for wading birds than other human activities. According to these results, wildfowling disturbance incites responses in wildfowl that are greater than other forms of human disturbance, but this does not always translate to impacts, for example in terms of increased mortality. Therefore, there is a need for more information on how wildfowling disturbance effects result in impacts and how those projected impacts compare to other forms of human activity.

Because different human activities have many different characteristics and ways of influencing animals, in order to compare them, multiple factors must be taken into consideration, not just in terms of disturbance but also in terms of factors leading to those disturbances. Risk assessments have been used in many capacities to determine variables that ultimately result in a hazardous situation (Crichton 1999; Wolf 2012). The hazardous situation in the context of human disturbance is the disturbance event itself. Therefore, one method for comparing human activities relative to disturbance is through a risk assessment that combines variables leading up to a disturbance. One method of risk assessment is through the use of a risk triangle that employs three main variables: exposure, vulnerability and hazard (Crichton 1999). With respect to human disturbance events, the characteristics that could be classified into the exposure category are conditions that are conducive to exposing an animal to a disturbance event, such as abundance of a human activity. While vulnerability refers to conditions that mean the animal is likely to be disturbed, such as overlap. Then the hazard, as mentioned earlier, is the disturbance event itself and the variation within those disturbance events. As a result, a useful way of comparing human activities in terms of human disturbance is through a risk assessment because it combines multiple variables into on value.

To more fully examine the distinctions in disturbance associated with different human activity types, and wildfowling in particular, this chapter evaluates the degree of overlap between birds and different types of human activities and the resulting costs of disturbance. Using these costs, projections are made of how increases in different activity types can lead to impacts, measured as reduced energy consumption. This chapter also implements a risk assessment analysis for identifying activity types that are potentially the most significant source for concern.

4.2.2. AIMS AND OBJECTIVES

This chapter contrasts different types of human activity in terms of their extent of overlap with Brent goose and wigeon, and the associated time and energy costs incurred by the birds.

This chapter has the following objectives:

- To measure the degree of overlap between Brent goose and wigeon and various human activities, including wildfowling events
- To quantify time and energy costs associated with wildfowling activity alone relative to other human activities

4.3. METHODS

4.3.1. STUDY SITE

The study site was the Exe Estuary, described in further detail in Section 2.2.

4.3.2. OBSERVATIONS

General observations of all human activity types were recorded using the methods in Chapters 2 and 3. These activities fit into 14 primary categories (Table 4.1). Walkers with dogs were split between the categories of ‘People’ and ‘Animals’. This separation means that disturbances from dog walkers are still represented, but distinctions can be made as to whether the disturbance is the result of the dog or the human. In addition, 49 separate wildfowling trips took place with members of the Devon Wildfowling Club during the wildfowling seasons of 2017-2018 and 2018-2019. Each trip simulated an actual wildfowling visit. Hunters only fired shots if quarry species were within range (45-140 meters) and dogs only left the hunter’s side if there was a bird to retrieve. Quarry species on the Exe Estuary included: teal (*Anas crecca*, L.), pintail (*Anas acuta*, L.), mallard (*Anas platyrhynchos*, L.), wigeon (*Mareca penelope*), Canada geese (*Branta canadensis*), and greylag geese (*Anser anser*, L.).

Two observers were present for each recorded wildfowling trip. Observers stood within 20 meters, or less, of a hunter, and data were recorded with the mixed scan and continuous collection methods described in section 2.2 and 3.2 (Chapters 2 & 3). Wildfowler presence as well as human activity presence were recorded on a continuous sampling basis by the minute for the duration of the wildfowling visit. All bird counts and distributions were recorded via scan sampling every 30minutes for the duration of the wildfowling visit. Due to the nature of the observations, all data collected during wildfowling observations included the presence of the wildfowler and the proximity of the wildfowler to all birds observed within the subsite by the minute. Wildfowlers, dogs, and shots fired were considered separate human activities due to the distinction between the inherent nature of a disturbance from these sources. However, any disturbance resulting from any one of those sources during a wildfowling visit was considered a 'wildfowling' disturbance. General observations incidentally collected data on wildfowling presence as well.

Table 4.1 General category assignments of specific human activities and other disturbance sources.

General Category	Specific Human Activity
Wind-water sport	Kite Surfers Wind Surfers Sailboats
Non-wind-water sport	Canoe Kayak Paddleboard
Motorized-land	Car Lorry Train Tractor Motorbike Trolley
Noise	Non-wildfowling gunfire Unidentified noise Fireworks
People	Walker Dog walker (excl. dog) Golfer Birdwatcher
Animals	Dog Horse
Predator	Peregrine Fox
Harvester	Fisher Crab-tiler Bait-digger
Air	Plane

General Category	Specific Human Activity
	Helicopter Paraglider
Fast-land	Cycle Jog
Other	Smoke
Wildfowler	Wildfowler Wildfowler shots Wildfowler dog
Motorized-water	Motorboat Jet-ski Tour-boat

4.3.3. BRITISH ASSOCIATION FOR SHOOTING AND CONSERVATION (BASC) DATA

BASC provided data on wildfowling that occurs on the Crown foreshore within the Exe Estuary with permission from the Devon Wildfowling Club. Data included all dates and duration of any wildfowling trips that took place. Additionally, data included the number of shots fired, the number of birds killed, dates and duration of wildfowling visits. This data provided a visitation rate of wildfowlers that could be compared to the incidental observation rate of wildfowlers in general observations. Furthermore, the records of the shots fired from the BASC data allowed comparison of shot percentages from the wildfowling trips to determine if wildfowling trips were truly representative of real wildfowling visits.

4.3.4. ENVIRONMENTAL VARIABLES

The following environmental variables were measured during wildfowling visits: date, time, minutes from high tide, wind speed, wind direction, temperature, precipitation, fog, substrate, accessibility, and moon phase. Additionally, historical weather data was paired with archived BASC datasets. Environmental variables were collected according to the methods in section 2.2 (Chapter 2).

4.3.5. EQUIPMENT

Two individuals conducted all observational surveys. Kit included a Swarovski STS 80 High Definition (HD) Straight Spotting Scope and accompanying tripod, as well as Swarovski 10x42 Swaro-Aim EL RANGE Binoculars.

4.3.6. ANALYSIS

All analyses used RStudio statistical software Version 1.0.136 (© 2009-2016 RStudio Inc.) with R version 3.3.3 (© 2017-03-06 R Inc.).

4.3.6.1. BIRDS OVERLAPPING PEOPLE

'Birds Overlapping People' (BOP) indexes were calculated (see Chapter 2) for the degree of overlap between birds and each human activity type. Comparisons used the BOP index values between for each Brent goose and wigeon as the dependent variable and human activity type, wind chill, tidal state and substrate type as the independent variables. This analysis used the 'General Linear Model' GLM command in the package multcomp_1.4-8.

4.3.6.2. WILDFOWLING DATA

Because wildfowling data was collected on different scales standardizing was necessary in order to be able to compare it with other human activities. This was achieved by using incidental wildfowling observations and BASC data to generate occurrence rates of wildfowlers on the Estuary relative to other human activities. Then disturbance rates and overlaps of wildfowling with Brent goose and wigeon was calculated from the accompanied wildfowling trips.

4.3.6.3. COST OF DISTURBANCE

Time and energy costs associated with each human activity type were calculated using the 'Cost of Disturbance' (COD) equation (Chapter 3; Equation 3.1).

4.3.6.4. RISK ASSESSMENT

Risk assessment analysis used the risk triangle of hazard, exposure, and vulnerability as a method for identifying activity types that are potentially the most significant source for disturbance concerns (Crichton 1999; Wolf 2012). Different activity types were ranked based on the combined variables of activity occurrence, degree of activity overlap with birds, whether the event disturbed birds more while feeding or resting, and the observed rate of disturbance per hour associated with the activity. Activity occurrence was considered to be an exposure variable. As the more often an activity occurs, the more a bird is likely to be exposed to this activity. Degree of activity overlap was considered to be a vulnerability variable, because once the activity overlaps with a bird then the bird become vulnerable to disturbance because the conditions are greater for the disturbance to happen. Ratio of disturbance while feeding or resting and rate of disturbance per hour were both considered hazards, because birds have already been exposed to the disturbance at this point and now it is a matter of how bad the hazard actually is.

4.4. RESULTS

Differences were apparent between different human activity types and the degree of overlap of those activities with Brent goose and wigeon. Differences were also present in the time and energy costs associated with disturbance caused by different human activity types.

4.4.1. OVERLAPS AND BOP INDEX

Of the 14 primary human activity groups (Table 4.1), pedestrians, animals and wind watersports were the three most commonly observed on the estuary. These same groups also had the highest frequency of overlap events with wildfowl on the estuary (Figure 4.1; Figure 4.2). Not including the separate BASC trips, wildfowling was the fourth most commonly observed activity on the estuary; however, only approximately 10% of wildfowling occurrences were accompanied by an overlap with either Brent goose or wigeon, compared with the near 40% of incidents of people resulting in an overlap with Brent goose and wigeon (Figure 4.1).

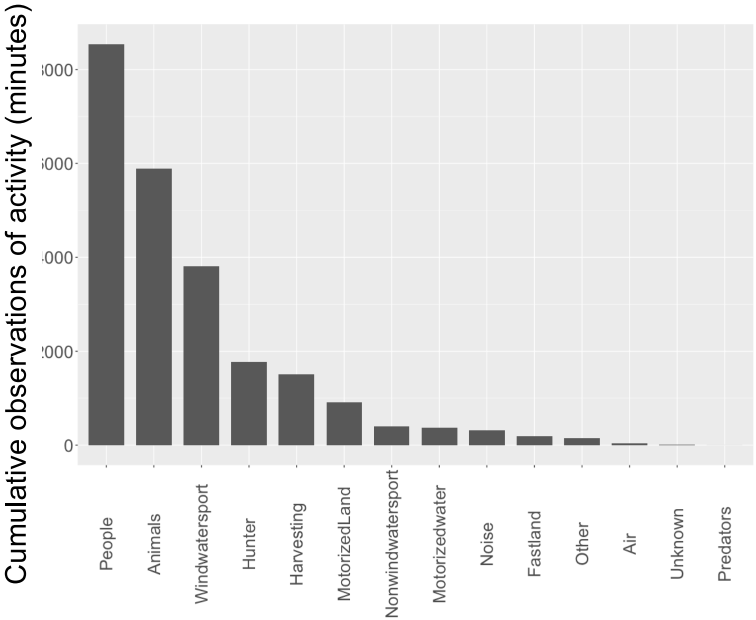


Figure 4.1 The number of minutes that different human activity types were observed on the Exe Estuary.

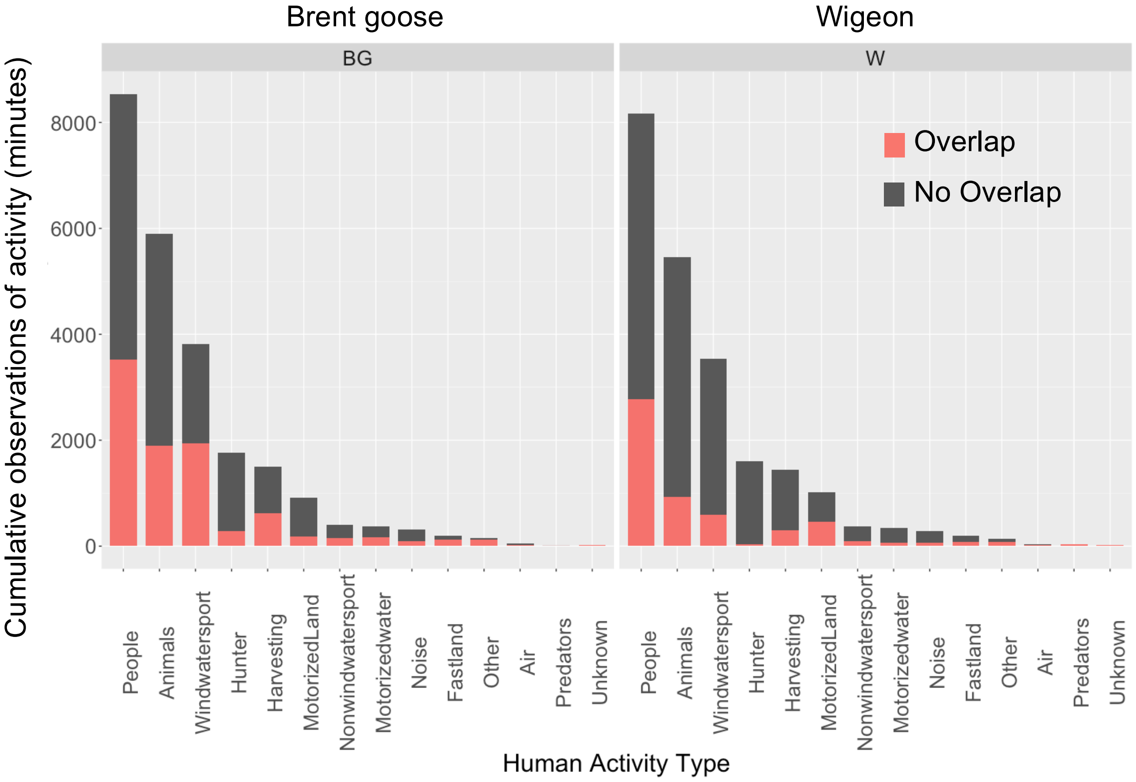


Figure 4.2 The number of minutes that different human activity types were observed and the number of those minutes where an overlap (pink) occurred between human activities and Brent goose (left) and wigeon (right)

Substantial visual variation was evident between the number of recorded minutes of human activity types and different environmental variables (Figure 4.3; Figure 4.4; Figure 4.5). Based on results from Chapter 2, bird presence and absence, as well as density, are dependent on several environmental variables. These results provided initial evidence that BOP index values were likely to be different between different human activity types.

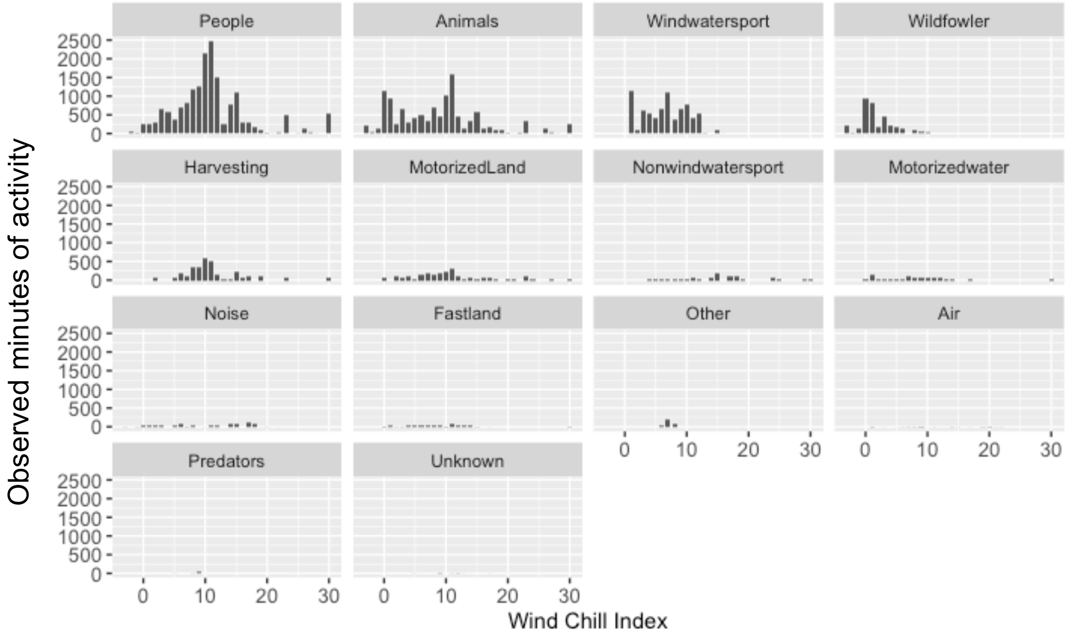


Figure 4.3 Observed minutes of different human activity types relative to wind chill values.

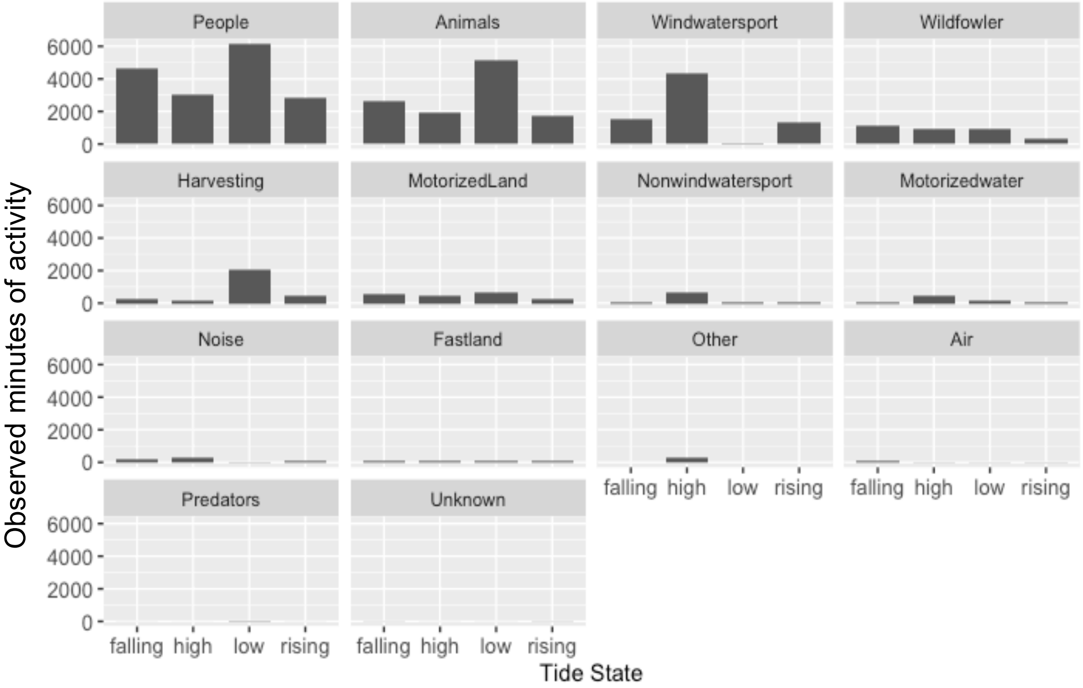


Figure 4.4 Observed instances of different human activity types relative to tide states.

Figure 4.5 Different human activity types relative to the location within the site and substrate types.

There were statistically significant differences in BOP index values detected between human activity types (Figure 4.5). ‘Air’, ‘Fast-Land’, and ‘People’ activities (Table 4.2) had the highest average BOP values with Brent goose. ‘Air’, ‘Non-wind water-sports’, and ‘Predators’ (Table 4.2) had the highest average BOP values with wigeon.

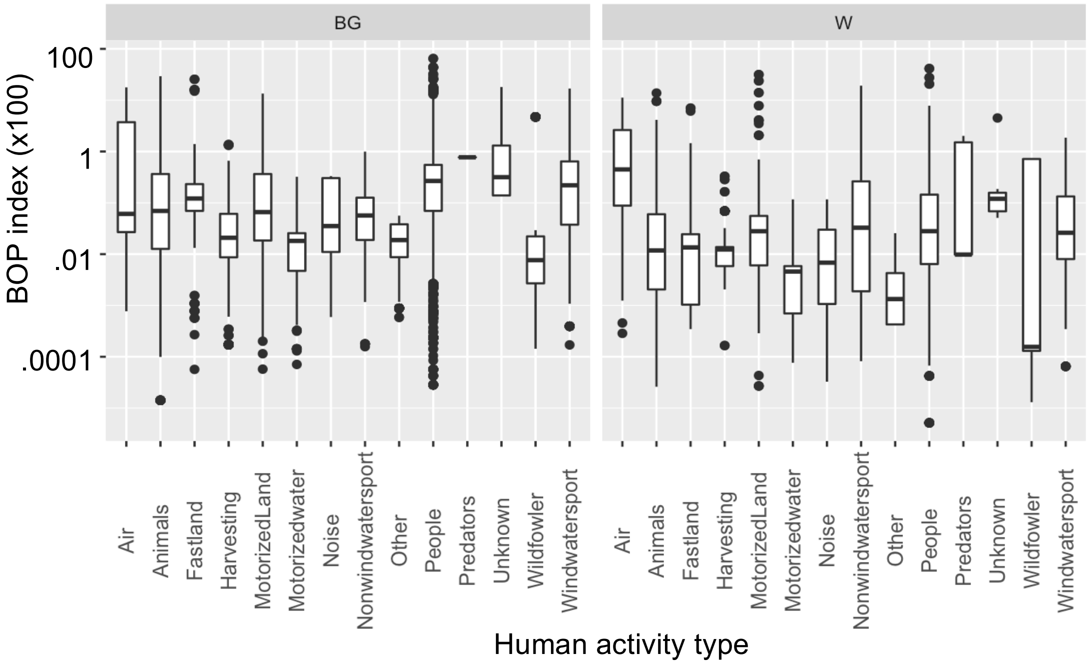


Figure 4.6 Comparison of average BOP values of different human activity types for Brent goose (left) and wigeon (right). Highest BOP values for Brent goose were: ‘Air’, ‘Fast-Land’, ‘People’ (Table 4.1). For wigeon, the highest BOP values were: ‘Air’, ‘Non-wind watersports’, and ‘Predators’ (Table 4.1).

Table 4.2 Statistical output from glm analysis of BOP index of Brent goose and wigeon relative to activity type and environmental variables.

Dependent Variable	Independent Variables	Estimate	SE	T value	Pr(>|t|
BOP index Brent Goose (n=10860)	Animals	-0.02	0.008	-2.512	0.012***
	Fast-land	-0.019	0.008	-2.367	0.018***
	Harvesting	-0.018	0.008	-2.234	0.025***
	Motorized-land	-0.034	0.008	-4.088	4.37e-05***
	Motorized-water	-0.022	0.008	-2.62	0.009***
	Noise	-0.026	0.009	-2.997	0.003***
	Non-wind-water sport	-0.023	0.009	-2.626	0.009***
	Other	-0.027	0.009	-3.111	0.002***
	People	-0.015	0.008	-1.896	0.058
	Predators	-0.018	0.026	-0.676	0.499
	Unknown	-0.017	0.013	-1.259	0.208
	Wildfowler	-0.013	0.008	-1.598	0.11
	Wind-water sport	-0.02	0.008	-2.521	0.012***
	Windchill index	-9.9e-05	8.9e-05	-1.118	0.263
	Tide state: high	0.002	0.001	1.748	0.08
	Tide state: low	-0.011	0.001	-7.731	1.17e-14***

Dependent Variable	Independent Variables	Estimate	SE	T value	Pr(>|t|
	Tide state: rising	0.01	0.001	7.969	1.76e-15***
	Substrate: mixed	-0.066	0.003	-25.803	< 2e-16***
	Substrate: mud	-0.069	0.002	-37.12	< 2e-16***
	Substrate: sand	-0.073	0.002	-32.347	< 2e-16***
BOP index Wigeon (n=6842)	Animals	-0.013	0.003	-4.384	1.18e-05***
	Fast-land	-0.013	0.003	-4.131	3.66e-05***
	Harvesting	-0.014	0.003	-4.524	6.18e-06***
	Motorized-land	-0.012	0.003	-3.811	1.4e-04***
	Motorized-water	-0.015	0.003	-4.318	1.6e-05***
	Noise	-0.015	0.003	-4.655	3.3e-06***
	Non-wind-water sport	-0.006	0.003	-1.712	0.087
	Other	-0.016	0.003	-4.758	2e-06***
	People	-0.013	0.003	-4.238	2.28e-05***
	Predators	-0.008	0.007	-1.24	0.215
	Unknown	-0.011	0.004	-2.578	0.01***
	Wildfowler	-0.012	0.003	-3.686	2.3e-04***
	Wind-water sport	-0.013	0.003	-4.422	9.95e-06***
	Windchill index	1.96e-05	3.8e-05	5.139	2.84e-07***
	Tide state: high	0.001	4.3e-04	2.092	0.036***
	Tide state: low	-0.002	0.001	-2.764	0.006***
	Tide state: rising	-5.7e-05	0.001	-0.106	0.915
	Substrate: mixed	-0.05	0.002	-22.913	< 2e-16***
	Substrate: mud	-0.05	0.002	-24.59	< 2e-16***
	Substrate: sand	-0.05	0.003	-19.218	< 2e-16***

*** Statistically significant

4.4.2. DISTURBANCE COST

According to the COD equation (Chapter 3), the greatest sources of disturbance were 'Wind-water sport' for Brent goose and 'Non-wind-water sport' for wigeon. This implies that these activities cost Brent goose and wigeon the most energy (Table 4.3). However, the action a bird is engaged in when it is disturbed can affect how much energy the bird loses to the disturbance event. If a bird is disturbed while feeding, it will cost the bird energy in flight as well as energy from lost feeding time. Whereas if a bird is disturbed while resting, it will cost only energy in flight. Therefore, the total time lost to disturbance is not sufficient to describe the cost of the disturbance. Instead, the proportion of that total time lost to disturbance while an animal is feeding and while it is resting is more representative of the costs of a disturbance source.

Table 4.3 The current rates of disturbance experienced by Brent goose and wigeon on the estuary and the projected disturbance threshold rates of disturbance of any individual activity that Brent goose and wigeon could withstand before running out of time to compensate based on the COD equation calculation (see Chapter 3).

Species	Human Activity Type	Observed rate of feeding disturbance (hr^{-1}) (λ_F)	Observed rate of resting disturbance (hr^{-1}) (λ_R)	Total observed rate of disturbance (hr^{-1}) ($\lambda_F + \lambda_R$)	Total predicted threshold rate of disturbance (hr^{-1})
Brent goose	Wind-water sport	0.15	0.22*	0.37*	33.65
	Non-wind-water sport	0.01	0.08	0.09	37.93
	Motorized-land	0.013	0.012	0.03	31.15
	Noise	0.003	0.002	0.01	22.40
	People	0.17*	0.05	0.22	16.99
	Animals	0.153	0.083	0.24	20.96
	Predator	0	0.01	0.01	18.40
	Harvester	0.01	0.13	0.14	38.67
	Air	0.005	0.005	0.01	7.88**
	Fast-land	0	0	0	0
	Other	0.003	0	0	9.41
	Wildfowler	0	0.01	0.01	47.43
	Motorized-water	0.006	0.036	0.04	29.94

Species	Human Activity Type	Observed rate of feeding disturbance (hr^{-1}) (λ_F)	Observed rate of resting disturbance (hr^{-1}) (λ_R)	Total observed rate of disturbance (hr^{-1}) ($\lambda_F + \lambda_R$)	Total predicted threshold rate of disturbance (hr^{-1})
Wigeon	Wind-water sport	0.01	0.08	0.09	30.46
	Non-wind-watersport	0	0.10	0.10	45.00
	Motorized-land	0.03	0.02	0.05	23.06
	Noise	0.01	0	0.01	8.65**
	People	0.082*	0.164*	0.25*	90.06
	Animals	0.027	0.064	0.09	46.81
	Predator	0	0.01	0.01	23.68
	Harvester	0.01	0.03	0.04	29.53
	Air	0.01	0.01	0.02	10.77
	Fast-land	0	0	0	0
	Other	0	0	0	0
	Wildfowler	0.002	0	0.002	15.89
	Motorized-water	0.02	0.03	0.05	13.39

* The highest rate of disturbance in each category for each species
** The lowest calculated rate of activity required to reach threshold levels

Both Brent goose and wigeon on the Exe Estuary were disturbed to different degrees when resting and feeding, which varied depending on the source of the disturbance

(Table 4.3). Resting Brent goose were disturbed the most by 'Wind-water sport'. Feeding Brent goose were disturbed the most by 'People'. Whereas 'Non-wind-water sports' disturbed wigeon the greatest while they were resting and Motorized-water' activities disturbed them most while they were feeding (Table 4.3). As some activities disturb birds more while they are feeding than when they are resting, if disturbances from these activities were to increase on the estuary, over time, birds would run out of energy more quickly (Figure 4.7; Figure 4.8). Whereas if activities that disturb birds more while they are resting were to increase, over time, birds would run out of energy more slowly (Figure 4.7; Figure 4.8).

The proportion of feeding time lost to disturbance 'Wildfowlers' is one of the lowest recorded for both Brent goose and wigeon. Furthermore, cumulative time lost to disturbance 'Wildfowlers' is also one of the lowest compared to other activities. These findings suggest that Brent goose and wigeon lose very little energy to disturbance from 'Wildfowlers'.

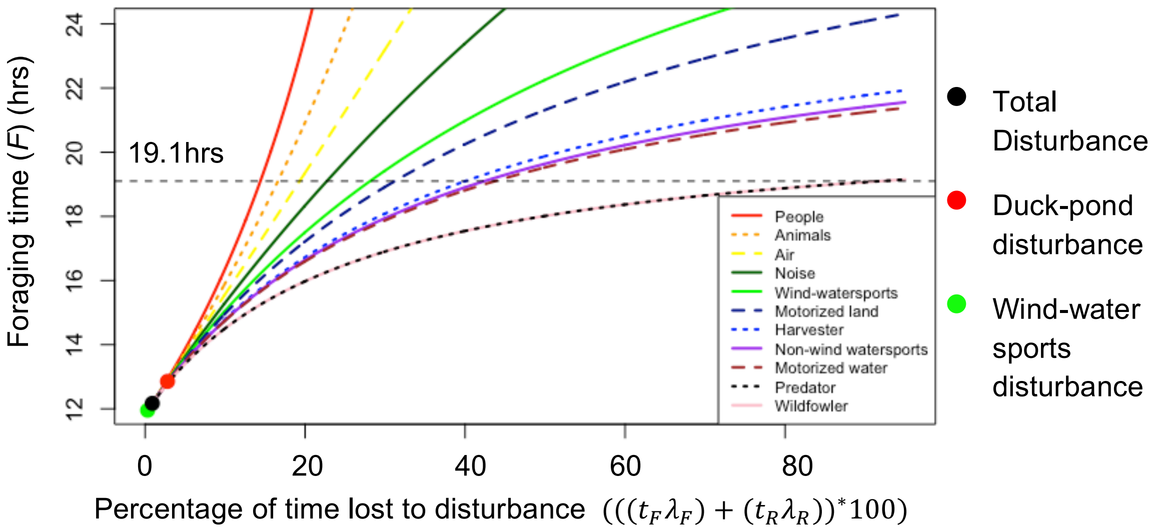


Figure 4.7 Representative projection how of much total feeding time is needed for energy balance at low to high levels of disturbance (left to right on x-axis). As birds spend more time and energy being disturbed, they must compensate with additional feeding time. Lines plot the effects of increases in different types of disturbance on Brent goose. The curve of the line depicts whether the activity disturbs birds more while feeding or resting. The dots on top of the lines represent current conditions in the Exe Estuary. The horizontal dotted grey line represents the maximum amount of time Brent goose could feed before being unable to compensate (19.1hrs).

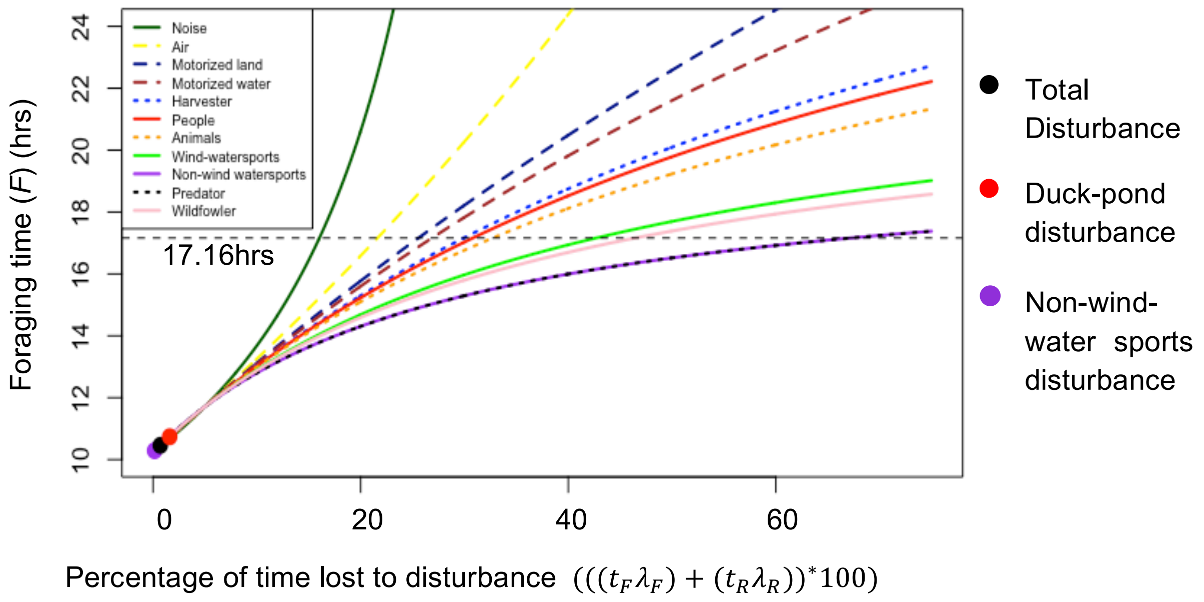


Figure 4.8 Representative projection how of much total feeding time is needed for energy balance at low to high levels of disturbance (left to right on x-axis). As birds spend more time and energy being disturbed, they must compensate with additional feeding time. Lines plot the effects of increases in different types of disturbance on wigeon. The curve of the line depicts whether the activity disturbs birds more while feeding or resting. The dots on top of the lines represent current conditions in the Exe Estuary. The horizontal dotted grey line represents the maximum amount of time wigeon could feed before being unable to compensate (17.16hrs).

No individual or cumulative human activities observed in this chapter were close to pushing Brent goose or wigeon on the Exe Estuary beyond their ability to compensate with increased feeding time (Chapter 3; Table 4.3; Figure 4.7; Figure 4.8). The maximum amount of time that Brent goose can feed on the Exe Estuary is 19.1 hours and for wigeon is 17.1 hours (See Chapter 3). Therefore, on top of a base feeding time of 11.83 hours, Brent goose could feasibly feed for an additional 7.27 hours before running out of time to compensate. For wigeon, that have a base feeding time of 10.24 hours, they could support a maximum of an additional 6.87 hours of feeding. ‘Wind-water sports’ disturbed Brent goose for 0.312 percent of their total time and ‘Non-wind-water sports’ disturbed wigeon for 0.148 percent of their total time. For Brent goose, this amounts to an increase in feeding time of approximately seven minutes and for wigeon nearly four minutes. When combining all human activity types, the percentage of total time spent being disturbed equates to 0.11 percent of Brent goose time and 0.072 percent of wigeon time. These disturbances equate to 22 minutes of extra feeding time for Brent goose and

14 minutes of extra feeding time for wigeon. In the Duck Pond, one of the most disturbed regions of the estuary, combined disturbance events amounted to 2.8 percent of brent goose time and 1.6 percent of wigeon time. Therefore, if birds only used the Duck Pond, Brent goose would need to feed an extra 67 minutes, and wigeon would need to feed an extra 31 minutes. These figures are still well below the additional time threshold of 7.27 hours for Brent goose and 6.87 hours for wigeon (Figure 4.7; Figure 4.8).

4.4.3. RISK ASSESSMENT INDEX

The risk assessment ranked each activity type based on each of the following categories: abundance, BOP index, ratio of disturbance during feeding vs. resting, and overall rate of disturbance. Activities were given a score in each category. Those activities that had the highest value were given a score of one, activities with the lowest value for a category were given a score of 13. Activities with the same values were given the same score. These scores were then summed to provide a single final score. This meant that activities with a low final scores had consistently higher values in each category than other activities. The activity that had the lowest final score, and thus the highest cumulative values for all categories, for both Brent goose and wigeon was ‘People’ (Table 4.4). 'People' scored the highest because they had a combination of high values in the following variables: observed minutes of activity, degree of BOP overlap index, the ratio of disturbances when birds were feeding, and overall rates of disturbance per hour on the Exe Estuary. Wildfowling had the fourth most observed minutes of activity on the estuary and had the seventh-highest degree of overlap. However, the ratio of disturbance during feeding vs resting was one of the lowest as was the overall rate of disturbance, making wildfowling one of the smallest ranking activities in terms of risk from disturbance for both Brent goose and wigeon.

Table 4.4 Risk assessment scores of different activity types in each category.

Species	Activity type	Abundance (exposure)	BOP index (vulnerability)	The current ratio of disturbance during feeding vs rest (hazard)	The current rate of disturbance (hazard)	Final score
Brent Goose	Wind watersport	3	6	5	1	15
	Non-wind watersport	7	9	8	5	29
	Motorized land	6	8	6	7	27
	Noise	9	10	4	11	34
	People	1	3	1	2	7*
	Animals	2	5	2	3	12
	Predator	13	4	10	8	35
	Harvester	5	11	7	4	27
	Air	12	1	3	8	24
	Fast land	10	2	13	0	25
	Other	11	13	13	12	49
	Wildfowler	4	7	11	10	32
	Motorized water	8	12	9	6	35
Wigeon	Wind watersport	3	9	8	3	23
	Non-wind watersport	7	2	9	2	20
	Motorized land	6	4	3	5	18
	Noise	9	11	1	9	30
	People	1	6	6	1	14*
	Animals	2	8	7	3	20
	Predator	13	3	10	9	35
	Harvester	5	10	5	7	27
	Air	12	1	2	8	23
	Fast land	10	5	13	13	41
	Other	11	13	13	13	50
	Wildfowler	4	7	11	11	33
	Motorized water	8	12	4	5	29

*Highest ranking activity for disturbance risk for each species

4.5. DISCUSSION

This chapter investigated the relative role of human activities in disturbing Brent goose and wigeon and evaluated how wildfowling compares to other human disturbance activities. The results show that different human activities influence wildfowl on the Exe Estuary in different ways. There are differences in shared time and space between birds and people and in how animals react to various human activities. Although wildfowling had a high incidence of occurrence on the estuary, the associated overlap and disturbance were much lower than other forms of disturbance.

