Three-dimensional foraging behaviour of Northern gannets

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Abstract

Movements of animals form a vital link between individual behaviour and spatial processes affecting populations, communities and ecosystems. Predators often have to search for prey that is unpredictable or patchily distributed and increasingly have to do so in habitats that are changing as a result of climate change or anthropogenic activity. Our understanding of animal movement has been revolutionised by the development of miniaturised loggers which allow tracking of individual animals over a range of spatial and temporal scales. However, while flight heights of birds are a critical component of avian movement ecology, they have been little-studied in comparison to horizontal movements. In this thesis I examine the three-dimensional foraging behaviour of northern gannets (*Morus bassanus*) at the world's largest breeding colony, at Bass Rock, Scotland. I first combine GPS and pressure data to estimate flight heights, and develop a novel refinement that uses sea surface pressure data to correct estimated heights during long periods of sustained flight. I then investigate sexual differences and effects of weather on three-dimensional foraging behaviour, before examining potential population-level consequences of mortality from collisions with offshore wind turbines. I found that sexual differences in foraging behaviour extend to the heights at which birds fly, and that wind speed in particular has a marked effect on movements and behaviour at sea. I also found that predicted levels of mortality from offshore wind farms would be likely to retard population growth but unlikely to drive the population into long-term decline. My thesis describes some of the complexity and flexibility of gannet foraging behaviour and highlights the importance of understanding movements in three dimensions.

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Chapter 1 : Introduction

1.1 Three-dimensional tracking of animal movement

Movements of individuals are a key component of population ecology and central to species' responses to the global challenges of climate change, habitat loss, invasive species and infectious diseases (Wikelski et al., 2007). Animal movement is orientated to foraging, avoiding predators, finding shelter and reproduction but is limited and scaled by time and space (Nathan et al., 2008). Foraging theory suggests that behaviour should be adjusted to optimise foraging efficiency and maximise fitness, requiring complex movement decisions at multiple spatial and temporal scales (Baker et al., 2004, Hamer et al., 2009, Reynolds, 2012). Predators often have to search for patchy or unpredictable prey (Eide et al., 2004, Benoit-Bird et al., 2013, Kittle et al., 2017) using strategies that can be broadly grouped into two types; ambush and active searching (Higginson and Ruxton, 2015). Those that actively search for prey use a variety of strategies to maximise prey encounter over different scales (Weimerskirch, 2007, Auger-Methe et al., 2016, Dannemann et al., 2018, Freitas et al., 2018).

Until recent decades, knowledge of foraging movements was limited to visual observations but technology now allows us to track individual animals, with important consequences for studying the ecology, evolution and conservation of species (Webster et al., 2002). The first devices transmitting radio signals were deployed on animals in the 1950's, providing a much greater insight into horizontal movement behaviour (LeMunyan et al., 1959, Cochran and Lord, 1963, Southern, 1964, Southern, 1970). Initially these devices were relatively large, heavy and limited in range and accuracy, but advances in radio telemetry technology now make it possible to track fine-scale movements of animals as small as insects along with long-distance migratory journeys of small passerines (Entwistle et al., 1996, Bowlin et al., 2005, Decourtye et al., 2011, Hagen et al., 2011, Knutson et al., 2018).

The tools available for animal tracking have now increased in number and include light-level geolocators, archival Global Positioning System (GPS) loggers and ARGOS-GPS PTTs (platform terminal transmitters) (Lopez et al., 2015). Geolocators, which record light level from which latitude and longitude can be estimated, are small, light-weight devices that can provide data for up to several years, making them suitable for tracking large-scale movements including migrations. However, a disadvantage of these devices is poor spatial resolution (Egevang et al., 2010, Heckscher et al., 2011, Ouwehand et al., 2016). GPS-based devices provide latitude and longitude data with the greatest precision and temporal resolution, with the additional advantage in the case of archival GPS devices that they are small and light. However these require the animal to be recaptured to retrieve the data. If recapture is unlikely, remote download GPS devices such as GPS-RF (radio-frequency), GPS-GSM (linked to the GSM (Global System for Mobile) network) and those linked to the ARGOS satellite system allow remote data access (Bridge et al., 2011).

To build a more complete understanding of space use by animals, it is important to study the vertical as well as horizontal dimensions of movement. The height at which birds and mammals fly has been of interest since long before it was possible to measure flight height reliably (Stebbins, 1906, Meinertzhagen, 1954). Flight height has important consequences for flight speed and energetics (Bruderer et al., 1995, Mandel et al., 2008), the detection and capture of prey (Garthe et al., 2014, Helms et al., 2016) and energy and water budgets (Klaassen, 1996, Carmi et al., 1992). Estimates of flight height can be made using a variety of methods. Visual observations and radar can estimate heights within a limited range of the observer but are restricted by light and weather conditions and they do not often allow recording of individuals over entire trips (Johnston et al., 2014a, Johnston et al., 2014b, Cleasby et al., 2015a, Borkenhagen et al., 2018). Radar also underestimates the abundance of low-flying individuals and visual estimates are difficult for birds at high elevations (Huppop et al., 2006). GPS loggers can be used to provide estimates of the height of the device above the ellipsoid, a mathematically generated surface of the earth based on Cartesian coordinates, but with an error typically ± 20 m (Cook et al., 2012). As a result they are not useful for most biological contexts although the accuracy can be increased by allowing longer power-up time and shorter intervals between fixes (Bouten et al., 2013, Ross-Smith et al., 2016). However, high power requirements (approximately 0.15 Watts over about 30 seconds) required to obtain GPS locations result in reduced battery life and limited deployment durations (Corman and Garthe, 2014, Ross-Smith et al., 2016).

1.2 External influences on flight behaviour

Birds exhibit a wide variety of foraging strategies which utilise airspace in different ways, from high-speed flight at low altitudes to capture insects in the air column to soaring, high-elevation flight to locate ephemeral food resources on the ground (Shepard and Lambertucci, 2013, Warrick et al., 2016). All flight modes are influenced by morphology (Shatkovska and Ghazali, 2017) but require individuals to adapt to rapidly changing environmental conditions to reduce the energy costs of movement or adjust movement speed (Kogure et al., 2016, Shamoun-Baranes et al., 2016, Richardson et al., 2018).

Tracking birds during long-distance migrations has revealed the impact of global wind patterns on behaviour, influencing the timing of departure, speed of travel and flight paths (Alves et al., 2016, Horton et al., 2016a, Hedenstrom and Akesson, 2017). High-resolution tracking over shorter time periods has also revealed how behaviour is influenced by wind at much finer scales (Gibb et al., 2017). Flight altitude may be adjusted in response to weather conditions, playing a key role in reducing energy costs and determining speed of travel, but it is also activity-specific (Kahlert et al., 2012, Gerdzhikov et al., 2014, Malmiga et al., 2014, Weimerskirch et al., 2016, Bruderer et al., 2018) as well as varying with time of day and topography (Bruderer et al., 1995, Liechti, 2006, Avery et al., 2011).

To understand how birds respond to the environmental conditions during flight it is now possible to annotate movement tracks with additional information about conditions encountered whilst on a particular path (Dodge and Bohrer, 2013). Weather reanalysis datasets, products of global atmospheric models with assimilated meteorological observations, are increasingly being used to annotate animal movement tracks (Safi et al., 2013, Vansteelant et al., 2017). The applicability of these datasets for integration with animal movement data has improved greatly as the resolution of the weather data has decreased, with global data now available at spatial resolutions of < 10 km and at temporal resolutions of 3 - 6 hours (Dee et al., 2011).

1.3 Importance of understanding space use by birds

In recent decades the importance of estimating how birds and mammals use the aerial environment has increased as rising global temperatures have affected atmospheric circulation, with impacts on rainfall, storm frequencies and wind regimes (McInnes et al., 2011, Trenberth, 2011). Anthropogenic structures and air-borne vehicles have also encroached on habitats, introducing potential hazards for both wildlife and people (Dolbeer, 2006, Barrios and Rodriguez, 2004, Biondi et al., 2013, Voigt et al., 2018). These anthropogenic changes to the environment in addition to the changes to atmospheric conditions in the context of climate change make it important to predict how avian behaviour may be influenced (Gibb et al. 2017). For instance, the height at which vultures fly, which is dependent on time of day and season, can have implications for potential bird strike with aircraft (Avery et al., 2011).

Evidence of observed climate change impacts is strongest and most comprehensive for natural systems (IPCC, 2014). Increases in global temperatures during the 20th century have been linked to wide-spread range shifts in flora and fauna with the geographical ranges of marine species ranges shifting at an order of magnitude faster than those of terrestrial species as a result of warming seas (Sorte et al., 2010). In response to threats from global climate change, a large increase in renewable energy infrastructure is planned in the marine environment, including wind and tidal turbines and wave energy devices (Pelc and Fujita, 2002). These may cause collision mortality, disturbance and habitat loss to marine taxa (Furness et al., 2012, Wade et al., 2016, Johnston et al., 2018) raising concerns about potential adverse effects on populations of seabirds and other species (Furness et al., 2012, Sebastian-Gonzalez et al., 2018).

1.4 Three-dimensional behaviour of seabirds

Seabirds are the most threatened group of birds in the world, facing threats from climate change, energy generation, fisheries and invasive alien species (Croxall et al., 2012). During the breeding season, seabirds need to balance their own nutritional needs with those of their offspring whilst being constrained to return repeatedly to the nest. They are therefore restricted in the distances they can travel and the duration of time they can be absent from the nest-site (Elliott et al., 2009). Seabirds forage for patchily distributed prey whose location is strongly influenced by environmental conditions (Santora et al., 2017). These prey patches are often predictable (Weimerskirch, 2007) but threats to the marine environment have raised increasing concerns about adverse changes in prey quantity, nutritional quality and distribution, and the ability of seabirds to adapt to these changes (Howells et al., 2017, Schoen et al., 2018).

Until recently, relatively little was known about the behaviour of seabirds at sea. Early surveys were ship-based, until aerial surveys and radar were employed to establish densities at sea (Briggs et al., 1985). Much of this work was driven by a need to understand the potential impact of offshore developments (Ainley et al., 2012). Now, bird-borne loggers are increasingly being used to identify important feeding areas and migration routes, providing data to inform the designation of Marine Protected Areas and the monitoring of ocean health (Parsons et al., 2008, Mallory et al., 2010, Masello et al., 2010, Camphuysen et al., 2012, Ceia et al., 2015, Arizaga et al., 2018). Many such tracking studies, however, and particularly those requiring high-resolution GPS data, have been restricted to particular stages of the breeding season when birds can most easily be captured, with the pre-laying stage in particular often being missed (Isaksson et al., 2016).

Seabirds can make long foraging trips during chick rearing that may cover 1000s of km and last up to several weeks (Phalan et al., 2007, Magalhaes et al., 2008). Sex-specific foraging behaviour is a common trait among seabirds, initially linked to sexual size dimorphism but now known to also occur in a variety of sexually monomorphic species (Gray and Hamer, 2001, Thaxter et al., 2009). Sexual differences in foraging areas, diets and parental duties among monomorphic species have been attributed to intra-specific competition, sex-specific nutritional requirements or differences in parental investment strategies (Lormee et al., 1999, Elliott et al., 2010, Phillips et al., 2011).

Flight heights of seabirds are known to vary between species and with behaviour and weather conditions (Schreiber and Burger, 2001, Cleasby et al., 2015a). Lesser black-backed gulls (*Larus fuscus*) fly higher over land than sea and higher at night than during the day (Ross-Smith et al., 2016) while red-footed boobies (*Sula sula*) double their height at the end of each foraging trip, probably to facilitate locating the colony or avoid attacks from great frigatebirds (*Fregata minor*) (Weimerskirch et al., 2005a). Frigatebirds can use uplift beneath clouds to gain altitudes of over 4000 m, allowing them to cover long distances by gliding until they reach another cloud updraft (Weimerskirch et al., 2016). In contrast, albatrosses cover long distances with little mechanical cost by moving within the shear wind directly above the surface of the ocean (Sachs et al., 2012).

1.5 Study species

Northern gannets (*Morus bassanus*) (hereafter gannets) are the largest breeding seabird in the North Atlantic Ocean (Nelson, 2002). Gannets have a single egg clutch which they incubate for approximately 6 weeks after which it takes 13 weeks for the chick, being brought food by both parents to reach fledging age (Nelson, 2002). Breeding success is typically 0.60 – 0.90 chicks fledged per breeding pair (Nelson, 2002, JNCC, 2016). The survival estimate for gannets in their first year after fledging varies between colonies but for the birds from the Bass Rock the estimate is ~ 0.542 (Wanless et al., 2006). Gannets typically have a period of 4-5 years of immaturity during which annual survival probabilities increase each year after the first year (Table 1.1). Once they become adults, gannets can no longer be aged from their plumage and so changes in productivity and survival associated with senescence are difficult to assess (Wanless et al., 2006). Immature gannets are pelagic in their first and second years and as a result are rarely seen at colonies. However, from their third summer they begin to associate with breeding colonies and act increasingly as central place foragers (Votier et al., 2011, Grecian et al., 2018).

Table 1.1. Mean estimates of age-specific survival of gannets from Bass Rock taken from Wanless et al. (2006).