4.5.1. OVERLAPS AND BOP INDEX

The activities associated with the most considerable number of overlaps and highest BOP index values were ‘People’, ‘Wind water-sports’, ‘Air’ and ‘Non-wind water-sports’. All of these activities, barring, ‘Air’, were also in the top five most frequently observed events on the estuary. These activities occurred at times on the estuary when there were also higher numbers of birds on the estuary (Chapter 2). Furthermore, different human activity types overlapped differently for Brent goose and wigeon, which is consistent with findings in Chapter 2 that revealed differences in how all human activity types combined differed between the two species. These results suggest that it is the combination of abundance as well as the occurrence in space and time that is influential in overlap events between different human activity types and animals.

These findings are consistent with the literature on niche, and predator-prey overlaps. A review by Carroll et al. (2019) highlights how population aggregation and densities affect the degree of shared time and space between predators and prey. Although this paper references competitors and predator-prey interactions, they maintain the same principles of shared space and interaction as this study with wildfowl and humans. Furthermore, models developed in Broennimann et al. (2012) were able to depict species distributions accurately and overlaps based on spatial environmental data. These studies indicate that by identifying ecological variables that influence species distributions, they can be used to depict niche overlap accurately. In addition to this, a model developed by Bennett et al. (2009) used to predict human disturbance effects on barbastelle bats (*Barbastella barbastellus*, S.) indicated that distribution and abundance of human activities and bats affected the degrees of disturbance experienced by the bats. These studies suggest that although the results depicted in this chapter are on human and animal overlaps, they are similar to those of niche overlap and similar principles can be applied.

4.5.2. DISTURBANCE COST

The human activities with the highest number of overlaps and highest BOP index values were also responsible for the greatest degree of disturbance of Brent goose and wigeon in the form of combined lost feeding and resting time. A study conducted on great bustards (*Otis tarda,* L.) in Spain found similar results that human activity density along with spatial overlap and environmental variables contributed to increases in disturbance rates (Sastre et al. 2009). The human activities that were the costliest for Brent goose, on the Exe Estuary, were ‘Wind watersports’ and ‘People’. Whereas, the human activities that were the most energetically expensive for wigeon on the Exe Estuary were ‘Non-wind watersports’ and ‘Wind watersports’ activities. Each of these activities was either in the top three most abundant activities on the estuary or were in the top three highest recorded BOP index values (Figure 4.1; Figure 4.2;Figure 4.6). Therefore, abundance and degree of overlap can potentially help predict the degree of disturbance an activity may be causing relative to other activities (Burger and Gochfeld 1991a & 1991b; Beale and Monaghan 2004; Sastre et al. 2009).

All activities recorded in this chapter were well below any thresholds for compensation for both Brent goose and wigeon. However, birds may tolerate greater increases of some activities than others. For instance, ‘People’ were recorded to cause more disturbances during brent goose feeding times than resting, and therefore, had higher associated costs (Table 4.3). Because of this, the overall cost of disturbance associated with ‘People’ increased at a greater rate than with activities such as ‘Motorized water sports’, in which costs were less associated with feeding. Therefore, human activities that disturb animals while they are feeding are a potentially greater concern than other activities that only cause disturbances while animals are resting.

4.5.3. WILDFOWLING

Wildfowling was one of the fourth most common activities observed on the estuary. However, unlike other activities with high abundance, wildfowlers had very low overlaps with Brent goose and wigeon. Additionally, for both Brent goose and wigeon, wildfowlers were among the least energetically costly activities affecting wildfowl on the Exe Estuary. The literature on wildfowling disturbance has found supporting results. In the review by Sokos et al. (2013) many studies failed to detect differences in feeding rates, body condition, breeding success, or population numbers when evaluating the presence and absence of wildfowling disturbance (Sokos et al. 2013).

The inherent differences in wildfowling compared to other typical human activities may explain why this is the case. First and foremost, wildfowling is an activity restricted to specific areas on the estuary as well as particular conditions. While this is not necessarily unique to wildfowling, as other human activities are often restricted based on location and conditions, it does influence how much wildfowlers overlap with Brent goose and wigeon on the Exe Estuary. Wildfowlers only have three primary regions in which they are permitted to hunt on the estuary, and two of these regions rarely had recordings of Brent goose or wigeon feeding or roosting. The one area that had records of wigeon, Brent goose, and wildfowlers, was only accessible when the tide was at its absolute lowest. A time that was coincidently, also when Brent goose and wigeon were least likely to be present in that location (Chapter 2). Therefore, the initial likelihood of overlap was limited based on regions and conditions. This finding may seem contradictory, as the purpose of wildfowling is, after all, to overlap with wildfowl. However, wildfowling is designed to result in a flight overlap, which is accomplished by a 'sit and wait' approach. This approach intends to avoid detection from target species while waiting for the animal to pass by. This method of wildfowling is most similar to that of stalking an animal, which causes the lowest cortisol response in ungulates in a traumatic situation, making it one the least stressful types of hunting (Gentsch et al. 2018). Therefore, wildfowlers can spend from three to four hours in marsh grasses and mud for the chance at just one or two flocks of birds to fly over. This translates to long periods of wildfowling presence, combined with overlaps that can span a matter of seconds. When an overlap does occur, the wildfowler must decide any birds, within a flock that flies over, are within a range to shoot.

Additionally, because wildfowlers want to avoid detection from the target species while waiting they very rarely incidentally disturb any birds in between shooting events. Ultimately, the outcome is a low probability of overlap and then even lower possibilities of disturbances within those overlaps. The combination of these factors helps to explain why wildfowlers are a small source of disturbance cost on the Exe Estuary.

Although wildfowlers are considered one of the lowest sources of disturbance on the Exe Estuary at present, they are still associated with high degrees of response when they do occur. When Brent goose and wigeon responded to a wildfowling disturbance on the estuary, the typical response time before settling was on average 69 seconds for Brent goose and 128 seconds for wigeon. The only other form of disturbance that was close to this response time was ‘Air’ activity which averaged 101-second response for Brent goose and 127-second response for wigeon. These response times mean that, although Brent goose and wigeon are currently unaffected by wildfowling disturbance on the estuary, assuming no habituation, they will be less tolerant of increases in wildfowling disturbance relative to increases in other forms of disturbance. However, it would still take up to 18 disturbances of Brent goose and 9 disturbances of wigeon per hour every day during the winter months before Brent goose and wigeon would reach their energetic threshold for dealing with wildfowling disturbance. The current average rate of disturbances per hour is 0.002 for Brent goose 0.01 for wigeon per hour per day on the Exe Estuary.

It is also important to mention the differences detected in response between Brent goose and wigeon to wildfowling. Brent goose response to wildfowling events were much lower than that of wigeon. This difference could be due to body size and exposure time. However, the results indicate that both Brent goose and wigeon had similar exposures to disturbance from shooting events. Furthermore, based on the literature on how body size relates to escape distance, Brent goose should technically have had longer flight time due to being larger (Collop et al. 2016). The most likely explanation for this result is that wigeon are a quarry species and Brent goose are not. Studies have shown that quarry species tend to have a more significant reaction to shooting disturbance than non-quarry species (Madsen & Fox 1995; Laursen et al. 2005; Sastre et al. 2009). This difference indicates that wigeon learn over time that shooting events are associated with a threat, while Brent goose learn the opposite, which is consistent with the predator-risk hypothesis. Animals learn to assess the risk associated with specific events and change their reactions accordingly (Urfi et al. 1996; Beale & Monaghan 2004; Frid & Dill 2002; Sastre et al. 2009). Therefore, further increases in wildfowling disturbance to quarry species could have more considerable implications than that of non-quarry species. However, more research is needed into how whether quarry species have maximum flight times in response to a disturbance, in which case, increases in response to wildfowling disturbance would only cause increased reactions up to a point.

4.5.4. RISK ASSESSMENT INDEX

According to risk assessment theory, when evaluating the risk associated with any event, three main categories must be addressed. These categories are hazard, exposure, and vulnerability (Crichton 2008; Wolf 2012). Concerning this chapter, the hazard is a disturbance, exposure is overlap and the degree of disturbance, and vulnerability is the animal’s capability of coping with that disturbance. In an attempt to consider these variables, this chapter compared the overall abundance of activity presence, the occurrence of overlap with wildfowl, degree of overlap when present, the ratio of feeding vs resting disturbance, and the current rate of disturbance. The human activities that presented themselves as the highest-ranking among these categories for Brent goose were: 'People', 'Animals', and 'Wind water-sports'. Therefore, these three activities are potentially the most threatening for Brent goose on the Exe Estuary. For wigeon, the three top-ranking activities for disturbance risk also included 'People' and 'Animals' but also, 'Motorized-Land' activity. These results are consistent with responses of other wildfowl in the literature to different disturbance activities (Marsden 2000; Pease et al. 2005; Sastre et al. 2009). For example, in a study conducted on pochard (*Aythya farina*, L.) and tufted duck (*Aythya fuligula*, L.), over 57% of all disturbance responses were attributed to pedestrians (Marsden 2000). Another study by Sastre et al. (2009) found that walkers and cars caused the highest amount of time loss in Great Bustards. Although these activities were high ranking in the risk assessment in this chapter, all of these activities, are responsible for very low levels of disturbances on the estuary. It would require a minimum of 60 times, the current level of any individual activity before Brent goose would struggle to meet energetic demands and nearly 340 times more disturbance before wigeon would struggle. Nonetheless, it is still a useful observation, as these are the activities, based on assessments addressed in this chapter, that could potentially pose the most significant risk for wildfowl in the future on the Exe Estuary.

4.6. CONCLUSION

This chapter highlighted the differences in how various human activities interact with and affect animal energetics. Activities in this chapter that were associated with the greatest disturbance costs were those activities that occurred most often and during times and places where animals were most likely to be present and feeding. These costs were evident in both the proportion of time lost to disturbance types as well as maximum tolerable disturbance rates of activity types. Furthermore, when comparing activity types, the results have shown that wildfowling is the fourth most commonly observed activity on the Estuary. However, wildfowling disturbance costs are much lower than those associated with other activity types, making it a much lower concern compared to other activity types. The concept of overlap and energetic cost is not unique to wildfowl. Therefore, the results of this chapter have the potential to be translated into many different species. Thus, research in this chapter provides a basis for evaluating various human activities for potential risk to surrounding wildlife.

4.7. FUTURE WORK

Although this chapter has highlighted the differences in how human activities can affect animals in different ways, it has only investigated these effects concerning Brent goose and wigeon on the Exe Estuary. Future work could attempt to apply these methods to other species in other situations. Additionally, this chapter could be further supported by understanding how animals might change responses over time to different activities. All future projections in this chapter are based on consistent reactions from animals over time. If animals were to either reduce or increase responses to various activities, projections might change.

Furthermore, activity rate threshold values are based on activities occurring individually. As a result, projections associated with them are assuming no other activities are happening to reach that threshold. Therefore, more research is needed into what threshold values are when activities are co-occurring.

5. CHAPTER 5: TIME BUDGETS: HOW WILDFOWL CAN USE TIME TO COMPENSATE FOR HUMAN DISTURBANCE

5.1. ABSTRACT

Time budgets can assess animal behaviour and can evaluate energetic needs. Therefore, time budgets may be able to help us understand how capable animals are of coping with energetically costly events, such as human disturbance. This chapter reviews published data on the time budgets of wildfowl to determine how they change relative to disturbance related activities, as well as body mass and environmental variables. Findings indicate that there is little association between wildfowl mass and the time allocated to feeding. However, differences in feeding time were significantly related to environmental variables that affected food availability and energetic costs. Furthermore, time feeding increased, and resting time decreased with increased time being alert, indicating a possible trade-off mechanism. This trade-off suggests that resting time in animals may be a measure of how capable animals are of compensating for disturbance events. By understanding which species-specific and environmental variables are associated with lower resting time, it may be possible to identify when animal species may be most susceptible to disturbance effects before they translate to population-level impacts.

5.2. INTRODUCTION

5.2.1. BACKGROUND

Time is a limiting factor for every form of life. It is time that ultimately provides boundaries to what activities an organism is capable of fulfilling. According to optimal foraging theory, activities that animals choose to engage in are those that maximise fitness (Evans 1976; Norberg 1977; Ydenberg et al. 1994). A measure of the use of time can provide insights into the requirements or constraints imposed on an animal (Evans 1976; Norberg 1977; Lindstedt & Calder 1981; Kvist & Lindström 2000). Additionally, if an animal has any time that it does not use, i.e.- ‘spare time’, it might be assumed that the animal has capacity for compensating for additional energy or time demands (Urfi et al. 1996; Dunbar et al. 2009). Human disturbance events are incidents that cause interruptions within an animal’s natural time budget. Therefore, an animal’s time budget may be a way of identifying whether it is capable of compensating for human disturbance events.

Human disturbance is often categorized as a predator avoidance reaction in birds (Frid & Dill 2002; Beale & Monaghan 2004), and predator avoidance is characterized by increased vigilance or alertness. Therefore, understanding how vigilance time changes relative to other bird activities can provide insight into how animal time budgets might change relative to human disturbance. When in high predator-risk situations, animals will often allocate extra time to being alert (Sutherland 1996). As would be expected, this allocation of time comes at the expense of other activities (Sutherland 1996). The risk allocation theory states that animals in high-risk situations will often sacrifice foraging time in the short term to gain increased vigilance (Sutherland 1996; Lima 1998; Ferrari et al. 2009). However, this loss of foraging time would mean that the animal is achieving a reduced energy input, meaning that foraging in the long term must increase to regain energy. This increased foraging time must come at the cost of some other activity (Stillman & Goss-Custard 2002). Vigilance or alert time can be an activity that an animal chooses to do, whereas activities such as resting and feeding are physiological requirements of an animal. Therefore, the reallocation of time to other activities can give insight into which activities an animal is physiologically capable of sacrificing (Urfi et al. 1996; Stillman & Goss-Custard 2002).

Several studies demonstrate how time budgets change relative to the presence and absence of human disturbance (Schummer & Eddelman 2003; Li & Rogers 2004). However, little work has been done to understand the ability of animals to compensate for these changes (Urfi et al. 1996). This chapter focuses on understanding wintering wildfowl time budgets found in literature and how they change relative to different environmental variables, with particular attention to varying levels of time allocated to being alert.

5.2.2. AIMS AND OBJECTIVES

This chapter aims to understand how wildfowl time budgets change relative to various environmental variables and what this means in the context of energetic compensation.

This chapter will address the following objectives:

- Review the literature to collect time budgets of various species of wildfowl
- Calculate how time budgets differ between variations in bird mass(kg), winter stage, presence of tide, latitude, and bird diet
- Establish what time budgets variations mean for the ability of wildfowl to compensate

5.3. METHODS

5.3.1. LITERATURE SEARCH

The following search engines were used to locate the literature on time budgets of wildfowl in winter months: GoogleScholar, Jstor.org, Springer.org, Web of Science, and Science Direct. Multiple combinations of the following search terms were used: 'time budget(s)', 'energy-budget(s)', 'wildfowl', 'winter(ing)', 'feeding-time', 'winter-month(s)', 'non-breeding', 'spare-time', 'rest-time', 'duck(s)', 'geese', as well as, common and scientific names of ducks and geese known to winter in the UK. Related papers cited within the searched papers were also evaluated.

Variables obtained from selected research papers included: species, protection status, coordinates of data collected, sample size, duration of study, time of year, sampling method, rate of human disturbance in study, temperature, percentage of time feeding, percentage of time resting, percentage of time alert, percentage of time flying, and percentage of time small locomotion. Biometric data such as diet, mass, wingspan, body length, life span for each species were obtained from the *Handbook of the Birds of the World Alive* database (del Hoyo et al. 2020). All behaviours described in the literature were grouped using a simplified ethogram, to harmonise the classification of bird activities (Table 5.1). Additionally, winter-stage categories were used to give consistent groupings of wintering months (Table 5.2), and diet classification was assigned to birds based on literature listed food sources (Table 5.3).

Table 5.1 General categorization of different literature defined behavioural categories.

Behavioural assignment	Literature classification
Rest	rest, preening, comfort, sleep
Small locomotion	walk, swim, social
Flight	flight
Feed	feeding, foraging
Alert	alert, vigilance

Table 5.2 General categorizations of winter-stage to data collected from different winter months.

Winter-stage assignment	Literature sample months*
Early	Sep - Nov
Mid	Nov - Jan
Late	Jan - Mar
All	Sep - Mar

*All samples were taken from Northern hemisphere.

Table 5.3 General diet classification based on food sources consumed.

Diet	Food sources consumed
Carnivore	Fish, mammals, insects, invertebrates
Herbivore	Plants, fruits, seeds, tubers, leaves
Omnivore	Plants, fruits, seeds, insects, fish, mammals, inverts, tubers, leaves

5.3.2. ANALYSIS

Mixed models were used to evaluate feeding time separately and resting time relative to the following variables: bird mass(kg), winter stage, latitude, tidal presence and bird diet. This analysis was performed using RStudio statistical software Version 1.0.136 (© 2009-2016 RStudio Inc.) with R version 3.3.3 (© 2017-03-06 R Inc.). The procedure lmer from R-package 'lme4', was carried out using feed time and rest time as the dependent variables and body mass, diet and environmental conditions as independent variable, while species and study were considered random variables.

5.3.1. PHYLOGENETIC RELATEDNESS

When comparing species, there is the possibility of non-independence due to phylogenetic relatedness (Felsenstein 1985; Harvey and Pagel 1991; Freckelton et al. 2002). To test for this, the methods described in Orme et al. (2013) were used to incorporate the phylogenetic tree of the species in question, and test for significant effects on factor comparisons due to relatedness. This test revealed no significant effect of phylogenetic relatedness on the comparative analysis in this study. This indicates that any relationships detected in this study are not a result of phylogenetic connection.

5.4. RESULTS

A total of 49 papers were reviewed that contained information on 40 species of wildfowl. Out of these papers, 132 data points were obtained for wildfowl feeding time (Appendix 3).

5.4.1. TIME BUDGET VARIATION RELATIVE TO CHANGES IN ENVIRONMENTAL CONDITIONS

Out of the 132 feeding time budgets obtained from the literature, 97 also contained information on environmental variables (Table 5.2; Table 5.3; Appendix 3). There were no significant differences detected between feeding times and body mass, or winter month (Table 5.4; Figure 5.2). Significant differences were detected between feeding time and the presence of tide, latitude and diet (Table 5.4; Figure 5.3; Figure 5.4; Figure 5.5). Additionally, post-hoc analysis between diets, revealed there were significant differences in feeding time between herbivores and omnivores (Figure 5.5). Herbivores fed for significantly more time than omnivores but not carnivores.

Table 5.4 Results of mixed model analysis of feeding time as the dependent variable and mass, winter month, tide presence, latitude, and diet as the independent variables, and study and species as random effects (n = 97).

Dependent Variable	Independent Variables	Estimate	SE	t value	Pr(>F)
Rest time	mass	-2.52	1.44	-1.75	0.09
	diet: herbivore	21.76	10.97	1.98	0.31
	diet: omnivore	6.06	11.88	0.51	0.68
	latitude	1.08	0.42	2.61	0.01***
	winter month: Early	-0.67	5.89	-0.11	0.91
	winter month: Late	5.61	4.65	1.21	0.23
	winter month: Mid	-0.53	4.48	-0.12	0.91
	tidal: yes	11.67	4.10	2.85	0.01***

*** Statistically significant

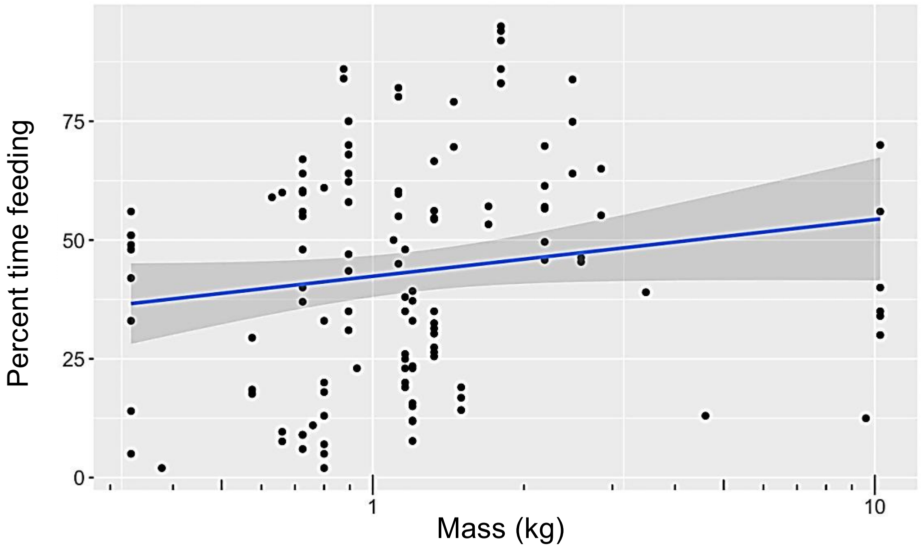


Figure 5.1 Comparison of wildfowl feeding time relative to the average weight of species with different diets. Shaded regions represent confidence intervals. No significant relationship was detected between mass and percent time feeding (n = 122; p-value = 0.09; Adj. R^2 = -0.007). The mean value of all feed times was 43.1%.

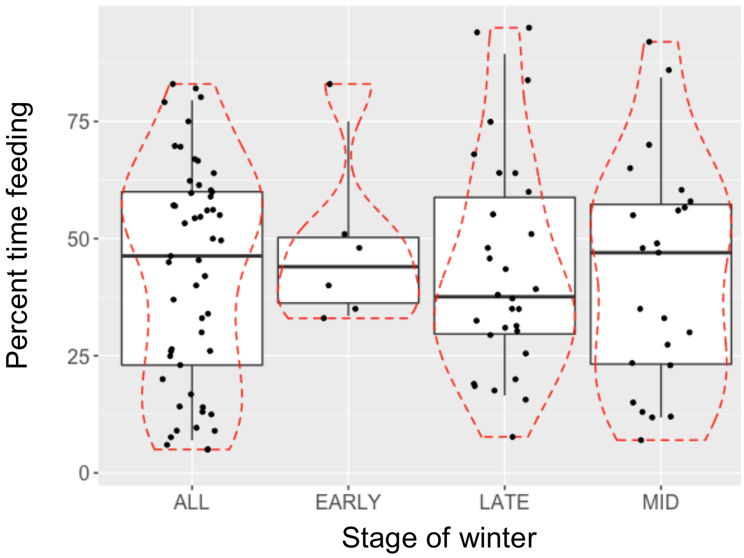


Figure 5.2 The recorded feeding times of wildfowl relative to the stage of winter. Dots represent data points. Red dashed lines signify the distribution of the data around the mean and boxplots indicate the 95% confidence intervals. No significant differences were detected between time feeding and winter stage (n = 94).

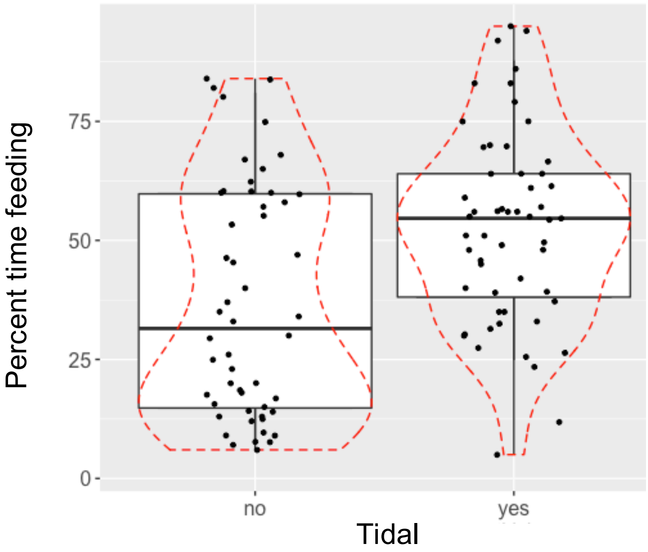


Figure 5.3 The recorded feeding times of wildfowl relative to sites that were tidally influenced and not. Dots represent data points. Red dashed lined signify the distribution of the data around the mean and boxplots indicate the 95% confidence intervals. Time feeding was significantly different between sites that were tidally influenced and not (n = 94; p-value = 0.01).

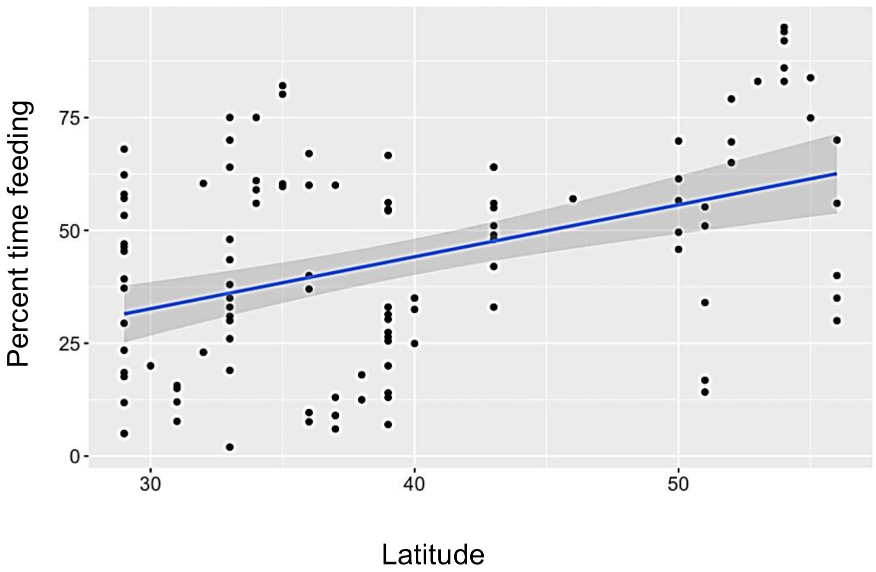


Figure 5.4 Time feeding varied significantly across different latitudes with higher latitudes being associated with greater feeding times (n = 97; p-value < 0.01; Adj. R^2 = 0.17).

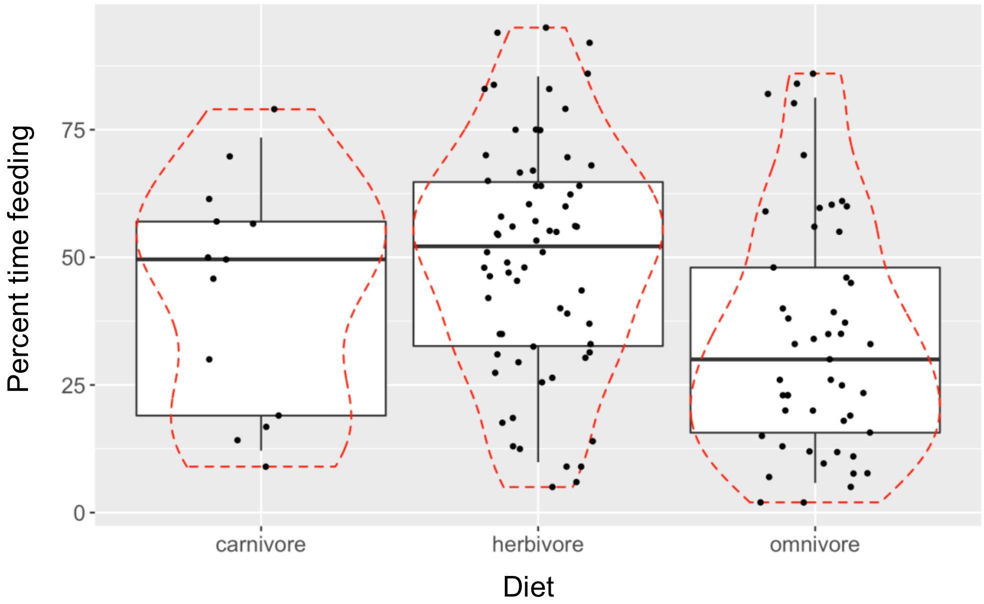


Figure 5.5 The recorded feeding times of wildfowl relative to different diets. Dots represent data points. Red dashed lined signify the distribution of the data around the mean and boxplots indicate the 95% confidence intervals. Time feeding was not significantly different between different diets.

5.4.2. TIME BUDGET RE-ALLOCATION AND COMPENSATION ABILITY

Time budgets revealed significant correlations between alert time and feeding time and resting time.

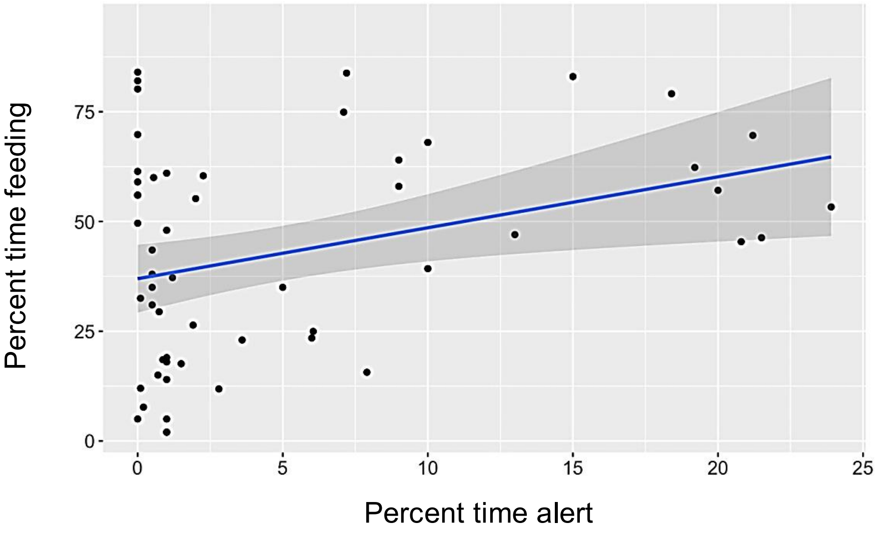


Figure 5.6 The differences in time spent feeding as it relates to time spent being alert in wildfowl. As time spent being alert increases, so does time spent feeding. Dots represent data points. The blue line indicates the linear relationship of the data means and the shading representing the 95% confidence intervals around that mean. Changes in feed time were significantly positively associated with changes in alert time (n = 54; p-value = 0.01; Adj R^2 0.10).

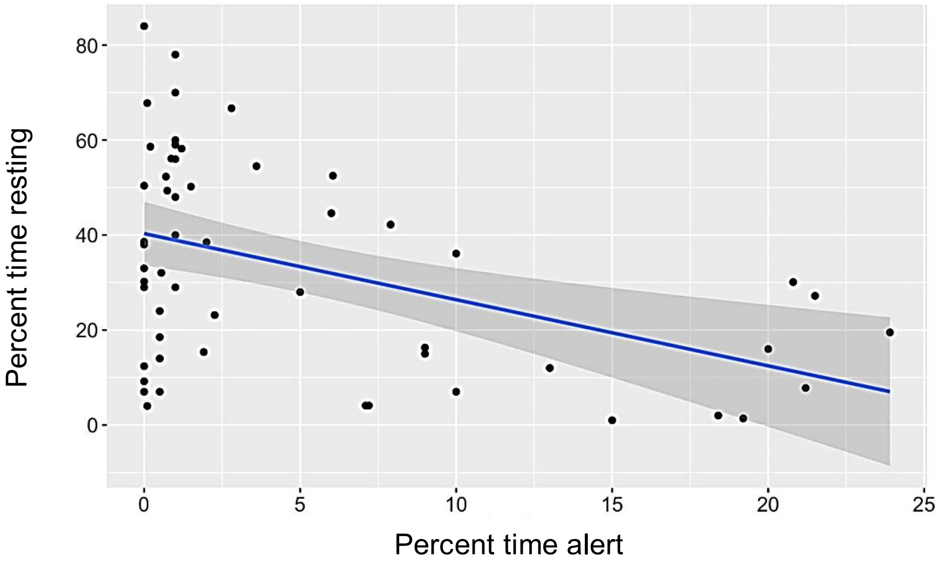


Figure 5.7 The differences in time spent resting as it relates to time spent being alert in wildfowl. As time spent being alert increases, time spent resting decreases. Dots

represent data points. The blue line indicates the linear relationship of the data means and the shading representing the 95% confidence intervals around that mean. Changes in rest time were significantly negatively associated with alert time ($n = 54$; p-value < 0.01; Adj. $R^2 = 0.18$).

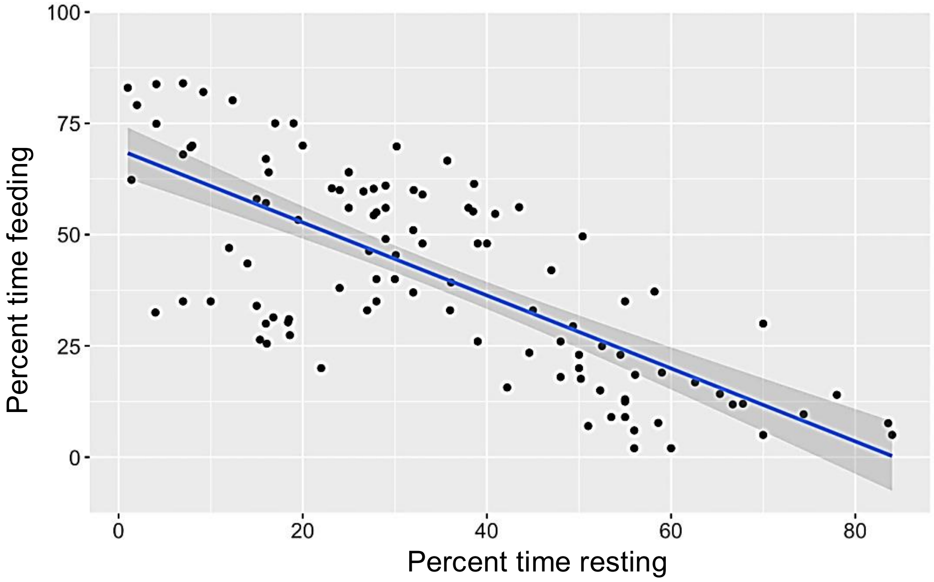


Figure 5.8 The differences in time spent feeding time as it relates to time spent resting in wildfowl. As time spent resting increases, time spent feeding decreases. Dots represent data points. The blue line indicates the linear relationship of the data means and the shading representing the 95% confidence intervals around that mean. Time feeding was significantly negatively associated with increased rest time (n=105; p-value < 0.01; Adj. R2 = 0.53).

Based on the correlation of feeding time to rest time, if a bird feeds more, it rests less. Thus, low rest time could mean that a bird is already feeding at close to maximum capacity. Consequently, wildfowl that exhibit the lowest rest times are the least able feed more, to compensate for increased energy demands.

Diet was considered to significantly explain variability in rest time (Table 5.5; Figure 5.9). Herbivores rested significantly less than both omnivores, indicating a possible increased risk from disturbance to herbivores due to having less overall rest time (Figure 5.9).

Table 5.5 Results of mixed model analysis with the dependent variable of rest time and environmental variables as fixed effects and species and study as a random effects (n = 86).

Dependent Variable	**Independent Variables**	**Estimate**	**SE**	**t value**	**Pr(>F)**
Rest time	mass	0.62	1.31	0.47	0.64
	diet: herbivore	-33.28	13.08	-2.55	0.02***
	diet: omnivore	-13.17	13.61	-0.97	0.34
	latitude	-0.60	0.44	-1.35	0.19
	winter month: Early	-6.36	7.03	-0.91	0.37
	winter month: Late	-6.59	5.03	-1.31	0.19
	winter month: Mid	-2.03	4.91	-0.41	0.68
	tidal: yes	-2.16	4.29	-0.50	0.62

*** Statistically significant

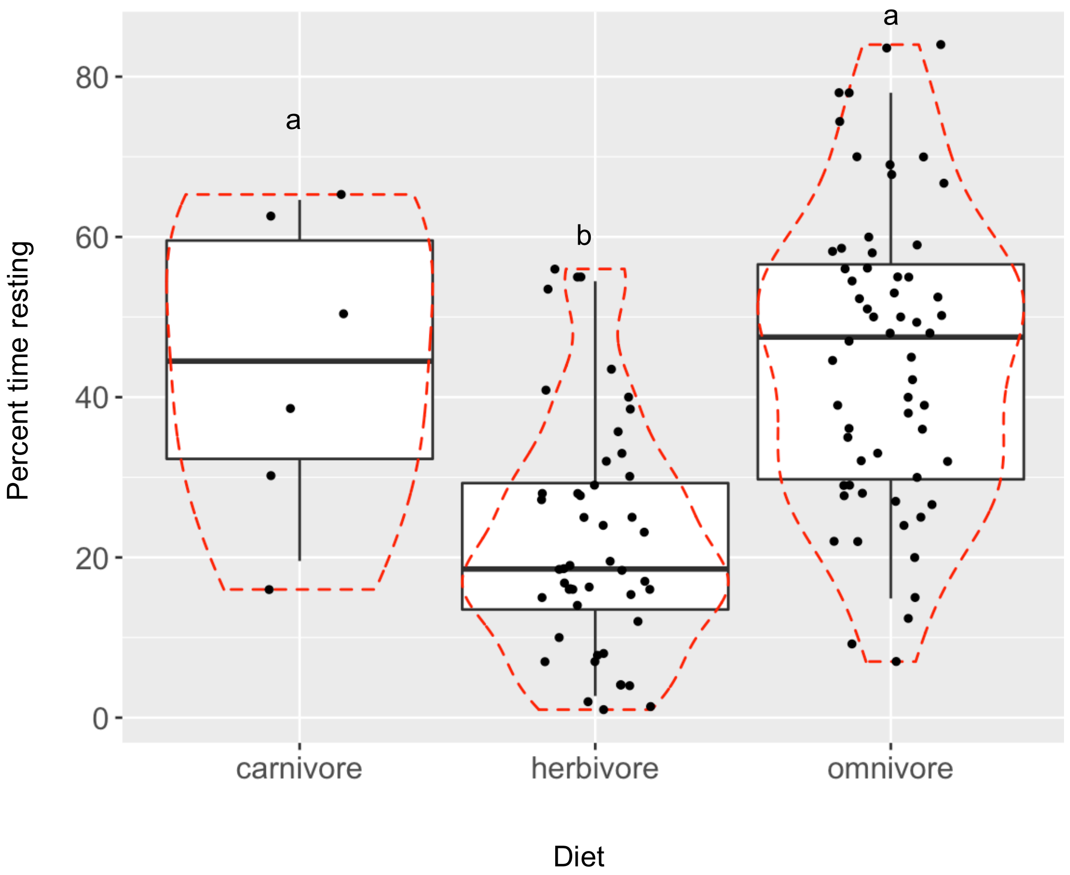


Figure 5.9 Comparison of wildfowl diets relative to time spent resting. Dots represent data points. The red dashed lines signify the distribution of the data around the mean and boxplots indicate the 95% confidence intervals. Herbivores rested significantly less than omnivores and carnivores (n=86; p-value = 0.02). Different letters indicate significant differences.

5.5. DISCUSSION

5.5.1. TIME BUDGETS AND BODY MASS

The literature indicates that an animal's energetic needs can be predicted based on animal mass and time budgets (Hemmingsen 1950; Lasiewski & Dawson 1967; Lindström & Kvist 1995). Larger animals require greater amounts of energy to survive (Lasiewski & Dawson 1967). For example, Basal Metabolic Rate (BMR), which is considered the minimal metabolic needs of an animal, can be calculated for non-passerine birds with only knowledge of body mass (Table 5.6). Furthermore, the Daily Energy Expenditure (DEE) an animal uses each day, can be calculated as a multiple of this BMR (Table 5.6). Moreover, a study by Kirkwood (1983) derives the Daily Metabolized Energy (DME) an animal can intake based on an animal's mass, by equating mass to digestive organ size (Table 5.6). Animal time-activity budgets are dependent on energetic requirements of the animal in combination with food resources (Table 5.6; Norberg 1977; Nagy 1987; Kvist & Lindström 2000; Houston et al. 2012). Therefore, it is logical to assume that an animal's mass could be an indicator for an animal's time budget allocations, and consequently, could potentially be an indicator for an animal's capacity to deal with human disturbance events.

Table 5.6 Calculation of metabolic need based on animal mass.

Variable Calculated	Equation	Source
Basal Metabolic Rate (kJ/day)	$BMR = 308 * Mass(kg)^{0.73}$	Aschoff & Pohl 1970; Lindström 1991; McKechnie 2006
Daily Energy Expenditure(kJ/day)	$DEE = 2.5 * BMR$	Aschoff & Pohl 1970; Kirkwood 1983; Kersten 1987
Daily Metabolized Energy Intake (kJ/day)	$DME = 1713 * Mass(kg)^{0.72}$	Kirkwood 1983
Proportion of time Feeding	$p^* = \frac{DEE}{DME}$ or $p^* = \frac{e_1}{f_1} M^{(e_m - f_m)}$	Stillman 2019; Appendix 2

However, because DEE and DME are nearly proportional as mass increases, feeding time should technically be independent of body mass (Equation 5.1; Table 5.6; Daan et al. 1990; Lindström and Kvist 1995; Maurer 1996; McKechnie 2006). This independence would imply that animals of all sizes that are not aiming to gain or lose mass, in controlled conditions, would have the same general feeding time regardless of size. In support of this, there was no significant difference detected between wildfowl body mass and feeding time and the average wildfowl feeding time was close to 0.45, as predicted by the equations.

$$p^* = \frac{2.5 * 308}{1713} M^{(0.73-0.72)}$$

Equation 5.1

$$p^* = \frac{770.5}{1713} = 0.45$$

5.5.2. TIME BUDGET VARIABILITY

That feeding time is independent of body mass means that any changes in feeding time of an animal can be primarily attributed to changes in environmental circumstances.

Wildfowl feeding times changed significantly relative to latitude. Latitude can be considered a measure of temperature, but also food availability. Average temperatures, day length, and the length of growing seasons decrease with increasing distance from the equator. Decreased temperature means animals must expend a greater amount of energy to maintain body temperatures (Kendeigh et al. 1977; Castro et al. 1992). As a result, animals in colder climates require longer feeding times to compensate, which is reflected in the data from this chapter.

Furthermore, changing temperatures in regions and different growing season lengths, mean that various food resources and food nutrients will be prevalent (Reich & Oleksyn 2002). Digestion time and energy assimilation can vary significantly within just one species depending on the food source (Kushlan 1981). Therefore, variation in time budgets associated with latitude is a reflection of temperature and food quality.

Tides also affect food availability, which influences animal feeding time. Throughout a tidal cycle, food resources become limited by water depth. For example, during high tide, eelgrass, *Zostera* spp., can be unreachable, and access to invertebrates, found in substrates, is restricted to the water's edge (Evans 1976; Lindström 1991). Therefore, it is understandable why there would be significant differences in feeding time at sites with tides versus those without tides.

Diet was also significantly associated with differences in rest time. Herbivores spent significantly less time resting than both omnivores and carnivores. This difference is likely due to omnivores having a broader range of food sources to choose from, especially on tidally influenced regions, where some food is inaccessible for significant portions of time. Omnivores can exploit multiple resources when others become inaccessible, whereas herbivores may be more restricted (Evans 1976; Lindström 1991). Furthermore, omnivorous diets have higher energy content per gram consumed than those of strict herbivores, meaning that omnivores can obtain energetic requirements by wasting less food than herbivores (Robbins 1993; Karasov 1996).

The failure to detect significant differences in feeding time relative to winter-stage may be due to food resource switching. Many wildfowl species switch food resources when the quality of food they are currently feeding on, decreases with the wintering season (Robbins 1993). For example, dark-bellied Brent goose, *Branta bernicla* (L.), on the Norfolk coast shift habitats upon resource depletion (Vickery et al. 1995). This resource switching could mean that wildfowl can maintain a consistent rate of feeding throughout the wintering months by always selecting food resources that are above a certain quality.

Another explanation for the failure to detect significant differences in feeding time relative to winter-stage is the lack of distinctive seasonal recording within the literature. Many records referred to the entire winter season and didn't distinguish winter months. Others had inconsistent groupings of winter months. Therefore, the winter-stage classification in this chapter may not have adequately captured the monthly variation in seasons.

5.5.3. TIME RE-ALLOCATION AND COMPENSATION ABILITY

Within environmental variability is the presence of human disturbance. Only a handful of the papers used in this chapter measured human disturbance as a proportion of wildfowl time budgets. Therefore, this chapter used 'alert' time as a proxy for human disturbance, due to its similarity as a response to human activity. Changes within time budgets relative to this variable could then be potential mechanisms for coping with human disturbance. If an animal is already operating at maximum capacity of energy intake to maintain body mass, that animal will struggle to cope with increases in energetic demands and will be more susceptible to disruptions in their time budgets (Lindström 1991).

When evaluating the change in wildfowl time budgets relative to alert time, this chapter identified that feeding time increased and resting time decreased. This correlation indicates several possibilities; when wildfowl feed more, they are more alert; when wildfowl are more alert, they feed more; when wildfowl rest they are less alert; or when wildfowl are alert, they rest less. Some literature indicates that predation risk increases when animals are feeding (Lima & Dill 1990). However, other papers have suggested that predation risk is based on the prey's perception, which may vary depending on circumstances (Lima & Dill 1990; Bednekoff & Lima 2002). For example, animals that rest on the edge of groups will have increased alert levels compared to those animals that rest in the centre of the groups (Di Blanco & Hirsch 2006).

Furthermore, if animals sacrifice feeding time to be alert, they will lose energy, which would, in turn, force the animals to feed for longer to compensate. Based on this, animals that spend more time feeding due to more spending more time vigilant must sacrifice time somewhere in their budget. That, reduced resting time is correlated with both increased feeding and alert time indicates that it is rest time that is forfeited.

If rest time is a measure of compensation for the alert time, it means that the overall measure of rest time for an animal has the potential to be used to infer the ability of an animal to cope with human disturbance. However, before rest time is used as a measure for compensation ability, some additional considerations must be made, because some environments enforce rest time due to restricted resource availability (Evans 1976; Lindström 1991). Additionally, some animals require increased rest time due to digestibility and intake restraints depending on the what food resource is available (Robbins 1993). Therefore, environmentally enforced rest time must be separated from overall rest time to determine 'spare-rest' time before it can be a measure for the ability to cope with human disturbance.

5.5.4. CASE STUDY OF BRENT GOOSE AND WIGEON ON THE EXE ESTUARY

Brent goose (*Branta bernicla*) on the Exe estuary spent approximately 34.1% of time resting and wigeon (*Mareca penelope*) were recorded to spend about 43.6% of time resting (See Chapter 3). These rest times would indicate that both species are at low risk from human disturbance. However, Brent goose are slightly less capable of coping with disturbance than wigeon due to different 'spare-rest' time. This result is supported by cost of disturbance equation (See Chapter 3) that indicates that Brent goose on the Exe estuary were capable of coping with approximately 24 disturbances per hour and. In contrast, wigeon were able to cope with around 34 disturbances per hour, before they would be at an energetic deficit.

5.6. CONCLUSION

This chapter indicates this although there is high variation in time budgets of different species, there may be a simple approach to determine if wildlife may be particularly susceptible to human disturbance. This approach is to measure the time that animals currently allocate to 'spare-rest'. There is evidence that rest time is sacrificed to allow increased feeding time due to increased energetic needs. Therefore, animals that spend less time resting will be less capable of coping with disturbance than animals that spend a more significant proportion of time resting.

5.7. FUTURE WORK

This chapter highlighted differences in animal time budgets and how time is reallocated for wildfowl under different circumstances. Few measurements of the effect of human disturbance on time budgets were found, and so alert time was used to indicate how animals time budgets vary with the presence of a potential disturbance source. However, alert time in this chapter does not mean that these animals were necessarily experiencing human disturbance. In contrast, the wildfowl in this chapter could also have been alert because they were in high predator risk areas. Therefore, future work could follow the approach used in Chapter 3 and 4 to address how human disturbance directly influences time budgets. Furthermore, this chapter focused primarily on wildfowl. Although the general concepts of time allocation apply to other species, future work could evaluate various animal species and determine if the same overall patterns hold.

6. CHAPTER 6: PREDICTING THE CONSEQUENCES OF DISTURBANCE ON WILDLIFE USING AN INDIVIDUAL-BASED MODEL: INSIGHTS FROM WINTERING WILDFOWL ON THE EXE ESTUARY

6.1. ABSTRACT

Determining if human disturbance has an impact on wildlife populations is a pressing question faced by ecologists. Many studies have shown that human interference can cause short term effects on wildlife, but few studies have been able to translate what these effects mean for wildlife populations. This chapter uses data on distribution, behavioural responses and fitness costs of two wildfowl species on the Exe Estuary during the winters of 2017-2018 and 2018-2019 to evaluate human disturbance impacts on wildfowl populations. Population effects were assessed by parameterising an individual-based model that combined the data collected, along with fitness maximising decision-making, to create a validated model environment similar to that observed on the Exe Estuary. Birds in the model environment had similar time budgets, distributions and disturbance rates to those seen on the Exe Estuary. Humans within the model environment also displayed a similar distribution behaviour to those observed on the Exe Estuary. Significant differences in model bird energy levels, behaviour and distribution were detected when human activity levels in the model increased beyond what was witnessed on the Exe Estuary. Brent goose within the model had bird threshold rates of 7 disturbances per hour, while wigeon had bird threshold rates of 12 disturbances per hour before being unable to compensate through increased feeding. To reach these disturbance rates, over 100 people needed to be on the model environment for 24 hours. These bird threshold rates were lower than those predicted by mathematical models in Chapters 3 and 4, where Brent goose could withstand up to 24 disturbances per hour, and wigeon could withstand up to 34 disturbances per hour. Both the individual-based model and mathematical model results indicate that current levels of human disturbance experienced by wildfowl populations on the Exe estuary are well below bird thresholds. Although the individual-based model is parameterized for Brent goose and wigeon on the Exe Estuary, its design and implementation allow flexibility and broader applicability. Thus, this model is also a useful tool for ecologists in understanding human disturbance in many contexts with a variety of animals.

6.2. INTRODUCTION

6.2.1. BACKGROUND

The literature indicates that human disturbance has measurable effects on wildlife. Studies have highlighted that human activities can influence animal behaviours and distributions (Gill 2007; Bennett et al. 2009; Pirotta et al. 2018). However, only a handful of these research studies have managed to determine if these effects translate to population-level impacts (Gill et al. 2001; Christiansen & Lusseau 2015); there are multiple reasons for this.

Multiple factors must be accounted for when assessing population-level impacts on wildlife from human disturbance (Gill et al. 2001; Pirotta et al. 2018). These include distribution and behaviour but also require a measure of the fitness costs associated with any changes in behaviour (Gill et al. 2001; Pirotta et al. 2018). It is difficult to measure individual fitness costs accurately and to incorporate them into population models within a useful time frame (Pirotta et al. 2018). Therefore, much of the research to date has primarily focussed on only the distribution or behaviour and not the combined fitness costs (Christiansen & Lusseau 2015; Pirotta et al. 2018).

The study of population dynamics uses two primary methods: population models and individual-based models. Population models can look at historical and current changes in a population, such as mortality and survivability, and to identify factors correlated to those changes and then, use those factors to help predict future fluctuations (Murdoch 1994; Evans 2012). Population models can also be behaviour-based and can calculate the population level costs of observed behaviours. However, individuals within numerical models are grouped into a single entity of population and are identical, meaning fitness costs are applied universally and equally to all individuals (DeAngelis 2018). Furthermore, the set of conditions that derive variable values may not be applicable under future prediction scenarios (Evans 2012). Conversely, individual-based modelling (IBM), also known as agent-based modelling (ABM), evaluates the individual behaviour of animals and determines how that behaviour results in a population-level change (DeAngelis & Grimm 2014; Stillman et al. 2014). The translation of individual response to population-level is achieved by using simulations that program discrete individuals to operate based on fundamental ecological principles, such as fitness-maximising decisions and the ability to make choices and adapt (DeAngelis & Grimm 2014). These methods mean individuals vary and adjust to changing environmental conditions. Both population and individual-based models have been successful in helping to predict and understand population fluctuations in animals. However, IBMs may be best suited for situations that involve accounting for animal adaptability and the fitness costs associated with changes in animal behaviour (Stillman et al. 2014).

It is the ability to account for adaptability, as well as individuality, that makes IBMs the method that best suits the study of how animal populations respond to human disturbance (Beale 2007; Pirotta et al. 2018). Whether through measures of reaction time or flight initiation distances, it is observations of individual behavioural changes, combined with the individual fitness costs associated with these behaviours, that measure human disturbance effects. Therefore, understanding if the human disturbance is impacting a population, requires a method that takes into account this individuality (Beale 2007).

In concordance with this, many studies within the literature evaluating the impacts of human disturbance on different wildlife populations, use individual-based models (Grimm & Railsback 2013; Stillman et al. 2014). For example, van Beest et al. (2017) was able to use individual-based modelling to predict the population-level effects of combined fishing closures and bycatch mitigation measures. However, the nature of individual-based models requires intricate understandings of the decision making processes of the animals involved, which can be different from species to species, as well as, vary from location to location (Grimm & Railsback 2013; DeAngelis & Grimm 2014). Furthermore, the data for testing various scenarios may be difficult to acquire or is limited in the literature, which makes understanding and implementing findings from individual-based models useful but sometimes complex for managers without specialist knowledge (Bennett et al. 2009). As a result, there is a demand for more models with the ability to be generalized and that are also relatively easy to implement.

6.2.2. THIS CHAPTER

This chapter uses Netlogo, as well as knowledge of wildfowl energetics relative to human disturbance effects on the Exe estuary, found in Chapters 2-5, to generate an IBM that is both generalizable and easy to use. Netlogo is an individual-based modelling platform developed by Uri Wilensky of Northwestern University that is user-friendly and intuitive (Tisue & Wilensky 2004). Netlogo has base coding built-in, referred to as primitives, that perform most primary tasks that a typical ecologist will need. Furthermore, Netlogo's coding language is one that is intuitive and easy to understand, which makes it ideal for researchers that are not familiar with technical coding, jargon, and implementation.

Although this chapter focuses on wildfowl on a specific site, the foundations of the model are energy budgets, food availability, and site accessibility. These are all factors that are widely applicable to many species, are the basis for optimal foraging theory and fitness-maximising decisions and are therefore, generally relatively easy to acquire through observation or the literature. As a result, the model developed for this chapter is both easy to understand as well as widely applicable.

6.2.3. AIMS AND OBJECTIVES

This chapter aims to understand how human disturbance effects translate to the population level effects in animals. The intention is to develop an individual-based model that is capable of determining bird thresholds of disturbance that animals can experience before population-level impact occurs.

This chapter addresses the following objectives:

- Develop, parameterize and validate an individual-based model based on Brent goose and wigeon on the Exe estuary
- Calculate population-level impacts of different degrees of human disturbance on Brent goose and wigeon
- Establish means for transferability of the model beyond Brent goose and wigeon and the Exe estuary

6.3. METHODS

6.3.1. MODEL DEVELOPMENT AND IMPLEMENTATION

Literature research on life histories of Brent goose and wigeon, as well as compiled information from Chapters 2-5, formed the basis of model parameters. Chapter 2 provided information and evidence on environmental characteristics that determine spatial-temporal distributions of birds and humans on the Exe estuary. In Chapter 2, these environmental states corresponded with food availability for birds and ease of access for humans. Therefore, individuals in the individual-based model were programmed using the basic principles of food availability, ease of access and energy-efficient decisions. Furthermore, characteristics of the site were programmed to most accurately represent the Exe, while maintaining simplicity and flexibility. These features consist of the tidal movement to partially restrict food availability and site accessibility over time, and also varied substrate types, which affected bird and human distribution on the Exe estuary in Chapter 2. A full list of the parameters used for the model can be found in the ‘Input’ section of Table 6.1. The model assumes that birds make decisions based on fitness-related rules (Grimm & Railsback 2005;Table 6.1; Figure 6.1). For this model, human proximity, energy level, and food availability determined fitness-related decisions. Additionally, birds in the IBM were programmed to ‘die’ (leave the system) if their energy level fell below 20% of their energy minimum. This was added after preliminary investigation indicated that once model birds fell below this minimum, they never returned to energy equilibrium within the model run. As a result, this function acted as an indicator that model birds were beyond their threshold for compensation or ‘Bird Threshold’. Measures of time budgets, energy levels and distribution of model birds against real-world birds validated the model, to test whether these processes accurately mimicked real bird behaviour (Table 6.1; Table 6.3; Figure 6.2).

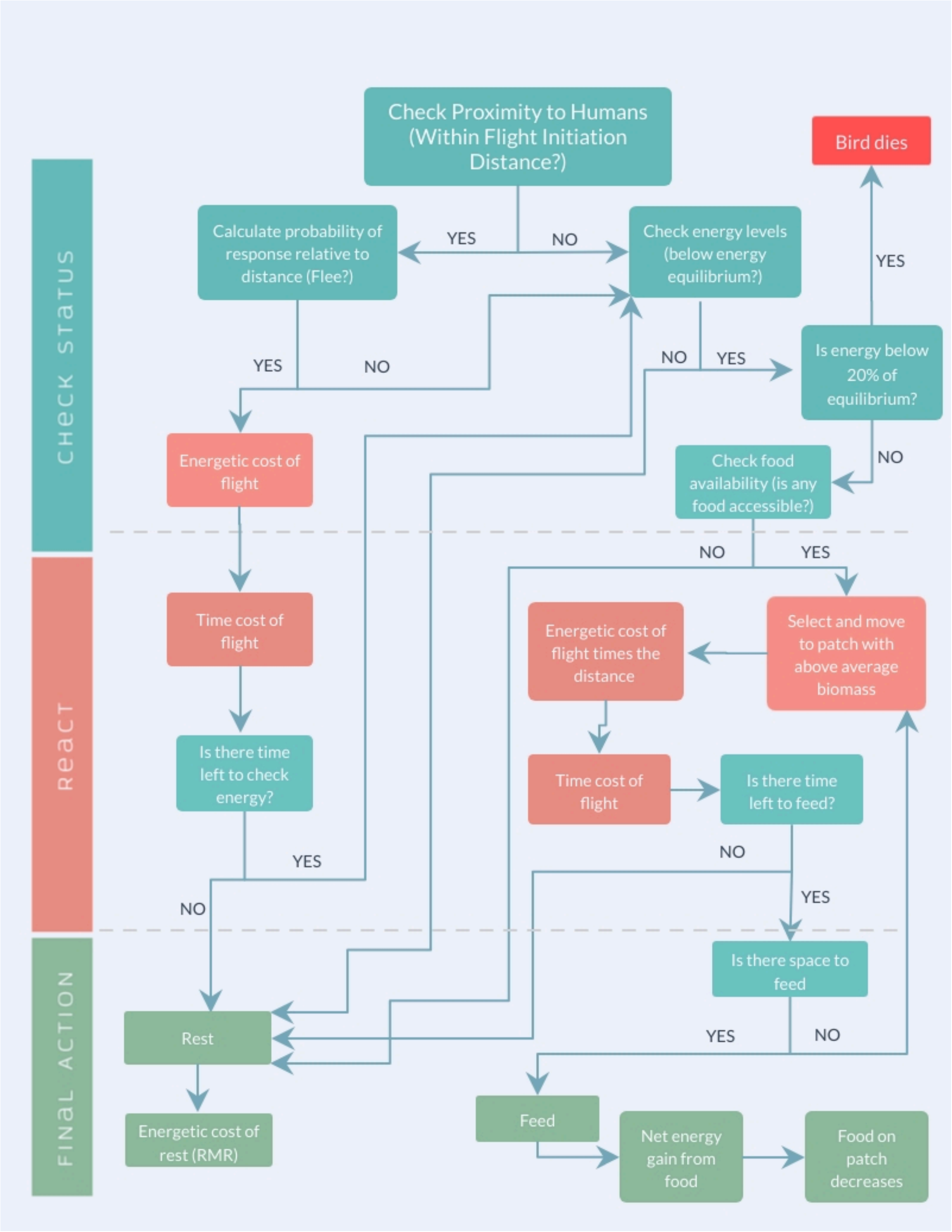


Figure 6.1 Conceptual framework for wildfowl decision making processes within the model during each time step (one minute).

Table 6.1 ODD protocol description of the model developed.

Overview	Purpose	This model simulates fitness-maximising decision making of birds on an estuarine environment in the presence of human activity. The goal is, to accurately represent bird behaviour through foraging and fleeing responses to human activity and to understand how bird distribution, energy and time budgets change relative to different levels of human activity over time.
	State variables and scales	This model includes the following entities that have state variables: individual, population, and environment. There are three different types of individual agents within the model: humans, Brent goose, and wigeons Defining characteristics of model birds: At the start of each model run, birds randomly distribute on patches that have an elevation less than 2.5 meters, which ensures birds start on the estuary and not on land. Brent goose and wigeon 'own' the same types of characteristics but the values assigned to these characteristics are species-specific. The following terms define these characteristics: • energy – the starting energy of a bird • energy-min – the minimum energy a bird strives to maintain • flight-cost – the energetic cost of flight • feed-depth – the depth at which a bird is capable of feeding • flight-prob – an equation representing the probability of flight relative to the distance • flight-dist – the distance a bird flees when disturbed • flight-speed – how fast a bird flies over a distance • body-mass – the starting body mass of an individual bird • rmr – the resting metabolic rate which is the rate a bird expends energy while resting • thermo-cost – equation of the energetic cost of maintaining temperature when the temperature is below the critical threshold • activity – the activity a bird is partaking in (resting, fleeing, feeding or locomotion)

		• start-patch – the location of a where a bird starts before moving • patches-visited – a running list of the patches a bird has visited • FID – flight initiation distance which is the recorded distance for that species that has resulted in an escape response Defining characteristics of model humans: Humans in the environment hold the characteristic of walking speed. The average walking speeds of humans observed on the Exe Estuary determines this speed. The primary behaviour they function on is to not go into areas that are muddy or mixed and to not enter regions with depths too shallow for water activity and too deep for walking. These were variables considered to best describe the variability in overall human activity on the estuary. Furthermore, humans can change their activity relative to the time of day. All humans randomly start on the very edge of land or in the middle of the estuary. These starting points are to replicate access points on the site and to avoid humans starting in areas that they would not usually be able to access. Defining characteristics of patches: The environment has a total area of 1200m^2 divided by a 60 x 60 grid of square patches. Each square patch, therefore, represents an area of 20m^2. Each patch has a randomly assigned substrate that varies between, sand, mud, mixed and rock. Patches also have depth and elevation to simulate an estuarine environment. Depth is then assigned based on the elevation of the patch. If a patch has a positive elevation, then the starting depth of that patch is 0. If a patch has a negative elevation, then the starting depth of that patch is equal to the absolute value of the elevation. This depth then varies each time step with the introduction of the tide function. The resulting environment is a region of land that is never covered by water and a sort of island region that requires crossing

		water to access. Patches that have a substrate of mud or mixed have vegetation mass, which represents eelgrass (*Zostera* spp.) presence. The seagrass is only present at patches with these substrates at elevations/depths that represent realistic growing conditions.
	Process overview and scheduling	Decision-making processes of model Birds: During each time-step, each bird performs the following actions (Figure 6.1): (i) Check their proximity to humans (ii) If proximity is within flight initiation distance birds react proportionally to the distance they are from the human (Based on reaction data relative to the proximity of humans observed on the Exe estuary). (iii) If the reaction takes longer than two-thirds of a time step, that bird must rest once arriving at the site, because it has used the majority of the time step for flight. (iv) If humans are not within flight initiation distance, or birds do not react, or the flight reaction takes less than two-thirds of the time step, birds check their energetic state (v) If energy is below the assigned energy-minimum, birds check to see if any food is available on the estuary (vi) If food is available, then birds forage (vii) To forage, birds randomly select a patch within the environment with above-average biomass available and move to those sites. (viii) If the location of the site would take longer than two-thirds of a time step, for the bird to reach, that bird must rest once arriving at the site, because it has used the majority of the time step for flight. (ix) If the site takes less than two-thirds of the time step for the bird to reach, then it checks the patch for bird density. (x) If bird density is less than 40 individuals on a patch, then the bird can eat (This density was selected based on the average maximum number of birds witnessed on 20m^2 areas on the Exe estuary). (xi) If the density is greater than 40 individuals on a patch, the bird must take note of the patch it

		is on and move to a patch other than the one it is on that has above average biomass (xii) If a bird has energy above the energetic minimum, then it rests. (xiii) Birds die if their energy falls below 20% of their minimum energy. (20% of energy minimum was used to provide a conservative cushion for bird thresholds and is the point at which birds struggled ever to regain energy equilibrium in the model). Decision-making process of model humans: During each time step, each human performs the following actions: (i) Check the substrate they are occupying and the substrates ahead for unfavourable substrates. These substrates are either too deep for walking, too shallow for water-sports, or when exposed, are poor substrates for walking on, such as mud or mixed substrate. (ii) If substrate ahead is favourable, move forward at a rate of 4.2 patches (equal to average human walking pace) per time step. (iii) Humans also check the time, have a user-defined period of activity. Two scenarios were simulated for this model: one where humans are active only 9 hrs of the day, and the other, where humans are active the entire 24 hrs. Patch variation in time: Patches during each time step are responsible for recording the following information: (i) Depth relative to tide (ii) Food availability relative to a depth. (iii) Favourability of the substrate relative to depth and substrate combined (iv) Both bird and human visitation rates. The state of these patches is pivotal to dictating both bird and human movement and for evaluating changes in distribution.

Design	Basic principles	This model is designed to be based on fitness-related decision making, and results from studies on behaviour and distribution of Brent goose and wigeon relative to human activity observed on the Exe Estuary (see Chapters 2 and 3)
	Emergence	The patterns that emerge from running this model are bird time budgets, spatial-temporal distribution of birds and energetics of birds. These patterns are driven by individual decision-making to either forage, rest, or flee depending on energy state and spatial location.
	Adaptation	Adaptations occur in several forms. Birds select regions with above-average biomass and rest in the absence of food availability to minimise energetic loss. Additionally, when birds meet energy needs, they cease to feed. Furthermore, birds adapt to the density of other birds on a site by moving to a different location if too many birds already occupy the patch they are on.
	Sensing	Model birds are able to sense food availability that varies in space relative to tide state and site geography. Furthermore, birds sense the proximity of human activity and density of birds on patches they occupy.
	Interaction	Direct interaction occurs between model birds and model humans. Model birds flee from model humans based on a proportion of response relative to proximity. Model birds also interact indirectly with each other via food bio-mass consumption and density dependence.
	Stochasticity	The model introduces stochasticity via random food distribution, random initial bird distribution, as well as random initial human distribution and movements. Additionally, model birds are assigned an arbitrary starting energy level, as well as random body-mass, within the appropriate species range, to represent birds with various body conditions on an estuary. Therefore, bird reactions to the environment change accordingly. The function 'set-seed' allowed for reproducibility by enabling the use of the same set of random numbers for each model run.
	Observation	The observer records the following variables: bird time budgets, spatial-temporal distribution of birds, energy levels of birds and spatial-temporal distribution of humans. These variables represent measures to help validate the model to the real-world and also offer information on the influence of model human activity on model study species.

<table>
<tr><td></td><td></td><td>They detect behavioural changes while simultaneously measuring energetic costs associated with those behavioural changes.</td></tr>
<tr><td>Detail</td><td>Initialization</td><td>The first step of initialization uses the 'Setup' button. The ‘Setup’ button creates the environmental conditions for the model to start. Background coding and sliders on the interface of the model determine this environment. Background coding includes:

Patch substrates
Patch starting vegetation
Patch elevation
Parameters for starting humans
visual aspects of humans such as colour, shape and size
walking speed
starting location
Parameters for starting birds
visual elements of the birds
starting energy
minimum energy requirements
body mass
flight-cost
feeding depth
flight probability
flee distance
flight-speed
resting metabolic rate
thermo-regulatory costs
records of patch visitation
and activity state
Parameters defined by interface sliders include:
numbers of birds
numbers of humans
time of high-tide
energy from each gram of grass
flight initiation distances
time humans are active
parameters regarding environmental geography.

After the initial setup, to get the model to progress in time, the 'go' button must be pressed. Pressing the 'go' button</td></tr>
</table>

		causes all of the steps listed in the 'go-procedure' in the background coding to take place. These steps include: • patches advance tide • patches report total biomass available • Brent goose and wigeon set their patch • Brent goose and wigeon check their status • humans move • Brent goose and wigeon check whether they are dead • humans check the time • patches record human and bird distribution. Ticks are limited at 1440 to replicate the total minutes in a 24hr day.
	Input	Input for modelling the Brent goose and wigeon on the Exe Estuary are as follows: Coding: **Set Seed: 727** produces a repeatable randomized environment tied to the number '727' **Globals:** numerical values applied to various terms used ubiquitously in the model so that the terms can be used in the coding instead of numbers set mud 1 set mixed 2 set sand 3 set land 5 set intertidal 0 set water 6 set feeding 2 set disturbed 3 set undisturbed 0 set resting 0 set locomotion 1

		Humans: **Colour:** red **Shape:** ‘person’ **Size:** 2 **Walking-speed:** 4.2 patches per minutes average walking speed recorded in observations for a human was 84m per minute/20m per patch **Brent goose:** **Colour:** black + 2 **Shape:** ‘bird side’ **Size:** 1.5 **Start-energy:** random between 840 and 1000 (Stillman et al. 2015) **Energy minimum:** start-energy **Energy:** start-energy **Body mass:** random between 1200 and 1540 (Fog 1967 as cited in Clausen et al. 2012) **Flight cost:** ((0.679 * (body-mass ^ 0.818)) / 1800) (Castro & Myers 1988) **Feeding depth:** -0.4 meters (Clausen 2000) **Flight probability:** 10% based on observational data of brent goose increase in the probability of flight relative to every 20m increment in proximity to human activity **Flight distance:** 12.84 patches (256.8m) Average recorded observed fleeing distance for Brent goose (m) / flight speed (m/min) / 20m per patch **Flight speed:** 1038m/min (Green & Alerstam 2000) **Resting metabolic rate:** (308 * ((body-mass / 1000) ^ 0.73)/ 1440) (Aschoff & Pohl 1970; Lindström 1991) **Thermoregulatory costs:** 0.004kJ/min * (Lower critical threshold – average temp) (Collop 2017)

		Patches-visited: list patch-here **Activity:** resting **Disturbance:** undisturbed **Wigeon:** **Colour:** brown + 1 **Shape:** 'bird side' **Size:** 1.5 **Start-energy:** random between 660 and 715 (Mayhew 1988) **Energy minimum:** start-energy **Energy:** start-energy **Body mass:** random between 539 and 723 (American Wigeon in winter; Rhodes et al. 2006) **Flight cost:** ((0.679 * (body-mass ^ 0.818)) / 1800) (Castro & Myers 1988) **Feeding depth:** -0.3 meters (Pöysä 1983) **Flight probability:** 7%based on observational data of wigeon increase in the likelihood of flight relative to every 20m increment in proximity to human activity **Flight distance:** 10.6 patches (212m) Average recorded observed fleeing distance for wigeon (m) / flight speed (m/min) / 20m per patch **Flight speed:** 1080m/min (Pennycuick et al. 2013) **Resting metabolic rate:** (308 * ((body-mass / 1000) ^ 0.73)/ 1440) (Aschoff & Pohl 1970; Lindström 1991) **Thermoregulatory costs:** 0.004kJ/min * (Lower critical threshold – average temp) (Collop 2017) **Patches-visited:** list patch-here **Activity:** resting **Disturbance:** undisturbed

		Interface sliders (Figure 6.2): **Time-high-tide:** set at 584 to represent a high tide in the middle of the day. **Number-of-wigeons:** set at 100 as this represents the average number of wigeon in a similar area on the estuary. **Number-of-brentgeese:** set at 100 as this represents the average number of brent-geese in a similar area on the estuary. **Energy-from-grass:** Set at 16.5 kJ/g but not implemented in this model, because intake energy is based on mass and calibrated energy intake for estuary, rather than patch vegetation. However, this provides the scope to implement such an equation if this variable is known. **Energy-from-rhizome:** This is left blank for the Exe Estuary model but is kept to show the possible scope of the model if the user desired to implement the effects of rhizome consumption. **FID:** set at 14 This is the minimum number of patches required for birds to consider reacting. Because this changes for different species as well as for different human activity types, this has high flexibility. For this model, it was 14 patches (14 * 20m = 280m). The average response distance for Brent goose and wigeon is technically less than this distance; however, for this model, it was increased to produce a conservative estimate of response rate to the presence of human activity. **Humans-active:** This defines the number of ticks (minutes) for which humans are active within the environment. For this model, two settings are used: one where activity ceases after dark (9.5hrs of time elapse = 570min), and the other where the activity is constant throughout a model run (24hrs = 1440min). These two settings depict two scenarios: the

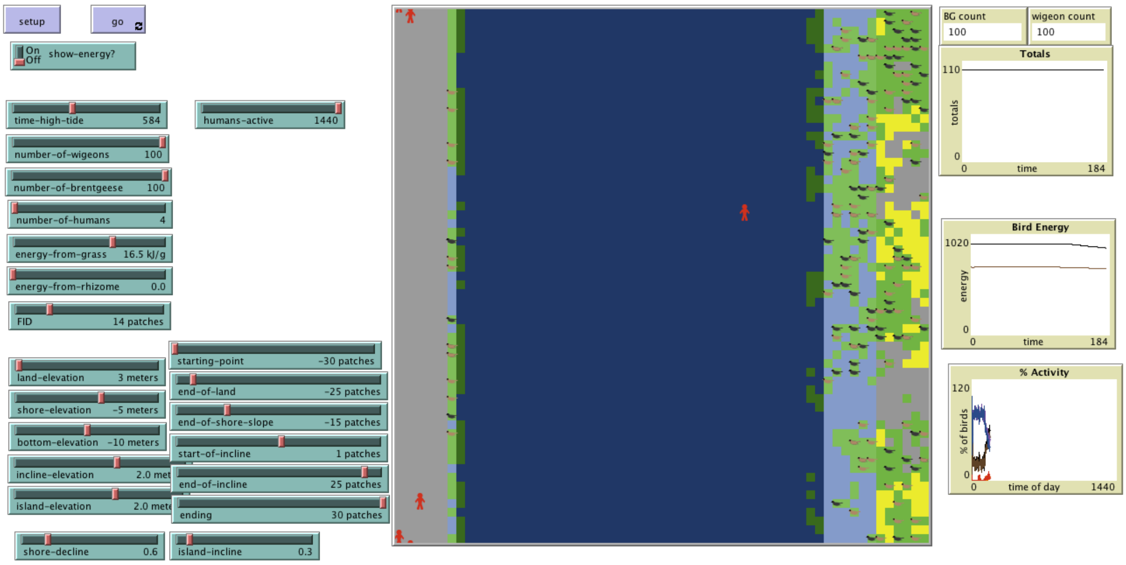
		first being closer to reality, and the second being more conservative. **Land-elevation:** This controls the height of the areas from 'starting-point' to 'end-of-land'. For this model, land height is 5 meters. **Shore-elevation:** This controls the lowest point of elevation of the shore, which is the area from 'end-of-land' to 'end-of-shore-slope'. For this model, shore elevation is -5 meters. **Bottom-elevation:** This controls the deepest portion of the environment and is the portion between 'end-of-shore-slope' and 'start-of-incline'. For this model, it is -10meters. **Incline-elevation:** This controls the overall elevation of the incline to the island. The boundaries of this are defined by 'start-of-incline' and 'end-of-incline'. For this model, it is 2 meters. **Island-elevation:** This controls the height of the island in the environment defined by the region between 'end-of-incline' to 'ending'. For this model, it is 3 meters. **Shore-decline:** This controls the decline along segment considered shore (between 'end-of-land' to 'end-of-shore-slope'). The gradient here will decrease at a slope defined on the slider from starting point height to the ending point depth. For this model, this is 0.6 meters per patch decline for every increase in the x-coordinate direction. **Starting-point:** This is the starting point of land and for this model is defined as the farthest edge patch at -30 for the x-coordinate. **End-of-land:** This is the endpoint of land and starting point for the shore. For this model is at -25 patches for the x-coordinate. **End-of-shore-slope:** This is the ending point of the shore and starting point for the bottom. For this model, this is at -15 patches for the x-coordinate.