Age Class	**Annual survival estimate**	**95% confidence limits**
1st year	0.542	0.516 – 0.567
2nd year	0.779	0.765 – 0.793
3rd year	0.859	0.848 – 0.869
4th year	0.863	0.852 – 0.874
5th year	0.863	0.852 – 0.874
Adult	0.916	0.910 – 0.922

Adult gannets are present at colonies between March and September each year. Outside of these months they are pelagic and occur further south than their breeding areas (Stone et al., 1995, Fort et al., 2012). Colonies vary in size from just a few pairs to tens of thousands and are found around the coast of the UK (Figure 1.1) and in the Channel Islands, Faeroes, Norway, Iceland and north-east Canada (Nelson, 2002). The population in the UK has been increasing steadily since the early 20th century when they were first afforded protection from culling at the colonies (Nelson, 2002). Between the first full census of all UK gannet colonies in 2003-04 and the most recent in 2013-2015 the population increased by 34 % (JNCC, 2016).

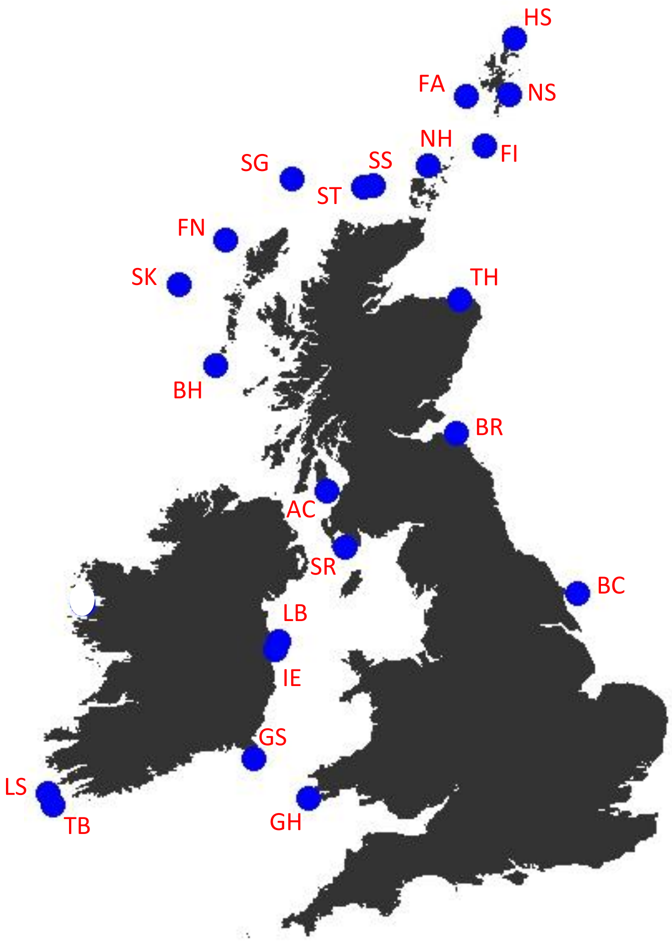

Figure 1.1. Locations of UK gannet colonies with 100 AON's (apparently occupied nests) during their most recent count. HS - Hermaness, FA – Foula, NS - Noss, FI - Fair Isle, NH - Noup Head, SS - Sule Skerry, ST - Sule Stack, SG - Sule Sgeir, FN - Flannan Isles, SK - St Kilda, BH – Barra Head, AC - Ailsa Craig, SR - Scar Rocks, LB - Lambray, IE - Ireland's Eye, GS - Great Saltee, TB - Bull Rock, LS - Little Skellig, GH - Grassholm, BC - Bempton Cliff, BR - Bass Rock, TH - Troup Head.

1.6 Foraging behaviour

Gannets are medium-range foragers capable of travelling more than 1000 km on a single trip (Hamer et al., 2007) although trip distance is dependent on population size and proximity to other colonies (Lewis et al., 2001, Wakefield et al., 2013). At Bass Rock, the typical range of trips is 150 – 300 km over 20 – 30 h (Hamer et al., 2009, Cleasby et al., 2015b). Gannets target frontal areas (Scales et al., 2014, Cox et al., 2016) where they feed on lipid-rich pelagic fish such as mackerel (*Scomber scombrus*), herring (*Clupea harengus*), sprats (*Sprattus sprattus*) and sandeels (mainly *Ammodytes marinus*) (Lewis et al., 2003, Hamer et al., 2007). Fish are caught using a variety of techniques including plunge diving, scooping from the surface and by scavenging discards from fishing vessels (Hamer et al., 2009, Camphuysen, 2011, Votier et al., 2010, Votier et al., 2013) although a discard ban is now in place on pelagic stocks meaning that gannets are no longer able to obtain as much food by scavenging from fishing vessels (Catchpole et al., 2018). Breeding adults are repeatable in their foraging behaviour, making consecutive trips over a narrow range of bearings both within and across years, providing some evidence that they may learn and remember the locations of profitable feeding areas from one year to the next (Patrick et al., 2014, Wakefield et al., 2015). However, durations and ranges of trips are less repeatable, probably reflecting variation in environmental conditions (e.g. wind speed and direction) and feeding opportunities encountered at sea (Hamer et al., 2001). Foraging areas also differ among years and, at least in some years, between sexes (Lewis et al., 2002, Hamer et al., 2007, Pettex et al., 2012, Davies et al., 2013). Immature gannets have been less well studied than adults but have less repeatable foraging tracks than adults, ranging more widely as they develop their individual foraging strategies (Votier et al., 2017, Grecian et al., 2018).

1.7 Study site

The Bass Rock, situated approximately 2 km off the coast of East Lothian in the Firth of Forth, SE Scotland (6º 6’ N, 2º 36’ W) has been associated with gannets since at least 1447 with records of chicks being culled for food there between 1511 and 1865 (Nelson, 2002). Since the first official count of apparently occupied nests (AONs) in the early 1900’s the Bass Rock population has risen from approximately 2000 breeding pairs to become the largest colony of gannets in the world with an estimated 75,259 apparently occupied nests in 2014 (Murray 2015) (Figure 1.2). Population growth at gannet colonies is density-dependent with per-capita growth declining as population size increases (Lewis et al., 2001). Despite this decline, a 57% increase in the number of apparently occupied nests between 2004 and 2014 has seen the Bass Rock colony brought to the point where there is little unoccupied nesting space available (Figure 1.3a) (Murray et al., 2015).

The main study site for gannets on Bass Rock is located next to the remains of an old chapel, above the cliffs fringing the rock (Figure 1.3b). This area is well suited to fieldwork with a large area in which to work and access to ample numbers of breeding birds.

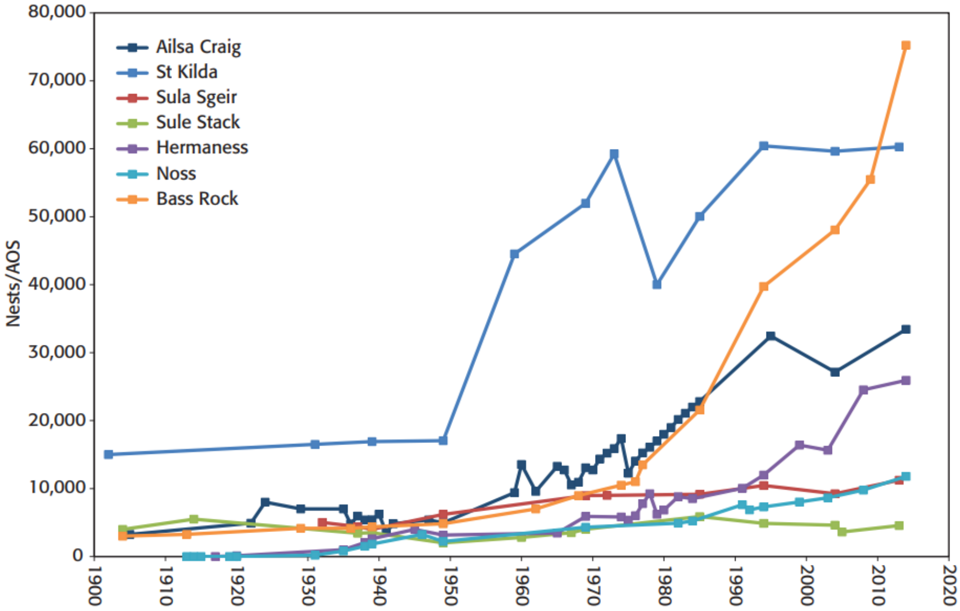

Figure 1.2. Population growth rate of the Bass Rock gannet colony in the context of six other Scottish gannetries. Plot taken from Murray et al. (2015).

The gannets on the Bass Rock have been studied extensively since the early 1960s, both by observations at the colony (Nelson, 1964, Nelson, 1966, Davies et al., 2013) and, since 1998, using tracking devices (Hamer et al., 2000, Lewis et al., 2003, Kubetzki et al., 2009, Wakefield et al., 2015, Cleasby et al., 2015a). These studies have identified foraging ranges, core foraging areas and identified traits in individual foraging behaviour. Wind farm developments which have been planned and consented for construction in the North Sea fall within the foraging range of gannets from Bass Rock, making it a colony for which is it particularly pertinent to examine foraging behaviour (The Crown Estate, 2017).

1.8 Outline and aims of this thesis

This thesis aims to increase knowledge and understanding of gannets' foraging behaviour, with the main aim being to investigate variation in flight height during foraging trips.

Chapter 2, the first data chapter, introduces the method I use for estimating flight height in the subsequent data chapters. Estimates of flight height in seabirds have not been studied as comprehensively as horizontal movements yet have important consequences for ecology and conservation. Seabirds can make journeys during the breeding season of hundreds of km during which they allocate their time between periods on the water and periods in flight. This means height can be estimated using changes in pressure between time on the water and time in flight. However, long periods of time in flight are known to increase the error in height estimates. Here I outline a novel refinement to using atmospheric pressure where I incorporate reanalysis pressure data to improve height estimates during longer periods in flight.

In Chapter 3 I investigate behavioural differences between male and female gannets. Previous work has recorded differences in foraging locations, dive behaviour and diet, and I was therefore interested to see whether these differences extended to height and how this might have potential consequences for conservation in the context of prey distribution and installation of wind farm developments.

Chapter 4 considers environmental influences on foraging behaviour. The marine environment experiences particularly challenging weather conditions known to affect seabird behaviour. Here I incorporate weather data from a reanalysis dataset to investigate how weather conditions affected the behaviour of gannets at sea.

Among the uncertainties identified in estimating collision risk at offshore wind farm sites is variation in the behaviour of birds in relation to sex, age and breeding stage. In Chapter 5 I use a combination of GPS and altitude data from adults at two breeding stages and from immature birds to examine how potential collision risk might change throughout the year and for birds of different age and sex. I then make a projection for how predicted collision risk might impact population growth.

In Chapter 6 I draw the conclusions of the four data chapters together and suggest future areas for research that have arisen from this work.

Figure 1.3. (a) The Bass Rock gannet colony on 23rd July 2014. The area within the red shape is the area is the study site; **(b)** is a close up on the study area, the building is the remains of St Baldred's chapel, yellow line indicates the path, blue indicates non-breeders displaced when we are present and the red shapes indicate the areas from which birds are caught and tagged. Access to the rest of the island is impossible due to breeding birds. Photo credits; **(a)** Murray et al. (2014), **(b)** Murray et al. (2015).

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Chapter 2 : Estimating flight heights of seabirds using atmospheric pressure and a global reanalysis dataset

Abstract

Flight heights of birds are a critical component of avian movement ecology but little-studied in comparison to horizontal movements. Flight height can be assessed by equipping birds with pressure loggers and calibrating pressures obtained during flight against atmospheric pressure at ground level. However, changes in surface atmospheric pressure over both time and space can introduce potentially large errors into height estimates obtained this way, particularly during long periods of sustained flight. Here I combine GPS and pressure data to examine the variability in flight height estimates during foraging trips of a mid-ranging marine predator, the northern gannet. I first use GPS data to identify when birds settle on the water during trips and calibrate pressures obtained during flight against sea surface pressure at the start or end of each flight bout (Method 1). I then develop and explore a novel refinement that uses ERA-Interim reanalysis sea surface pressure data to correct estimated heights during long sustained periods of flight, accounting for both temporal and spatial changes in atmospheric pressure throughout each bout (Method 2). I found that individual flight bouts lasted up to 514 minutes and covered up to 381 km, with ~10 % of bouts longer than 2 hours and 15 % covering > 50 km. Consequently, the median error in flight height assessments using Method 1 was calculated to be 3.9 m, with estimated heights often showing continued drift during long periods of sustained flight, in some cases resulting in negative height estimates. This problem was greatly reduced using Method 2, with a significant positive relationship between both the distance and duration of a flight bout and the absolute difference in mean heights estimated using each method. These results indicate that the use of environmental re-analysis data to correct for spatial and temporal changes in atmospheric pressure during individual flight bouts could greatly improve flight height estimates, particularly for species that spend long periods in sustained flight and/or cover

large distances without landing and/or in regions or at times of year when atmospheric circulation is highly variable.