		Start-of-incline: This is the starting point for the island incline and the ending point for the island. For this model, it is one patch for the x-coordinate. **End-of-incline:** This is the ending point of the incline and the starting point of the island. For this model, this is patch 25 for the x-coordinate **Ending:** This is the end of the island, which is patch 30 for the x-coordinate in this model. **Island-incline:** This represents the rate of incline for the slope up to the island. For this model, this rate is 0.3 meters for every increase in x-coordinate patch. To test for other birds and other estuaries, modifications to the following parameters will be necessary: For other birds/animals: - Number of birds - energy-from-grass (food energy) - Energy - Energy minimum - Body mass - Feeding depth - Flight probability - Flight distance - Flight speed - Thermoregulatory costs (if below lower critical threshold). **For other estuaries:** All sliders concerning environment geography that best reflects the area of interest.
	Sub-models	Each step in the go procedure implements the following sub-models: i) **Patches advance-tide:** patches set a depth based on current elevation and then apply a tidal equation that functions as a unit of time which is defined by the ticks and the 'time-high-tide' set on the interface slider. Biomass availability changes as the depth of patches exceed feeding depths for birds. Furthermore,

		the visual dynamics of patches change to reflect inundation by water as the depth decrease below 0. Additionally, favourability of substrates for human movement and accessibility changes according to travel depths of humans. ii) **Patches check for total-biomass-available:** this is a reporter that checks to see if there are patches above a certain depth where biomass is available. If all patches with veg-mass are deeper than feeding depth, then total-biomass-available is set to 0. iii) **Brent geese and wigeons patchset:** this is a sub-model that sets the patch that each brent goose and wigeon starts on and the starting activity state for every tick. iv) **Brent geese and wigeons check-status:** This sub-model has several sub-models**. I)** First Brent goose and wigeon determine whether they need to flee any humans in the vicinity. If there are humans, birds determine their proximity, and if humans are within the FID defined by the slider on the interface, then birds pick a number between 1 and 100. If that number is the same or less than their flight probability for the distance within the FID, then the bird sets its disturbance state to 'disturbed' and flies back the distance that the average bird flies when disturbed. Then that bird loses energy at the rate of the length of the flight*the cost of the flight. Then if that distance takes longer than 30 seconds to get to, that bird must rest. If it takes less to get to, then that bird checks its energy. If its energy is less than its energy minimum, then that bird forages. **II)** To forage, a bird first checks if the total-biomass-available. If that biomass is greater than 0, then the bird will move to a random patch with an above-average amount of biomass and subtract the cost of the movement from it energy based on flight-cost, and the distance travelled. **III)** Once at the patch, then birds will check to see if the distance travelled takes more than the two-thirds of a minute. If so, that bird must rest because it has lost its feeding time to travel time. **IV)** If it takes less than two-

			thirds of a minute, then the bird will check the density of birds on the patch. If the density is greater than 40 birds within a 20m^2 patch (the maximum number of real birds witnessed in the Estuary in a 20m^2 patch), then the bird will take note of that patch and move to a neighbouring patch with maximum biomass. If that patch is also too high of a density, then the bird will also note this patch and select a random patch with above-average biomass that is not one of the patches it has already visited. For each movement, a bird loses energy according to flight cost and distance. **V)** Once a patch meets requirements, then birds can eat the grass. Within this model, birds increase energy relative to body mass and calibrated average energy available on the estuary. When birds are feeding, they set their activity state to feeding. Biomass on that patch then decreases by the energy level that birds have consumed. **VI)** Birds rest if they have enough energy or have used up their time step in a movement. To rest birds stay in their position and lose energy at a rate of resting metabolism and set their activity state to rest. v) **Humans move-humans:** if there are humans on the site, then humans will randomly set a heading, and move forward. Before they move forward, they check that the substrate is favourable within each of the four patches ahead (because humans move 4.2 patches per time-step so if any one of the patches within 4 is unfavourable they must know). If one of those patches is unsuitable, then the human will turn around and move. If there are no favourable patches to move on, then the human is reset at the coordinate -30 -30 which is considered a land access point. vi) **Brent geese and wigeons check-death:** for every time step, birds check their energy. If their energy is below 20 percent of their minimum energy requirements, then birds leave the system. vii) **Humans check-time:** If the ticks have progressed beyond the ticks listed for humans-active then humans move to a designated

		point on the map and no longer move, represent a limited source of disturbance representative of the night time. viii) **Patches record-distribution:** In this sub-model, each patch records the number of times it has been visited by either a brent-goose, wigeon, or human and continuously adds to this number as it is visited, which allows for information on visitation rates and distribution.



show-energy? Off
time-high-tide 584
humans-active 1440
number-of-wigeons 100
number-of-brentgeese 100
number-of-humans 4
energy-from-grass 16.5 kJ/g
energy-from-rhizome 0.0
FID 14 patches
starting-point -30 patches
land-elevation 3 meters
end-of-land -25 patches
shore-elevation -5 meters
end-of-shore-slope -15 patches
bottom-elevation -10 meters
start-of-incline 1 patches
incline-elevation 2.0 met
end-of-incline 25 patches
island-elevation 2.0 mete
ending 30 patches
shore-decline 0.6
island-incline 0.3
BG count 100
wigeon count 100

Figure 6.2 A snapshot of the interface of the individual-based model and slider settings to represent the Exe Estuary.

6.3.2. MODEL VALIDATION

There are various methods for performing individual-based model validation and verification. In this chapter, the methods used are graphical representation, historical data validation, and predictive validation (Xiang et al. 2005). Model variables used in these tests for validation were bird time budgets, bird habitat use, and human distribution. These variables were selected for validation because they were measures that emerged from the model and were not used for parameterizing the model. Values for these variables were obtained by running model simulations at similar disturbance rates to those that were witnessed on the Exe Estuary. Predicted model bird time budgets, model bird habitat-use, and model human distribution were compared to real bird time budgets, real bird habitat-use and real human distributions observed on the Exe estuary. Because 100 model birds were present in the model, comparisons were made on observations where at least 100 real birds were present to be observed on the Exe Estuary. Comparisons between model predictions and observed values were made by visual analysis, percentage difference from the observed values, as well as, statistical analysis (Xiange et al. 2005). Statistical analysis used proportion test analysis (prop.test in RStudio statistical software Version 1.0.136; © 2009-2016 RStudio Inc.; R version 3.3.3; © 2017-03-06 R Inc.) to compare the predicted results vs observed results. Prop.test analysis is a comparison of equal proportions and therefore was used to compared real bird activity proportions to model bird activity proportions as well as real bird distributions on substrates to model bird distributions on substrates. Furthermore, model outputs were measured against COD outputs from Chapter 3 by comparing model bird compensatory feeding times and model bird thresholds to COD bird compensatory feeding times and COD bird thresholds.

6.3.3. MODEL EXPERIMENTS

After the chosen model variables were validated and verified, several scenarios examined how bird time budgets and distributions changed relative to varying levels of human activity and presence (Table 6.2). The same random distribution of food was used in each Individual simulation. Model birds were exposed to increasing levels of human activity, both in the number of humans, and the time exposed to those humans. The resulting time budgets, distribution and energy levels of model birds were examined to determine whether there were significant differences. Data from the model was collected on a minute by minute basis, meaning each run produced a total of 1440 observations of activity budgets, distribution and energy levels. The examination of these differences used analysis of variance (ANOVA) and multiple analysis of variance (MANOVA) using the ‘aov’ and ‘manova’ procedures in RStudio statistical software Version 1.0.136 (© 2009-2016 RStudio Inc.) with R version 3.3.3 (© 2017-03-06 R Inc.). If birds either did not meet minimum energy requirements or if birds died, the number of humans and the time they were active in the environment was beyond the threshold for compensation for the birds.

Table 6.2 Model structure for testing model scenarios

	Model structure		Sampling	
Question:	**Dependent variable**	**Independent variable**		**Analysis**
How does bird energy change relative to number of humans?	Bird energy	Number of humans present	1 measure on 14 groups of 2880	ANOVA
How does bird energy change relative to the amount of time birds are exposed to human activity?	Bird energy	Time humans are active	1 measure on 2 groups of 20160	ANOVA
How does bird activity change relative to number of humans?	Bird activity: • Feeding • Resting • Disturbed	Number of humans present	3 different measures on 14 groups of 2880	MANOVA
How does bird activity change relative to the amount of time birds are exposed to human activity?	Bird activity: • Feeding • Resting • Disturbed	Time humans are active	3 different measures on 2 groups of 20160	MANOVA
How does bird distribution change relative to number of humans?	Bird substrate: • Mud • Mixed • Sand • Land • Water • Intertidal	Number of humans present	6 different measures on 14 groups of 2880	MANOVA

	Model structure		**Sampling**	
Question:	**Dependent variable**	**Independent variable**		**Analysis**
How does bird distribution change relative to the amount of time birds are exposed to human activity?	Bird substrate: • Mud • Mixed • Sand • Land • Water • Intertidal	Time humans are active	6 different measures on 2 groups of 20160	MANOVA

6.4. RESULTS

6.4.1. *MODEL VALIDATION*

Brent goose and wigeon in the model showed similar time budgets to the observed time budgets of real birds on the Exe Estuary (Table 6.3; Figure 6.3). Percent differences indicated that model birds fed and rested slightly more than those observed. However, proportion test analysis failed to detect any significant differences between the proportions of model birds engaged in both feeding and resting, compared to proportions of real birds engaged in both feeding and resting (Table 6.3; Figure 6.3). Furthermore, bird and human distributions on habitat in the model were similar to that observed on the Exe Estuary. Both birds and humans spent similar proportions of time on different substrates, as was witnessed on the Exe estuary (Table 6.3). However, there were significant differences in the percentage of time Brent goose spent on mud and sand. Model Brent goose spent more time on mud and mixed substrate and less time on the sandy substrate than real Brent goose observed on the Exe estuary (Table 6.3). Furthermore, standard errors were high for human distribution on substrates indicating that although significant differences weren’t detected between real human distributions and model human distribution, the variation of how humans use the substrates in the model may differ from that of real humans.

Table 6.3 Validation parameters for Brent goose, wigeon, and humans within the individual-based model. Observed parameters and model outputs were very similar, indicating that the model closely simulated human and bird movements and interactions on the Exe Estuary.

	Trait	***Variable***	***Observed (%)***	***Standard Error of observed values***	***Model prediction (%)***	***Standard error of model predictions***	***% difference (Pred-Obs/Pred* 100)***	***Prop.Test Analysis (p-value)***
Brent Goose	***Time budgets***	Feed	48.2	3.3	53.8	5.0	10.4	0.37
		Rest	41.1	3.2	46.2	5.0	11.0	0.38
		Flee	0.5	0.5	0.5	0.7	0.0	0.95
	Bird Habitat use	Mud/ Mixed	93	0.1	99	1.0	6.1	0.05***
		Sand	5	0.1	0.5	0.7	-900.0	0.03***
		Water/ Intertidal	98	0.1	100	0	2.0	0.15
		Land	0	0	0	0	0.0	0.85
Wigeon	***Time budgets***	Feed	47.4	2.9	47.7	5.0	0.6	0.95
		Rest	44.4	2.8	52.2	5.0	14.9	0.17
		Flee	0.3	0.3	0.3	0.6	0.0	0.99

	Trait	**_Variable_**	**_Observed (%)_**	**_Standard Error of observed values_**	**_Model prediction (%)_**	**_Standard error of model predictions_**	**_% difference (Pred-Obs/Pred* 100)_**	**_Prop.Test Analysis (p-value)_**
Wigeon	**_Bird Habitat use_**	Mud/ Mixed	99	0.03	99	1.1	0.0	0.48
		Sand	0.4	0.03	0.8	0.1	50.0	0.59
		Water/ Intertidal	100	0.04	100	0	0.0	0.42
		Land	0	0	0	0	0.0	N/A
Human activity	**_Human Distribution_**	Mud/ Mixed	71	0.5	45	40.6	-57.8	0.49
		Sand	29	0.5	25	35.1	-16.0	0.90
		Water/ Intertidal	53	0.5	75	35.5	29.3	0.59
		Land	47	0.5	25	35.5	-88.0	0.59

*** Statistically significant

There were similar patterns in the way model and real bird time budgets changed through the tidal cycle. Both model and real birds foraged most over mid-tide and least over high tide (Figure 6.3). There were small differences apparent following high tide times. Model birds after high tide fed much more quickly than real birds. This outcome is a result of the simplified model environment compared to an actual estuary. The simplification means that although the length of time that food is available for birds in the model is the same as real birds on the estuary, the food becomes available more quickly than it would on an actual estuary. The more rapid availability means that birds in the model are slightly less restricted in feeding as the tide falls than real birds. Because there is greater human accessibility at high tide, this change in feeding behaviour could mean that model birds will experience greater disturbance effects from humans than those of real birds. Greater disturbance while feeding costs birds more and thus effects on the model bird will represent a more energetically taxing situation than real birds on the estuary.

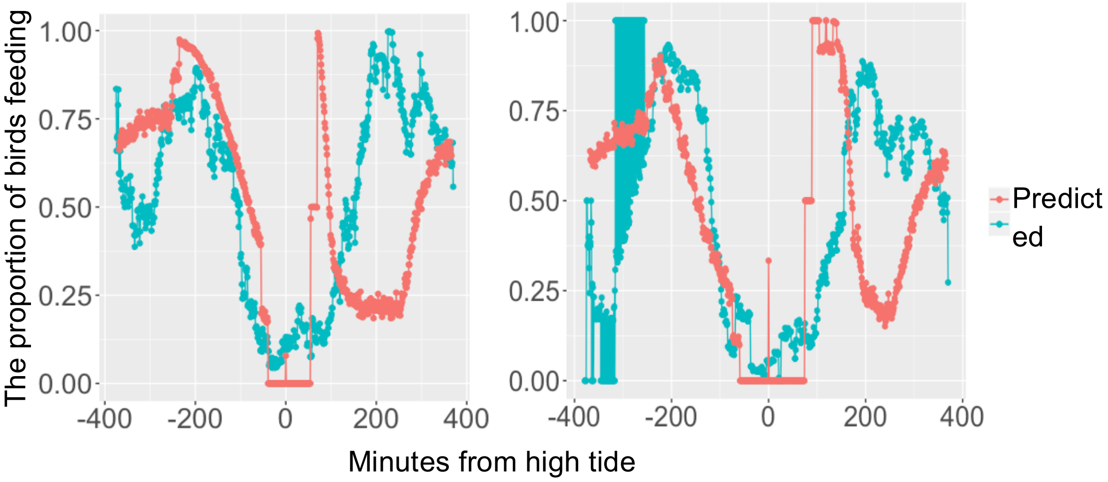


Figure 6.3 Proportion of Brent goose (left) and wigeon (right) feeding predicted by the model (orange) vs observed (green) relative to minutes from high tide (0).

6.4.2. MODEL EXPERIMENTS

There were significant differences in model bird energy, behaviour and habitat-use relative to both number of humans present as well as the amount of time the humans were active for (Table 6.4). Increases in human activity coincided with changes in bird distribution, both relative to the substrate, but also in regions of use within the environment (Table 6.4; Figure 6.4 - Figure 6.7). Furthermore, increasing the number of model humans and the amount of time they were active, were associated with decreases in the energy levels of both model Brent goose and wigeon (Figure 6.8; Figure 6.9). These decreased energy levels consequently increased the time model birds needed to feed to compensate for energy losses (Figure 6.10; Figure 6.11). Model birds exceeded their bird thresholds for compensation when they were not able to feed enough to make up for energetic losses (Figure 6.12; Figure 6.13).

Table 6.4 ANOVA and MANOVA analysis of changes in bird energy, time budget, and distribution on habitat type relative to different numbers of humans and the amount of time humans were active.

Independent variable	Response Variable (n = 40317)	categories	MANOVA Estimate	Df	Sum of Squares	F-value	Pr > F
Varied number of humans (0 – 2000)	Brent goose energy levels *(based on* average energy levels of birds each time step)	N/A	N/A	1	206341337	19170	< 0.0001
	Wigeon energy levels *(based on average energy levels of birds each time step)*	N/A	N/A	1	37956792	14576	< 0.0001
	Brent goose time budgets *(based on the percentage of*	Feeding	0.317	1	171.000	1510.320	< 0.0001
		Resting	0.317	1	171.000	1510.320	< 0.0001

Independent variable	Response Variable (n = 40317)	categories	MANOVA Estimate	Df	Sum of Squares	F-value	Pr > F
	birds engaged in each activity type each time step)	Disturbed	0.317	1	268.960	18003.700	< 0.0001
	Wigeon time budgets *(based on the percentage of birds engaged in each activity type each time step)*	Feeding	0.308	1	118.300	991.464	< 0.0001
		Resting	0.308	1	118.300	991.464	< 0.0001
		Disturbed	0.308	1	285.25	18229.24	< 0.0001
	Brent goose use of habitat types *(based on the percentage of birds in each habitat type*	Mud	0.013	1	1.400	154.315	< 0.0001
		Mixed	0.013	1	1.330	159.120	< 0.0001

Independent variable	**Response Variable (n = 40317)**	**categories**	**MANOVA Estimate**	**Df**	**Sum of Squares**	**F-value**	**Pr > F**
	during each time step)	Sand	0.013	1	1.961	520.520	< 0.0001
		Land	0.017	1	4.784	709.330	< 0.0001
		Water	0.017	1	0.013	20.840	0.1043
		Intertidal	0.017	1	5.290	634.140	< 0.0001
	Wigeon use of habitat types (*based on percentage of birds in each habitat type during each time step)*	Mud	0.027	1	0.790	84.886	< 0.0001
		Mixed	0.027	1	3.450	403.070	< 0.0001
		Sand	0.027	1	3.060	827.830	< 0.0001
		Land	0.016	1	4.588	659.390	< 0.0001
		Water	0.016	1	0.015	21.862	< 0.0001
		Intertidal	0.016	1	5.130	569.370	< 0.0001

Independent variable	**Response Variable (n = 40317)**	**categories**	**MANOVA Estimate**	**Df**	**Sum of Squares**	**F-value**	**Pr > F**
Varied time humans were active (9.5hrs & 24hrs)	Brent goose energy levels *(based on average energy levels of birds each time step)*	N/A	N/A	1	39278429	3649	< 0.0001
	Wigeon energy levels *(based on average energy levels of birds each time step)*	N/A	N/A	1	10571922	4060	< 0.0001
	Brent goose time budgets *(based on the percentage of birds engaged in each activity type each time step)*	Feeding	0.146	1	16.000	140.880	< 0.0001
		Resting	0.146	1	16.000	140.880	< 0.0001
		Disturbed	0.146	1	107.740	7212.400	< 0.0001

Independent variable	Response Variable (n = 40317)	categories	MANOVA Estimate	Df	Sum of Squares	F-value	Pr > F
	Wigeon time budgets *(based on the percentage of birds engaged in each activity type each time step)*	Feeding	0.148	1	11.700	98.359	< 0.0001
		Resting	0.148	1	11.700	98.359	< 0.0001
		Disturbed	0.148	1	120.350	7690.900	< 0.0001
	Brent goose use of habitat types *(based on the percentage of birds in each habitat type during each time step)*	Mud	0.011	1	0.640	70.494	< 0.0001
		Mixed	0.011	1	1.740	208.550	< 0.0001
		Sand	0.011	1	1.577	418.660	< 0.0001
		Land	0.009	1	2.042	302.680	< 0.0001

Independent variable	**Response Variable (n = 40317)**	**categories**	**MANOVA Estimate**	**Df**	**Sum of Squares**	**F-value**	**Pr > F**
	Wigeon use of habitat types *(based on percentage of birds in each habitat type during each time step)*	Water	0.009	1	0.098	160.860	< 0.0001
		Intertidal	0.009	1	3.040	363.800	< 0.0001
		Mud	0.013	1	0.370	39.336	< 0.0001
		Mixed	0.013	1	2.680	312.530	< 0.0001
		Sand	0.013	1	1.758	475.600	< 0.0001
		Land	0.010	1	2.690	386.660	< 0.0001
		Water	0.010	1	0.101	145.180	< 0.0001
		Intertidal	0.010	1	3.840	425.530	< 0.0001

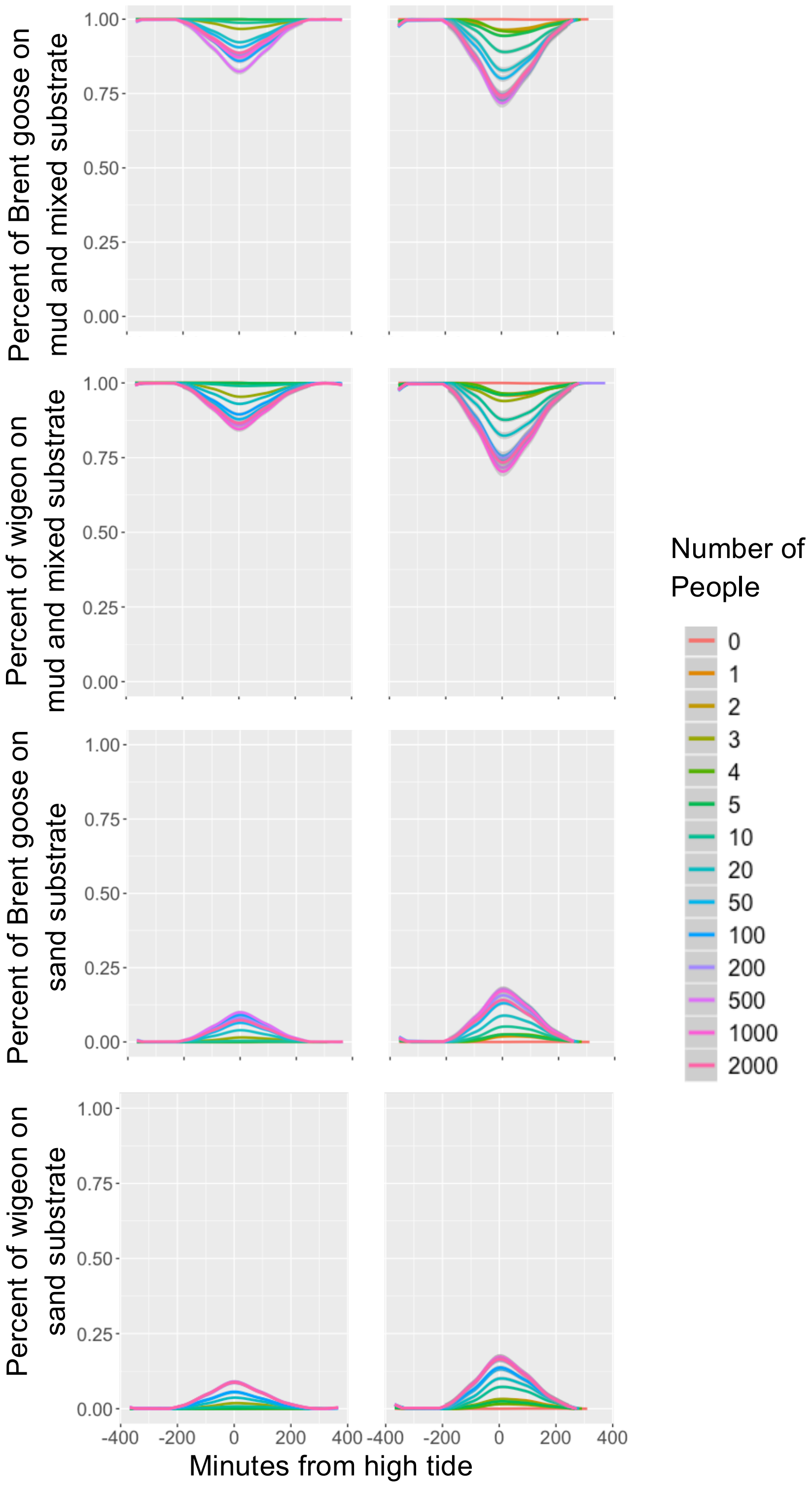


Figure 6.4 Depiction of how percentage of time birds spend on different substrates relative to tide time depends on the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right).

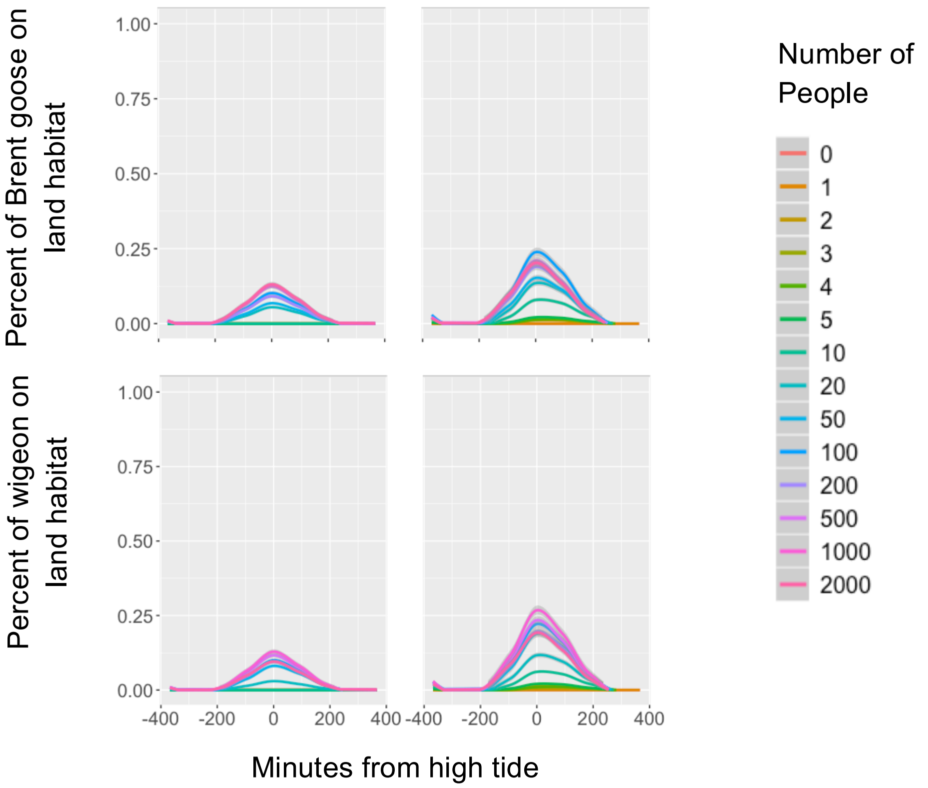


Figure 6.5 Depiction of how percentage of time birds spend on land habitats relative to tide time depends on the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right).

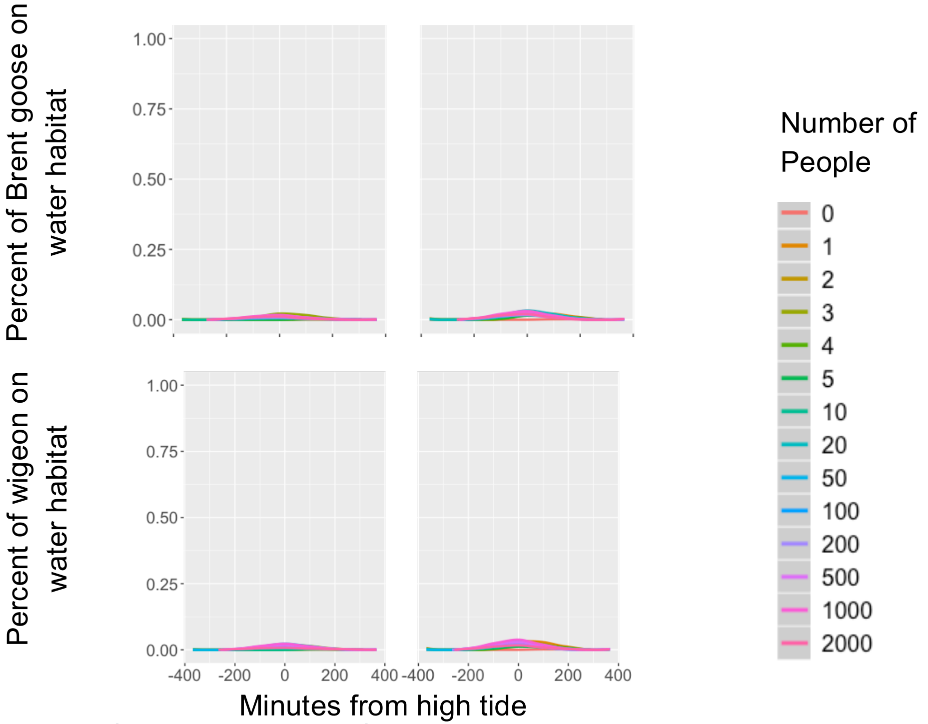


Figure 6.6 Depiction of how percentage of time birds spend on water habitats relative to tide time depends on the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right).

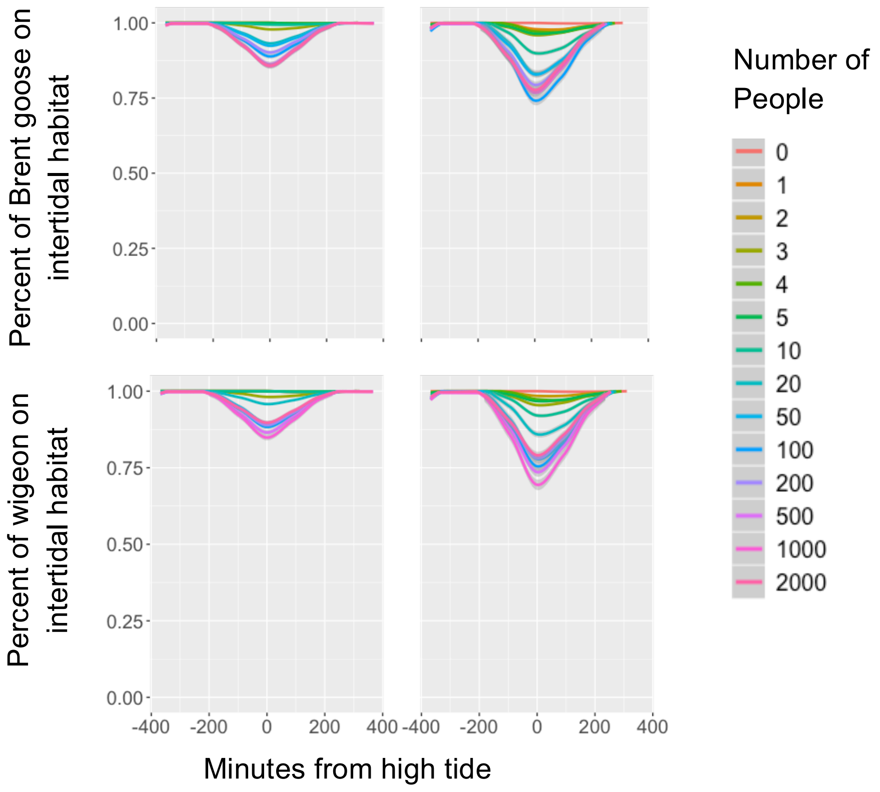


Figure 6.7 Depiction of how percentage of time birds spend on intertidal habitat relative to tide time depends on the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right).

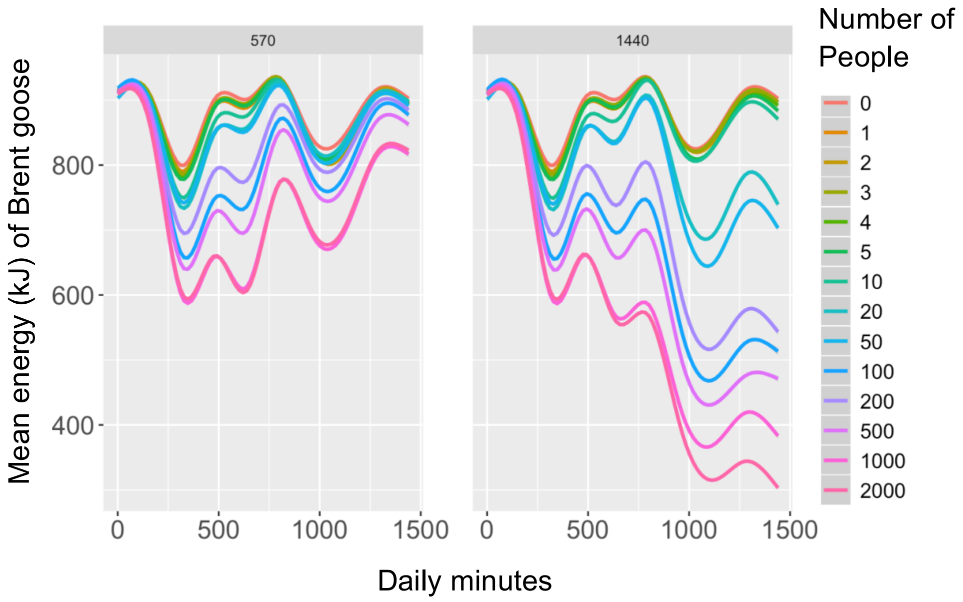


Figure 6.8 Depiction of how overall brent goose energy levels were affected by the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right). Increases in human activity number and exposure time decrease the energy birds acquire.

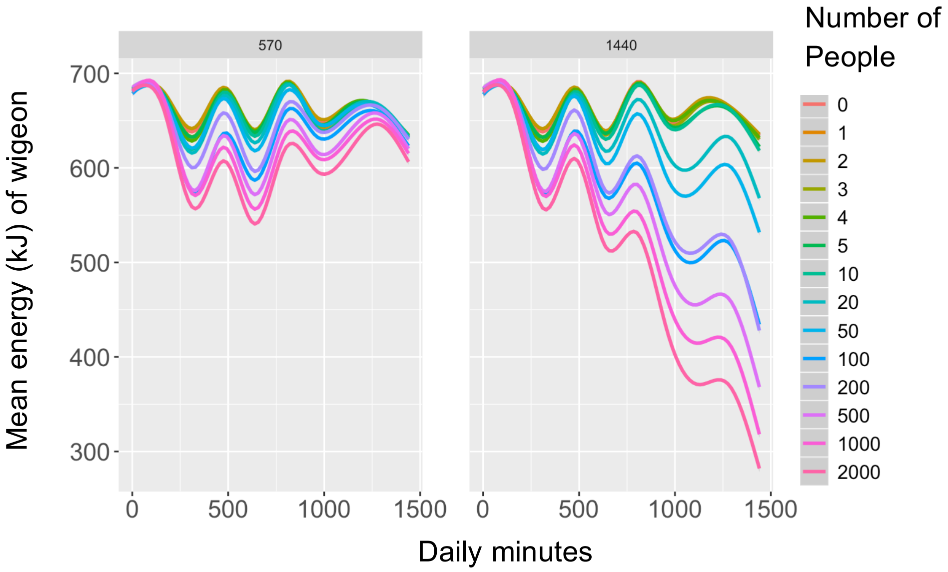


Figure 6.9 Depiction of how overall wigeon energy levels were affected by the number of humans within the environment and if humans were active for 9hrs (570 minutes; left) or the full 24hrs (1440 minutes; right). Increases in human activity number and exposure time decrease the energy birds acquire.

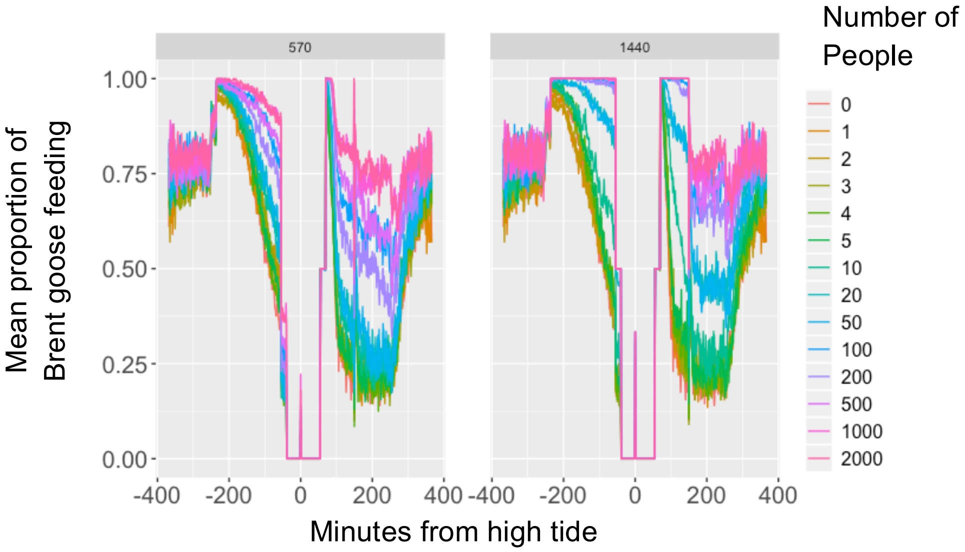


Figure 6.10 Depiction of how overall brent goose percentage feeding was affected by the number of humans within the environment, and whether humans were active 9hrs (570 minutes; left) or for the full 24hrs (1440 minutes; right).

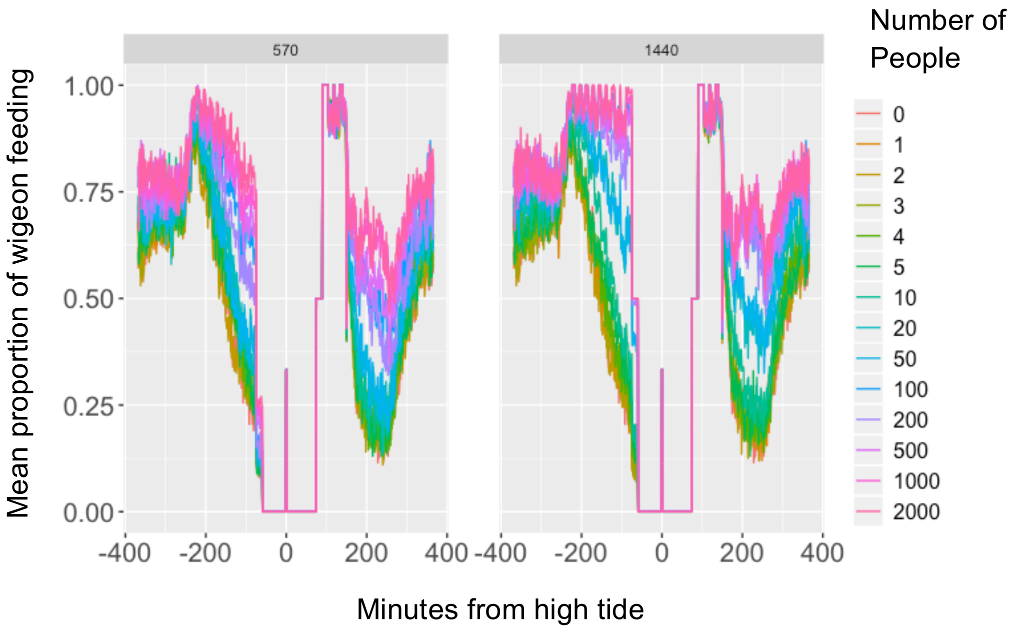


Figure 6.11 Depiction of how overall wigeon percentage feeding was affected by the number of humans within the environment, and whether humans were active 9hrs (570 minutes; left) or for the full 24hrs (1440 minutes; right).

In the IBM, if model birds had sustained energy deficits, they ‘died’, meaning they had reached their bird threshold and were removed from the system. Model brent goose reached their bird threshold when disturbance rates increased above seven disturbances per hour and wigeon reached their bird threshold when disturbances rates increased to over 12 disturbances per hour (Figure 6.12; Figure 6.13). This model bird threshold rate was less than COD bird threshold rate in Chapter 3. This reduction is due to model birds leaving the model if energy levels reach below 20% of their minimum rather than at 0%. Therefore, model birds reach their bird threshold at 80% of their maximum feed time instead of 100% like COD birds (Figure 6.14; Figure 6.15).

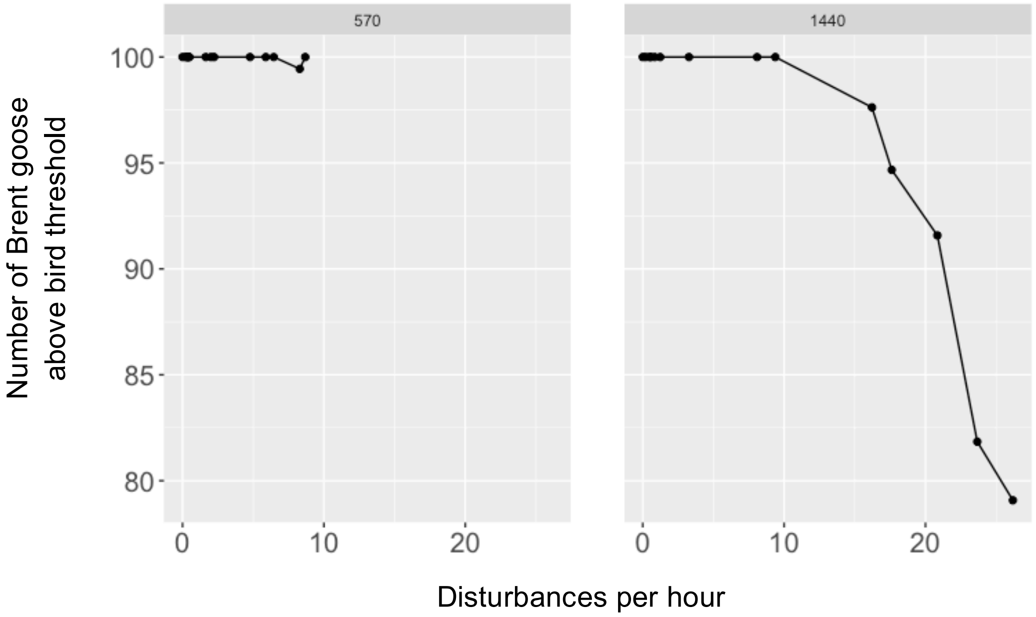


Figure 6.12 The number of Brent goose with energy levels above bird threshold rates relative to increasing number of humans and whether humans were active 9hrs (570 minutes; left) or for the full 24hrs (1440 minutes; right). Brent goose in the model reach their bird threshold at approximately 7 disturbances per hour.

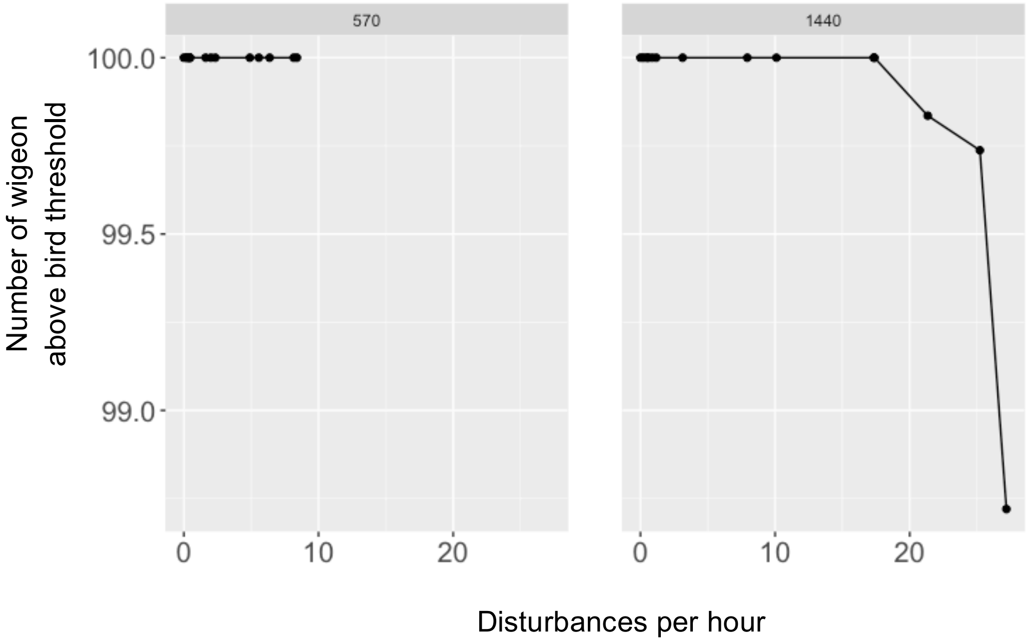


Figure 6.13 The number of wigeon with energy levels above bird threshold rates relative to increasing number of humans and whether humans were active 9hrs (570 minutes; left) or for the full 24hrs (1440 minutes; right). Wigeon in the IBM reach their bird threshold at approximately 12 disturbances per hour.

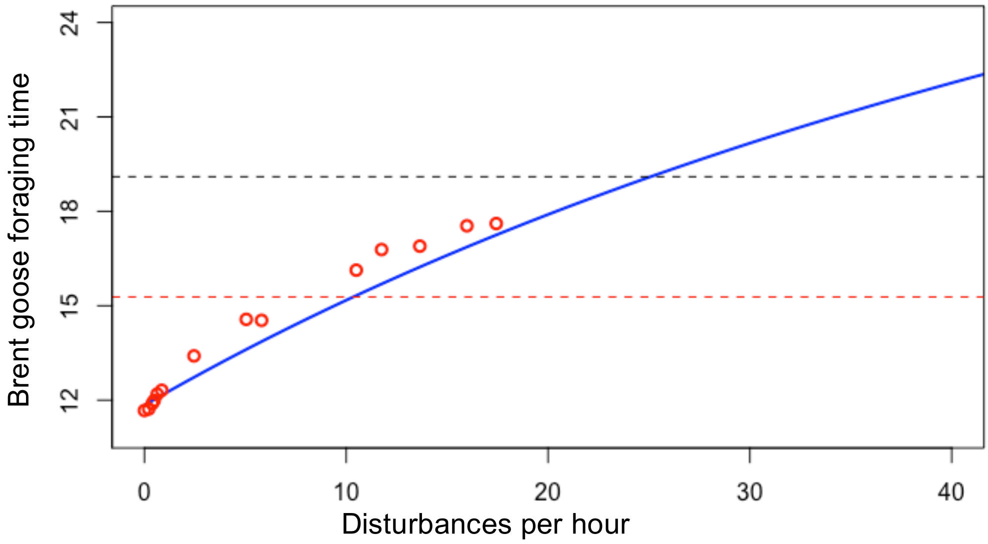


Figure 6.14 Feeding times of Brent goose relative to disturbance rates predicted by the individual-based model (red dots) and predicted by the cost of disturbance equation from Chapter 3 (blue line). The dotted line is when COD birds run out of feeding time to compensate for energy loss and reach their COD bird threshold (19.1hrs of feeding). The red dotted line represents when model birds in the IBM reach bird thresholds (20% of energy minimum and are removed from the model).

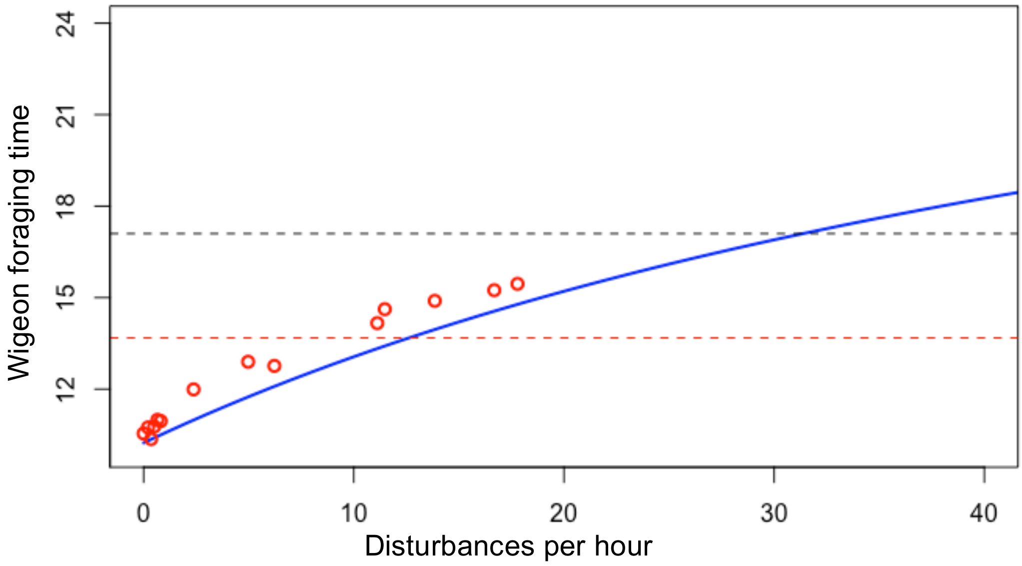


Figure 6.15 Feeding times of wigeon relative to disturbance rates predicted by the individual-based model (red dots) and predicted by the cost of disturbance equation from

Chapter 3 (blue line). The dotted line is when COD birds run out of feeding time to compensate for energy loss and reach their COD bird threshold (17.1hrs of feeding). The red dotted line represents when model birds in the IBM reach bird thresholds (20% of energy minimum and are removed from the model).

When equating disturbance rate to the number of humans on the estuary, to equal seven brent goose disturbances per hour, there had to be 1000 humans active for 9hrs of the day or 50 humans active for the entire day (Figure 6.16). For there to be 12 wigeon disturbances per hour, there needed to be over 2000 humans on the estuary for 9hrs or over 100 humans on the estuary for the entire 24 hours (Figure 6.17).

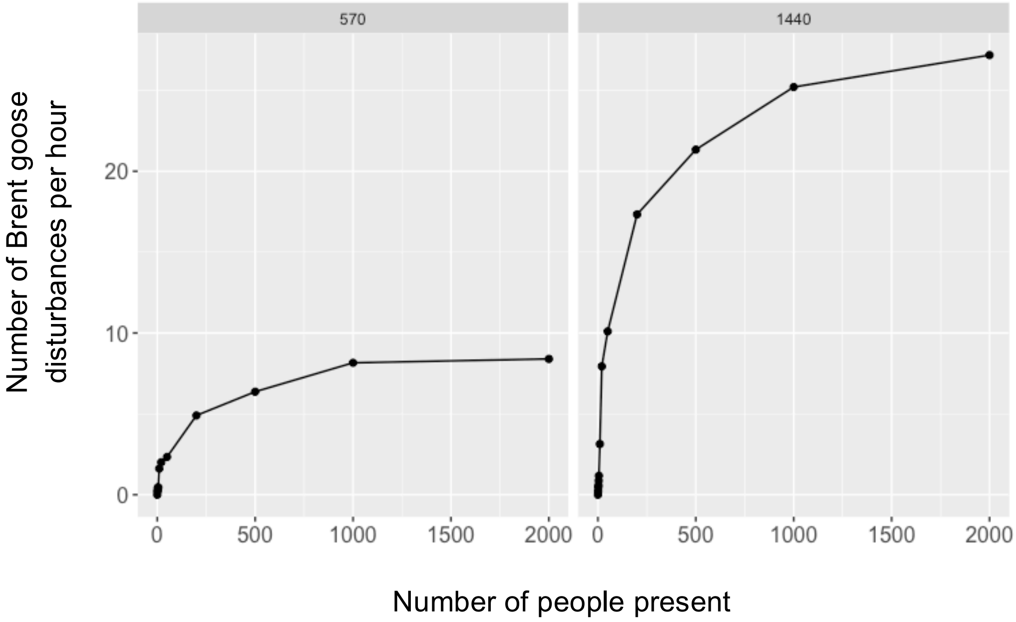


Figure 6.16 How the rate of disturbance experienced by Brent goose changed relative to the number of people present and whether people were active for 9hrs (570 minutes; left) or 24hrs (1440 minutes; right).

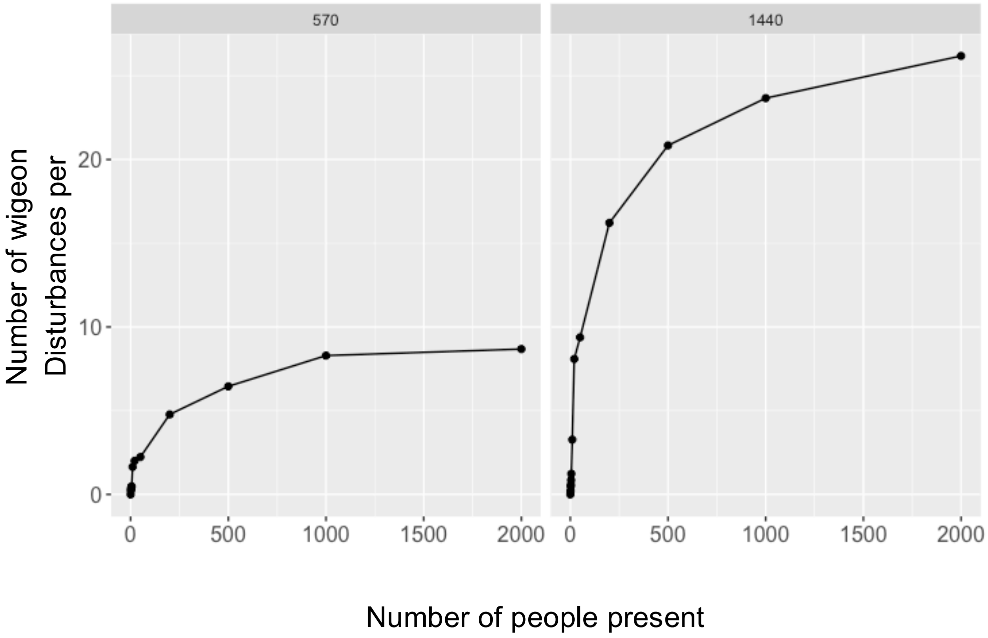


Figure 6.17 How the rate of disturbance experienced by wigeon changed relative to the number of people present and whether people were active for 9hrs (570 minutes; left) or 24hrs (1440 minutes; right).

6.5. DISCUSSION

6.5.1. MODEL VALIDATION

Model validation is an essential aspect of model development that is necessary to have confidence in the predictions associated with a model. There were no significant differences detected in the feeding behaviour of Brent goose and wigeon in the model compared to that of real birds on the Exe Estuary under similar disturbance rates. When the predicted feeding times of Brent goose and wigeon relative to disturbance rates were compared to those predicted by the COD equations in Chapter 3 and 4, outputs were also very similar. There were some differences detected in habitat use, with use of mud and mixed substrates being used significantly more by Brent goose in the model and sand used significantly less by Brent goose in the model, than observations. However, this is likely a result of imperfect substrate classification in observations compared to that of model outputs. This possibility is supported by the absence of these differences when observational sites that had broad substrate classifications are removed from the comparative analysis. Furthermore, some differences were detected in the patterns of feeding between model birds and real birds just after high tide. Model birds feed in more significant numbers just after high tide than real birds. This increase was attributed to simplification of the estuarine environment in the model, meaning that food became accessible more quickly in the model than it would on an actual estuary. Increased model bird feeding closer to high tide puts model birds at greater risk of disturbance while feeding than on the Exe Estuary. Therefore, costs associated with disturbance in the model will be higher than those observed, and resulting predictions from model outputs will be conservative. According to Grimm & Railsback (2013), it is not necessarily true that a model is or is not valid but rather how valid it is. Based on the similarities between the model bird behaviour and distribution compared to that of real birds on the Exe Estuary, this model was deemed agreeable for testing the scenario of the effects of increasing human disturbance on bird behaviour, habitat use, and survival.

6.5.2. MODEL EXPERIMENTS

6.5.2.1. BIRD BEHAVIOUR

There were significant changes detected in both Brent goose and wigeon behaviour relative to different degrees of human activity. These differences indicate that the human activity within the model was adequately mimicking human disturbance events by changing bird behaviour (Frid and Dill 2002). Furthermore, the nature of the differences in bird behaviour showed increases in feeding and decreases in resting activity with increasing degrees of human activity. Within the literature, it is well known that human disturbance is an energetically costly event (Steven et al. 2011; Houston et al. 2012; Pirotta et al. 2018). Additionally, evidence within the literature reviewed in Chapter 5 showed that wildfowl sacrifice resting time in favour of feeding time to make up for time and energy lost to disturbance related events. This evidence indicates that the model managed to capture the appropriate responses to increasing levels of human activity.

The point at which birds began to struggle to survive occurred when birds no longer had an adequate amount of time to feed to make up for the costs associated with disturbance. The rate disturbance at which this occurred was lower than that predicted by the Cost of Disturbance (COD) equation in Chapter 3. In Chapter 3 COD equation output, the threshold rate was 24 disturbances per hour for Brent goose and 33 disturbances per hour for wigeon. In contrast, in the IBM, the threshold rate for Brent goose was seven disturbances per hour and for wigeon was 12 disturbances per hour. This difference was because birds in the IBM died if they fell below 20% of their energy minimum rather than when they were at zero energy. This lower threshold was implemented in the IBM as a conservative approach.

The IBM also predicted higher proportions of disturbances while birds were feeding as disturbance events increased, compared to that predicted by the COD equation. The higher degree of disturbance while birds are feeding indicates that the individual-based model predictions are more representative of the real system than those of the COD equations. When birds are disturbed, they must feed more to regain the energy lost. Therefore, increases in disturbance logically lead to increased time birds are feeding. If birds are spending increased time feeding, that means the probability of them being disturbed while feeding also increases. The COD equations do not take this change into account because they assume constant disturbance while feeding and resting. Observational data on activities that occurred the most often on the Exe estuary support these results (walkers; See Chapter 4). Walkers were the most abundant activity on the estuary and also proportionally, disturbed birds more while they were feeding than while they were resting.

6.5.2.2. BIRD DISTRIBUTION

In addition to significant differences in bird behaviour relative to different numbers of humans and the duration of their presence, significant differences were also detected in bird distributions. As the number of humans in the model increased, model birds spent significantly less time on muddy and mixed substrates and significantly more time on sandy substrates. Furthermore, model birds increased the amount of time they spent on land and water and decreased the amount of time they spent on intertidal substrates.

Muddy and mixed substrates, as well as intertidal habitat in the model, represented regions with food availability. Therefore, increases in the number and duration of human activity increasingly restricted model birds from food resources. This meant that the costs associated with disturbance were not only energetic from reduced feeding and increased use of energy, but also in decreased access to food habitat. This is consistent with a study on pink-footed geese by Gill et al. (1996) that reported decreasing use of feeding ground with increasing human disturbance.

However, the increase in differences in both substrate and habitat use was most prominent at high tide period. This is due to human access to the estuary increasing with increasing tide. Model humans had greatest accessibility at high tide, because they were only able to reach certain sections of the estuary at high tide. This also meant, model birds were restricted most from regions of food availability when food was underwater and therefore birds were more likely to be resting than feeding. This result is consistent with findings in Chapter 4 where water activities disturbed birds more when resting than when feeding. If birds are disturbed off of suitable feeding habitat when they are resting, then the energetic consequences are less than if they were feeding.

6.5.2.3. BIRD THRESHOLDS

The amount of human activity required to meet bird threshold rates of disturbance varied depending on how long humans were active. Two scenarios were run that both had increasing numbers of humans: One, where humans were only active during the average daylight hours of winter, and another where humans were active continuously for 24 hours. The scenario in which humans were only active during daylight hours is consistent with the majority of outdoor recreational activities including such as walking, water-sports and birdwatching. However, because it is plausible that in some regions, humans could be active for a full 24hrs, this scenario was also simulated. In the situation where humans were only active for daylight hours, no Brent goose or wigeon died even when the human visitation rate was at 2000 visitors. However, there was a slight energy deficit in Brent goose after human counts reached 200.

On the other hand, when visitors were present for the entire 24 hours, it took a much smaller number of humans to reach the same disturbance rates. Just over 50 humans were required for Brent goose to be at an energy deficit and for there to be a decrease in survival. For wigeon energy deficits started when just 20 humans were present, but it took over 100 humans to decrease survival rates. This finding indicates that understanding the level of human activity throughout a full 24-hour cycle is necessary to know how much scope animals have to cope with disturbance.

6.5.3. MODEL ASSUMPTIONS

Several critical assumptions within the model could potentially affect the outputs of the model. One is that all human activity is considered equal within this model. Within the model, all humans are similarly restricted and move at the same rates and produced the same rates of response. This was implemented to increase simplicity and generalizability of the model. However, as it is evident in Chapter 4, not all human activity is equal and different degrees of different activity types could change how birds meet these threshold values. For instance, it would take the presence of fewer activities that have higher bird response rates to reach bird thresholds than those activities that have lower response rates. This become evident in the fact that model humans appeared to have a greater variability in habitat use compared to real humans. This means that the frequency in which humans interact with birds in the model may have different variability that what exists in real life. This is likely due to model humans being lumped into one human type rather than varied as they would be in reality. The grounds for this change in limit is evident in a study by Steven et al. (2011), where the ecological significance of human disturbance increased with the level of response and intensity of the activity. Response rates within the IBM in this chapter were based on average response rates to all different types of activities at the ratios they currently occur on the estuary. However, it is plausible that if activity increased on the estuary, it might not increase proportionally. Therefore, future refinement should include a range of different activity types to investigate how this might influence threshold rates of disturbance.

Furthermore, the bird response rate in the IBM is maintained regardless of how often a bird has been disturbed. Whittaker & Knight (1998) as well as Blumstein (2016) both highlighted that some species might react more strongly with each passing disturbance, while other species may respond less with increases in disturbance levels. Therefore, it is conceivable that individual Brent goose and wigeon may either increase their response or decrease it relative to exposure. Increases or decreases in response would then affect the point at which model birds meet threshold values.

6.5.4. WIDER APPLICATION

This model was designed and calibrated for both Brent goose and wigeon observed on the Exe Estuary. However, the nature of the model design means that it can be calibrated and designed for many different species and environments. This design is similar to that of the MORPH model that is capable of adapting to a variety of species and habitats (Stillman 2008). However, this model differs in the platform and the parameters used. The parameters that define the animals and their movements within this model are all variables that were readily available within the literature and are representative of widely applicable driving forces. For example, time and environmental variables constrain energy levels and proximities to human activities, which drive bird movements. These variables can all be modified and calibrated to the animal of interest. For Brent goose a primary environmental factor was tide times, however, for other animals such as nocturnally active animals, this might be time of day. For example, bats, *Chiroptera*, L., that feed nocturnally due to both predator avoidance and food resources availability (Erkert 2000) could be modelled by restricting food accessibility to night-time hours and introducing a predator presence during daytime hours. Furthermore, for animals where time budgets are easy to assess, validation measures of time budgets and distribution, if not already available in the literature, can be relatively non-invasive (Lehner 1987). In addition to this, the model environment can represent a variety of elevations, substrate types and vegetation cover, to mimic a suite of different geographical scenarios. Therefore, this model can be generalized and applied to a variety of animals and environments to investigate and predict human disturbance impacts.

6.6. CONCLUSION

Understanding the point at which any external influence begins to affect an animal population is an important question that is frequently posed by ecologists. This chapter applied this question to human disturbance on wildfowl on the Exe estuary by developing and validating a generalizable individual-based model. The model was developed based on general principles of fitness-maximising decision making, combined with observed responses to disturbance. In this model, increasing human activity was recorded to result in significant differences in bird behaviour as well as distribution. Bird behaviour indicated that birds spent more energy and fed more with increasing human activity. Bird distribution showed that with increasing human activity birds spent less time in suitable feeding habitat, but primarily during times when they would normally not be feeding anyway, which reduced the effects of redistribution. These findings highlight the importance of evaluating animal behaviour, in combination with spatial-temporal distributions for understanding the consequences of disturbance effects. Furthermore, evidence provided by the IBM indicates that current rates of disturbance that Brent goose and wigeon are experiencing on the Exe estuary pose no threat to their survival. Additionally, the IBM identified that it would require up to 23 times more disturbance for Brent goose and 67 times more disturbance for wigeon before there was a decrease in either brent goose or wigeon survival. The success in applying this model to Brent goose and wigeon provides credibility for its use to examine human disturbance on a variety of different species and environments in the future.

6.7. FUTURE WORK

There are several future avenues for the application of this model as well as improvements that could be made to this model's parameters. Firstly, energetic equilibrium was the driving force for bird movements in the model. However, in some situations, animals will be attempting to exceed balance. For example, both migration and reproduction are events where animals need to be above equilibrium beforehand.

Furthermore, when animals are in the process of migration, reproduction or experiencing extreme temperature events, energy levels will likely be at a deficit as animals will be using more energy than they are gaining. In these instances, energetic parameters would need to be changed to reflect this. For example, increasing energy minimums may need to be higher than starting energy values, or there may be increases in movement or energetic costs of resting. Along with this, animals in this model could include behaviour changes after exposure to disturbance. Such as sensitization and habituation, which would require individuals to record every disturbance they experienced. This could then be applied to the 'flee?' sub-model meaning flee responses change relative to individual bird exposure. Another avenue of improvement is through the modelling of humans in this model. This model considered all humans to be created equal. Therefore, differences associated with reactions to changing human activity types are not explicitly represented. For example, in a model developed by Bennett et al. (2009), different human activities were represented by two kinds of movement, linear and non-linear. Future work could also model humans with different accessibilities, speeds, a more extensive array of movement patterns, and FID distances. Lastly, this model calibrated intake rates relative to feeding proportion times, which works for implementation when both intake rate and total biomass of a site is unknown. However, in instances where intake rate and biomass is known, those parameters could be implemented to more closely reflect the environment birds are experiencing as they are in the MORPH model (Stillman 2008). Future work could then see how changes in that biomass would affect the way birds are capable of responding to the same rates of disturbance.

Additionally, if biomass distribution is known, then changes in that biomass distribution, such as development and sea-level rise, might also influence animal reactions to disturbance. Lastly, as this model was designed for herbivores, therefore, additional coding would be required to represent a predator with moving prey. This foraging pattern could be implemented in several ways, either another set of individuals represent prey in the environment or as a patch variable that changes with each time step to reflect varying densities of prey. These suggestions for improvement and future work, highlight the flexibility and applicability of this model for answering many questions regarding human disturbance, in the present and the future.

7. DISCUSSION

7.1. UNDERSTANDING HUMAN DISTURBANCE IMPACTS

Human disturbance is one potential mechanism leading to wildlife population declines and biodiversity loss. Loss of biodiversity can mean reduced productivity and value of regions to humans (Díaz et al. 2006; Duffy 2009; Cardinale et al. 2012). Therefore, identifying, understanding, and mitigating sources of human activity that result in biodiversity loss is directly beneficial to human life. However, more work is needed to understand how human disturbance effects lead to population-level impacts.

Estuaries provide a common ground for both human and wildlife to interact and are therefore a natural habitat for investigating the influence of human activity on wildlife. With this in mind, this study investigated the impacts of human activity on wildfowl on the Exe Estuary.

Using the insight from wildfowl on the Exe Estuary, this research examined the translation of human disturbance effects to population-level impacts. For human disturbance effects to occur, it requires a shared time and space between humans and animals (Chapter 2). When this shared time and space then results in a disturbance event, it will cost animals time and energy (Chapter 3). This time and energy loss can vary depending on the source of the disturbance (Chapter 4). If animals cannot compensate for the time and energy loss, they will die or reduce their reproductive output (Chapter 5 and 6). When animals die or reproduce less, then population-level impacts can result (Chapter 6; Figure 1.6).

7.2. KEY FINDINGS

7.2.1. OVERLAPS BETWEEN PEOPLE AND WILDLIFE IN SPACE AND TIME

Several environmental variables significantly explained wildfowl and human distributions in space and time. Environmental conditions associated with both, food availability for wildfowl, and accessibility for humans on the Exe Estuary, correspond significantly with spatiotemporal overlap events. This result is consistent with what other research has found when evaluating distributions of humans and wildlife separately (Wilson et al. 1996; Hoare 1999). Environmental conditions, therefore, have the potential to help predict scenarios that are more likely to lead to human disturbance before its occurrence.

7.2.2. THE RESPONSE OF WILDLIFE WHEN OVERLAP WITH HUMANS OCCURS

Costs of human disturbance are measured by an animal's combined loss of time and energy (Riddington et al. 1996; Houston et al. 2012). This cost depends on the degree of response and whether a brent goose or wigeon is feeding or resting. These results indicate that wildfowl that are disturbed more when feeding are affected more than those that are disturbed more when resting.

7.2.3. VARIATION IN DISTURBANCE RESPONSE TO DIFFERENT HUMAN ACTIVITY TYPES

Different human activities have distinctive characteristics, and therefore, animals respond differently to various activity sources (MacArthur et al. 1982; Cole 1991). This chapter revealed that disturbance from some human activities cost wildfowl more than other activities. The results show that those activities that are; most abundant; overlap the most with birds; disturb birds more while feeding; have a high overall rate of disturbance, are of greater concern for disturbance effects than other sources.

7.2.4. HOW ANIMALS CAN USE THE TIME TO COMPENSATE FOR HUMAN DISTURBANCE

Time budgets are proxies for an animal's energetic needs (Evans 1976; Norberg 1977; Lindstedt & Calder 1981; Kvist & Lindström 2000). A meta-analysis of the literature on multiple species of wildfowl and their time budgets provided evidence that wildfowl will sacrifice resting time in favour of increased feeding time. These findings mean that animals that have less rest time in their time budgets are less able to compensate for the energetic costs associated with human disturbance.

7.2.5. PREDICTING CONSEQUENCES OF DISTURBANCE ON WILDLIFE USING AN IBM

Consistent with the literature review, when evaluating wildfowl in both a mathematical and an individual-based model, the level at which wildfowl on the Exe Estuary were unable to compensate for human disturbance, was when they ran out of feeding time to make up for the disturbance cost. Wildfowl, in both the COD model (Chapters 3 and 4) and the IBM (Chapter 6), were capable of experiencing levels of disturbance much greater than those observed before being at risk of not being able to compensate. Consequently, Brent goose and wigeon on the Exe Estuary at the time of this study are at no risk of population-level impacts from human disturbance.

7.3. MANAGEMENT IMPLICATIONS

Because Brent goose and wigeon were the study species and the Exe Estuary was the study site, all research findings have direct relevance to the management of these species on this site. Results from this study indicate that neither Brent goose and wigeon populations on the Exe Estuary are under threat from human disturbance effects detected on the Exe Estuary. This finding was attributed to minimal spatial-temporal overlap, minimal disturbance costs within overlaps, and high compensation ability within brent goose and wigeon time budgets. Therefore, from a management perspective, this offers the ideal scenario; a space that is used in high numbers by both humans and wildfowl and yet there is little resulting human disturbance.

Although human disturbance is no threat wildfowl on the Exe Estuary, findings did suggest that some human activities have more significant effects on Brent goose and wigeon than other activities. The risk assessment index in Chapter 4 highlights these differences. Activities that ranked highest on the risk assessment index should be those that are most closely monitored for increases on the Exe estuary.

According to Ross et al. (2015 unpublished), the Exe Estuary is potentially the fourth most disturbed estuary in the UK. Therefore, finding that wildfowl disturbance on the Exe Estuary is minimal, bears a potentially positive outlook for wildfowl on estuaries that ranked lower than the Exe. However, it is important to recognize that humans and wildfowl may use these other estuaries differently than they use the Exe, which could produce different results.

Many of the variables measured in this study can be generalized for broader implications. For example, although specific sites and times on the Exe estuary had a high spatial-temporal overlap between birds and humans, the conditions leading to the overlap, were food availability and human accessibility. These two variables are not site-specific. Therefore, results from this research can advise management of human disturbance on a much wider scale as well.

One of the primary conditions that was integral for the ability of Brent goose and wigeon, in this study, to mitigate disturbance effects, was ‘spare-time’. If a brent goose or wigeon ran out of time to feed in both the COD model (Chapter 3 and 4) and the IBM (Chapter 6), the result was a sustained negative energy budget. The meta-analysis of the literature in Chapter 5 supported this. Therefore, the first step to identifying whether human disturbance may impact a species is to evaluate its time budget (Table 7.1). Animals that are already feeding at maximum capacity are those least able to compensate for disturbance costs with extra feeding.

Brent goose and wigeon in this study experienced very little disturbance because of several variables. There was minimal spatial-temporal overlap between the wildfowl and humans, and within that overlap, there was still minimal disturbance. Additionally, those activities that did disturb Brent goose and wigeon had equal disturbances of birds while feeding as resting, which means disturbance costs were relatively low. Therefore, in situations and regions were animals may already at the threshold for dealing with disturbance, it is recommended that effort is made to reduce overlap conditions, particularly in areas and times associated with food availability for the animal of interest. This reduction may be achieved in the form of restricting access of regions to humans both spatially and temporally. Further action may also be necessary to limit activities that are considered the costliest for the animal of interest-based on the risk assessment index in Chapter 4 (Table 4.4; Table 7.2).