2.1 Introduction

Understanding how birds use aerial environments is a critical component of avian movement ecology. Variation in flight altitude has potential consequences for the detection and capture of prey (Garthe et al., 2014), energy and water budgets (Finn et al., 2012, Carmi et al., 1992) and interactions with humans (Horton et al., 2016b). In turn, flight height is influenced by weather conditions including wind and rain (Liechti, 2006, Kemp et al., 2013), which are likely to be affected by changes in climate (Kovats et al., 2014). The ability to gather fine-scale three-dimensional movement data from free-ranging birds is of increasing importance in the context of wind power. Generation of electricity from wind energy is rapidly increasing (Kumar et al., 2016), raising concerns about potential ecological impacts, including both displacement and mortality of birds from collision with turbine blades (Masden et al., 2009, Boehlert and Gill, 2010). The impacts of wind turbines on seabirds, one of the most threatened groups of birds globally (Croxall et al., 2012), are a particular concern as the number of offshore wind farms in European, North American and Chinese waters in particular is likely to increase greatly over the next few decades (Sun et al., 2012, European Wind Energy Association, 2016, U.S. Department of Energy, 2016).

Flight heights of birds can be estimated from land or ship-based visual observations and radar but these methods are restricted by light and weather conditions and do not allow recording of individuals over entire trips (Cleasby et al., 2015a, Borkenhagen et al., 2018). Bird-borne GPS loggers are well established tools for recording horizontal movements (Hamer et al., 2007, Sala et al., 2012, Wakefield et al., 2013, Hallworth and Marra, 2015, Gilbert et al., 2016) and can also provide information on height, but the accuracy of recorded flight heights (typically ± 20 m; (Cook et al., 2012)) is too low for most biological contexts

(Johnston et al., 2014a) as discussed in Chapter 1. Consequently, despite rapid advances in bio-logging technology (Evans et al., 2013, Gibb et al., 2017), bird-borne measurements of flight height over entire trips are still lacking for most species.

An alternative method for determining flight height is to use a bird-borne sensor to record atmospheric pressure. Using this method, pressures when the bird is in flight can be combined with the pressure at sea level (hereafter calibration pressure) to calculate flight height using the barometric formula (BerberanSantos et al., 1997, Wallace and Hobbs, 2006, Cleasby et al., 2015a, Helms et al., 2016). This method has been used in tropical regions (Weimerskirch et al., 2003, Weimerskirch et al., 2004, Weimerskirch et al., 2005b) where pressure systems are more stable over both time and space than at higher latitudes (Manabe and Hahn, 1981). Under these conditions atmospheric pressure at sea level may remain more-or-less constant across the temporal and spatial extent of foraging trips, making it possible to calibrate flight heights with sea level pressure measured at the colony. Difficulties arise, however, using this approach in regions or during times of year when atmospheric circulation is more variable. For instance, an error of 1 mb in calibration pressure equates to an error of approximately 8.4 m in flight altitude (Wallace and Hobbs, 2006).

During foraging trips, seabirds intersperse periods of flight with other activities including time on the water surface (Edwards et al., 2007, Gutowsky et al., 2014). If the latter can be identified, for instance using salt-water immersion loggers (Afanasyev and Prince, 1993, Edwards et al., 2007) or from behavioural classification of GPS data (Wakefield et al., 2013, Bennison et al., 2017), the atmospheric pressure recorded by a logger on the bird during this period can be used to re-calibrate pressure at sea level (Garthe et al., 2014, Cleasby et al., 2015a). However, this may be insufficient to reduce errors to manageable levels during long periods of sustained flight as the accuracy of height estimates decreases with time since calibration (Cleasby et al., 2015a).

Northern gannets (hereafter gannets) are medium-ranging neritic foragers that breed at sites in the North Atlantic Ocean and have been identified as one of the species at greatest potential risk from collision with offshore wind turbines (Furness et al., 2013). Approximately 60 % of the world’s breeding population of gannets breeds in the UK (Mitchell et al., 2004) with an estimated 75,000 pairs at the world’s largest colony, Bass Rock in SE Scotland (6^{o} 6’ N, 2^{o} 36’ W) (Murray et al., 2015). Foraging trips during chick-rearing at this colony can cover > 1000 km and last over 40 hours, with long periods of sustained flight interspersed with periods of active foraging including diving for prey and time at the water surface (Hamer et al., 2000, Hamer et al., 2007, Cleasby et al., 2015b). In this chapter I estimate the flight heights of gannets over entire trips using GPS and pressure loggers and explore how spatial and temporal changes in atmospheric pressure affect calculated heights. I also develop and explore a novel refinement that corrects estimated heights during long periods of flight by accounting for both temporal and spatial changes in atmospheric pressure.

2.2 Materials and methods

2.2.1 Study site and sampling

Fieldwork took place at Bass Rock, UK (6^{o} 6’ N, 2° 36’ W) between mid-June and mid-August of 2015 and 2016. Adult gannets with chicks (n = 32 in 2015, n = 29 in 2016; eight birds were sampled in both years) were caught at the nest using a 6-meter telescopic pole fitted with a metal noose or hook. Each bird was fitted with a metal British Trust for Ornithology ring and a coloured plastic ring with a unique alphanumeric code for easy identification at the nest site. A GPS logger (igotU-GT600, Mobile Action Technology, Taipei, Taiwan) was then attached to the upper side of the central tail feathers and a logger recording atmospheric pressure and temperature (MSR-145W, MSR Electronics, Seuzach, Switzerland) was attached to the central tail feathers, on the underside to reduce Bernoulli effects during take-off from the water. The GPS logger weighed 30 g and recorded location at 2-minute intervals; the pressure logger weighed 18 g and recorded at 1 Hz; both were attached using Tesa© tape. All sampled birds were recaptured after 7 - 14 days to retrieve loggers. Handling time of birds at both deployment and recapture was no longer than 15 minutes and on both occasions' birds returned to their chick almost immediately and resumed normal behaviour. The combined weight of loggers used in this study was < 2 % of body mass, well within the critical threshold of ~3 % of body mass (Phillips et al., 2003). Previous studies of gannets at this colony recorded that such deployments had no significant impact on trip duration or body mass (Hamer et al., 2007, Hamer et al., 2009, Cleasby et al., 2015b) however, the deployment of tags > 1% of body mass can have small but significant negative impacts on survival, reproduction, parental care and trip durations in birds.

2.2.2 Classification of behaviour at sea

I defined foraging trips as periods when the bird was greater than 500 m from the colony for more than 40 minutes (Carter et al., 2016). To remove any irregularities in the GPS data due to variation in satellite uplink time, I regularised the data by linear interpolation to 2-minute intervals using the package adehabitatLT v.0.3.20 (Calenge, 2006). Following Wakefield et al. (2013) I then used the speed and turning angles of birds to define three categories of behaviour at sea: commuting, active foraging (i.e. searching or diving for prey) and sitting on the water. Validation of these criteria against a separate sample of birds equipped with GPS loggers and time-depth recorders (TDRs) showed that, within individuals, 99 % of GPS locations occurring within 10 minutes of dives detected using TDRs were classified as foraging and 62 % of GPS locations classified as foraging occurred within 10 minutes of dives (Wakefield et al., 2013). I chose this method over alternatives such as Hidden Markov models (HMMs) (Bennison et al., 2017, Grecian et al., 2018) because the latter emphasise foraging bouts that include diving whereas gannets frequently exhibit search behaviour without diving (Hamer et al., 2009) and I was interested in all periods of active foraging whether they included dives or not.

2.2.3 Estimation of flight heights

I used the barometric formula (BerberanSantos et al., 1997, Wallace and Hobbs, 2006) to estimate height h (m) above sea level:

$$h = -\frac{KT}{mg}\ln\left(\frac{P}{P_0}\right) \qquad \text{Equation 2.1}$$

where P_0 and P are the atmospheric pressures (Pascals) at sea level and at height h (m), respectively; K is the universal gas constant for air (8.31432 N m mol^{-1} K^{-1}); m is the molar mass of air (0.0289644 kg mol^{-1}); g is the acceleration due to gravity (9.80665 ms^{-2}); and T is the temperature (K) of the atmosphere between P_0 and P. Validation of this method using loggers placed at different known heights indicated that the mean absolute error of height estimated by recording pressure was 0.88 m (range 0.32–1.92 m), although the precision of height estimates decreased linearly as the interval between observations of P_0 and P increased (Cleasby et al., 2015a).

To calculate birds' heights during periods of flight, I first removed pressure observations ≤ 5 seconds before and ≤ 3 seconds after dives (identified by a rapid increase in pressure above ambient), as there was typically high variation in pressure within these periods due to acceleration and turbulence. I also removed individual anomalous pressure readings (i.e. 1-second 'spikes') suggesting abrupt and implausibly rapid changes in height or turbulence around the logger, for instance as a result of the bird flexing its tail in flight. Following Cleasby et al. (2015a) I next smoothed the pressure data using a running median calculated using a moving window of 11 observations centred on each successive pressure reading (i.e. over a period of 5 s before and after each reading). I then selected those smoothed pressure records that coincided with GPS data-points, to give a location- and activity-specific measurement of pressure every 2 minutes. In doing so I discounted short periods of flight and on the water (< 6 min; i.e. fewer than 3 consecutive GPS points) to ensure accurate classification of behaviour from GPS data (see 2.2.2 above).

I used periods classified as in flight, whether commuting or active foraging, to obtain height-specific pressure data P and I used either the previous or the subsequent period on the water (whichever was closer in time) to estimate calibration pressure P_0 in each case. Before calculating P_0 I removed the first and final pressure records for each period on the water, to avoid including pressures during take-off or landing. P_0 was then calculated as the mean smoothed pressure over either the final remaining 8 minutes of the previous period or the first remaining 8 minutes of the subsequent period on the water (i.e. a mean of four smoothed data points generated from a total of 44 unsmoothed pressure readings in each case). This procedure required a minimum period of 10 minutes on the water to estimate P_0. Hence, because periods on water were often shorter than 10 minutes, in those cases I allowed up to two intervening flight periods before or after the period on the water used to estimate P_0.

This method (hereafter Method 1) allowed me to obtain estimates of P_0 during foraging trips, accounting for both spatial and temporal variation in atmospheric pressure at sea level. However, a previous analysis of how temporal changes in atmospheric pressure affected estimates of height at a single location indicated an average error of ~5 m in heights estimated with an interval of 2 h between measurement of P and P_0 (calculated from data in Cleasby et al. 2015a SOM). Hence, since gannets can sustain flight for much longer than this (Hamer et al. 2007), I additionally refined estimates of P_0 during flights using ERA-Interim reanalysis sea surface pressure data (6-hourly data at 0.125 × 0.125 degree or approximately 8 km resolution) produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) (Dee et al., 2011). To achieve this, I first established the interpolated ERA-Interim pressure for each of a bird's locations at sea. Then for every location in flight, the corresponding calibration pressure was adjusted by applying the change in interpolated ERA-Interim pressure between the time and place of measurement of P_0 and P. This method (hereafter Method 2) therefore accounted for both temporal and spatial changes in sea surface pressure throughout a flight bout, not just between bouts.

2.2.4 Potential errors in flight height estimates

I calculated the error in estimated flight height throughout a flight bout, due to spatial and temporal changes in pressure at sea level, by calculating the time (Δt; seconds) and distance (Δd; meters) elapsed between measuring P_0 and P. The error in flight height (σ_z) due to temporal changes in pressure over Δt was estimated according to the following equation (from Cleasby et al. 2015a):

$$\sigma z = 0.39 + 5.27 \times 10^{-4}\, \Delta t \qquad \text{Equation 2.2}$$

This equation is based on changes in atmospheric pressure at a static reference point (Bass Rock) during the summer of 2011 (Cleasby et al., 2015a), which were similar to those during the current study (summer 2015 and 2016; Appendix A).

I calculated the error in flight height due to spatial changes in pressure over Δd using ECMWF surface pressure data. I calculated the median change in surface pressure over Δd for the period 1st June – 31st August 2015 over a domain of 53° 5’ – 60° 0’ N, 3° 5’ – 5° 0’ E, then used Equation 2.1 to estimate the error in flight height. I assumed spatial and temporal errors were independent and estimated the combined spatial and temporal error to be the square root of the sum of squares.

2.2.5 Statistical analysis

All analysis was carried out in R version 3.3.1 (R Development Core Team, 2016b). To examine whether or not there were significant differences between the height estimates derived using each method I used a generalised linear mixed model (GLMM) in the R package ‘lme4’ (Bates et al., 2015). To account for autocorrelation and repeated measures I used the median height per flight bout and included individual bird as a random effect.

2.3 Results

2.3.1 Trip and flight-bout durations and distances travelled

I obtained combined GPS and pressure data from 159 trips by 38 individuals (29 in 2015, 16 in 2016; seven birds were sampled in both years) encompassing 2128 flight bouts (mean ± SD = 15.1 ± 7.1 per trip). Trip durations (24.7 ± 9.7 h in 2015; 20.5 ± 13 h in 2016) and total distances travelled (567.8 ± 250.4 km and 432.2 ± 261.6 km, respectively) were similar to those in previous years at this colony (Hamer et al., 2007, Cleasby et al., 2015a). The duration of individual flight bouts varied from 6 – 514 minutes (median = 20 min; Figure 2.1a) and the distance covered over a single flight bout ranged varied 0.4 to 381 km (median = 8.2 km; Figure 2.1b). Overall, 8 % of flight bouts lasted more than 120 minutes and 14 % of bouts were longer than 50 km. There was a significant positive relationship between the duration of each trip and the number of flight bouts ($F_{1,174} = 333.7$, $P < 0.001$) and between the total distance travelled per trip and the median distance covered during a flight bout ($F_{1,174} = 6.72$, $P < 0.05$). There was, however, no relationship between trip duration and the median duration of each flight bout ($F_{1,174} = 0.07$, $P > 0.5$).

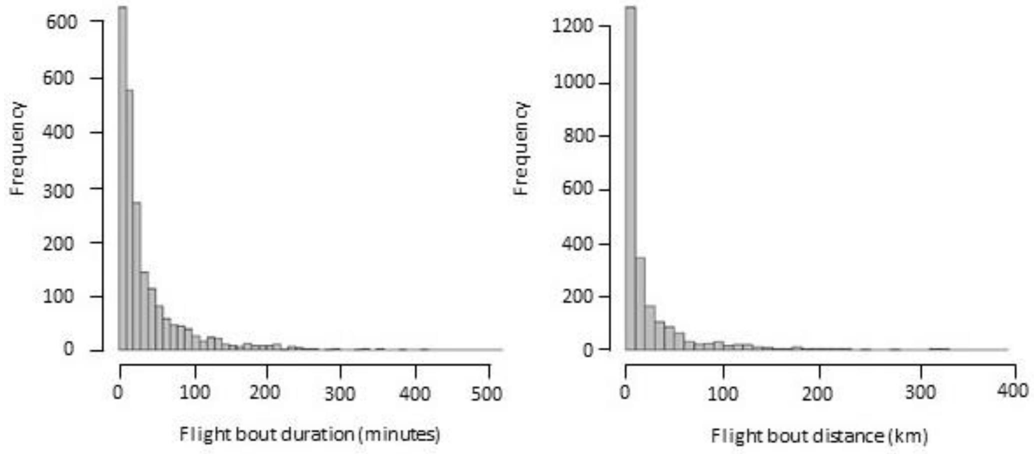

Figure 2.1. Frequency distributions of **(a)** duration (minutes) and **(b)** distance travelled (km) for individual flight bouts of chick-rearing gannets during foraging trips from Bass Rock (combined data for 2015 and 2016).

2.3.2 Estimated flight heights

The median time interval between measurement of P and P_0 (Δt) was 50 minutes (IQR = 20.0 – 114.0) and the median distance travelled between measurements (Δd) was 22.2 km (IQR = 5.7 – 68.0). Consequently, using Method 1, the median errors in flight height assessment due to temporal and spatial changes in atmospheric pressure during flight bouts were estimated to be 3.6 m and 1.5 m, respectively (from eqns 2.1 & 2.2). Assuming these errors were independent, the estimated combined error in flight height using this method was therefore 3.9 m. Moreover, heights estimated using Method 1 tended to exhibit continual drift during longer flight bouts. For long flights (> 60 min), this drift resulted in some cases in estimated heights becoming negative however, this phenomenon was greatly reduced using Method 2 (Figure 2.2), with a significant positive relationship between both the distance ($F_{1,\,329} = 77.34$, $P < 0.001$) and duration ($F_{1,171} = 34.48$, $P < 0.001$) of a flight bout and the absolute difference in mean heights estimated using each method (Figure 2.3).

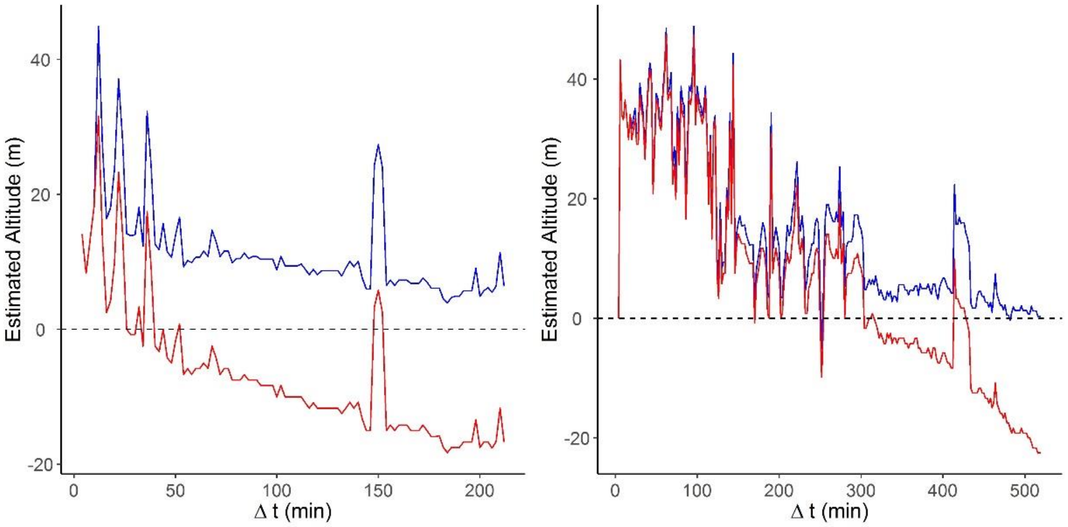

Figure 2.2. Examples of estimated flight height during two long flight bouts. The x-axis in each case is time elapsed since the calibration pressure was measured (Δt, minutes). Spurious drifts in flight height due to changes in atmospheric pressure over long flight bouts (Method 1, red) were greatly reduced when ECWMF surface pressure data were used to correct calibration pressures (Method 2, blue).

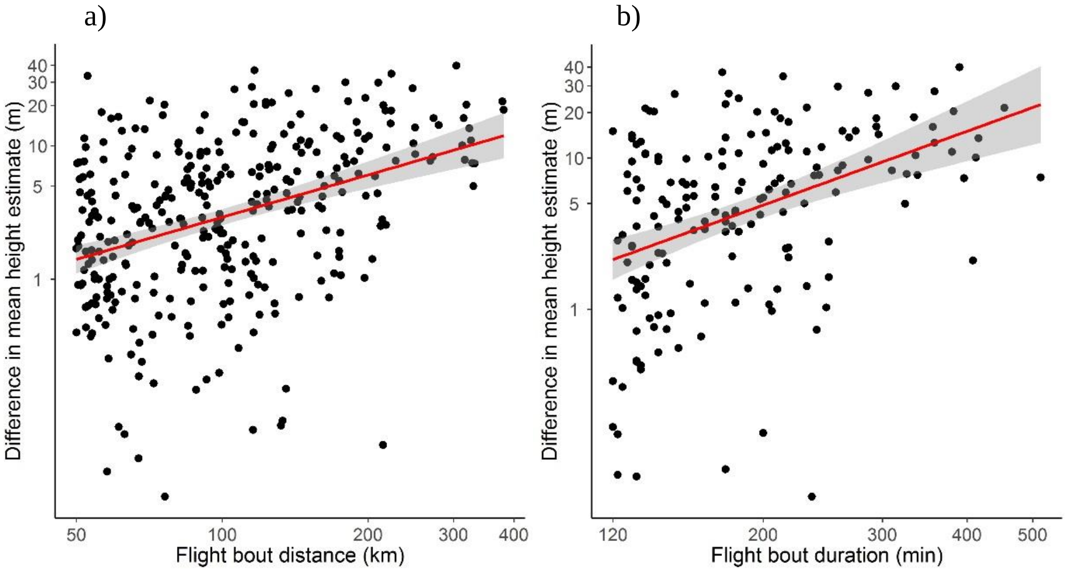

Figure 2.3. Absolute difference in mean flight heights between Method 1 and Method 2 for flight bouts **(a)** > 50 km and **(b)** > 120 minutes. Red line and grey shading show linear model and 95% confidence level, respectively.

Despite the potentially large sampling errors using Method 1, the median flight height estimated using this method (21.3 m, IQR = 7.5 – 40.5) was not significantly different from that estimated using Method 2 (20.2 m, IQR = 7.4 – 39.9) (GLMM: $\chi^2_1 = 1.59$, $P = 0.2$), presumably because atmospheric pressure could drift either upwards or downwards during flight bouts. However, as flight bout duration increased the difference between methods in H-spread (Q3 – Q1) also increased (Table 2.1), indicating an increasing disparity between methods in the variability of height estimates.

Table 2.1. IQRs of flight heights estimated during long flight bouts using Methods 1 and 2.

Flight bout duration (min)	**Method 1**		**Method 2**		**Diff in H-spread (m)**
	IQR (m)	H-spread (m)	IQR (m)	H-spread (m)	
≤ 60	10.9 – 44.5	33.6	10.9 – 43.8	32.9	0.7
60.1 – 120	10.0 – 44.2	34.1	9 – 43.0	34	0.1
> 120	3.4 – 33.1	29.7	4.6 – 31.8	27.4	2.5

2.4 Discussion

Initial studies using pressure loggers to estimate flight heights accounted for changes in atmospheric pressure over time by correcting measurements from the bird using atmospheric pressure recorded by a fixed altimeter at the colony (Weimerskirch et al., 2005b, Garthe et al., 2014). This method was refined by re-calibrating sea-level pressure from periods the bird spent on the water (Cleasby et al., 2015a) to account for changes in atmospheric pressure over short periods of time. However, over sustained flights or during unstable weather conditions, changes in atmospheric pressure may introduce unmanageable errors into estimated flight heights. This could be a particular problem for species that make long sustained flights and/or occupy regions with unstable weather patterns and/or for studies of how flight height varies with weather conditions.

In this study I used GPS data obtained at 2-minute resolution to estimate flight heights throughout the full durations of foraging trips. Using this resolution resulted in a median interval of 50 minutes between the time the calibration pressure was estimated and the time the flight height of the bird was estimated because flight bouts durations were a median of 20 min long and the bird needed to be on the water for a minimum of 10 minutes to measure P_0. This interval could be reduced using higher resolution GPS data (e.g. 1-10 Hz) (Cleasby et al., 2015a, Gibb et al., 2017) but limited device storage capacity restricts this method to short trips or parts of longer trips.

To help overcome these problems, here I tested a novel method to account for spatial and temporal changes in pressure over individual flight bouts. I found that estimated heights were similar to those recorded by Cleasby et al. (2015a) with the advantage of being able to estimate flight heights for multiple complete trips per bird. Although using reanalysis data to correct for pressure changes (Method 2) had no significant effect on the median flight height calculated, improvements in flight height estimates were evident in some long flight bouts, and there was increasing disparity between methods in the variability of height estimates as flight bout duration increased. Longer trips involved flight bouts of longer duration and so height estimates during long trip durations will be particularly improved using Method 2.

These results indicate that the use of environmental re-analysis data to correct for spatial and temporal changes in atmospheric pressure during individual flight bouts could greatly improve flight height estimates, particularly for species that spend long periods in flight (Gill et al., 2009, Liechti et al., 2013b) and/or cover large distances without landing (e.g. during migration; (Catry et al., 2004, Egevang et al., 2010) and/or in regions or at times of year when atmospheric circulation is highly variable. The spatial and temporal resolution of environmental re-analysis datasets are steadily improving (Gleeson et al., 2017) which could lead to further increases in the efficacy of such data in the future.

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Chapter 3 : Three-dimensional tracking of a wide-ranging marine predator: sex-specific foraging behaviour of northern gannets

Abstract

Sexual differences in foraging behaviour are widespread among sexually dimorphic species but also occur in species with little or no dimorphism, including many seabirds. However the selective advantage of sex-specific foraging behaviour among monomorphic species remains unclear. In this chapter I use GPS and pressure data to examine sexual differences in the three-dimensional foraging behaviour of northern gannets, a sexually monomorphic species in which sexes differ in foraging habitat and dive depths, although sex differences in trip durations and ranges have been recorded in some years but not in others. I examine whether or not sex-specific behaviour extends to flight height and whether or not differences in male and female foraging behaviour are influenced by annual variation in prey abundance. Over three consecutive years I found that females foraged more frequently in offshore waters to the east of the colony, whereas males foraged more frequently in coastal waters to the north-east and south-east of the colony, as also found in previous years. I recorded no difference between sexes in the durations of trips or distances travelled at sea, in contrast to some previous years, and I present data for multiple years suggesting that the difference in foraging trip durations of males and females may be positively related to the abundance of 0-group sandeels in surrounding waters. I also found that females not only dived deeper than males but also flew higher than males, particularly during active foraging, probably to gain greater momentum during V-shaped dives. Differences in the foraging distributions and flight heights of males and females led to different patterns of spatial variation in flight height, providing evidence of sexual segregation in three dimensions. This study adds to the body of work revealing differences in the foraging behaviour of males and females in sexually monomorphic species and highlights the importance of including sex-specific foraging information in impact assessments for renewable energy developments.

3.1 Introduction

Sexual differences in foraging niches and behaviour occur in a wide range of socially monogamous but sexually dimorphic birds including passerines, raptors and seabirds (Cook et al., 2013, Duron et al., 2018, Kruger, 2005). These differences are often attributed to the influence of body size on foraging efficiency and competitive ability (Pearson et al., 2002, Rey et al., 2012, Gwiazda and Ledwon, 2016). In some cases, the degree of difference between sexes in foraging behaviour reflects the extent of sexual size dimorphism among closely-related species (Lewis et al., 2005). However, sex-specific foraging behaviour also occurs in species with little or no dimorphism, including many seabirds (Lewis et al., 2002, Phillips et al., 2004, Gladbach et al., 2009, Paredes and Insley, 2009, Thaxter et al., 2009).