Table 7.1 Management suggestions for assessing sites and species for risk of disturbance impacts

Site Assessment procedures		
Actions	**Details**	**Rationale**
Conditions for disturbance	Identify shared space and time between animals and humans	Figure 2.20 & Figure 2.21: Sites with high food availability and high human accessibility had the highest BOP index values
Disturbance cost	Calculate disturbance costs with the associated ability of animals to compensate and identify thresholds	Figure 3.3, Figure 3.5, Figure 3.8, and Figure 3.10: Changes to wildfowl energy levels, time budgets and distribution revealed disturbance costs
Disturbance risk	Determine activities that have the highest associated risk of disturbance cost	Table 4.4: activities with most considerable overlaps also had the highest disturbance rates

Site Assessment procedures		
Actions	**Details**	**Rationale**
Bird vulnerability	Measure time budgets to assess the ability to cope with disturbance effects	Figure 5.8: wildfowl already feeding at maximum levels have less time to spare for additional feeding to compensate for the disturbance
Threshold values	Determine if disturbance costs exceed bird compensation ability	Figure 6.8, Figure 6.9, Figure 6.10, and Figure 6.11: Wildfowl experienced sustained energy deficits when energy costs associated with disturbance exceeded feeding time to compensate

Table 7.2 Management suggestions for managing a site that has evidence of disturbance impacts (Table 7.1)

Site mitigation procedures		
Actions	**Details**	**Rationale**
Restrict access	Restrict access to sites at times that are associated with the animal presence and accessibility of food resources for animals	• Figure 2.12 & Figure 2.13: Wildfowl distribution and abundance was associated with variables that increased food availability • Figure 3.9 & Figure 3.11: When wildfowl were disturbed more often when feeding, it costs birds a more considerable amount of energy, and thresholds for disturbance were reached faster

Site mitigation procedures		
Actions	**Details**	**Rationale**
Regulate activities	Limit activity types that are most associated with high risk of disturbance costs	Table 4.4: Risk assessment indexes indicate that some activities are potentially more costly for wildfowl than other activities

7.4. RESEARCH LIMITATIONS AND FUTURE WORK

This research primarily focused on two wildfowl species in one location. Although findings are supported by research on other species and situations, the actual application of these methods to other animals and different circumstances is still theoretical. Therefore, a future investigation could benefit from applying similar methods as this research to other locations and species to further validate the broader applicability.

Furthermore, predictions within the models in this study relied on several assumptions that are worth investigating further. One of these assumptions was that reactions of wildfowl, over time, did not change relative to increasing levels of disturbance. Some species may become sensitized and increase their responses, and other species may decrease their reactions as a form of habituation or desperation (Whittaker & Knight 1998; Blumstein 2016). Due to time limitations, this research was unable to investigate whether Brent goose or wigeon exhibited these behaviours and therefore, how these variables may have affected wildfowl within the models. As a result, future work could investigate this component of wildfowl behaviour and how model predictions change with these variables. Another assumption within the COD model was that disturbance, associated with human activity, would continue to proportionally disturb wildfowl at the same rates when birds were feeding and resting as they were recorded. The IBM could investigate changes in feeding and resting disturbance rates by explicitly modelling human activity types and observing how disturbance these rates change with increasing numbers of activities. Lastly, threshold rates for individual disturbance calculated within the COD model were only applicable to each particular activity without the influence or presence of other activities. This shortcoming could also be an avenue of future exploration within the IBM, that could investigate threshold disturbance rates of different combinations of human activity types.

7.5. FINAL REMARKS

Human disturbance has the potential to result in population-level impacts. Therefore, any research contributions to understanding the mechanisms that lead to this are useful in helping to prevent biodiversity loss. This study was able to evaluate and identify several factors that can contribute population-level impacts on Brent goose and wigeon on the Exe Estuary. Results from this research will help in advising the management of wildfowl on the Exe Estuary as well as human disturbance events in a more general context. As with any research project, there are several possible avenues for future studies.

REFERENCES

AEWA, Agreement on the Conservation of African-Eurasian Migratory Waterbirds, 2016, *Definition of Disturbance*, Platz der Veneinten Nationen, Bonn, Germany

Allport, G., 1991. The feeding ecology and habitat requirements of overwintering Western Taiga Bean Geese (Anser fabalis fabalis).

Allen, M.C. and Read, A.J., 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. *Marine Mammal Science*, *16*(4), 815-824.

Amat, J. A. and Green, A. J., 2010. Waterbirds as bioindicators of environmental conditions. *Conservation Monitoring in Freshwater Habitats A Practical Guide and Case Studies*, 45–52.

Anderson, D.W. and Keith, J.O., 1980. The human influence on seabird nesting success: conservation implications. *Biological Conservation*, *18*(1), 65-80.

Ankney, C.D. and MacInnes, C.D., 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *The Auk*, 459-471.

Arzel, C., Elmberg, J. and Guillemain, M., 2006. Ecology of spring-migrating Anatidae: a review. *Journal of Ornithology*, *147*(2), 167-184

Aschoff, J. and Pohl, H., 1970. Der ruheumsatz von vögeln als funktion der tageszeit und der körpergrösse. *Journal für Ornithologie*, *111*(1), 38-47.

Ashe, J.B., 2012. Fall-winter habitat utilization of Eurasian Wigeon and American Wigeon with notes on migration and highly pathogenic avian influenza H5N1 virus.

Atkinson-Willes, G.L. and Frith, J.C., 1965. Trends in the population of British wintering ducks 1961-64. *Wildfowl*, *16*(16), 9.

Backman, T.W. and Barilotti, D.C., 1976. Irradiance reduction: effects on standing crops of the eelgrass Zostera marina in a coastal lagoon. *Marine Biology*, *34*(1), 33-40.

Barton, K. and Barton, M.K., 2015. Package ‘MuMIn’. *Version*, *1*, 18.

Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology*, *18*(6), 1482-1491.

Beale, C.M. and Monaghan, P., 2004. Human disturbance: people as predation-free predators?. *Journal of applied ecology*, *41*(2), 335-343.

Beale, C. M., 2007. The Behavioral Ecology of Disturbance Responses. *International Journal of Comparative Psychology*, 20 (20), 111–120.

Bednekoff, P.A. and Lima, S.L., 2002. Why are scanning patterns so variable? An overlooked question in the study of anti-predator vigilance. *Journal of Avian Biology*, *33*(2), 143-149.

Beeco, J.A. and Brown, G., 2013. Integrating space, spatial tools, and spatial analysis into the human dimensions of parks and outdoor recreation. *Applied Geography*, *38*, 76-85.

Bennett, V.J., Beard, M., Zollner, P.A., Fernandez-Juricic, E., Westphal, L. and LeBlanc, C.L., 2009. Understanding wildlife responses to human disturbance through simulation modelling: a management tool. *Ecological Complexity*, *6*(2), 113-134.

Bensizerara, D. and Chenchouni, H., 2019. Are diurnal time-budgets and activity patterns density-dependent in the Shelduck (Tadorna tadorna) wintering in Algeria? An analysis across multiple temporal scales. *Avian Research*, 10 (1), 1–15.

Bergan, J.F., Smith, L.M. and Mayer, J.J., 1989. Time-activity budgets of diving ducks wintering in South Carolina. The Journal of Wildlife Management, 769-776.

Bezzalla, A., Houhamdi, M., Cherif Maazi, M., and Chenchouni, H., 2019. Modelling climate influences on population dynamics and diurnal time budget of the Shelduck (Tadorna tadorna) wintering in Ramsar wetlands of Algeria. *Avian Biology Research*, 12 (3), 77–95.

Bishop, J. D., McKay, H. V., Parrott, D., and Allan, J., 2003. Review of international research literature regarding the effectiveness of auditory bird scaring techniques and potential alternatives. *Food and Rural Affairs*, (December), 1–52.

Black, J.M., Carbone, C., Wells, R.L. and Owen, M., 1992. Foraging dynamics in goose flocks: the cost of living on the edge._Animal Behaviour,_44(1), 41-50.

Blake, R.W., 1979. Exploitation of a natural population of Arenicola marina (L.) from the north-east coast of England. *Journal of Applied Ecology*, 663-670.

Blumstein, D.T., 2016. Habituation and sensitization: new thoughts about old ideas. *Animal Behaviour*, *120*, 255-262.

Bötsch, Y., Tablado, Z., and Jenni, L., 2017. Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B: Biological Sciences*, 284 (1858).

Bouchaala, L., Elafri, A., Charchar, N., Boukhemza, M. and Houhamdi, M., 2017. Wintering behaviour and spatial ecology of Eurasian Wigeon Anas penelope in a coastal Mediterranean wetland complex (Guerbes-Sanhadja) of northeastern Algeria. Avian Biology Research, 10(2), 84-91.

Boyle, S.A. and Samson, F.B., 1985. alien press. *Wildl. Soc. Bull*, *13*, 110-116.

Bregnballe, T., Speich, C., Horsten, A. and Fox, A.D., 2017. Differential flight responses of spring staging Teal Anas crecca and Wigeon A. penelope to human vs. natural disturbance. *Wildfowl*, *67*.

Brodsky, L.M. and Weatherhead, P.J., 1984. Behavioural thermoregulation in wintering black ducks: roosting and resting. *Canadian Journal of Zoology*, *62*(7), 1223-1226.

Broennimann, O., Fitzpatrick, M.C., Pearman, P.B., Petitpierre, B., Pellissier, L., Yoccoz, N.G., Thuiller, W., Fortin, M.J., Randin, C., Zimmermann, N.E. and Graham, C.H., 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. *Global ecology and biogeography*, *21*(4), 481-497.

Brunnschweiler, J. M. and Baensch, H., 2011. Seasonal and long-term changes in relative abundance of bull sharks from a tourist shark feeding site in Fiji. *PLoS ONE*, 6 (1).

Bryant, D.M. and Leng, J., 1975. Feeding distribution and behaviour of shelduck in relation to food supply. *Wildfowl*, *26*(26), 20-30.

Burger, J. and Gochfeld, M., 1991a. Human activity influence and diurnal and nocturnal foraging of sanderlings (Calidris alba). *The Condor*, *93*(2), 259-265.

Burger, J. and Gochfeld, M., 1991b. Human distance and birds: tolerance and response distances of resident and migrant species in India. *Environmental Conservation*, *18*(2), 158-165.

Burger, J. and Gochfeld, M., 1993. Tourism and short-term behavioural responses of nesting masked, red-footed, and blue-footed, boobies in the Galapagos. *Environmental Conservation*, *20*(3), 255-259

Burger, J. and Gochfeld, M., 1999. Role of human disturbance in response behavior of Laysan albatrosses (Diomedea immutabilis). *Bird Behavior*, *13*(1), 23-30.

Campbell, J.W., 1946. The food of the wigeon and brent goose. *British Birds*, *39*, 194-200.

Campbell, L.H., 1978. Diurnal and tidal behaviour patterns of eiders wintering at Leith. *Wildfowl*, *29*.

Campredon, P., 1981. Hivernage du Canard Siffleur Anas penelope L. en Camargue (France) stationnements et activités. .*Alauda 49*, 161–19

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A. and Kinzig, A.P., 2012. Biodiversity loss and its impact on humanity. *Nature*, *486*(7401), 59.

Carroll, G., Holsman, K.K., Brodie, S., Thorson, J.T., Hazen, E.L., Bograd, S.J., Haltuch, M.A., Kotwicki, S., Samhouri, J., Spencer, P. and Willis-Norton, E., 2019. A review of methods for quantifying spatial predator–prey overlap. *Global Ecology and Biogeography*, *28*(11), 1561-1577.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B. and Liu, J., 2012. Coexistence between wildlife and humans at fine spatial scales. *Proceedings of the National Academy of Sciences*, *109*(38), 15360-15365.

Castro, G. and Myers, J.P., 1988. A Statistical Method to Estimate the Cost of Flight in Birds (Un Método Estadístico para Estimar el Costo Energético del Vuelo en Aves). *Journal of Field Ornithology*, 369-380.

Castro, G., Myers, J.P. and Ricklefs, R.E., 1992. Ecology and energetics of sandlerlings migrating to four latitudes. *Ecology*, *73*(3), 833-844.

Charman, K., 1979. Feeding ecology and energetics of the dark-bellied brent goose (Branta bernicla bernicla) in Essex and Kent. *Ecological processes in coastal environments*, 451-465.

Chiba, S., 2010. Invasive non-native species' provision of refugia for endangered native species. *Conservation Biology*, *24*(4), 1141-1147.

Christiansen, F. and Lusseau, D., 2015. Linking behavior to vital rates to measure the effects of non-lethal disturbance on wildlife. *Conservation Letters*, *8*(6), 424-431

Christiansen, F., Rasmussen, M. and Lusseau, D., 2013. Whale watching disrupts feeding activities of minke whales on a feeding ground. *Marine Ecology Progress Series*, *478*, 239-251.

Clark, H.B. and Whiting Jr, R.M., 1994. Time budgets of Mallards and Wood Ducks wintering in a flooded bottomland hardwood forest. *In Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies, 48*, 22-30.

Clausen, K.K., Clausen, P., Fælled, C.C. and Mouritsen, K.N., 2012. Energetic consequences of a major change in habitat use: endangered Brent Geese Branta bernicla hrota losing their main food resource. *Ibis*, *154*(4), 803-814.

Clausen, K.K., Clausen, P., Fox, A.D., Fælled, C.C. and Madsen, J., 2013. Varying energetic costs of Brent Geese along a continuum from aquatic to agricultural habitats: the importance of habitat-specific energy expenditure. *Journal of Ornithology*, *154*(1), 155-162.

Clausen, K.K., Dalby, L., Sunde, P., Christensen, T.K., Egelund, B. and Fox, A.D., 2013. Seasonal variation in Eurasian wigeon Anas penelope sex and age ratios from hunter-based surveys. *Journal of ornithology*, *154*(3), 769-774.

Clausen, P., 2000. Modelling water level influence on habitat choice and food availability for Zostera feeding Brent Geese Branta bernicla in non-tidal areas. *Wildlife Biology*, *6*(4), 75-87.

Cole, D.N., 1991. Effects of recreational activity on wildlife in wildlands. In *Transactions of the North American Wildlife and Natural Resources Conference, 56,* 238-247.

Collop, C. H., 2016. Impact of human disturbance on coastal birds: Population consequences derived from behavioural responses, (July), 322.

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

Corcoran, M. J., Wetherbee, B. M., Shivji, M. S., Potenski, M. D., Chapman, D. D., and Harvey, G. M., 2013. Supplemental Feeding for Ecotourism Reverses Diel Activity and Alters Movement Patterns and Spatial Distribution of the Southern Stingray, Dasyatis americana. *PLoS ONE*, 8 (3).

Crichton, D., 1999. The risk triangle. *Natural disaster management*, *102*, 103.

Crichton, D., 2008. Role of insurance in reducing flood risk. *The Geneva Papers on Risk and Insurance-Issues and Practice*, *33*(1), 117-132.

Culik, B., Adelung, D. and Woakes, A.J., 1990. The effect of disturbance on the heart rate and behaviour of Adélie penguins (Pygoscelis adeliae) during the breeding season. In *Antarctic ecosystems,* Springer, Berlin, Heidelberg, 177-182.

Daan, S., Masman, D., and Groenewold, A., 1990. Avian basal metabolic rates: Their association with body composition and energy expenditure in nature. *American Journal of Physiology - Regulatory Integrative and Comparative Physiology*, 259 (2 28-2), 333–340.

Davidson, N.C. and Rothwell, P.I., 1993. Human disturbance to waterfowl on estuaries: conservation and coastal management implications of current knowledge. *Wader Study Group Bulletin*, *68*, 97-105.

Davies, J.C. and Cooke, F., 1983. Annual nesting productivity in snow geese: prairie droughts and arctic springs. *The Journal of Wildlife Management*, 291-296.

Davis, B.E. and Afton, A.D., 2010. Movement distances and habitat switching by female mallards wintering in the lower Mississippi alluvial valley. *Waterbirds*, *33*(3), 349-357.

de Freitas, C.R., 2003. Tourism climatology: evaluating environmental information for decision making and business planning in the recreation and tourism sector. *international Journal of Biometeorology*, *48*(1), 45-54.

del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (2020). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona.

De Roos, A.M., 2008. Demographic analysis of continuous-time life-history models. *Ecology Letters*, *11*(1), 1-15.

DeAngelis, D. L. and Grimm, V., 2014. Individual-based models in ecology after four decades. *F1000Prime Reports*, 6 (June).

DeAngelis, D.L., 2018. Individual-based models and approaches in ecology: populations, communities and ecosystems. CRC Press.

DesGranges, J.L. and Reed, A., 1981. Disturbance and control of selected colonies of Double-crested Cormorants in Quebec. *Colonial Waterbirds*, 12-19.

Di Blanco, Y. and Hirsch, B.T., 2006. Determinants of vigilance behavior in the ring-tailed coati (Nasua nasua): the importance of within-group spatial position. *Behavioral Ecology and Sociobiology*, *61*(2), 173-182.

Díaz, S., Fargione, J., Chapin, F. S., and Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biology*, 4 (8), 1300–1305.

Drent, R. and Klaassen, M., 1989. Energetics of avian growth: the causal link with BMR and metabolic scope. In *Physiology of cold adaptation in birds*. Springer, Boston, MA, 349-359.

Duffy, J.E., 2009. Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, *7*(8), 437-444.

Dunbar, R.I., Korstjens, A.H., Lehmann, J. and British Academy Centenary Research Project, 2009. Time as an ecological constraint. *Biological Reviews*, *84*(3), 413-429.

Ebbinge, B., Canters, K. and Drent, R., 1975. Foraging routines and estimated daily food intake in Barnacle Geese wintering in the northern Netherlands. Wildfowl, 26(26), 5-19.

Ebbinge, B.S., 1992. Regulation of numbers of dark-bellied brent geese. *Ardea*, *80*, 203-228.

Encyclopedia of Life. Available from http://eol.org. Accessed 15 July 2018

Environment Agency. 2017. Exe Estuary, *50°36'53"N 3°25'30".* Zoster Extent Map. Viewed 5 August 2018, http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/

Erkert, H.G., 2000. Bats—flying nocturnal mammals. In Activity patterns in small mammals, Springer, Berlin, Heidelberg, 253-272.

Erwin, R.M., 1989. Responses to human intruders by birds nesting in colonies: experimental results and management guidelines. *Colonial Waterbirds*, 104-108.

Evans, J., Boudreau, K. and Hyman, J., 2010. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology*, *116*(7), 588-595.

Evans, M.R., 2012. Modelling ecological systems in a changing world. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1586), 181-190.

Evans, P.R. and Pienkowski, M.W., 1982. Behaviour of shelducks Tadorna tadorna in a winter flock: does regulation occur?. The Journal of Animal Ecology, 241-262.

Evans, P.R., 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea*, *55*(1–2), 117-140.

Ferrari, S. and Cribari-Neto, F., 2004. Beta regression for modelling rates and proportions. Journal of applied statistics, 31(7), 799-815.

Ferrari, M.C., Sih, A. and Chivers, D.P., 2009. The paradox of risk allocation: a review and prospectus. *Animal Behaviour*, *78*(3), 579-585.

Fog, M., 1967. investigation on the Brent Goose (Branta bernicla) in Denmark. *Danish Rev. Game Biol., 5(1),* 1-40.

Fox, A.D., 1996. Zostera exploitation by Brent geese and wigeon on the Exe estuary, southern England. *Bird Study*, *43*(3), 257-268.

Fox, A.D., Clausen, K.K., Dalby, L., Christensen, T.K. and Sunde, P., 2016. Between-year variations in sex/age ratio bias in hunter wings of Eurasian Wigeon (Anas penelope) compared to field samples. Ornis Fennica, 93(1), 26.

Fraser, W.R. and Patterson, D.L., 1997. Human disturbance and long-term changes in Adélie penguin populations: a natural experiment at Palmer Station, Antarctic Peninsula. *Antarctic Communities: Species, Structure and Survival.*, 445-446.

Frederick, R.B. and Klaas, E.E., 1982. Resource use and behaviour of migrating snow geese. *The Journal of Wildlife Management*, 601-614.

Frid, A. and Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1).

Frost, T. M., Austin, G. E., Calbrade, N. A., Mellan, H. J., Hearn, R. D., Robinson, A. E., Stroud, D. A., Wotton, S. R., and Balmer, D. E., 2019. *Waterbirds in the UK 2017/18: The Wetland Bird Survey. BTO, RSPB and JNCC, in association with WWT*.

Ganter, B., 2000. Seagrass (Zostera s) as food for brent geese (Branta bernicla): an overview. *Helgoland Marine Research*, *54*(2), 63.

Gavrilov, V., & Handling Editor Daniel Dykhuizen., 2014. Ecological and Scaling Analysis of the Energy Expenditure of Rest, Activity, Flight, and Evaporative Water Loss in Passeriformes and Non-Passeriformes in Relation to Seasonal Migrations and to the Occupation of Boreal Stations in High and Moderate Latitudes. *The Quarterly Review of Biology, 89*(2), 107-150.

Geffroy, B., Samia, D.S., Bessa, E. and Blumstein, D.T., 2015. How nature-based tourism might increase prey vulnerability to predators. *Trends in Ecology & Evolution*, *30*(12), 755-765.

Gentsch, R.P., Kjellander, P. and Röken, B.O., 2018. Cortisol response of wild ungulates to trauma situations: hunting is not necessarily the worst stressor. *European journal of wildlife research*, *64*(1), 11.

Giese, M., 1996. Effects of human activity on Adelie penguin Pygoscelis adeliae breeding success. *Biological Conservation*, *75*(2), 157-164.

Gill, J.A., 1996. Habitat choice in pink-footed geese: quantifying the constraints determining winter site use. *Journal of Applied Ecology*, 884-892.

Gill, J.A., 2007. Approaches to measuring the effects of human disturbance on birds. *Ibis*, *149*, 9-14.

Gill, J.A., Norris, K. and Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, *97*(2), 265-268.

Gill, J.A., Sutherland, W.J. and Watkinson, A.R., 1996. A method to quantify the effects of human disturbance on animal populations. *Journal of applied Ecology*, 786-792.

Goss-Custard, J.D., Triplet, P., Sueur, F. and West, A.D., 2006. Critical thresholds of disturbance by people and raptors in foraging wading birds. *Biological Conservation*, *127*(1), 88-97.

Goudie, A.S. and Viles, H.A., 2013. The earth transformed: an introduction to human impacts on the environment. John Wiley & Sons.

Goudie, R.I. and Ankney, C.D., 1986. Body size, activity budgets, and diets of sea ducks wintering in Newfoundland. Ecology, 67(6), 1475-1482.

Grant, S. and Berkes, F., 2007. Fisher knowledge as expert system: A case from the longline fishery of Grenada, the Eastern Caribbean. *Fisheries Research*, *84*(2), 162-170.

Green, A.J., Fox, A.D., Hughes, B.A.R.R.Y. and Hilton, G.M., 1999. Time_activity budgets and site selection of White-headed Ducks Oxyura leucocephala at Burdur Lake, Turkey in late winter._Bird Study,_46(1), 62-73.

Green, M. and Alerstam, T., 2000. Flight speeds and climb rates of Brent Geese: mass-dependent differences between spring and autumn migration. *Journal of Avian Biology*, *31*(2), 215-225.

Gregory, R.D. and van Strien, A., 2010. Wild bird indicators: using composite population trends of birds as measures of environmental health. *Ornithological Science*, *9*(1), 3-22.

Grimm V, Railsback SF. 2005. Individual-Based Modeling and Ecology. Princeton University Press.

Grimm, V. and Railsback, S. F., 2006. Agent-Based Models in Ecology: Patterns and Alternative Theories of Adaptive Behaviour. *Agent-Based Computational Modelling*, 139–152.

Grimm, V. and Railsback, S.F., 2013. Individual-based Modeling and Ecology. Princeton university press.

Gudmundsson, G.A., Benvenuti, S., Alerstam, T., Papi, F., Lilliendahl, K. and Åkesson, S., 1995. Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *261*(1360), 73-79.

Guillemette, M., 1998. The effect of time and digestion constraints in common eiders while feeding and diving over blue mussel beds. Functional Ecology, 12(1), 123-131.

Guillemette, M., Ydenberg, R.C. and Himmelman, J.H., 1992. The role of energy intake rate in prey and habitat selection of common eiders Somateria mollissima in winter: a risk-sensitive interpretation. Journal of Animal Ecology, 599-610.

Hagy, H.M., Straub, J.N., Schummer, M.L. and Kaminski, R.M., 2014. Annual variation in food densities and factors affecting wetland use by waterfowl in the Mississippi Alluvial Valley. Wildfowl, 436-450.

Hammond, K.A. and Diamond, J., 1997. Maximal sustained energy budgets in humans and animals. *Nature*, *386*(6624), 457.

Hansen, J.W., Udy, J.W., Perry, C.J., Dennison, W.C. and Lomstein, B.A., 2000. Effect of the seagrass Zostera capricorni on sediment microbial processes. *Marine Ecology Progress Series*, *199*, 83-96.

Heise, J.R., Williams, C.K. and Castelli, P.M., 2019. Factors Influencing a 24-Hour Time-Budget for Wintering Atlantic Brant. Journal of Fish and Wildlife Management, 10(1), 79-90.

Hels, T. and Buchwald, E., 2001. The effect of road kills on amphibian populations. *Biological conservation*, *99*(3), 331-340.

Hemmingsen, A.M., 1950. The relation of standard (basal) energy metabolism to total fresh weight of living organisms. *Rep. Steno Mem. Hosp.*, *4*, 7-58.

Henny, C.E.J., Blus, L.J. and Tomson, S.P., 1989. Environmental Contaminants, Hurnan Disturbance cand Nesting of Double-crested Cormorants in Northwestern Washington. *Colonial Waterbirds*, *12*(2), 198-206.

Hepp, G.R., 1982. Behavioral ecology of waterfowl (Anatini) wintering in coastal North Carolina. Doctoral dissertation, North Carolina State University, North Carolina.

Hill, G.J.E. and Barnes, A., 1989. Census and distribution of Wedge-tailed Shearwater Puffinus pacificus burrows on Heron Island, November 1985. *Emu*, *89*(3), 135-139.

Hoare, R.E., 1999. Determinants of human–elephant conflict in a land-use mosaic. *Journal of applied ecology*, *36*(5), 689-700.

Hohman, W. and Rave, D., 1990. Diurnal time-activity budgets of wintering canvasbacks in Louisiana. *The Wilson bulletin (Wilson Ornithological Society)*, 102 (4), 645–654.

Holm, T.E., 2002. Habitat use and activity patterns of Mute Swans at a molting and a wintering site in Denmark. Waterbirds, 183-191.

Houhamdi, M. and Samraoui, B., 2013. Diurnal behaviour of wintering Wigeon Anas penelope at Lac des Oiseaux, northeast Algeria. *Wildfowl*, *54*(54), 51-62.

Houston, A.I., Prosser, E. and Sans, E., 2012. The cost of disturbance: a waste of time and energy?. *Oikos*, *121*(4), 597-604.

Hughes, K.A., Waluda, C.M., Stone, R.E., Ridout, M.S. and Shears, J.R., 2008. Short-term responses of king penguins Aptenodytes patagonicus to helicopter disturbance at South Georgia. *Polar biology*, *31*(12), 1521-1530.

Huveneers, C., Rogers, P.J., Beckmann, C., Semmens, J.M., Bruce, B.D. and Seuront, L., 2013. The effects of cage-diving activities on the fine-scale swimming behaviour and space use of white sharks. *Marine Biology*, *160*(11), 2863-2875.

Ihwagi, F.W., Thouless, C., Wang, T., Skidmore, A.K., Omondi, P. and Douglas-Hamilton, I., 2018. Night-day speed ratio of elephants as indicator of poaching levels. Ecological indicators, 84, 38-44.

JNCC, Joint Nature Conservation Committee, 2011. *The deliberate disturbance of a European species*. Monkstone House, City Road, Peterborough.

Jonsson, J.E. and Afton, A.D., 2009. Time budgets of Snow Geese Chen caerulescens and Ross's Geese Chen rossii in mixed flocks: Implications of body size, ambient temperature and family associations._Ibis,_151(1), 134-144.

Jorde, D. G., 1981. Winter and spring staging ecology of mallards in south central Nebraska, (Masters dissertation, University of North Dakota). 116.

Kam, M. and Degen, A.A., 1997. Energy requirements and the efficiency of utilization of metabolizable energy in free-living animals: evaluation of existing theories and generation of a new model. *Journal of Theoretical Biology*, *184*(2), 101-104.

Kastelein, R.A., Jennings, N., Verboom, W.C., De Haan, D. and Schooneman, N.M., 2006. Differences in the response of a striped dolphin (Stenella coeruleoalba) and a harbour porpoise (Phocoena phocoena) to an acoustic alarm. *Marine Environmental Research*, *61*(3), 363-378.

Karasov, W.H., 1996. Digestive plasticity in avian energetics and feeding ecology. In *Avian energetics and nutritional ecology,* Springer, Boston, MA, 61-84.

Keane, E.M. and O'Halloran, J., 1992. The behaviour of a wintering flock of Mute Swans Cygnus olor in southern Ireland. Wildfowl, 43(43), 12-19.

Kear, J 2005 Bird Families of the World: Ducks, Geese and Swans.-Oxford University Press, Oxford: 1-930

Keim, J.L., DeWitt, P.D., Fitzpatrick, J.J. and Jenni, N.S., 2017. Estimating plant abundance using inflated beta distributions: Applied learnings from a lichen–caribou ecosystem. *Ecology and evolution*, *7*(2), 486-493.

Kendeigh, S.C., 1970. Energy requirements for existence in relation to size of bird. *The Condor*, *72*(1), 60-65.

Kendeigh, S.C., Dol'Nik, V.R. and Gavrilov, V.M., 1977. Avian energetics. Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impacts and control, 127-203.

Kennish, Michael J., 2002. Environmental threats and environmental future of estuaries. *Environmental conservation* 29(1), 78-107.

Kerley, L.L., Goodrich, J.M., Miquelle, D.G., Smirnov, E.N., Quigley, H.B. and Hornocker, M.G., 2002. Effects of roads and human disturbance on Amur tigers. *Conservation Biology*, *16*(1), 97-108.

Kersten, M. and Piersma, T., 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea*, *75*(2), 175-187.

Kirkwood, J.K., 1983. A limit to metabolisable energy intake in mammals and birds. *Comparative Biochemistry and Physiology Part A: Physiology*, *75*(1), 1-3.

Klaassen, M., 1996. Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology*, *199*(1), 57-64.

Knight, R.L. and Cole, D.N., 1995. Wildlife Responses to. Wildlife and recreationists: Coexistence through management and research, 51.

Korschgen, C.E. and Dahlgren, R.B., 1992. 13.2. 15. Human Disturbances of Waterfowl: Causes, Effects, and Management. *Waterfowl management handbook*, 12.

Krüger, O., 2005. The role of ecotourism in conservation: panacea or Pandora's box?. Biodiversity & Conservation, 14(3), 579-600.

Kushlan, J.A., 1981. Resource use strategies of wading birds. *The Wilson Bulletin*, 145-163.

Kushlan, J.A., 1993. Colonial waterbirds as bioindicators of environmental change. *Colonial waterbirds*, 223-251.

Kvist, A. and Lindström, Å., 2000. Maximum daily energy intake: it takes time to lift the metabolic ceiling. *Physiological and Biochemical Zoology*, *73*(1), 30-36.

Ladin, Z.S., Castelli, P.M., Mcwilliams, S.R. and Williams, C.K., 2011. Time energy budgets and food use of Atlantic brant across their wintering range. The Journal of Wildlife Management, 75(2), 273-282.

Lasiewski, R.C. and Dawson, W.R., 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *The Condor*, *69*(1), 13-23.

Laursen, K., Kahlert, J. and Frikke, J., 2005. Factors affecting escape distances of staging waterbirds. *Wildlife Biology*, *11*(1), 13-20.

Lebret, T., 1970. Nocturnal feeding and other activities of the Greylag Goose (Anser anser) in fresh water tidal habitat in the Netherlands._Limosa, *43(1-2),* 11-30.

Lehikoinen, A. and Jaatinen, K., 2012. Delayed autumn migration in northern European waterfowl. *Journal of Ornithology*, *153*(2), 563-570.

Lehner, P.N., 1987. Design and execution of animal behavior research: an overview. *Journal of Animal Science*, *65*(5), 1213-1219.

Li, Z. and Rogers, E., 2004. Habitat quality and activity budgets of white-headed langurs in Fusui, China. *International Journal of Primatology*, *25*(1), 41-54.

Liley, D. and Sutherland, W.J., 2007. Predicting the population consequences of human disturbance for Ringed Plovers Charadrius hiaticula: a game theory approach. *Ibis*, *149*, 82-94.

Liley, D., Cruickshanks, K., Waldon, J., and Fearnley, H., 2011. Exe Disturbance Study. *Footprint Ecology, 1*, 98.

Lima, S.L. and Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian journal of zoology, 68(4), 619-640.

Lima, S.L., 1998. Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behaviour*, *27*(8), 215-290.

Lindstedt, S.L. and Calder III, W.A., 1981. Body size, physiological time, and longevity of homeothermic animals. *The Quarterly Review of Biology*, *56*(1), 1-16.

Lindström, Å. and Kvist, A., 1995. Maximum energy intake rate is proportional to basal metabolic rate in passerine birds. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *261*(1362), 337-343.

Lindström, Å., 1991. Maximum fat deposition rates in migrating birds. *Ornis Scandinavica*, 12-19.

MacArthur, R.A., Geist, V. and Johnston, R.H., 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. *Journal of Wildlife management*, *46*(2), 351-358.

Madsen, J. and Fox, A.D., 1995. Impacts of hunting disturbance on waterbirds-a review. *Wildlife biology*, *1*(1), 193-208.

Madsen, J., 1988. Autumn feeding ecology of herbivorous wildfowl in the Danish Wadden Sea, and impact of food supplies and shooting on movements. *Dan. Rev. Game Biol. 13,* 1-32.

Madsen, J., 1995. Impacts of disturbance on migratory waterfowl. *Ibis*, 137, S67–S74.

Madsen, J., 1998a. Experimental refuges for migratory waterfowl in Danish wetlands. I. Baseline assessment of the disturbance effects of recreational activities. *Journal of Applied Ecology*, *35*(3), 386-397.

Madsen, J., 1998b. Experimental refuges for migratory waterfowl in Danish wetlands. II. Tests of hunting disturbance effects. *Journal of Applied Ecology*, *35*(3), 398-417.

Maljković, A. and Côté, I.M., 2011. Effects of tourism-related provisioning on the trophic signatures and movement patterns of an apex predator, the Caribbean reef shark. *Biological Conservation*, *144*(2), 859-865.

Mallory, M.L., Gilchrist, H.G., Braune, B.M. and Gaston, A.J., 2006. Marine birds as indicators of Arctic marine ecosystem health: linking the Northern Ecosystem Initiative to long-term studies. *Environmental Monitoring and Assessment*, *113*(1-3), 31-48.

Map data, Google Maps. 2018. Exe Estuary, *50°36'53"N 3°25'30".* Overview Map. Viewed 5 August 2018, <https://goo.gl/maps/C7Po6ZsZbzi6RHDR9>.

Márquez-Farias, J.F. and Castillo-Geniz, J.L., 1998. Fishery biology and demography of the Atlantic sharpnose shark, Rhizoprionodon terraenovae, in the southern Gulf of Mexico. *Fisheries Research*, *39*(2), 183-198.

Marsden, S.J., 2000. Impact of disturbance on waterfowl wintering in a UK dockland redevelopment area. *Environmental management*, *26*(2), 207-213.

Marsh, G.P., 1867. *Man and Nature: Or, Physical Geography as Modified by Human Action (1864)*. Kessinger Publishing.

Martin, J., Basille, M., Van Moorter, B., Kindberg, J., Allaine, D. and Swenson, J.E., 2010. Coping with human disturbance: spatial and temporal tactics of the brown bear (Ursus arctos). *Canadian Journal of Zoology*, *88*(9), 875-883.

Martin, P., Bateson, P.P.G. and Bateson, P., 1993. Measuring behaviour: an introductory guide. Cambridge University Press.

Marzluff, J. and Rodewald, A., 2008. Conserving biodiversity in urbanizing areas: nontraditional views from a bird's perspective. *Cities and the Environment (CATE)*, *1*(2), 6.

Mason, C.D., Whiting, R.M. and Conway, W.C., 2013. Time-activity budgets of waterfowl wintering on livestock ponds in Northeast Texas. Southeastern naturalist, 12(4), 757-769.

Mathers, A. R. G., Montgomery, W. I., Biology, S., Proceedings, E., Irish, R., and Brent, P., 2014. Quality of Food Consumed by over Wintering Pale-Bellied Brent Geese

Branta bernicla hrota and Wigeon Anas penelope. In *Biology and Environment: Proceedings of the Royal Irish Academy*, 97 (1), 81–89.

Maurer, B.A., 1996. Energetics of avian foraging. In *Avian energetics and nutritional ecology,* Springer, Boston, MA, 250-279.

Mayhew, P.W. and Houston, D.C., 1993. Food throughput time in European wigeon Anas penelope and other grazing waterfowl. *Wildfowl*, *44*(44), 174-177.

Mayhew, P.W., 1985. *The feeding ecology and behavior of wigeon (Anas penelope)* (Doctoral dissertation, University of Glasgow). 241.

Mayhew, P.W., 1988. The daily energy intake of European Wigeon in winter. *Ornis Scandinavica*, 217-223.

McDonough, C., Jaffe D., Watzin, M., McGinley, M., 2012. "Indicator species". In: Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment).

McGarigal, K., Anthony, R.G. and Isaacs, F.B., 1991. Interactions of humans and bald eagles on the Columbia River estuary. *Wildlife Monographs*, 3-47.

McKechnie, A.E., Freckleton, R.P. and Jetz, W., 2006. Phenotypic plasticity in the scaling of avian basal metabolic rate. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1589), 931-937.

McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. *Urban ecosystems*, *11*(2), 161-176.

McNamara, J.M. and Houston, A.I., 1986. The common currency for behavioral decisions. *The American Naturalist*, *127*(3), 358-378.

McNamara, J.M. and Houston, A.I., 1987. Starvation and predation as factors limiting population size. *Ecology*, *68*(5), 1515-1519.

McWilliams, S.R., Guglielmo, C., Pierce, B. and Klaassen, M., 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. *Journal of Avian Biology*, *35*(5), 377-393.

Met Office. (2019). *Global circulation patters – Met Office.* [online] Available at: https:// https://www.metoffice.gov.uk/weather/learn-about/weather/atmosphere/global-circulation-patterns [Accessed 7 Apr. 2019].

Meziane, N., Samraoui, F. and Samraoui, B., 2014. Status and diurnal activity budget of non-breeding White-headed Ducks Oxyura leucocephala in Algeria._Ostrich,_85(2), 177-184.

Miller, M.R., 1985. Time budgets of northern pintails wintering in the Sacramento Valley, California. Wildfowl, 36(36), 53-64.

Møller, A.P., Fiedler, W. and Berthold, P. eds., 2010. Effects of climate change on birds. OUP Oxford.

Mooij, J.H., 1992. Behaviour and energy budget of wintering geese in the Lower Rhine area of North Rhine-Westphalia, Germany._Wildfowl,_43(43), 121-138.

Moore, K.A. and Wetzel, R.L., 2000. Seasonal variations in eelgrass (Zostera marina L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. *Journal of Experimental Marine Biology and Ecology*, *244*(1), 1-28.

Murdoch, W.W., 1994. Population regulation in theory and practice. *Ecology*, *75*(2), 271-287.

Nagy, K. A., Girard, I. A., and Brown, T. K., 1999. Energetics of free-ranging mammals reptiles and birds. *Annual Review of Nutrition*, 19, 247–277.

Nagy, K.A., 1987. Field metabolic rate and food requirement scaling in mammals and birds. *Ecological monographs*, *57*(2), 111-128.

Natural England and Environment Agency. 2013. Exe Estuary, *50°36'53"N 3°25'30".* Sublittoral Map. Viewed 5 August 2018, http://www.nationalarchives.gov.uk/doc/open-government-licence/version/3/

Nergiz, H., 2019. Habitat utilization and winter time-activity budgets of the whooper swan Cygnus cygnus (Linnaeus, 1758) population wintering at the Van Lake basin, Turkey. *Applied ecology and environmental research*, 17(2), 2179-2185.

Neuvonen, M., Pouta, E., Puustinen, J. and Sievänen, T., 2010. Visits to national parks: Effects of park characteristics and spatial demand. *Journal for Nature Conservation*, *18*(3), 224-229.

Newson, S.E. and Hughes, B., 1998. Diurnal activity and energy budgets of Goosander Mergus merganser wintering on Chew Valley Lake, North Somerset: influence of time of day and sex. Wildfowl, 49(49), 173-180.

Nilsson, L., 1970. Food-seeking activity of south Swedish diving ducks in the non-breeding season. Oikos, 145-154.

Nimon, A.J., Schroter, R.C. and Oxenham, R.K., 1996. Artificial eggs: measuring heart rate and effects of disturbance in nesting penguins. *Physiology & Behavior*, *60*(3), 1019-1022.

Nishijima, W., Nakano, Y., Hizon-Fradejas, A.B. and Nakai, S., 2015. Evaluation of substrates for constructing beds for the marine macrophyte Zostera marina L. *Ecological Engineering*, *83*, 43-48.

Norberg, R.A., 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *The Journal of Animal Ecology*, 511-529.

Noseworthy, S.M., 1981. Distribution, sex ratios and behavior of diving ducks wintering on the Detroit River (Doctoral dissertation).

O'Shea, T.J., 1995. Waterborne recreation and the Florida manatee. *Wildlife and recreationists: Coexistence through management and research*, 297-312.

Ogden, J.C., Baldwin, J.D., Bass, O.L., Browder, J.A., Cook, M.I., Frederick, P.C., Frezza, P.E., Galvez, R.A., Hodgson, A.B., Meyer, K.D. and Oberhofer, L.D., 2014. Waterbirds as indicators of ecosystem health in the coastal marine habitats of southern Florida: 1. Selection and justification for a suite of indicator species. *Ecological indicators*, *44*, 148-163.

Ogilvie, M.A. and St Joseph, A.K.M., 1976. Dark-bellied brent geese in Britain and Europe 1955-76. *Brit. Birds*, *69*, 422-439.

Ohashi, H., Saito, M., Horie, R., Tsunoda, H., Noba, H., Ishii, H., Kuwabara, T., Hiroshige, Y., Koike, S., Hoshino, Y. and Toda, H., 2013. Differences in the activity pattern of the wild boar Sus scrofa related to human disturbance. *European journal of wildlife research*, *59*(2), 167-177.

Ollason, J.C. and Dunnet, G.M., 1978. Age, experience and other factors affecting the breeding success of the Fulmar, Fulmarus glacialis, in Orkney. *The Journal of Animal Ecology*, 961-976.

Ordnance Survey Limited. 2018. *Exe Estuary, 50°36'53"N 3°25'30".* Overview Map. Viewed 5 August 2018, <http://ordnancesurvey.co.uk/open>.

Ospina, R. and Ferrari, S.L., 2010. Inflated beta distributions. *Statistical Papers*, *51*(1), 111.

Owen, M., 1993. The UK shooting disturbance project. *Wader Study Group Bulletin*, *68*, 35-46.

Parsons, M., Mitchell, I., Butler, A., Ratcliffe, N., Frederiksen, M., Foster, S. and Reid, J.B., 2008. Seabirds as indicators of the marine environment. *ICES Journal of Marine Science*, *65*(8), 1520-1526.

Paulus, S.L., 1984. Activity budgets of nonbreeding gadwalls in Louisiana. The Journal of wildlife management, 371-380.

Paulus, S.L., 1988. Time-activity budgets of nonbreeding Anatidae: a review. *Waterfowl in winter*, 135-152.

Pawley, M.D. and McArdle, B.H., 2018. Spatial autocorrelation: bane or bonus?. *BioRxiv*, 385526.

Pease, M.L., Rose, R.K. and Butler, M.J., 2005. Effects of human disturbances on the behavior of wintering ducks. *Wildlife Society Bulletin*, *33*(1), 103-112.

Pennycuick, C.J., Åkesson, S. and Hedenström, A., 2013. Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. *Journal of the Royal Society Interface*, *10*(86), 20130419.

Phithakkitnukoon, S., Horanont, T., Di Lorenzo, G., Shibasaki, R. and Ratti, C., 2010, August. Activity-aware map: Identifying human daily activity pattern using mobile phone data. In *International Workshop on Human Behavior Understanding,* Springer, Berlin, Heidelberg, 14-25.

Pirotta, E., Booth, C.G., Costa, D.P., Fleishman, E., Kraus, S.D., Lusseau, D., Moretti, D., New, L.F., Schick, R.S., Schwarz, L.K. and Simmons, S.E., 2018. Understanding the population consequences of disturbance. *Ecology and Evolution*, *8*(19), 9934-9946.

Popkin, B.M., Duffey, K. and Gordon-Larsen, P., 2005. Environmental influences on food choice, physical activity and energy balance. *Physiology & behavior*, *86*(5), 603-613.

Pöysä, H., 1983. Morphology-mediated niche organization in a guild of dabbling ducks. *Ornis Scandinavica*, 317-326.

Quinlan, E.E. and Baldassarre, G.A., 1984. Activity budgets of nonbreeding green-winged teal on playa lakes in Texas. The Journal of wildlife management, 838-845.

Rappole, J.H. and McDonald, M.V., 1994. Cause and effect in population declines of migratory birds. *The Auk*, 652-660.

Raveling, D.G., Crews, W.E. and Klimstra, W.D., 1972. Activity patterns of Canada Geese during winter. The Wilson Bulletin, 278-295

Reich, P.B. and Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences*, *101*(30), 11001-11006.

Rhodes Jr, O.E., DeVault, T.L. and Smith, L.M., 2006. Seasonal variation in carcass composition of American Wigeon wintering in the Southern High Plains. *Journal of Field Ornithology*, *77*(2), 220-228.

Richardson, R.B. and Loomis, J.B., 2005. Climate change and recreation benefits in an alpine national park. *Journal of Leisure Research*, *37*(3), 307-320.

Riddington, R., Hassall, M., Lane, S.J., Turner, P.A. and Walters, R., 1996. The impact of disturbance on the behaviour and energy budgets of Brent Geese Branta b. bernicla. *Bird study*, *43*(3), 269-279.

Robbins, C., 1993. Food intake regulation. In *Wildlife feeding and nutrition* (322-324). Elsevier, 2012.

Robinson, J.A. and Pollitt, M.S., 2002. Sources and extent of human disturbance to waterbirds in the UK: an analysis of Wetland Bird Survey data, 1995/96 to 1998/99. *Bird study*, *49*(3), 205-211.

Robinson, R.A. (2017) BirdFacts: profiles of birds occurring in Britain & Ireland (BTO Research Report 407). BTO, Thetford (http://www.bto.org/birdfacts, accessed on 27/November/2017)

Ross, K., Liley, D., Austin, G., Clarke, R.T., Burton, N.H., Stillman, R.A., Cruickshanks, K. and Underhill-Day, J., 2014. Housing Development and Estuaries in England: Developing Methodologies for Assessing the Impacts of Disturbance to Non-Breeding Waterfowl. *Footprint Ecology, unpublished report for Natural England*.

Saker, H., Rouaiguia, M., Talai-harbi, S., Bara, M., Bouslama, Z., and Houhamdi, M., 2016. Diurnal time budget of the Eurasian Wigeon (Anas penelope) at Lac des Oiseaux (northeast of Algeria), *4(4)*, 248–251.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A. and Leemans, R., 2000. Global biodiversity scenarios for the year 2100. *science*, *287*(5459), 1770-1774.

Sastre, P., Ponce, C., Palacín, C., Martín, C.A. and Alonso, J.C., 2009. Disturbances to great bustards (Otis tarda) in central Spain: human activities, bird responses and management implications. *European Journal of Wildlife Research*, *55*(4), 425-432.

Savard, J.P.L., Clergeau, P. and Mennechez, G., 2000. Biodiversity concepts and urban ecosystems. *Landscape and urban planning*, *48*(3-4), 131-142.

Schlaepfer, M.A., Sax, D.F. and Olden, J.D., 2011. The potential conservation value of non-native species. *Conservation Biology*, *25*(3), 428-437.

Schmidt, P.E., 1999. Population counts, time budgets, and disturbance factors of black brant (Branta bernicla nigricans) at Humboldt Bay, California (Doctoral dissertation, Humboldt State University).

Schulz, R. and Stock, M., 1993. Kentish Plovers and tourists: competitors on sandy coasts. *Wader Study Group Bulletin*, *68*, 83-91.

Schummer, M.L. and Eddleman, W.R., 2003. Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma. *The Journal of wildlife management*, 789-795.

Scott, I., Mitchell, P.I. and Evans, P.R., 1994. Seasonal changes in body mass, body composition and food requirements in wild migratory birds. *Proceedings of the Nutrition Society*, *53*(3), 521-531.

Sedinger, J.S. and Raveling, D.G., 1988. Foraging behavior of cackling Canada goose goslings: implications for the roles of food availability and processing rate. *Oecologia*, *75*(1), 119-124.

Semeniuk, C.A. and Rothley, K.D., 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays Dasyatis americana. Marine Ecology Progress Series, 357, 271-282.

Silberhorn, G.M., Orth, R.J. and Moore, K.A., 1983. Anthesis and seed production in Zostera marina L.(eelgrass) from the Chesapeake bay. *Aquatic Botany*, *15*(2), 133-144.

Sokos, C.K., Birtsas, P.K., Connelly, J.W. and Papaspyropoulos, K.G., 2013. Hunting of migratory birds: disturbance intolerant or harvest tolerant? *Wildlife biology*, *19*(2), 113-126.

Stalmaster, M.V. and Gessaman, J.A., 1984. Ecological energetics and foraging behavior of overwintering bald eagles. *Ecological Monographs*, *54*(4), 407-428.

Stankowich, T., 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological conservation*, *141*(9), 2159-2173.

Steven, R., Pickering, C. and Castley, J.G., 2011. A review of the impacts of nature based recreation on birds. *Journal of environmental management*, *92*(10), 2287-2294.

Stillman, R.A. and Goss-Custard, J.D., 2002. Seasonal changes in the response of oystercatchers Haematopus ostralegus to human disturbance. *Journal of Avian Biology*, *33*(4), 358-365.

Stillman, R.A., 2008. MORPH—An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling*, *216*(3-4), 265-276.

Stillman, R.A., Railsback, S.F., Giske, J., Berger, U.T.A. and Grimm, V., 2014. Making predictions in a changing world: the benefits of individual-based ecology. *BioScience*, *65*(2), 140-150.

Stillman, R.A., West, A.D., Caldow, R.W. and DURELL, S.E.L.V.D., 2007. Predicting the effect of disturbance on coastal birds. *Ibis*, *149*, 73-81.

Stillman, R.A., Wood, K.A., Gilkerson, W., Elkinton, E., Black, J.M., Ward, D.H. and Petrie, M., 2015. Predicting effects of environmental change on a migratory herbivore. *Ecosphere*, *6*(7), 1-19.

SurferToday.com, (2019). *How much wind does a kiteboarder need to fly a kite?*. [online] Surfertoday. Available at: https://www.surfertoday.com/kiteboarding/how-much-wind-does-a-kiteboarder-need-to-fly-a-kite [Accessed 29 Mar. 2019].

Sutherland, W.J., 1996. *From individual behaviour to population ecology* (Vol. 11). Oxford University Press on Demand.

Sutherland, W.J., 1998. The effect of local change in habitat quality on populations of migratory species. *Journal of Applied Ecology*, *35*(3), 418-421.

Tamisier, A., 1972. Rythmes nycth_m_raux des sarcelles d□hiver pendant leur hivernage en Camargue. Alauda, 10(107135), 235-256.

Therkildsen, O.R. and Madsen, J., 2000. Energetics of feeding on winter wheat versus pasture grasses: a window of opportunity for winter range expansion in the pink-footed goose Anser brachyrhynchus._Wildlife Biology,_6(4), 65-74.

Thompson, D.B.A., 1981. Feeding behaviour of wintering Shelduck on the Clyde Estuary. Wildfowl, 32(32), 88-98.

Tides4fishing.com, (2019). *Tides and solar lunar charts Bournemouth and Southampton.* [online] Available at: https://tides4fishing.com/uk/england/bournemouth/southampton [Accessed 1 April 2020].

Tinkler, E., Montgomery, W.I. and Elwood, R.W., 2009. Foraging ecology, fluctuating food availability and energetics of wintering brent geese. *Journal of Zoology*, *278*(4), 313-323.

Tisue, S. and Wilensky, U., 2004. Netlogo: A simple environment for modeling complexity. *Conference on Complex Systems*, 21, 1–10.

Turnbull, R.E. and Baldassarre, G.A., 1987. Activity budgets of mallards and American wigeon wintering in east-central Alabama. The Wilson Bulletin, 457-464.

United Nations, Department of Economic and Social Affairs, Population Division (2017). *World Population Prospects: The 2017 Revision, Key Findings and Advance Tables*. Working Paper No. ESA/P/WP/248

Urfi, A.J., Goss-Custard, J.D., Lev, S.E.A. and Durell, D., 1996. The ability of oystercatchers Haematopus ostralegus to compensate for lost feeding time: field studies on individually marked birds. *Journal of Applied Ecology*, 873-883.

Van Beest, F. M., Kindt-Larsen, L., Bastardie, F., Bartolino, V., and Nabe-Nielsen, J., 2017. Predicting the population-level impact of mitigating harbor porpoise bycatch with pingers and time-area fishing closures. *Ecosphere*, 8 (4).

van Eerden, M.R. (1984) Waterfowl movements in relation to foodstocks. *Coastal Waders and Water- fowl in Winter*, (eds P.E. Evans, Goss-Custard, J.D. & Hale, W.G.), 84ñ100. Cambridge University Press, Cambridge.

Vickery, J.A., Sutherland, W.J., Watkinson, A.R., Rowcliffe, J.M. and Lane, S.J., 1995. Habitat switching by dark-bellied brent geese Branta b. bernicla (L.) in relation to food depletion. *Oecologia*, *103*(4), 499-508.

Vos, D.K., Ryder, R.A. and Graul, W.D., 1985. Response of breeding great blue herons to human disturbance in northcentral Colorado. *Colonial Waterbirds*, 13-22.

weather.gov. 2019. Wind Chill. [ONLINE] Available at: https://www.weather.gov/media/epz/wxcalc/windChill.pdf. [Accessed 25 April 2019].

West, A.D., Goss-Custard, J.D., Stillman, R.A., Caldow, R.W., dit Durell, S.E.L.V. and McGrorty, S., 2002. Predicting the impacts of disturbance on shorebird mortality using a behaviour-based model. *Biological Conservation*, *106*(3), 319-328.

White, D.H. and James, D., 1978. Differential use of fresh water environments by wintering waterfowl of coastal Texas. The Wilson Bulletin, 99-111.

Whittaker, D. and Knight, R.L., 1998. Understanding wildlife responses to humans. *Wildlife Society Bulletin*, *26*, 312-317.

Wilson, R.P., Coria, N.R., Spairani, H.J., Adelung, D. and Culik, B., 1989. Human-induced behaviour in Adélie penguins Pygoscelis adeliae. *Polar Biology*, *10*(1), 77-80.

Wilson, S.M., Madel, M.J., Mattson, D.J., Graham, J.M. and Merrill, T., 2006. Landscape conditions predisposing grizzly bears to conflicts on private agricultural lands in the western USA. *Biological Conservation*, *130*(1), 47-59.

Wolf, S., 2012. Vulnerability and risk: comparing assessment approaches. *Natural Hazards*, *61*(3), 1099-1113.

Wood, K.A., Stillman, R.A. and Goss-Custard, J.D., 2015. Co-creation of individual-based models by practitioners and modellers to inform environmental decision-making. *Journal of Applied Ecology*, *52*(4), 810-815.

Wooley Jr, J.B. and Owen Jr, R.B., 1978. Energy costs of activity and daily energy expenditure in the black duck. *The Journal of Wildlife Management*, 739-745.

Xiang, X., Kennedy, R., Madey, G. and Cabaniss, S., 2005, April. Verification and validation of agent-based scientific simulation models. In *Agent-directed simulation conference, 47,* 55.

Xu, S., Zhou, Y., Wang, P., Wang, F., Zhang, X., and Gu, R., 2016. Salinity and temperature significantly influence seed germination, seedling establishment, and seedling growth of eelgrass Zostera marina L. *PeerJ*, (11), 1–21.

Ydenberg, R.C., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P. and Beauchamp, G., 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behavioral Ecology*, *5*(1), 28-34.

YiJin, Z., MingQin, S., Peng, C., and Bin, C., 2019. Time budget and activity rhythm of the Mandarin duck aix galericulata in the poyang lake watershed. *Pakistan Journal of Zoology*, 51 (2), 725–730.

Zwarts, L., 1976. Density-related processes in feeding dispersion and feeding activity of teal (Anas crecca). *64*, 192–209.

APPENDICES

Appendix 1 Derivation of the COD Equation and add-ons to incorporate change energy change and behavioural habituation for Chapters 3 & 4 (Stillman 2019 unpublished)

Variables calculated by the equations below.

Symbol	Description
F	Total time spent feeding
R	Total time spent resting
D	Total time spent responding to disturbance
G	Total energy gain during time period

Parameters used in the equations below.

Symbol	Description
T	Total amount of time during which feeding can potentially occur
g	Gross rate of energy gain while feeding
E_F	Metabolic rate while feeding
E_R	Metabolic rate while resting
E_D	Metabolic rate while disturbed
E_Δ	Rate of change in energy balance over time period
λ_F	Rate at which disturbance encounters occur while feeding
λ_R	Rate at which disturbance encounters occur while resting
t_F	Average time spent responding to disturbance that occurs while feeding
t_R	Average time spent responding to disturbance that occurs while resting
r	Relative amount of habituation / sensitisation

Parameters that would be used to check whether time or energy have run out

Symbol	Description

F_{max}	Maximum amount of time for which feeding can occur during time period
G_{max}	Maximum amount of energy that can be gained during time period

Derivation of the model (text in yellow is to show the steps).

We consider a time and energy budget over a fixed period of time.

$$T = F + R + D, \qquad (1)$$

where T = total amount of time, F = time spent feeding, R = time spent resting and D = time spent responding to disturbance.

We assume that animals can be disturbed while feeding or resting with the total number of disturbance encounters given by

$$N = \lambda_F F + \lambda_R R, \qquad (2)$$

Where N = total number of disturbance encounters, λ_F = rate at which disturbance encounters occur while feeding and λ_R = rate at which disturbance encounters occur while resting.

The total time responding to disturbance is then given by

$$D = t_F \lambda_F F + t_R \lambda_R R, \quad (3)$$

where t_F = average time spent responding to disturbance that occurs while feeding and t_R = average time spent responding to disturbance that occurs while resting.

We assume that animals could potentially become habituated (reduced response) or sensitised (increased response) to disturbance sources, and so include an additional parameter to account for this

$D = rt_F\lambda_F F + rt_R\lambda_R R,$ (4)

where r = relative amount of habituation ($r < 1$) / sensitisation ($r > 1$) to disturbance sources. For simplicity, we assume that r is unrelated to the encounter rate with disturbance sources and test for its potential effect by varying its value. r would in reality be a function of the encounter rate with disturbance sources, but the exact form of function will be unavailable for most species.

Substituting equation 4 into equation 1 gives

$$T = F + R + rt_F\lambda_F F + rt_R\lambda_R R. \qquad (5)$$

Which can be simplified to

$$T = F(1 + rt_F\lambda_F) + R(1 + rt_R\lambda_R) \qquad (6)$$

and then rearranged to give

$$R = \frac{T - F(1 + rt_F\lambda_F)}{1 + rt_R\lambda_R}. \qquad (7)$$

We assume that the energy budget is either balanced or changing during the time period.

$$gF = E_F F + E_R R + E_D D + E_\Delta T \qquad (8)$$

where g = gross rate of energy gain while feeding, E_F = metabolic rate while feeding, E_R = metabolic rate while resting, E_D = metabolic rate while disturbed and E_Δ = rate of change in energy balance over time period.

Substituting equation 4 into equation 8 gives

$$gF = E_F F + E_R R + E_D(rt_F\lambda_F F + rt_R\lambda_R R) + E_\Delta T. \qquad (9)$$

which can be simplified to give

$$gF = E_F F + \mathrm{E}_R R + E_D r t_F \lambda_F F + E_D r t_R \lambda_R R + E_\Delta T$$

$$gF = E_F F + E_D r t_F \lambda_F F + E_R R + E_D r t_R \lambda_R R + E_\Delta T$$

$$gF = F(E_F + E_D r t_F \lambda_F) + R(E_R + E_D r t_R \lambda_R) + E_\Delta T \qquad (10)$$

Substituting equation 7 into equation 10 gives

$$gF = F(E_F + E_D r t_F \lambda_F) + \frac{T - F(1+rt_F\lambda_F)}{1+rt_R\lambda_R}(E_R + E_D r t_R \lambda_R) + E_\Delta T \qquad (11)$$

which can be simplified to give

$$gF = F(E_F + E_D r t_F \lambda_F) + \frac{T(E_R+E_D r t_R \lambda_R) - F(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R} + E_\Delta T$$

$$gF = F(E_F + E_D r t_F \lambda_F) + \frac{T(E_R+E_D r t_R \lambda_R)}{1+rt_R\lambda_R} - \frac{F(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R} + E_\Delta T$$

$$gF - F(E_F + E_D r t_F \lambda_F) + \frac{F(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R} = \frac{T(E_R+E_D r t_R \lambda_R)}{1+rt_R\lambda_R} + E_\Delta T$$

$$F\left(g - (E_F + E_D r t_F \lambda_F) + \frac{(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R}\right) = \frac{T(E_R+E_D r t_R \lambda_R)}{1+rt_R\lambda_R} + E_\Delta T$$

$$F = \frac{\frac{T(E_R+E_D r t_R \lambda_R)}{1+rt_R\lambda_R} + E_\Delta T}{g - (E_F + \mathrm{E}_D r t_F \lambda_F) + \frac{(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R}}$$

$$F = \frac{T\left(\frac{E_R+E_D r t_R \lambda_R}{1+rt_R\lambda_R} + E_\Delta\right)}{g - (E_F + E_D r t_F \lambda_F) + \frac{(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R}} \qquad (12)$$

From which the proportion time feeding can be calculated as

$$\frac{F}{T} = \frac{\frac{E_R+E_D r t_R \lambda_R}{1+rt_R\lambda_R} + E_\Delta}{g - (E_F + E_D r t_F \lambda_F) + \frac{(1+rt_F\lambda_F)(E_R+E_D r t_R\lambda_R)}{1+rt_R\lambda_R}} \qquad (13)$$

The total energy gain during the time period is calculated as

$$G = gF$$

To test whether time or energy have run out F and G can be compared to F_{max} and G_{max} respectively.

Appendix 2 Derivation of equation to determine feeding time based on body mass in Chapter 5.

Variable calculated by the equations below.

Symbol	Description
P^*	Proportion of time animals need to spend feeding to achieve energy balance

Parameters used in the equations below.

Symbol	Description
M	Body mass
e_1	Energy expenditure rate when body mass equals 1
e_m	Scaling factor relating energy expenditure to body mass
f_1	Energy gain rate when body mass equals 1
f_m	Scaling factor relating energy gain rate to body mass

Derivation of the model

The purpose of the model is to predict the proportion of time for which animals of different body mass would be expected to spend feeding. Animals with a higher proportion of time spent feeding have less ability to compensate for adverse environmental changes that may increase energy demands or decrease the rate at which prey can be consumed.

The net rate of gaining energy during a period of time (g) is given by

$$g = pf - pe_f - (1-p)e_r \tag{1}$$

where p = proportion of time spent feeding, f = rate of energy gain while feeding, e_f = energy expenditure while feeding and e_r = energy expenditure while resting.

We assume that the animals adjust their proportion of time spent feeding (p^*) so that net energy gain (g) equals a target amount (e_Δ).

Substituting e_Δ for g, and p^* for p in equation 1 gives

$$e_\Delta = p^* f - p^* e_f - (1 - p^*) e_r \tag{2}$$

where e_Δ = target rate of net energy change, and p^* = proportion of time animals need to spend feeding to achieve target rate of net energy change.

Which can be rearranged to give the proportion of time animals need to spend feeding to meet their energy demands

$$e_\Delta = p^* f - p^* e_f - e_r + p^* e_r$$

$$e_\Delta + e_r = p^* f - p^* e_f + p^* e_r$$

$$e_\Delta + e_r = p^* \left(f - e_f + e_r \right)$$

$$p^* = \frac{e_\Delta + e_r}{f - e_f + e_r} \tag{3}$$

For simplicity incorporating body mass, we assume that animals attempt to balance their energy budget (i.e. $e_\Delta = 0$) and that energy demands are the same while feeding and resting (i.e. $e_f = e_r$).

Setting e_Δ to zero and assuming $e_f = e_r$ (and terming e) gives

$$p^* = \frac{0 + e}{f - e + e} \tag{4}$$

where e = energy expenditure while feeding or resting, and p^* = proportion of time animals need to spend feeding to achieve energy balance. Which can be simplified to give

$$p^* = \frac{e}{f} \tag{5}$$

We assume that energy expenditure and energy gain rate while feeding have the following allometric relationships with body mass (M) (i.e. the relationships typically fitted in empirical studies scaling body mass to energetics)

$$e = e_1 M^{e_m} \tag{6}$$

$$f = f_1 M^{f_m} \tag{7}$$

Where e_1 = energy expenditure rate when body mass equals 1, f_1 = energy gain rate when body mass equals 1, e_m = scaling factor relating energy expenditure to body mass, and f_m = scaling factor relating energy gain rate to body mass. Substituting equations 6 and 7 into equation 5 gives

$$p^* = \frac{e_1 M^{e_m}}{f_1 M^{f_m}} \tag{8}$$

Which can be simplified to give

$$p^* = \frac{e_1}{f_1} M^{(e_m - f_m)} \tag{9}$$

The values of e_1, f_1, e_m and f_m can then be derived from the literature to determine how the proportion of time spent feeding would be expected to scale with body mass.

Appendix 3 Table of species reviewed in the literature for Chapter 5.

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Aix galericulata	omnivore	0.575	29.75	116.22	no	35	LATE	ISS	17.6	50.2	1.7	1.5	27.5	YiJin et al. 2019
Aix galericulata	omnivore	0.575	29.75	116.22	no	35	LATE	ISS	18.51	56.1	0.7	0.87	23.04	YiJin et al. 2019
Aix galericulata	omnivore	0.575	29.75	116.22	no	35	LATE	ISS	29.43	49.35	0.4	0.74	17.58	YiJin et al. 2019
Alopochen aegyptiacus	herbivore													
Anas acuta	omnivore	0.8							2	60		1	30	Roux et al. 1978
Anas acuta	omnivore	0.8	38.5842	-121.5007	no				18	48		1	13	Miller 1985
Anas acuta	omnivore	0.8	29.9659	-92.8777			ALL	ISS	5	70		1	9	Tamisier 1976
Anas acuta	omnivore	0.8	34.0352	-77.8936	yes				61	29		1	5	Hepp 1982
Anas acuta	omnivore	0.8	39.25	-122	no		EARLY	ISS	33	27			11	Miller 1985
Anas acuta	omnivore	0.8	39.25	-122	no		MID	ISS	13	55			12	Miller 1985

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Anas acuta	omnivore	0.8	39.25	-122	no		MID	ISS	7	51			13	Miller 1985
Anas acuta	omnivore	0.8	39.25	-122	no		LATE	ISS	20	50			11	Miller 1985
Anas americana	herbivore	0.725	32.0047	-85.0852	no		MID	FS	60.4	23.16		2.26	14.2	Turnbull and Baldassarre 1987
Anas clypeata	omnivore	0.63	34.0352	-77.8936	yes		ALL		59	33		0	8	Hepp 1982
Anas clypeata	omnivore	0.63	36.85	8.05	no		ALL	ISS	39	35		11	13	Ali 2019
Anas crecca	omnivore	0.33	51.73673	4.286258	yes	2855	EARLY		51					Zwarts 1976
Anas crecca	omnivore	0.33	29.9659	-92.8777	yes		ALL	ISS	5	84		0	9	Tamisier 1976
Anas crecca	omnivore	0.33	43.5939	4.469	yes		ALL		42	47				Tamisier 1972
Anas crecca	omnivore	0.33	43.5939	4.469	yes		EARLY		48	39			1	Tamisier 1972
Anas crecca	omnivore	0.33	43.5939	4.469	yes		MID		33	36			20	Tamisier 1972
Anas crecca	omnivore	0.33	43.5939	4.469	yes		MID		49	29			20	Tamisier 1972
Anas crecca	omnivore	0.33	43.5939	4.469	yes		LATE		51	32			16	Tamisier 1972
Anas crecca	omnivore	0.33	36.85	8.05	no		ALL	ISS	12	69		8	10	Ali 2019

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Anas crecca carolinensis	omnivore	0.33	34.0352	-77.8936	yes		ALL		56	38		0	4	Hepp 1982
Anas crecca carolinensis	omnivore	0.33	39	-102	no		ALL		14	78		1	7	Quinlan and Baldassarre 1984
Anas platyrhynchos	omnivore	1.16	40.6993	-99.0817	no		MID	FS	35	28		5	13	Jorde et al. 1984
Anas platyrhynchos	omnivore	1.16	40.6993	-99.0817	no		ALL		24.95	52.5	2.9	6.05	11.45	Jorde et al. 1984
Anas platyrhynchos	omnivore	1.16	32.0047	-85.0852	no		MID	FS	23	54.5		3.6	18.8	Turnbull and Baldassarre 1987
Anas platyrhynchos	omnivore	1.16	30.86561	-94.17953	no		ALL		20	22			43	Clark and Whiting 1994
Anas platyrhynchos	omnivore	1.16					ALL		26	39			13	Lee 1985
Anas platyrhynchos	omnivore	1.16	33.21456	-96.61445		281	LATE	FS	38	24		0.5	27	Mason, Whiting, and Conway 2013

Species	**Diet**	**Mass (kg)**	**Lat**	**Lon**	**Tide**	**N**	**Winter month**	**Sample method**	**% Feed**	**% Rest**	**% Flight**	**% Alert**	**% Small loco**	**Source**
Anas platyrhynchos	omnivore	1.16	33.21456	-96.61445		148	LATE	FS	48	40		1	30	Mason, Whiting, and Conway 2013
Anas platyrhynchos	omnivore	1.16	33.21456	-96.61445		70	LATE	FS	19	59		1	21	Mason, Whiting, and Conway 2013
Anas platyrhynchos	omnivore	1.16	36.85	8.05	no		ALL	ISS	8	22			60	Ali 2019
Anas querquedula	omnivore	0.38	33.21456	-96.61445					2	56		1	40	Roux et al. 1978
Anas strepera	herbivore	0.895	33.21456	-96.61445	yes				75	17			5	Hepp 1982
Anas strepera	herbivore	0.895	33.21456	-96.61445					70	8			8	Dwyer 1975
Anas strepera	herbivore	0.895	33.21456	-96.61445	yes		ALL		64	16.3		9	11.1	Paulus 1984
Anas strepera	herbivore	0.895	33.21456	-96.61445		251	LATE	FS	35	10			47	Mason, Whiting, and Conway 2013

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Anas strepera	herbivore	0.895	33.21456	-96.61445		251	LATE	FS	31	18.5		0.5	49	Mason, Whiting, and Conway 2013
Anas strepera	herbivore	0.895	33.21456	-96.61445		251	LATE	FS	43.5	14		0.5	42	Mason, Whiting, and Conway 2013
Anas strepera	herbivore	0.895	29.56675	-91.8513	no		MID	ISS	47	12		13	16	Paulus 1984
Anas strepera	herbivore	0.895	29.56675	-91.8513	no		MID	ISS	58	15		9	13	Paulus 1984
Anas strepera	herbivore	0.895	29.56675	-91.8513	no		LATE	ISS	68	7		10	9	Paulus 1984
Anas strepera	herbivore	0.895	29.56675	-91.8513	no		ALL	ISS	62.3	1.4		19.2	12.9	Paulus 1984
Anas strepera	herbivore	0.895	34.0352	-77.8936	yes		ALL		75	19			5	Hepp 1982
Anas strepera	herbivore	0.895	36.85	8.05	no		ALL	ISS	63	16			21	Ali 2019
Anser albifrons	herbivore	2.5	43.5939	4.469	yes		LATE	FS	64	25			6	Campredon 1981.
Anser anser	herbivore	3.5			yes				39				42	Lebret 1970

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Anser brachyrhynchus	herbivore	2.5	55.11667	8.666667	no	100-500	LATE	ISS	83.8	4.1	0.1	7.2	4.1	Therkildsen and Madsen 2000
Anser brachyrhynchus	herbivore	2.5	55.11667	8.666667	no	100-500	LATE	ISS	74.9	4.1	0.1	7.1	4.1	Therkildsen and Madsen 2000
Anser fabalis	herbivore	2.85	51.98167	4.080556	no	14552	LATE	ISS	55.2	38.5	2	2		Mooij 1992
Anser fabalis	herbivore	2.85	52.57722	1.5031	no		MID	ISS	65					Allport 1991
Aythya affinis	carnivore		33.2464	-81.6679	no		ALL	FS	30	16			30	Bergan, Smith, and Mayer 1989
Aythya ferina	omnivore	0.93							23					Nilsson 1987
Aythya ferina	omnivore	0.93	36.85	8.05	no		ALL	ISS	9	53	1		37	Ali 2019
Aythya fuligula	omnivore	0.76							11					Nilsson 1987
Aythya fuligula	omnivore	0.76	36.85	8.05	no		ALL	ISS	10	58			32	Ali 2019
Aythya marila	carnivore								9					Nilsson 1987

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Aythya valisineria	omnivore	1.2	32.3547	-89.3985			ALL		23	50			24	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	33.8361	-81.1637			ALL		33	45			20	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	31.25	-92	no	4245	MID	FS	15	52.3		0.7	30.6	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	31.25	-92	no	4245	MID	FS	12	67.8		0.1	19.9	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	31.25	-92	no	4245	LATE	FS	7.7	58.6		0.2	30.8	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	31.25	-92	no	4245	LATE	FS	15.65	42.2		7.9	33.4	Hohman, William and David 1990

Species	**Diet**	**Mass (kg)**	**Lat**	**Lon**	**Tide**	**N**	**Winter month**	**Sample method**	**% Feed**	**% Rest**	**% Flight**	**% Alert**	**% Small loco**	**Source**
Aythya valisineria	omnivore	1.2	29.25	-89.25	yes	4245	MID	FS	11.85	66.7		2.8	16.8	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	29.25	-89.25	yes	4245	MID	FS	23.45	44.6		6	24.5	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	29.25	-89.25	yes	4245	LATE	FS	39.25	36.1		10	12.6	Hohman, William and David 1990
Aythya valisineria	omnivore	1.2	29.25	-89.25	yes	4245	LATE	FS	37.2	58.2		1.2	21.5	Hohman, William and David 1990
Branta bernicla	herbivore	1.45	52.982	0.7067	yes	100	ALL	ISS	79.1	2	2.4	18.4		Riddington et al. 1996.
Branta bernicla	herbivore	1.45	52.982	0.7067	yes	100	ALL	ISS	69.6	7.8	1.6	21.2		Riddington et al. 1996.
Branta bernicla hrota	herbivore	1.325	39.51667	74.36667	yes	20	ALL	ISS	56.15	43.5	11.35		67.4	Heise, Williams, and Castelli 2019