During the breeding season, sex-specific foraging behaviour in seabirds with little or no size dimorphism includes segregation in foraging areas (Hedd et al., 2014) and differences in diets and rates of food provisioning to offspring (Gray and Hamer, 2001, Navarro et al., 2009, Ismar et al., 2017). Possible explanations for such sex-specific behaviour include differences between sexes in nutritional requirements (e.g. related to egg production by females; (Peters and Grubb, 1983, Lewis et al., 2002)), differences in foraging efficiency leading to competitive exclusion (Gonzalez-Solis et al., 2000) and, at least proximately, differences between sexes in sensitivity to chick condition and food solicitation (Hamer et al., 2006). However the selective advantage of sex-specific foraging behaviour among monomorphic species remains unclear. For instance, at present no proximate mechanism has been proposed for why one sex would consistently outcompete the other in a monomorphic species (Peck and Congdon, 2006).

3.1.1 Flight height

A relatively unexplored element of avian behaviour is how birds use airspace in the vertical dimension, an important knowledge gap with implications for foraging strategies

(Weimerskirch et al., 2005b, Helms et al., 2016, Warrick et al., 2016, Mills et al., 2018) and energetics (Dokter et al., 2011, Corman and Garthe, 2014, Sherub et al., 2016). By changing flight altitude birds can take advantage of ground effect and thermal lift to reduce costs of flight (Finn et al., 2012, Weimerskirch et al., 2016), and capture prey species found at different heights in the air column (Helms et al., 2016). Increasing height above the surface also enables birds to extend the distance over which they can potentially detect feeding opportunities (Andersson et al., 2009, Bodey et al., 2014a). Flight height has been shown to vary with activity, light levels, topography, wind speed and direction and between species (Katzner et al., 2012, Seeland et al., 2012, Johnston et al., 2014b, Cleasby et al., 2015a, Villegas-Patraca and Herrera-Alsina, 2015, Ross-Smith et al., 2016) but differences between sexes have seldom been considered.

3.1.2 Sex differences in foraging behaviour of northern gannets

Northern gannets (hereafter gannets) are medium-ranging neritic predators with little sexual size dimorphism (females are on average ~ 8% heavier (Stauss et al., 2012)). Female gannets have been recorded to make longer foraging trips than males in both distance and duration in some years, though not in others (Lewis et al., 2002, Cleasby et al., 2015b). Sex differences have also been recorded in foraging distribution, diet and diving behaviour (Lewis et al., 2002, Cleasby et al., 2015b). In common with many air-breathing diving species, gannets perform dives with two distinct time-depth profiles: V-shaped and U-shaped. V-shaped dives tend to be shallower and of shorter duration than U-shaped dives, which typically involve underwater propulsion (Garthe et al., 2000, Ropert-Coudert et al., 2009). By using momentum gannets can attain depths of up to ~10 m during V-shaped dives (Ropert-Coudert et al. (2009), and these dives are more common among females, which attain greater depths during such dives than males (Cleasby et al., 2015b). In contrast, males make more U-shaped dives involving underwater wing beats to actively pursue prey (Cleasby et al., 2015b). Dive profile is also linked to habitat, with U-shaped dives more common closer to the colony in mixed waters, possibly driven by prey type (Stauss et al., 2012) or because waters closer to the coast are typically more turbid than those further offshore (Melin and Vantrepotte, 2015) favouring underwater pursuit (Grémillet et al., 2012). A positive relationship exists between flight heights of gannets and subsequent dive depths (Garthe et al., 2014). However, it is not known whether or not differences in diving behaviour result in males and females flying at different heights, nor whether or not differences in foraging movements result in different spatial distributions of flight height in males and females.

Estimates of flight heights of birds are commonly made by visual observations (Liechti et al., 2013a), laser range finders (Kahlert et al., 2012) or radar (Kemp et al., 2013) but it is now possible to estimate heights throughout foraging trips using pressure loggers (Weimerskirch et al., 2005b, Cleasby et al., 2015a, Helms et al., 2016). In this chapter I investigate the foraging behaviour of male and female gannets in three dimensions by examining the relationship between sex-specific foraging behaviour and flight height. I combine GPS and pressure data to test the hypothesis that females fly higher than males during active foraging, and I examine whether or not segregation in foraging areas leads to different spatial distributions of flight heights in males and females. I then explore a potential link between sex differences in foraging behaviour and the abundance of 0-group sandeels, which comprise more than 50 % of the diet by biomass in some years but much less in others (Lewis et al. 2003; Hamer et al. 2007).

3.2 Methods

3.2.1 Study site and data collection

Fieldwork took place at the Bass Rock, UK (6º 6’ N, 2° 36’ W) between mid-June and mid-August of 2015 - 2017. In total 63 adult gannets with chicks (39 males, 24 females) were caught at the nest using a 6-meter telescopic pole fitted with a metal noose or hook. Each bird was fitted with a metal British Trust for Ornithology ring and a coloured plastic ring with a unique alphanumeric code for easy identification at the nest site. I then recorded body mass to the nearest 10 g using an electronic scale. Each bird had a GPS logger (igotU-GT600, Mobile Action Technology, Taipei, Taiwan) attached to the upper side of the central tail feathers and a logger recording atmospheric pressure and temperature (MSR-145W, MSR Electronics, Seuzach, Switzerland) attached to the underside of the central tail feathers as described in Chapter 2. Birds were sexed from observations of copulation and other sex-specific behaviour at the colony (Redman et al., 2002) and, at the Natural Environment Research Council (NERC) Biomolecular Analysis Facility, Sheffield, UK, using DNA extracted from breast feathers shed during handling and from blood collected in previous years under Home Office Licence (Wakefield et al., 2015).

3.2.2 Trip analysis

For each foraging trip, I determined the duration (h), total distance travelled (km), maximum distance (km) on a direct bearing from the colony and departure angle (degrees) from the colony (an average of the first 5 bearings > 10 km from the colony) (Patrick et al., 2014). I used speeds and turning angles derived from the GPS data to classify the behaviour of birds at sea into three categories: commuting, active foraging and time spent on the water (Wakefield et al., 2015). I used the furthest location from the colony during each trip to distinguish between outbound and inbound stages, and I identified individual flight bouts as periods of flight separated by periods on the water.

To compare the foraging locations of males and females, I used the utilisation distribution (UD) of locations at sea, estimated using kernel density analysis (Calenge, 2006) of those locations categorised as active foraging. Hence I excluded periods of commuting and time spent on the water surface between periods of flight and during hours of darkness (gannets do not forage at night; (Lewis et al., 2002, Furness et al., 2018)). This analysis was carried out using the R package adehabitatHR (Calenge, 2006) over a 1 km^{-2} grid with a smoothing parameter of 10 km (Stauss et al., 2012). I used the 50 % and 95 % UDs to represent core and overall foraging areas, respectively (Hamer et al., 2007, Cleasby et al., 2015b).

I investigated the link between male and female foraging behaviour and sandeel abundance by comparing the trip durations of males and females from this study and previous studies at this colony (Lewis et al. 2002; Cleasby et al. 2015b) with annual 0-group sandeel stock assessment data (billions of recruits) for the southern and central North Sea including Dogger Bank, and the central and northern North Sea (http://standardgraphs.ices.dk/stockList.aspx; datasets san.sa.1r and san.sa.4, respectively). I summed datasets to give an index of annual abundance weighted 1:2:1 for the southern, central and northern North Sea, respectively (i.e. weighting abundance data in proximity to Bass Rock more heavily).

3.2.3 Flight height and dive depth estimation

Following Cleasby et al.(2015a) I used the barometric formula (Equation 3.1) to estimate the heights of birds (h m) above sea level:

$$h = -\frac{KT}{mg}\ln\left(\frac{P}{P_0}\right) \qquad \text{Equation 3.1}$$

where K is the universal gas constant for air (8.31432 N m mol^{-1} K^{-1}); m is the molar mass of air (0.0289644 kg mol^{-1}); g is the acceleration due to gravity (9.80665 ms^{-2}); and T is the temperature (K) of the atmosphere between P_0 and P. P_0 and P are the atmospheric pressures (pascals) at sea level and at height h (m) respectively.

I accounted for spatial and temporal changes in atmospheric pressure at sea level by adjusting calibration pressures (P_0) throughout the duration of each flight bout using the ERA-Interim reanalysis sea surface pressure dataset (6-hourly data at 0.125 × 0.125 degree or approximately 8 km resolution) produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) (Dee et al., 2011), as described in Chapter 2.

Dive depths were estimated by identifying rapid increases in pressure above ambient (1000 mb) and converting them to depth below the water surface using the following equation:

$$D = \frac{Pb - Pa}{100} \qquad \text{Equation 3.2}$$

Where D = dive depth (m), Pb (mb) is the pressure recorded on the bird and Pa (mb) is ambient pressure. A standard ambient pressure of 1000 mb was applied to all pressure data because pressure increases rapidly with depth below the surface (by 1 mb per cm of depth), and so using an ambient pressure of 1000 mb gave confidence that all dives were captured.

3.2.4 Statistical analysis

I used linear mixed effects models (LMMs) fitted using the 'nlme' package (Pinheiro et al., 2018) to model the relationships among behaviour, sex, year and dive depth. Duration, distance and maximum displacement from the colony were square root transformed prior to analysis. Bird identity was included in all models as a random factor with trip nested within bird identity in flight height models. The serial autocorrelation in successive height measurements during trips was modelled using a first-order continuous autoregressive structure. Some estimated flight heights were below 0 m and following Cleasby et al.

(2015a) these were retained in the analysis by adding the minimum estimated height (absolute value) to all cases to permit square root-transformation. Spatial variation in flight height was modelled using a generalized additive mixed model (GAMM) with Gaussian errors in the R package mgcv (Wood, 2006). To explore the relationship between trip durations and sandeel abundance I used a linear model with a quasi-Poisson model structure to address over-dispersion in the data. All statistical tests and models were implemented using R statistical software (R Development Core Team, 2016b).

3.3 Results

3.3.1 Trip metrics and activity budgets

I acquired combined GPS and altitude data for 173 trips by 53 individuals (57 trips by 16 males and 40 trips by 10 females in 2015; 31 trips by 9 males and 16 trips by 7 females in 2016; 18 trips by 7 males and 11 trips by 4 females in 2017). I also obtained GPS data for an additional 46 trips by males and 33 trips by females over the three years of the study, included in the analysis of horizontal movements.

Overall, females foraged more frequently in offshore waters to the east of the colony, whereas males foraged most frequently in coastal waters to the north-east and south-east of the colony (Figure 3.1), as also found in previous years (Cleasby et al. 2015b). Despite this difference in distributions, however, there was no significant difference between sexes in foraging trip duration (LMM; $F_{1,\,47} = 1.4$, $P = 0.2$), total distance travelled ($F_{1,\,47} = 1.6$, $P = 0.2$), maximum displacement from the colony ($F_{1,\,47} = 1.3$, $P = 0.3$) or departure angle from the colony ($F_{1,\,47} = 1.0$, $P = 0.3$) (Table 3.1). There was no difference among years in maximum displacement from the colony ($F_{2,\,195} = 2.4$, $P = 0.09$) or departure angle ($F_{2,195} = 0.7$, $P = 0.5$) but both trip duration ($F_{2,195} = 6.7$, $P = 0.002$) and total distance travelled ($F_{2,195} = 3.9$, $P < 0.05$) were shorter in 2016 than the other two years studied (Table 3.2).

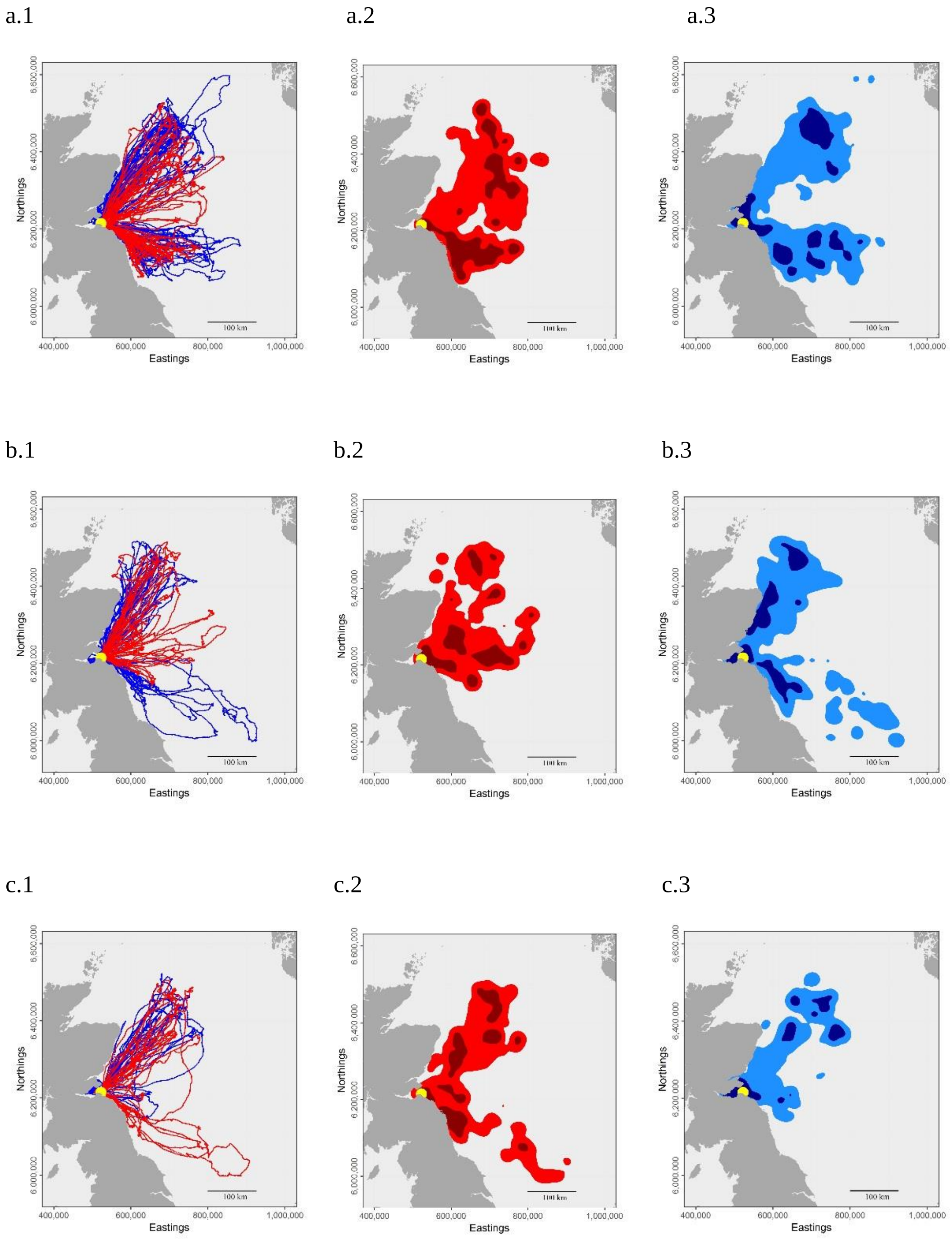

Figure 3.1. (1) Foraging tracks and **(2 and 3)** utilisation distributions (UDs) of **(2)** female and **(3)** male gannets during the breeding seasons of **(a)** 2015, **(b)** 2016 and **(c)** 2017. UDs are based on active foraging locations from 100 tracks by females (red) and 152 tracks by males (blue). Shading denotes UD contours (darker, 50%; lighter, 95%).

Table 3.1. Trip metrics of male and female gannets rearing chicks at Bass Rock in 2015-2017.

	Male			**Female**		
Variable	**Mean**	**n**	**SD**	**Mean**	**n**	**SD**
Trip duration (hours)	23.0	147	11.2	24.8	100	11.6
Total distance (km)	502.4	147	288.7	546.6	100	236.3
Maximum displacement (km)	201.6	147	117.0	218.1	100	90.4
Departure angle (deg)	31.7	147	64.1	15.0	100	35.4

Table 3.2. Trip metrics of male and female gannets rearing chicks at Bass Rock in 2015-2017.

	2015			**2016**			**2017**		
	Mean	**n**	**SD**	**Mean**	**n**	**SD**	**Mean**	**n**	**SD**
Trip duration (hours)	24.9	114	9.7	20.9	90	12.3	25.8	48	11.2
Total distance (km)	568.9	114	251.9	454.2	90	267.4	533.4	48	288.7
Maximum displacement (km)	226.4	114	102.4	187.5	90	105.3	208.6	48	116.9
Departure angle (deg)	21.4	114	47.3	22.4	90	62.1	42.7	48	55.1

3.3.2 Sex-, behaviour- and location-specific flight heights

Median flight height was 21.2 m (IQR 7.7 – 42.1 m). Flight height was significantly higher during periods of active foraging than commuting ($\chi^2 = 267.66$, $P < 0.001$) and significantly higher during outbound than inbound commuting ($\chi^2 = 54.3$, $P < 0.001$) (Figure 3.2).

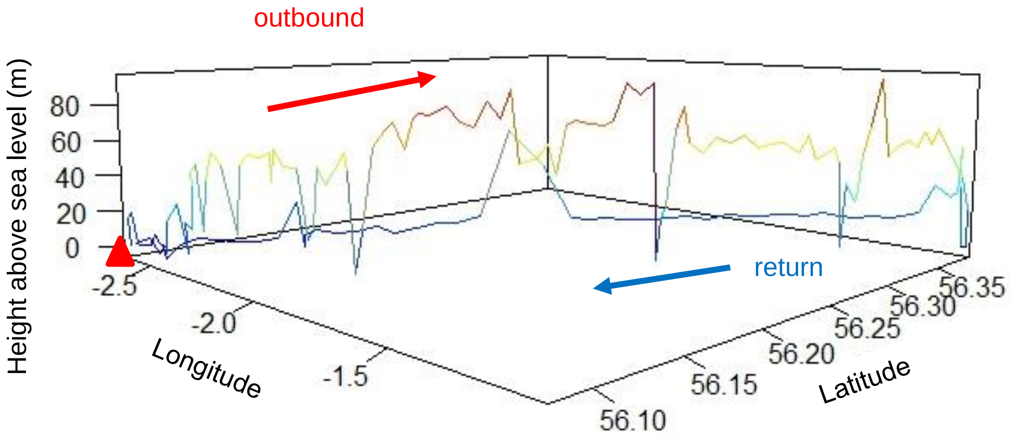

Figure 3.2. Illustration of the variation in flight height throughout a single foraging trip from Bass Rock (red triangle). Line shading represents height (m) from blue (lowest) to red (highest).

Females flew significantly higher than males when actively foraging ($\chi^2 = 6.39$, $P = 0.01$) and when commuting away from the colony ($\chi^2 = 4.53$, $P = 0.03$) but the difference was only marginally significant when returning to the colony ($\chi^2 = 2.99$, $P = 0.08$) (Figure 3.3). There was no difference among years in foraging or commuting flight heights ($P > 0.1$). Across the foraging distribution, birds of both sexes tended to fly lower over inshore waters than elsewhere, particularly along the coast NE of the colony, with the greatest difference between sexes occurring mainly over offshore waters, particularly to the east of the colony (Figure 3.4).

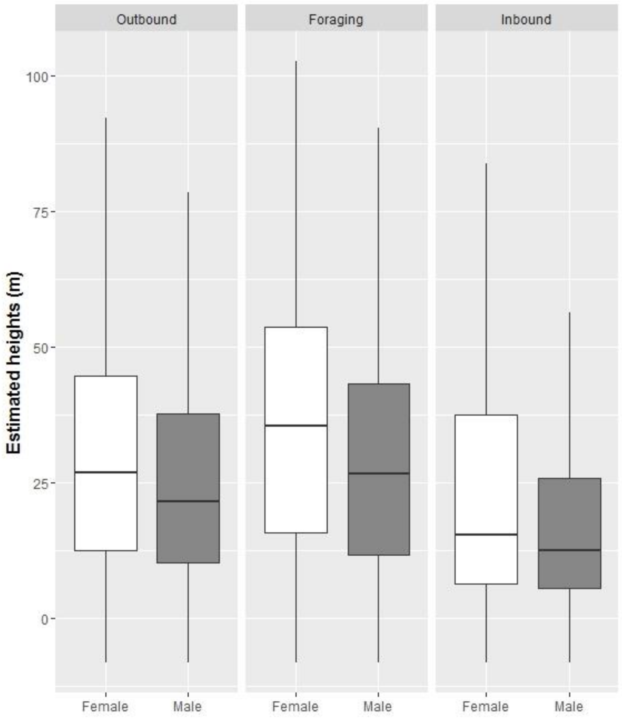

Figure 3.3. Flight heights (medians, IQRs and ranges) of female (white) and male (grey) gannets while commuting away from the colony, actively foraging and commuting back to the colony.

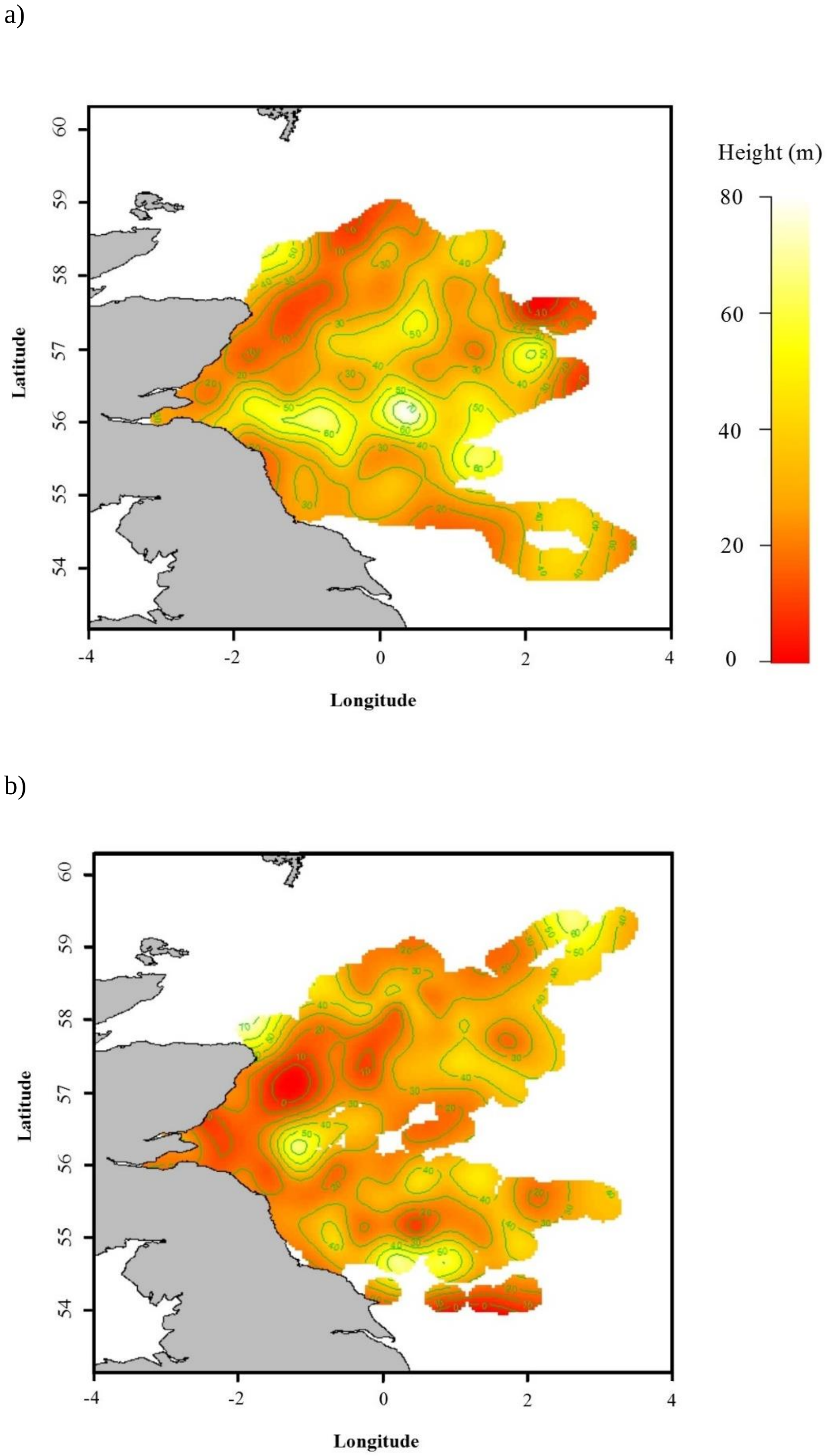

Figure 3.4. Spatial variation in flight heights of **(a)** female and **(b)** male gannets when actively foraging. Contours and shading show estimated heights (m) above sea level (brighter shading shows higher elevations).

3.4 Flight height and dive depth

Females were ~ 185 g heavier than males on average (mean ± SD; female, 3096 ± 308 g; male, 2910 ± 214 g; Student's *t*-test; $t_{83} = 3.32$, $P < 0.001$) and made deeper dives than males on average (median = 5.01 m, IQR 3.8 – 5.5 m and median = 3.74 m, IQR 2.8 – 4.9, respectively; LMM using log transformed depths, $\chi^2_{1,46} = 5.70$, $P = 0.017$). There was also a significant interaction between body mass and sex ($\chi^2_{1,46} = 5.03$, $P = 0.02$), due to a stronger effect of mass on dives depths of males than females (Figure 3.5), however these results should be viewed with some caution as removal of points makes the relationship non-significant ($\chi^2_{1,38} = 0.69$, $P = 0.4$).