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Branta bernicla hrota	herbivore	1.325	39.51667	74.36667	yes	24	ALL	ISS	54.35	27.7	9.2		81.25	Heise, Williams, and Castelli 2019
Branta bernicla hrota	herbivore	1.325	39.51667	74.36667	yes	44	ALL	ISS	26.39	15.36	7.67	1.91	48.59	Heise, Williams, and Castelli 2019
Branta bernicla hrota	herbivore	1.325	39.51667	74.36667	yes	20	ALL	ISS	54.65	40.9	19.5		56.1	Heise, Williams, and Castelli 2019
Branta bernicla hrota	herbivore	1.325	39.51667	74.36667	yes	24	ALL	ISS	66.6	35.7	10.95		71.05	Heise, Williams, and Castelli 2019
Branta bernicla hrota	herbivore	1.325	39.7	73.36667	yes	207	MID	ISS	27.4	18.6	13		28.5	Ladin et al. 2011
Branta bernicla hrota	herbivore	1.325	39.7	73.36667	yes	272	LATE	ISS	25.5	16.1	23.6		26.7	Ladin et al. 2011
Branta bernicla hrota	herbivore	1.325	39.7	73.36667	yes	256	LATE	ISS	31.4	16.8	15.3		30.7	Ladin et al. 2011

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Branta bernicla hrota	herbivore	1.325	39.7	73.36667	yes	270	LATE	ISS	30.3	18.4	13.7		29.6	Ladin et al. 2011
Branta bernicla hrota	herbivore	1.325	40.7195	-124.2426	yes	2146	LATE	FS	35	7	0.1	0.5	32.5	Schmidt 1999
Branta bernicla hrota	herbivore	1.325	40.7195	-124.2426	yes	2146	LATE	FS	32.5	4	0.1	0.1	45	Schmidt 1999
Branta canadensis	herbivore	4.6	37.71020	-89.06079	no		ALL		13					Raveling, Crews, and Klimstra 1972
Branta leucopsis	herbivore	1.8	54.9762	-3.4841	yes	300	EARLY	ISS	83					Black et al. 1992
Branta leucopsis	herbivore	1.8	54.9762	-3.4841	yes	300	MID	ISS	86					Black et al. 1992
Branta leucopsis	herbivore	1.8	54.9762	-3.4841	yes	300	MID	ISS	92					Black et al. 1992
Branta leucopsis	herbivore	1.8	54.9762	-3.4841	yes	300	LATE	ISS	95					Black et al. 1992

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Branta leucopsis	herbivore	1.8	54.9762	-3.4841	yes	300	LATE	ISS	94					Black et al. 1992
Branta leucopsis	herbivore	1.8	53.4894	6.2309	yes	100-200 birds	ALL	ISS	83	1		15		Ebbinge, Canters and Drent 1975
Bucephala clangula	omnivore	0.875							86					Nilsson 1970.
Bucephala clangula	omnivore	0.875			no				84	7		0	9	Noseworthy 1981
Chen caerulescens caerulescens	herbivore	2.6	29.91667	93.06667	no	707	ALL	FS	45.4	30.1		20.8	3.6	Jonsson and Afton 2009
Chen caerulescens caerulescens	herbivore	2.6	29.91667	93.06667	no	707	ALL	FS	46.3	27.2		21.5	5.6	Jonsson and Afton 2009
Chen rossii	herbivore	1.7	29.91667	93.06667	no	624	ALL	FS	53.3	19.5		23.9	2.9	Jonsson and Afton 2009
Chen rossii	herbivore	1.7	29.91667	93.06667	no	624	ALL	FS	57.1	16		20	7.2	Jonsson and Afton 2009

Species	**Diet**	**Mass (kg)**	**Lat**	**Lon**	**Tide**	**N**	**Winter month**	**Sample method**	**% Feed**	**% Rest**	**% Flight**	**% Alert**	**% Small loco**	**Source**
Clangula hyemalis	carnivore								79					Nilsson 1970
Cygnus columbianus	herbivore	6												
Cygnus cygnus	herbivore	9.6	38.32863	42.92717	no	1540	ALL	BOTH	12.48	55	4.87		27.65	Nergiz 2019
Cygnus olor	omnivore	10.25	51.8921	-8.4846	no	538	ALL	ISS	34	15	0.5		50	Keane and O'Halloran 1992
Cygnus olor	omnivore	10.25	56.71667	8.233333	yes	2138	EARLY	ISS	35	55				Holm 2002
Cygnus olor	omnivore	10.25	56.71667	8.233333	yes	2138	MID	ISS	56	25				Holm 2002
Cygnus olor	omnivore	10.25	56.71667	8.233333	yes	2138	MID	ISS	30	70				Holm 2002
Cygnus olor	omnivore	10.25	56.71667	8.233333	yes	2138	EARLY	ISS	40	30				Holm 2002
Cygnus olor	omnivore	10.25	56.71667	8.233333	yes	2138	MID	ISS	70	20				Holm 2002
Mareca penelope	herbivore	0.725	43.5939	4.469	yes				56	29		0	8	Campredon 1981
Mareca penelope	herbivore	0.725	43.5939	4.469	yes		MID		55	28			8	Campredon 1981

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Mareca penelope	herbivore	0.725	43.5939	4.469	yes		MID		48	33			11	Campredon 1981
Mareca penelope	herbivore	0.725	43.5939	4.469	yes		LATE		64	25			6	Campredon 1981
Mareca penelope	herbivore	0.725	37.00111	7.283611	no		ALL	ISS	9	53.5	1.5		36	Bouchaala et al. 2017
Mareca penelope	herbivore	0.725	37.00111	7.283611	no		ALL	ISS	6	56	1.5		37	Bouchaala et al. 2017
Mareca penelope	herbivore	0.725	37.00111	7.283611	no		ALL	ISS	9	55	1		35	Bouchaala et al. 2017
Mareca penelope	herbivore	0.725	36.81667	8.416667	no		ALL	FS	67	16	1		15	Houhamdi. and Samraoui 2013
Mareca penelope	herbivore	0.725	36.81667	8.416667	no		ALL	FS	60	24	1		14	Houhamdi. and Samraoui 2013
Mareca penelope	herbivore	0.725	36.78333	8.116667	no	260	ALL	ISS	40	28	3		28	Saker et al. 2016

Species	**Diet**	**Mass (kg)**	**Lat**	**Lon**	**Tide**	**N**	**Winter month**	**Sample method**	**% Feed**	**% Rest**	**% Flight**	**% Alert**	**% Small loco**	**Source**
Mareca penelope	herbivore	0.725	36.78333	8.116667	no	260	ALL	ISS	37	32	5		27	Saker et al. 2016
Mareca penelope	herbivore	0.725	36.85	8.05	no		ALL	ISS	59	40	1			Ali 2019
Melanitta fusca	omnivore													
Melanitta nigra	carnivore	1												
Mergus albellus	omnivore								46					Nilsson 1970
Mergus merganser	carnivore	1.5							19					Nilsson 1970
Mergus merganser	carnivore	1.5	51.3362	-2.6186	no	152.5	ALL	ISS	14.2	65.3	0.4		20.3	Newson and Hughes 1998
Mergus merganser	carnivore	1.5	51.3362	-2.6186	no	152.5	ALL	ISS	16.8	62.6	0.3		20.3	Newson and Hughes 1998
Mergus serrator	carnivore	1.1					ALL		50					Nilsson 1970

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Oxyura jamaicensis	omnivore		33.2464	-81.6679	no	870	ALL	FS	26	48			16	Bergan, Smith, and Mayer 1989
Oxyura leucocephala	omnivore	0.66	37.71667	35.25	no	3010	LATE	ISS	60	32.05		0.55	6.9	Green et al. 1999
Oxyura leucocephala	omnivore	0.66	36.85	8.5	no		ALL	ISS	9.63	74.39			15.07	Meziane, Samraoui, F. and Samraoui, B. 2014
Oxyura leucocephala	omnivore	0.66	36.84833	7.729722	no		ALL	ISS	7.62	83.57			8.29	Meziane, Samraoui, F. and Samraoui, B. 2014
Oxyura leucocephala	omnivore	0.66	36.85	8.05	no		ALL	ISS	11	78			9	Ali 2019
Somateria mollissima	carnivore	2.2	50.66667	63.11667	yes	30	MID	FS	56.6					Guillemette 1998

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Somateria mollissima	carnivore	2.2	50.66667	63.11667	yes	30	LATE	FS	45.8					Guillemette 1998
Somateria mollissima	carnivore	2.2	46.28333	54.2	yes		ALL	ISS	57					Goudie and Ankney 1986.
Somateria mollissima	carnivore	2.2	50.66667	63.11667	yes	30	ALL	FS	61.4	38.6	0	0	0	Guillemette, Ydenberg, and Himmelman 1992
Somateria mollissima	carnivore	2.2	50.66667	63.11667	yes	30	ALL	FS	49.6	50.4	0	0	0	Guillemette, Ydenberg, and Himmelman 1992
Somateria mollissima	carnivore	2.2	50.66667	63.11667	yes	30	ALL	FS	69.8	30.2	0	0	0	Guillemette, Ydenberg, and Himmelman 1992

Species	Diet	Mass (kg)	Lat	Lon	Tide	N	Winter month	Sample method	% Feed	% Rest	% Flight	% Alert	% Small loco	Source
Tadorna tadorna	omnivore	1.125	35.66667	6.45	no		ALL	ISS	59.7	26.6	3.7		10.1	Bensizerara and Chenchouni 2019
Tadorna tadorna	omnivore	1.125	35.66667	6.45	no		ALL	ISS	60.3	27.7	3.7		8.3	Bensizerara and Chenchouni 2019
Tadorna tadorna	omnivore	1.125			yes		ALL		55					Evans and Pienkowski 1982
Tadorna tadorna	omnivore	1.125			yes		ALL		45					Thompson 1981
Tadorna tadorna	omnivore	1.125	35.88333	6.483333	no	200	ALL	ISS	80.17	12.39	3.86	0	3.57	Bezzalla et al. 2019
Tadorna tadorna	omnivore	1.125	35.08333	6.5	no	200	ALL	ISS	82.04	9.2	4.38	0	4.38	Bezzalla et al. 2019

Appendix 4 Netlogo coding for IBM in Chapter 6.

```
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;; DEFINING VARIABLES ;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


globals [                     ;; variables terms used throughout the model that will be given
  mud                         ;; specified values
  mixed
  sand
  land
  water
  intertidal
  feeding
  disturbed
  undisturbed
  resting
```

```
  locomotion
]

breed [humans human]                 ;; each human is a group of humans ranging from 1 to 5 (based on observations where groups of
                                     humans generally do not exceed 5 person) also any groups that did, exceeded the area and
                                     therefore would constitute several groups when over 5
breed [brentgeese brentgoose]        ;; each brent goose is a group of brent geese ranging from 1 to 5 as this represents a single family
                                     unit which general move in groups and therefore assimilate and expend energy similarly
breed [wigeons wigeon]               ;; each wigeon is a group of wigeon ranging from 1 to 3 as this represents a social unit which
                                     general move in groups and therefore assimilate and expend energy similarly

humans-own[
  activity-type
  duration
  walking-speed
]
```

```
brentgeese-own[
  energy                    ;; energy the bird has at any moment in time
  energy-min                ;; the required daily energy needed
  energy-assimilation       ;; proportion of energy assimilated relative the energy equation
  flight-cost               ;; energetic cost of flight for this species
  feed-depth                ;; depth at which birds are capable of feeding
  flight-prob               ;; determined by the average flight probability when distance is 200m or less calculated from observation data
  flight-dist               ;; the average observed distance a brent goose flew when disturbed
  flight-speed              ;; the average flight speed for brent geese in autumn (Green & Alerstam 2000)
  body-mass                 ;; average body mass of brent geese during winter months
  rmr                       ;; the resting metabolic rate of brent geese
  thermo-cost               ;; the thermo-regulatory costs of wind chill temperatures below lower critical threshold
  activity                  ;; the activity birds are engaged in coded in numbers (0 = rest, 1 = small locomotion, 2 = feed, 3 = disturbed)
  disturbance               ;; keeps track of whether birds or disturbed or not (separate from other activities because they can happen
simultaneously)
  start-patch               ;; the patch that birds are on before moving to allow for calculating distance travelled
```

```
  patches-visited              ;; record of patches visited to avoid density clogging after moving
]

wigeons-own [                  ;; defining a new turtle variable for wigeon called energy *similar to turtles having colour options
  start-energy
  energy                       ;; "same as for brent geese"
  energy-min
  energy-assimilation
  flight-cost
  feed-depth
  feed-time
  flight-prob
  flight-dist
  flight-speed                 ;;Pennycuick et al. 2013
  body-mass
  rmr
  thermo-cost
```

```
  activity
  disturbance
  start-patch
  patches-visited
]

patches-own [
  depth                         ;; defining a new patch variable called depth that will change with tidal cycles
  cluster                       ;; give patch a cluster 'leader'
  elevation                     ;; establishing that patches all start with a constant height above low tide
  substrate                     ;; substrate type of each patch given in numbers that are explained in setup-function (mud, sand, or mixed)
  habitat                       ;; intertidal, water, land
  veg-mass                      ;; the biomass of eelgrass shoots, in gC/m2
  rhizome-mass                  ;; the biomass of eelgrass rhizomes, in gC/m2
  biomass-available             ;; the biomass on a patch open to feeding based on depth
  unfavourable-substrate        ;; the state of substrate based on favourability of substrate for traversing
  bg-visitation                 ;; the number of times a patch has been visited by a brent goose
```

```
  w-visitation                  ;; the number of times a patch has been visited by a wigeon
  human-visitation              ;; the number of times a patch has been visited by a human
  total-biomass-available       ;; overall count of patches that have available biomass
]



;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;; MODEL SETUP ;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;


to setup                        ;; defines procedure named setup
 clear-all                      ;; resets to the world to initial, empty state


  random-seed 727               ;; setting a standardized random number set so model is reproducible
```

```
 set mud 1                        ;; generating global variables with values so that the terms can be used in later models
 set mixed 2
 set sand 3
 set land 5
 set intertidal 0
 set water 6
 set feeding 2
 set disturbed 3
 set undisturbed 0
 set resting 0
 set locomotion 1

ask patches                                                                     ;; creating patches
 [ set pcolor one-of [brown yellow grey orange]                                 ;; use colours that represent substrates (brown = mud,
                                                                                yellow = sand, grey = shore, green = land, black =
                                                                                path)
```

```
  set cluster nobody ]                                                  ;; initially, patches are not in clusters
  repeat 10                                                              ;; telling the process to repeat x times
[ ask patches [
  set pcolor [pcolor] of one-of neighbors                                ;; spreads colours from patch to patch, and creates
                                                                        connected areas that are all the same colour 'clusters'
  set bg-visitation 0                                                    ;; setting initial bird visitation to 0
  set w-visitation 0
  set human-visitation 0                                                 ;; setting initial human visitation to 0
  set total-biomass-available 1
let decline shore-elevation - (shore-decline * (pxcor - end-of-shore-slope))   ;; defining the nature of how steep the shore is
                                                                        descending into water (controlled by slider on
                                                                        interface)
let incline incline-elevation + (island-incline * (pxcor - end-of-incline))    ;; defining the nature of how steep the incline out of
                                                                        water is on the opposite side of the shore (basically
                                                                        other shore but named it different because it is on the
                                                                        other side; also controlled by slider on interface)
```

```
 if pxcor <= end-of-land


  [set elevation land-elevation]


 if pxcor > end-of-land and pxcor <= end-of-shore-slope
  [set elevation decline]
 if pxcor > end-of-shore-slope and pxcor <= start-of-incline
  [set elevation bottom-elevation]
 if pxcor > start-of-incline and pxcor <= end-of-incline
  [set elevation incline]
 if pxcor > end-of-incline and pxcor <= ending
  [set elevation island-elevation]
  ]
]
```

```
;; the following set of coding controls sliders on the
interface that determine the nature of the environment
being examined
;; when sliders are changed, the landscape changes
therefore, patch elevation will be updated to reflect
this
```

```
  ask patches                                   ;; asking patches to perform the following tasks
  [if pcolor = brown                            ;; substrate that is brown is mud
      [set substrate mud]                       ;; 1 equals mud for future use in the model
  if pcolor = orange                            ;; substrate that is orange is mixed substrate
      [set substrate mixed]                     ;; 2 equals mixed for future use in the model
  if pcolor = yellow                            ;; substrate that is yellow is considered sand
      [set substrate sand]                      ;; 3 equals sand for future use in the model
  if elevation >= land-elevation                ;; establishing that if the elevation is 15m or greater than the substrate is
land
    [set pcolor black                           ;; for visual purposes this defines land as being the colour black
     set habitat land]                          ;; 5 equals land
  if elevation <= 0 and elevation > -1          ;; elevation below 0 but greater than -1 is intertidal
    [set pcolor blue - 2                        ;; if the elevation is intertidal it is coloured light-blue
     set habitat intertidal]                    ;; 0 equals intertidal for the future use in this model
  if elevation <= -1                            ;; elevation below -1 is underwater
    [set pcolor blue                            ;; if the elevation is underwater it is coloured blue
     set habitat water]                         ;; 6 equals water for the future use in this model
```

```
  if (elevation < land-elevation) and (elevation >= -0.4) and           ;; selecting specifically for patches that are considered intertidal influenced
     ((substrate = mud) or (substrate = mixed))                           ;; selecting specifically for patches that are the colour brown and yellow
      [ set veg-mass (random-float (500)) * energy-from-grass            ;; assigning a random value of energy that a patch of seagrass can offer to a
                                                                          bird calculated by taking range of biomass cover of typical eelgrass
                                                                         vegetation (0-25g/m2) and  multiplying by patch size (20m2) (energy from
                                                                         the grass then is varied based on a slider on the interface)
        set rhizome-mass (random-float (500)) * energy-from-rhizome  ;; again assigning a random value of biomass cover to each site for
                                                                         rhizomes (energy from the rhizomes then is varied based on a slider on the
interface)
        set pcolor scale-color green veg-mass 0 500]
    set pcolor scale-color pcolor elevation -20 20]                      ;; setting a scale of blue for different depths

  create-humans number-of-humans [                                       ;; creates number of humans based on slider 'number of humans'
    setxy random-pxcor random-pycor                                      ;; starts each human at random points on the map
    ]    ask humans [
         set color red                                                   ;; give properties the humans as the colour red
         set shape "person"                                              ;; make humans shape of a 'person'
```

```
          set size 2                                    ;; gives a size to humans
          set walking-speed 4.2                         ;; average human walking speed is 1.4m/s = 84m/min /20m =
4.2patches/min
          move-to one-of patches with [                 ;; establishing that we want humans to start on patches that are on land or
                                                        deep enough water
            ((elevation > 2) and                        ;; **could modify this to have more specific access points
        (pxcor = starting-point))
         or
        ((elevation < -3) and
        (pxcor = start-of-incline))]]


  create-brentgeese number-of-brentgeese [              ;; creates number of brent geese based on slider 'number of brentgeese'
    setxy random-xcor random-ycor                       ;; starts the brent geese at random coordinates anywhere on the site
  ]  ask brentgeese [
          set color black + 2                           ;; gives properties to the brent geese as the colour dark grey
          set shape "bird side"                         ;; giving brent geese a bird shape on visual model
```

```
set size 1.5                                              ;; giving brent geese a size on visual model
set start-energy random (1000 - 840) + 840                ;; giving each brent goose within the model an random starting energy
                                                          between 421 and 1000 based on avg energy stores of brant geese upon
                                                          arrival in wintering grounds (Stillman et al. 2015)
set energy-min start-energy                               ;; setting minimum energy requirements to that of energy birds start with
set energy start-energy                                   ;; giving energy current the value of starting energy (but this value will
                                                          change with the model)
set energy-assimilation .024                              ;; this value is taken from the energy balance equation for brent geese
                                                          observed on the Exe estuary (69.45 kJ/12.17hrs spent feeding = .095
                                                          kJ/min)
set body-mass random (1540 - 1200) + 1200                 ;; average range of brent goose mass during winter months
set flight-cost ((0.679 * (body-mass ^ 0.818)) / 1800)    ;; based on the equation of flight cost 'kj/hr = 0.679 x W^0.818'
set feed-depth -0.4                                       ;; feeding depth as defined in literature BRENT GOOSE max reach is 40 cm
set flight-prob 7.6                                       ;; flight probability based on mean percentage of bird reacting to a
                                                          disturbance source within 250m or less
set flight-dist 12.84                                     ;; mean flight distance when disturbed by a source within 250m (256.8 m /
                                                          20m patch size)
```

```
    set flight-speed 1038                               ;; average flight speed in autumn was recorded as 17.3m/sec = 1038m/min
    set rmr (308 * ((body-mass / 1000) ^ 0.73)/ 1440)   ;; resting metabolic rate of brent geese
    set thermo-cost 0.004 * (18.1 - 11)                 ;; 5.5 kj/24hrs per degree = .004 kj/min per degree below LCT which is
                                                        18.1 (Collop 2015). Average winter temperature exmouth in winter is 11
                                                        meaning. 0.004 * 7.1 = .03
    set patches-visited (list patch-here)               ;; telling birds to start creating a list of patches visited starting with the patch
                                                        they are on
    set activity resting                                ;; setting starting activity state to 0 (rest)
    set disturbance undisturbed                         ;; starting off birds as undisturbed state
    move-to one-of patches with [elevation < 2.5 ]      ;; assuming birds start at areas that are intertidal or water
    ]


create-wigeons number-of-wigeons [                      ;; creates number of wigeon based on slider 'number of wigeon' that start at
                                                        random coordinates that are generated
  setxy random-xcor random-ycor                         ;; starts the wigeon at random coordinates anywhere on the site
]  ask wigeons [
```

```
    set color brown + 1                                     ;; gives properties to the wigeon as the colour light brown
    set shape "bird side"                                   ;; type of shape used for wigeon
    set size 1.5                                            ;; size of wigeon in visual models
    set start-energy random (715 - 660) + 660               ;; giving each Wigeon within the model a random starting energy between
                                                            715 and 660kj based on avg energy stores of wigeon upon arrival on
                                                            wintering grounds
    set energy-min start-energy                             ;; want birds to reach equilibrium so the energy minimum will be the energy
                                                            they start with
    set energy start-energy
    set body-mass random (723 - 539) + 539                  ;; average range of wigeon mass during winter months
    set flight-cost ((0.679 * (body-mass ^ 0.818)) / 1800)  ;; kj/hr = 0.679 x W^0.818
    set feed-depth -0.34                                    ;; feeding depth this is based on approximately 70% of the body being able
                                                            to go under water with average length of wigeon being 45-51cm ;
    set flight-prob 7.6                                     ;; flight probability based on mean percentage of bird reacting to a
                                                            disturbance source within 250m or less
    set flight-dist 10.6                                    ;; mean flight distance when disturbed by a source within 250m (212.41 m /
20m patch size)
```

```
        set flight-speed 1080                                ;; 18m/s = 1080m/min
        set rmr (308 * ((body-mass / 1000) ^ 0.73)/ 1440)    ;; resting metabolic rate for wigeon; .013
        set thermo-cost 0.004 * (18.1 - 11)                  ;; 5.5 kj/24hrs per degree = .004 kj/min per degree below LCT which is 18.1
                                                             (Collop 2015). Average winter temperature Exmouth in winter is 11 meaning
                                                             0.004 * 7.1 = .03
        set patches-visited (list patch-here)                ;; telling birds to start creating a list of patches visited starting with the patch
                                                             they are on
        set activity resting                                 ;; setting starting activity state to 0 (rest)
        set disturbance undisturbed                          ;; starting off birds as undisturbed state
        move-to one-of patches with [elevation < 2.5 ]       ;; assuming birds start at areas that are intertidal or water
        ]
  reset-ticks
end                                                          ;; completes the procedure that sets up the patches

;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;; GO PROCEDURE ;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
```

```
to go                                              ;; defines the procedure named go
  ask patches[advance-tide]                        ;; procedure to change tide state
  ask patches[check-total-biomass-available]       ;; procedure to report if any biomass is available on the site to avoid foraging
                                                   when it isn't
  ask brentgeese[patchset]                         ;; procedure for brentgeese to record the patch they are on (used for
                                                   calculations of distance travelled)
  ask wigeons[patchset]                            ;; procedure for brentgeese to record the patch they are on (used for
                                                   calculations of distance travelled)
  ask brentgeese[check-status]                     ;; brent geese determine their current state to decide if they need to flee or
                                                   to forage
  ask wigeons[check-status]                        ;; wigeon determine their current state to decide if they need to flee or to
                                                   forage
  ask humans[move-humans]                          ;; procedure that makes humans move in space
  ask brentgeese[check-death]                      ;; procedure for Brent goose death based on energy levels
  ask wigeons[check-death]                         ;; procedure for wigeon death based on energy levels
  ask humans[check-time]                           ;; procedure to limit human access to the sites based on time of day
```

```
  ask patches[record-distribution]     ;; procedure to count number of times a patch has been visited by a bird and
                                       human
  tick                                 ;; primitive procedure created by netlogo that that advances the counter by
                                       one tick
  if ticks >= 1440 [ stop ]            ;; procedure that identifies if ticks have gone 1440 or more times and if so it
                                       stops the procedure (ticks represent minutes and 1440 minutes in a 24 hour
                                       day)
end                                    ;; completes the procedure named go


;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;
;;;; SUBMODELS ;;;;;;;;;;
;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;;

to advance-tide
   set depth
```

```
   elevation - (1.085 * cos (.5 * (ticks - time-high-tide)) + 1.435)   ;; inputting depth as a variable that depends on
                                                                       elevation (elevation is a value given based on dead
                                                                       low tide)
                                                                       ;; establishing an equation for the depth of water on
                                                                       patches based on the existing height of the patch
                                                                       (assigned randomly in clusters at setup)
if (depth > 0)                                                         ;; then inputting the equation for determining tidal
                                                                       height (this is based on the average tidal range
                                                                       associated with the Exe Estuary

  [set biomass-available veg-mass]
if (depth <= 0) and (depth > -0.4) and (veg-mass = 0)                  ;; this was listed as being from 0.35 to 2.52 meaning
                                                                       that the average is 1.435 with a fluctuation of 1.085)
 [set pcolor blue + 2                                                  ;; giving different visual attributes to different depths of
                                                                       water (0.4 is used as a cut off because that is the
                                                                       greatest depth Brent goose can feed)

    set biomass-available veg-mass]
if (depth <= 0) and (depth > -0.4) and (veg-mass > 0)
```

```
    [set pcolor green + 1
      set biomass-available veg-mass]
  if depth < -0.4  and (veg-mass = 0)                                                    ;; establishing that if the depth is greater than 0.4 then
                                                                                         biomass available is 0 because the depth is greater
                                                                                         than feeding depth
    [ set pcolor blue - 2]
  if depth < -0.4  and (veg-mass > 0)
   [set pcolor green - 2
      set biomass-available 0]
  ifelse ((depth <= 0 and depth >= -2)) or
        (depth > -2 and substrate = mud) or
        (depth > -2 and substrate = mixed)
       [set unfavourable-substrate 1]
       [set unfavourable-substrate 0]
end

to check-total-biomass-available
```

```
   ifelse count patches with [biomass-available > 0] > 0
   [set total-biomass-available 1]
   [set total-biomass-available 0]
end

to patchset                         ;; code for setting starting patch
  set start-patch patch-here        ;; restarts each time step to make sure all movements in next time step are based of where birds are at the end of
                                    the last time step
  set activity 0                     ;; setting starting activity to rest
end

to check-status
  flee?
end

to flee?                                                                                    ;;defining a procedure for birds to flee when they
                                                                                            encounter humans too close
```

```
ifelse count humans > 0 and
((distance min-one-of humans [distance myself] ) <= FID) and
                                                                   ;; at the moment this is defined as FID which is a
                                                                   slider on the interface
 ((random-float 100) <= (100 - (flight-prob * (distance min-one-of humans [distance myself]))))
                                                                   ;; establishing a way of randomly selecting a number
                                                                   between 1 and 100 and if that number is less than or
                                                                   equal to the prob-dist then bird reacts
[back flight-dist
                                                                   ;; average flee distances based on values observed
                                                                   on Exe when FID is less than 250m
 set energy
                                                                   ;; room here for implementing a habituation
                                                                   equation and distinction of reaction to disturbance
                                                                   sources
     energy - ((flight-dist * flight-cost))
```

```
                                                         ;; applying a cost to fleeing while foraging  to energy
                                                         budget which is in the form of distance times flight
                                                         cost and lost energy from feeding if they just fed
 set start-patch patch-here

 set disturbance disturbed
                                                         ;; giving an identity to being disturbed so it can be
                                                         measured
ifelse distance start-patch > ((flight-speed / 20) * 0.7 ) ;; average bird flight speed/min relative to species
                                                         divided by 20m (patch width) * 0.5 to reflect distance
                                                         covered in 30 seconds. Anything more and bird would
                                                         lose too much feeding time on the patch

[rest]
[ifelse energy <= energy-min                             ;; saying that if the energy level of the birds is below
                                                         the literature kj required for daily maintenance of then
                                                         birds must feed
[forage]                                                 ;; if birds need energy they forage if not they rest
```

```
      [rest]]]                                              ;; NOTE*** need to add value for efficiency of food
                                                            value conversion literature indicates between 28.8%
                                                            (Mayhew 1988) and 46% (Madsen 1988) for Wigeon
   [set disturbance undisturbed
    ifelse energy <= energy-min                             ;; saying that if the energy level of the birds is below
                                                            the literature kj required for daily maintenance of then
                                                            birds must feed
    [forage]                                                ;; if birds need energy they forage if not they rest
    [rest]]
end

to forage
  ifelse total-biomass-available > 0
    [move-to one-of patches with[biomass-available > (mean[biomass-available] of patches)]
                                                            ;; telling birds to move around the site to select the
                                                            highest biomass plants (based on optimal foraging
                                                            theory) and with necessary feeding depth
```

```
    set energy
    energy - (flight-cost * (distance start-patch))                ;; setting energy to reflect the cost of moving to the
                                                                   eelgrass patch using the flight cost for birds
    set activity locomotion
    check-movement]                                                ;; checking to see if bird has moved so far that it has
                                                                   lost more than half feeding time

  [rest]
end

to check-movement
  ifelse distance start-patch > ((flight-speed / 20) * 0.7 )      ;; average bird flight speed/min relative to species
                                                                   divided by 20m (patch width) * 0.5 to reflect distance
                                                                   covered in 30 seconds. Anything more and bird would
                                                                   lose too much feeding time on the patch
  [set start-patch patch-here
```

```
    rest]                                    ;; if too much feeding time is lost (greater than 30
                                             seconds) then birds must rest and lose the feeding
                                             time due to movement for that time step
  [set start-patch patch-here                ;; change start-patch because moved
    check-depth]                             ;; however if there is still 30 seconds, once at the site,
                                             birds have to check the density to see if room to
                                             forage
end

to check-depth                               ;; this step is commented out. For now assuming that
                                             biomass available does a sufficient job of limiting birds
                                             to resources without having to have birds specifically
                                             check for their species depth. In the future this may be
                                             useful with evaluating species with larger
                                             differences in feeding depth
    ifelse (depth >= feed-depth)              ;; establishing that for birds to feed on patches the
                                             food must first be within reach, this depth is species
```

```
                                                            specific and determined by the tidal cycle and the site
                                                            height
    [check-density]                                         ;; can add further detail for percentage reach at
                                                            greater depths but for now assuming that the birds
                                                            cannot feed at depths greater than defined feed-depth
    [rest]                                                  ;; if the depth is too great they rest
end

to check-density
  ifelse (count brentgeese-here + count wigeons-here) < 40
                                                            ;; setting a maximum density of a site so that not all
                                                            birds can go to one site; this was based on a two birds
                                                            per sq. meter which is typically observed during
                                                            feeding time when food is available
  [eat-grass]
                                                            ;; if less than max density then, birds eat grass
  [let unvisited patches with [not member? self [patches-visited] of myself]
```

```
                                                          ;; if more than max then birds record the patch as
                                                          visited
set patches-visited lput patch-here patches-visited
move-to one-of neighbors with-max[biomass-available]
                                                          ;; the birds move to a random neighbour with max
                                                          biomass
  ifelse (count brentgeese-here + count wigeons-here) < 40
                                                          ;; now the birds check the density on this new patch
  [eat-grass
                                                          ;; if the density is below the threshold then birds eat-
                                                          grass
   set start-patch patch-here]
                                                          ;; this patch is now the new start-patch
  [set patches-visited lput patch-here patches-visited
                                                          ;; the same process is repeated with the patch
                                                          previous being noted as the start patch
   move-to one-of unvisited with[biomass-available > (mean[biomass-available] of patches)]
```

```
                                                            ;; now birds will choose an entirely different regions
                                                            with the same rules as initial foraging
set energy
energy - (flight-cost * (distance start-patch))
ifelse (count brentgeese-here + count wigeons-here) < 40
[eat-grass
set start-patch patch-here]
[set patches-visited lput patch-here patches-visited
 move-to one-of unvisited with[biomass-available > (mean[biomass-available] of patches)]
   eat-grass
                                                            ;; there have been hopefully enough iterations to
                                                            break up any patches enough and prevent too many
                                                            birds visiting one patch
   set energy
   energy - (flight-cost * (distance start-patch))
                                                            ;; energy is changed to reflect the movement
   set start-patch patch-here
```

```
                                                                  ;; change start-patch because moved
        set patches-visited (list patch-here)]]]
                                                                  ;; to avoid a list of patches that birds can never visit
                                                                  again, birds refresh their list after all of the steps
end



to move-humans
  if count humans > 0
  [set heading (random (181) - 90)                                ;; starts each human headed in a random direction
                                                                  between 0 and 360 degrees
   ifelse (can-move? 1 and ([unfavourable-substrate] of patch-ahead 1) = 1) or      ;; if one of the five patches ahead of human is
                                                                  unfavourable (because humans move up to 4.2
                                                                  patches per step)
          (can-move? 2 and ([unfavourable-substrate] of patch-ahead 2) = 1) or
          (can-move? 3 and ([unfavourable-substrate] of patch-ahead 3) = 1) or
          (can-move? 4 and ([unfavourable-substrate] of patch-ahead 4) = 1) or
```

```
     (can-move? 5 and ([unfavourable-substrate] of patch-ahead 5) = 1) or
     (can-move? 1 and ([unfavourable-substrate] of patch-here) = 1)          ;; if the patch at location is unfavourable
      [set heading (180)]                                                    ;; human turns around and heads the other way
        [if not can-move? 1
          [setxy -30 -30]]                                                   ;; if humans can't move then they are placed at an
                                                                             access point
  forward walking-speed]                                                     ;; average walking speed for a human is 1.4m/sec and
                                                                             each tick is 1 minute so the humans move forward
                                                                             84m each time step and each patch represents 20
                                                                             meters so each person moves forward 4.2 patches
                                                                             from the direction they are initially placed at
end

to check-time                                                                ;; defines the procedure check-time
 if ticks > humans-active [                                                  ;; states that if ticks progress beyond slider 'humans-
                                                                             active'
   setxy -30 0]                                                               ;; all humans leave the environment (go to -30 0)
```

```
end

to eat-grass
  set energy
  energy  - (rmr) -  (0.06) + ((1.572 * (body-mass ^ 0.68)) / 60)            ;; bases intake rate on body mass and stays constant
    set activity feeding                                                     ;; activity state is now feeding
  ask patch-here
    [set veg-mass
      veg-mass - (0.0167 * (veg-mass / 20) - (3 * (10 ^ -15)))]               ;; establishing that once the bird selects and 'eats' the
                                                                             eelgrass, the eelgrass biomass in a patch will decline
  ifelse show-energy?                                                        ;; defines whether the show-energy? button on
                                                                             interface
    [set label energy]                                                        ;; if the show-energy? button is selected then the
                                                                             labels are set to energy
    [set label ""]                                                           ;; if the show-energy? button is not selected then the
                                                                             labels are set to nothing
```

```
end                                             ;; ending the procedure named eat-grass

to rest                                         ;; defining the procedure rest
  set energy                                    ;; tells the birds to lose energy while resting
      energy - (rmr)                            ;; energy is lost relative to resting metabolic rate
                                                owned by Brent goose and wigeon
  set activity resting
end

to check-death                                  ;; defining the procedure check-death
   if energy <= (0.2 * energy-min) [ die ]      ;; Birds will reach a point of no return limit of energy
                                                before reaching zero. For this model the point of no
                                                return has been defined as 20% energy-min ** may be
                                                able to establish this as BMR later
end                                              ;; ending the procedure named check-death
```

```
to record-distribution                              ;; defining the procedure to record bird and
distribution
  if count brentgeese-here > 0                      ;; saying that if there are Brent goose on the patch
     [set bg-visitation                             ;; add the count to the Brent goose-visitation
        bg-visitation + count brentgeese]           ;; same for wigeon
  if count wigeons-here > 0
     [set w-visitation
        w-visitation + count wigeons]
  if count humans-here > 0                          ;; same for humans
     [set human-visitation
        human-visitation + count humans]
end
```