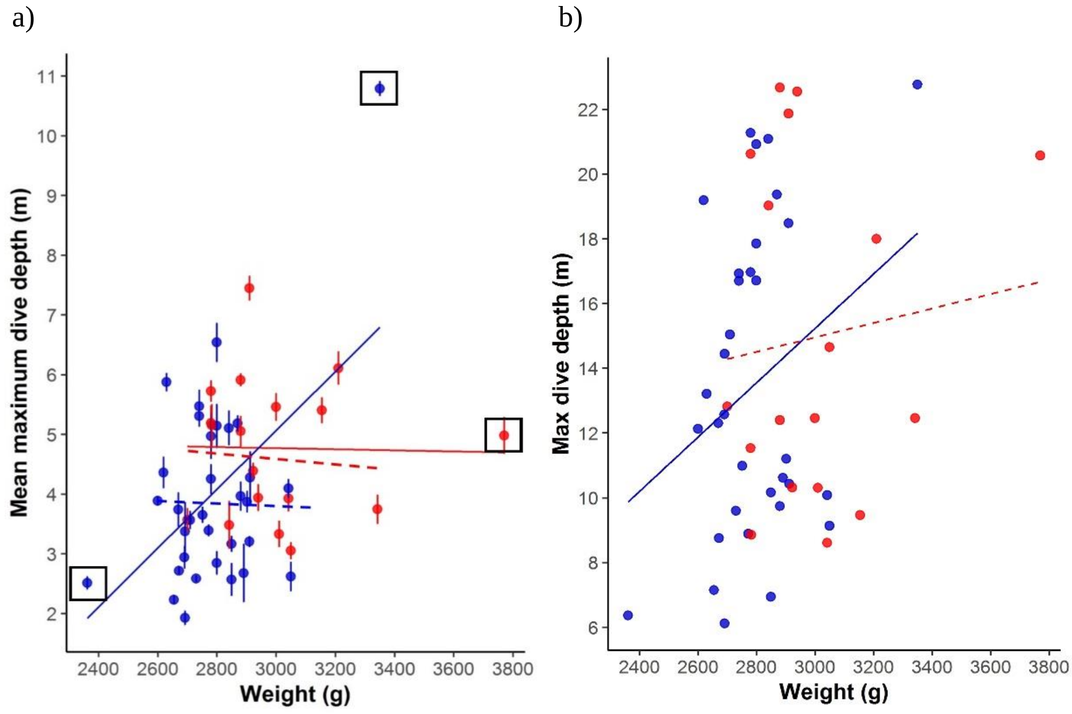

Figure 3.5. The relationship between body mass and **(a)** mean maximum dive depth and **(b)** maximum dive depth for males (blue) and females (red). Lines show linear model predictions (solid – all data; dashed – outliers (within squares) removed), error bars are standard error.

3.4.1 Trip durations and sandeel abundance

The index of 0-group sandeel abundance varied widely between years, ranging from < 100 billion in 2015 to > 400 billion in 2001. There was a significant negative relationship between trip duration and sandeel abundance index (LM; $\chi^2 = 8.03$, $P = 0.017$), with some indication of a steeper rate of decline for males than females (Figure 3.6); trips by females were longer than those by males in all years except the two with lowest sandeel abundance (2011 and 2015), with the difference between sexes tending to be greater in years with higher sandeel abundance. However the difference between sexes was only marginally significant ($P = 0.09$) and further data for more years are needed to confirm or refute this pattern.

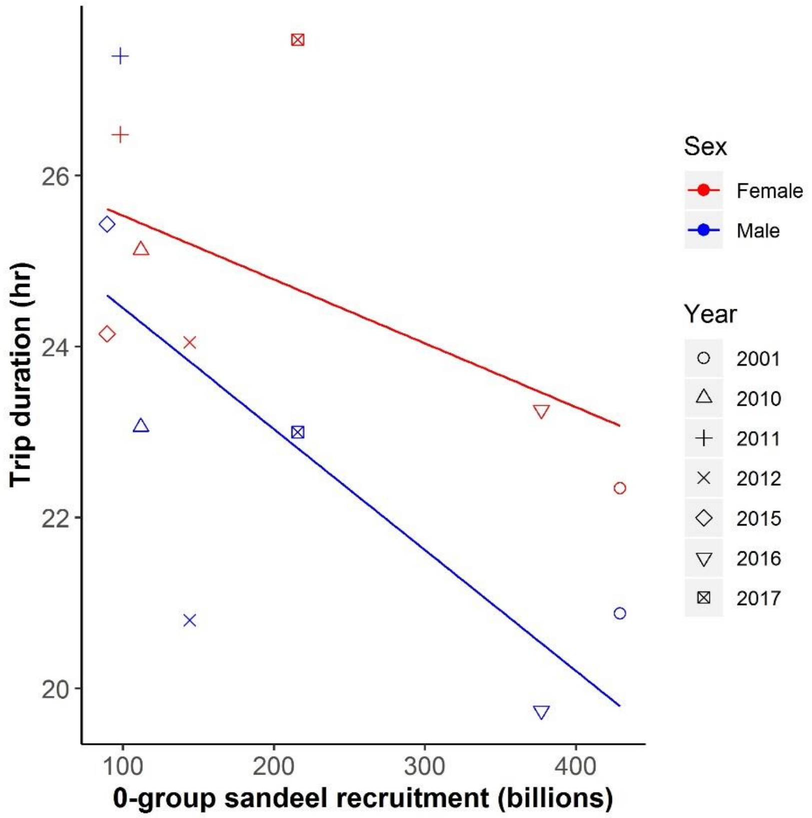

Figure 3.6. The relationship between the mean trip durations of male and female gannets and the abundance of 0-group sandeels in the North Sea.

3.5 Discussion

Previous studies of sex-specific foraging behaviour in gannets have highlighted differences in horizontal movements and dive depths (Lewis et al., 2002, Cleasby et al., 2015b). I found that these differences also extend to flight heights. Foraging trip durations and destinations in this study were similar to those in some previous years at this colony (Hamer et al., 2007, Wakefield et al., 2015) and I found no differences in these metrics between males and females, in accordance with results of a study at the same colony in 2001 (Lewis et al., 2002). In contrast, Cleasby et al. (2015b) found that males made significantly shorter trips than females in both distance and duration in 2010 to 2012, with a significant difference between years in the overlap between male and female foraging distributions. A possible explanation for this annual variation in sex differences could involve the abundance of sandeels. Gannets at Bass Rock feed extensively on 0-group sandeels in some years but not in others, and trip durations at the colony have been putatively linked to 0-group sandeel abundance in surrounding waters (Hamer et al., 2007). The foraging distribution of males has also been linked with sandeel habitat (Cleasby et al., 2015b). The data presented here suggest a possible link between the abundance of 0-group sandeels and the difference in trip durations of males and females. Trips were shorter in both sexes when sandeel numbers were higher, with some evidence of a steeper rate of decrease for males than females. This pattern suggests that males may prey upon sandeels to a greater extent than females when they are available, resulting in shorter trips by males in years of high sandeel abundance. However the difference between sexes was only marginally significant and this suggestion should be viewed with caution until further data are available for more years to confirm or refute it.

3.5.1 Differences in flight height

Flight height estimated in this study (median = 21 m) was very similar to that estimated by Cleasby et al. (2015a) (median = 22 m) with heights during active foraging higher than those during commuting in both sexes. Active foraging involves birds spending more time in areas where prey might be expected to be more plentiful by moving at slower speeds and along more tortuous paths (area-restricted search behaviour; (Pinaud and Weimerskirch, 2007, Hamer et al., 2009)). I found that active foraging in gannets not only involved reducing speed and increasing path tortuosity but also flying at greater heights. This combination of more time in an area at higher elevations may facilitate detection of prey either directly (Weimerskirch et al., 2005b, Bodey et al., 2014a) or through local enhancement (Haney et al., 1992, Hamer et al., 2000). Commencing plunge-dives from a greater height may also increase momentum, enabling attainment of greater depths (Garthe et al., 2014, Cleasby et al., 2015b).

I found support for the hypothesis that females fly higher than males during active foraging. Garthe et al. (2014) found that gannets making V-shaped dives for mackerel dived from a mean height of 37.1 m. This was very similar to the median height of 35.3 m for females during active foraging in this study, and much higher than the corresponding height of 25.7 m for males (Figure 3.3). Garthe et al. (2014) also found a positive relationship between flight height and dive depth, and I found that females not only flew higher than males during active foraging but also dived to greater depths. Cleasby et al. (2015b) found that females at Bass Rock made more V-shaped dives than males and foraged more over thermally stratified water off-shore, where they were presumed to be feeding mainly on mackerel. Together, these data suggest that sex differences in both mean flight heights and the spatial distribution of flight heights were associated with females making more V-shaped dives than males, particularly in thermally stratified waters offshore to the east of the colony.

Most active foraging by gannets occurs during the outbound leg of a trip or around the maximum range from the colony (Hamer et al., 2009), although birds do sometimes dive during the return leg (Lewis et al., 2004). Commuting flight height during the outbound leg was higher on average than during the return leg, probably to facilitate detection of feeding opportunities (Andersson et al., 2009, Votier et al., 2011, Bodey et al., 2014a, Corman and Garthe, 2014, Weimerskirch et al., 2016). That males and females flew at similar heights during the inbound leg of the trip strongly suggests that differences in flight heights during outbound commuting and active foraging were linked to foraging behaviour. Commuting flight height may also have been influenced by wind speed and direction (Krüger and Garthe, 2001), and the relationship between windscape and flight height is explored in Chapter 4.

My findings add to the body of work highlighting foraging differences between male and female gannets despite only slight sexual size dimorphism. Gannets have been identified as one of the seabirds at greatest potential risk from collision with offshore wind turbines (Furness et al., 2013) and so sex-specific foraging behaviour and flight heights raise concerns about potential sex-biased collision risks (Cleasby et al., 2015a). Sex-specific mortality has demographic implications (Martinez-Abrain et al., 2006) and with large increases in wind farm infrastructure planned for the North Sea over the coming decade, consideration should be taken to include sex-specific and three-dimensional behaviour in assessments of risk. This topic is examined further in Chapter 5.

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Chapter 4 : Effects of weather on three-dimensional foraging behaviour

Abstract

Foraging is a key component of time-activity budgets, forming an essential link between prey availability and predator breeding success. Gannets are large seabirds that make long foraging trips during the breeding season but the influence of weather conditions on their foraging behaviour is unclear. In this chapter I use data from GPS and pressure loggers to investigate the effects of weather on the three-dimensional foraging behaviour of gannets breeding at Bass Rock, Scotland. I found that birds spent a greater proportion of each trip actively foraging during stronger winds, suggesting more challenging conditions as wind speed increased, probably due to changes in prey visibility and behaviour. However, there was no increase in trip durations during stronger winds, because birds compensated for spending more time foraging by spending less time on the water. Wind speed and direction had a significant effect on ground speeds during both the outbound and return stages of trips and also influenced the height at which birds flew during both commuting and active foraging. Adults returned at higher speeds from more distant foraging locations up to ~200 km from the colony, due at least in part to a decrease in the proportion of time on the water. Over the longest return distances, birds encountering headwinds spent less time on the water and so were able to attain similar speeds of travel on average to those encountering crosswinds or tailwinds, suggesting that by adjusting time spent on the water, birds were able to buffer trip durations to some extent against adverse weather conditions encountered at sea.

4.1 Introduction

Global climate change is having a profound effect on terrestrial and aquatic biota, leading to pervasive changes in species abundance, distributions, demography and behaviour (Jones et al., 2018, Thackeray et al., 2016, Sydeman et al., 2015, Zuckerberg et al., 2018, Jenouvrier et al., 2018). Drivers of these changes include both indirect effects on prey availability and habitat quality (Regehr et al., 2007, Durant et al., 2007), and direct effects of changing weather conditions (McKechnie and Wolf, 2010, Lamarre et al., 2018). The impacts of changes in temperature and rainfall on species have been an increasing focus of recent research (Parmesan et al., 1999, Oswald et al., 2008, Terraube et al., 2017, Jones et al., 2018) yet while changes in other environmental variables such as cloud level and wind regime are also affecting species, these factors are less frequently considered (Foster, 2001, Bowlin and Wikelski, 2008, Gill et al., 2014). In temperate and polar latitudes environmental conditions are often highly variable and unpredictable, with increases in mean wind speeds and storm frequencies predicted as a result of anthropogenic climate change, particularly in mid-latitudes (McInnes et al., 2011, Young et al., 2011), although uncertainties still exist (Coumou et al., 2015).

Wind is a major component of the environmental conditions experienced by birds, affecting the cost of travel on migration (Gill et al., 2014, La Sorte and Fink, 2017) and on foraging trips during the breeding season (Hernandez-Pliego et al., 2017, Gibb et al., 2017), as well as affecting the efficiency of detecting and capturing prey (Nevitt et al., 2008, Moller, 2013). In aquatic environments wind influences wave patterns (Salisbury et al., 2013, Albert et al., 2016) and turbidity (Cho, 2007) which can alter the vertical distribution of forage fish in the water column (Konarzewski and Taylor, 1989, De Robertis et al., 2003, Parker-Stetter et al., 2016) making them more difficult to locate or pursue (Dodd and Vahle, 1998, Finney et al., 1999, Stienen et al., 2000, Baptist and Leopold, 2010). The effect of rainfall on the water surface is complex and dependent on rain intensity, raindrop size, terminal velocity and the angle at which the rain droplets strike the surface (Yang et al., 1997). At low wind speeds, rain dampens waves but at higher wind speeds the damping effect of the rain decreases (Zhao et al., 2013). Wave-breaking and rainfall also produce underwater sound (Nystuen et al., 1993, Thorpe, 1995) which may affect the ability of prey close to the surface to detect predators aurally. There may also be lagged effects of wind on foraging efficiency through increases in sea surface swell and choppiness after the wind has subsided (Dunn, 1973) .

In addition to affecting foraging efficiency, wind conditions also influence foraging flight height. Several studies have shown that birds alter their flight elevations in response to wind direction, with head winds associated with lower heights (Krüger and Garthe, 2001, Villegas-Patraca and Herrera-Alsina, 2015, Tarroux et al., 2016). Flying lower into headwinds allows birds to take advantage of wind shear, where wind speed may be reduced by ~15 - 20 % at heights below 4 m (Finn et al., 2012). Flying less than 1.5 × wingspan above the surface also allows birds to utilise ground effect, where lift is increased and aerodynamic drag is decreased as a result of the ground interrupting wingtip vortices and downwash behind the wing (Rayner, 1991). Hence flying close to the ground reduces flight costs when flying into head winds (Rayner, 1991, Finn et al., 2012) whereas flying higher with tail winds enables faster and more efficient flight (Liechti et al., 2000, Krüger and Garthe, 2001, Green, 2004).

Many seabirds forage over large areas of ocean and so how they respond to weather conditions across their foraging ranges may have consequences for trip durations, nest attendance patterns, foraging success and chick provisioning rates. Numerous studies of seabirds have highlighted changes in trip durations and distances travelled in response to changes in prey distributions and abundance (Hamer et al., 2007, Orben et al., 2015, Camprasse et al., 2017) but few have considered responses to weather conditions. Gannets (*Morus* spp.) are plunge diving predators that make foraging trips covering 10s to 100s of km (Hamer et al., 2000, Angel et al., 2016, Botha et al., 2017). They use vision to detect prey during the underwater phase of dives (Machovsky-Capuska et al., 2012), which are shallower at dawn and dusk than at other times of day (Cleasby et al., 2015b), probably due to changes in the vertical distribution of prey coupled with greater difficulty in visual detection of prey in low light conditions (Wanless et al., 1999, Elliott and Gaston, 2015). Similarly, a reliance on visual cues to identify suitable foraging locations (Tremblay et al., 2014, Bodey et al., 2014b) may explain the little time gannets spend flying at night (Hamer et al., 2000, Garthe et al., 2003, Furness et al., 2018).

Northern gannets (*M. bassanus*; hereafter gannets) are the largest seabird breeding in the North Atlantic Ocean with an increasing population in the United Kingdom (Murray et al., 2015). They exploit prey of a wide range of sizes from 0-group sandeels (< 10 cm length) to herring, mackerel and garfish (> 35 cm) and larger species obtained as fisheries discards (Hamer et al., 2000, Lewis et al., 2003). Energy expenditure in gannets is higher during active foraging than commuting to and from the colony but during both activities, less energy is expended when flying with the wind (Amelineau et al., 2014). However they spend more time actively foraging with a head wind than with a tail wind, possibly a consequence of numerous take-offs into the wind following dives or to reduce flight speed, which is advantageous in the detection of prey (Machovsky-Capuska et al., 2012, Amelineau et al., 2014). Gannets also fly higher during active foraging than commuting (Chapter 3) but it is not clear how weather conditions affect flight heights, time-activity budgets or overall durations of foraging trips.

In this chapter I investigate variation in the three-dimensional foraging behaviour of gannets at Bass Rock in response to weather conditions in the North Sea. I test the hypotheses (1) that trip duration and time spent foraging increase in deteriorating weather conditions, and (2) that weather conditions affect flight heights during commuting and active foraging. In light of the differences I found between male and female flight heights (Chapter 3) I also explore how males and females respond to weather conditions experienced at sea.

4.2 Methods

4.2.1 Study site and data collection

Fieldwork took place at the Bass Rock, UK (6º 6’ N, 2° 36’ W) between mid-June and mid-August of 2015 - 2017. In total 63 adult gannets with chicks (39 males, 24 females) were caught and fitted with identification rings, a GPS logger and a logger recording atmospheric pressure and temperature as described in Chapter 2. Birds were sexed from observations at the nest and from biomolecular analysis as described in Chapter 3.

4.2.2 Trip analysis

All location data were interpolated to 2 min intervals and behaviours at sea classified as described in Chapter 2. I determined the trip metrics as described in Chapter 3. I also calculated the direction of travel throughout each trip as the bearing between successive locations.

4.2.3 Flight height estimation

Flight heights were estimated using a combination of GPS and pressure data recorded using loggers attached to the bird, and reanalysis sea surface pressure data as described in Chapter 2.

4.2.4 Weather conditions

I downloaded the following data from the ERA-Interim reanalysis dataset (see above): 10 m zonal (U) and meridional (V) wind components at 10 m a.s.l, rainfall (mm h^{-1}) and low cloud cover (% of sky covered by low clouds, defined as those at pressures greater than 80 % of surface pressure, equivalent to altitude below ~1.9 km). I then selected those data closest in time and space to every bird location at sea (maximum distance was 4 km and maximum time difference was 3 h). I next used the U and V wind components to calculate wind speed (ms^{-1}) and direction (^{o}) using Equations 4.1 and 4.2, respectively.

$$Ws = \sqrt{Uw^2 + Vw^2} \qquad \text{Equation 4.1}$$

$$Wv = \frac{180}{\pi}(\text{atan}(Vw, Uw)) \qquad \text{Equation 4.2}$$

where Ws = wind speed, Uw = zonal (U) wind component, Vw = meridional (V) wind component, Wv = meteorological wind direction.

Following Amélineau et al. (2014), I used the bird-wind angle (BWA) to characterise the relationship between wind direction and the bird’s direction of travel. Values of 0 - 45^{o} were categorised as tail winds, 45 - 135^{o} as cross winds and 135 – 180^{o} as head winds (Figure 4.1). To examine the use of ground effect I assumed that birds experienced lift at heights < 2.74 m (i.e. 1.5 × wingspan) above sea level (Finn et al., 2012).

4.2.5 Statistical analysis

I modelled trip parameters and flight heights during active foraging and commuting in relation to weather variables using linear mixed-effects models (LMMs) fitted using the R package ‘nlme’ (Pinheiro et al., 2018). I included foraging trip identity nested within bird identity as a random effect to control for repeated measures across multiple trips per bird, and I included a temporal autocorrelation structure to control for non-independence of successive data within each trip. I used generalized linear models (GLM) to examine the relationship between speed, time on the water, distance travelled and wind direction. I used a Gamma error distribution to examine speed and a Poisson error distribution to examine time on the water both with an identity link function. I ran three models for both speed and time on the water so as to include all combinations of distance and distance^2 and selected the best model using Akaike Information Criterion (AIC) values.

Flight heights were treated as described in Chapter 3 for inclusion in models. All response variables, with the exception of trip distance, were right skewed and were therefore square-root transformed prior to analysis. Global models for each response variable included wind speed and direction at 10 m a.s.l., rainfall and low cloud cover and their two-way interactions. Sex was included as a fixed effect in the global models of flight height to see whether differences in flight heights of males and females (Chapter 3) were influenced by weather. Year was included as a fixed effect in trip parameter models due to it being a significant factor in explaining variation in trip distances and durations (Chapter 3) but I did not include it in flight height models as there was no annual variation found in flight height (Chapter 3). Continuous predictor variables were normalised to increase the interpretability of parameter estimates (Schielzeth, 2010) and I tested for collinearity between predictor variables to ensure this would not cause difficulties for determining true relationships (Freckleton, 2011).

All combinations of variables from the global model were modelled separately using the dredge function in the R package MuMln (Bartón, 2013) and the top ranked model was selected using the Akaike Information Criterion (AIC). Models with the greatest raw AIC weight and a ΔAIC < 2 from the next ranked model were considered to have the best model fit (Burnham and Anderson, 2002) but where there was uncertainty over the top model, the outputs of the top six models were examined (Harrison et al., 2018).

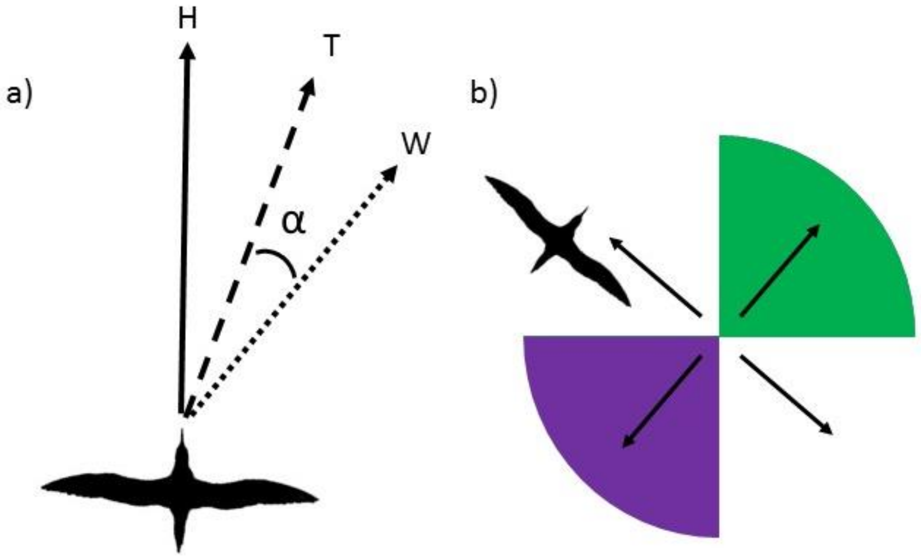

Figure 4.1. (a) Graphical representation of how bird-wind angle (α) was calculated from the direction of the birds ground track (dashed line – T) and the wind direction (dotted line – W). The birds heading (solid line – H) is the direction in which the bird is flying. In this example α represents a tail wind. **(b)** Illustration of wind directions classified as head winds (purple), cross winds (white) and tail winds (green). Arrows show mean wind direction in each case.

4.3 Results

I acquired combined GPS and altitude data for 189 trips by 48 individuals (107 trips by 29 birds in 2015; 47 trips by 16 birds in 2016; 35 trips by 13 birds in 2017) and GPS data for an additional 44 trips over the three years of the study (Figure 4.2a). Bearings between the colony and the terminal point of trip had a bimodal distribution with peaks between 30 - 40^{o} and 110 - 120^{o} (Figure 4.2b).

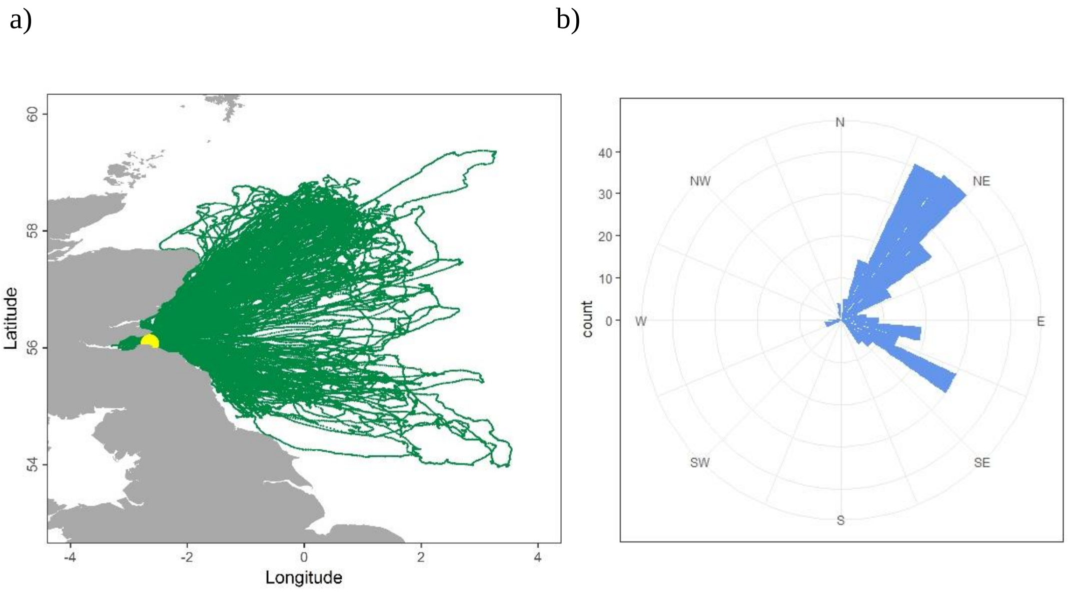

Figure 4.2. (a) Tracks of foraging trips and **(b)** bearings between the colony and the terminal point of the trip (n=189) by adult gannets rearing chicks at Bass Rock between mid-June and mid-August of 2015-2017.

The prevailing wind during each year of data collection was from the south and west, with wind speed most commonly 3 – 6 ms^{-1} at Bass Rock and stronger at greater distances from the coast (Figure 4.3). Rainfall at Bass Rock averaged 0.12 mm h^{-1} (range 0 – 2.76 mm h^{-1}). These weather conditions were in keeping with the long-term average (https://www.meteoblue.com/en/weather/forecast/modelclimate/dunbar_united-kingdom_2650776).

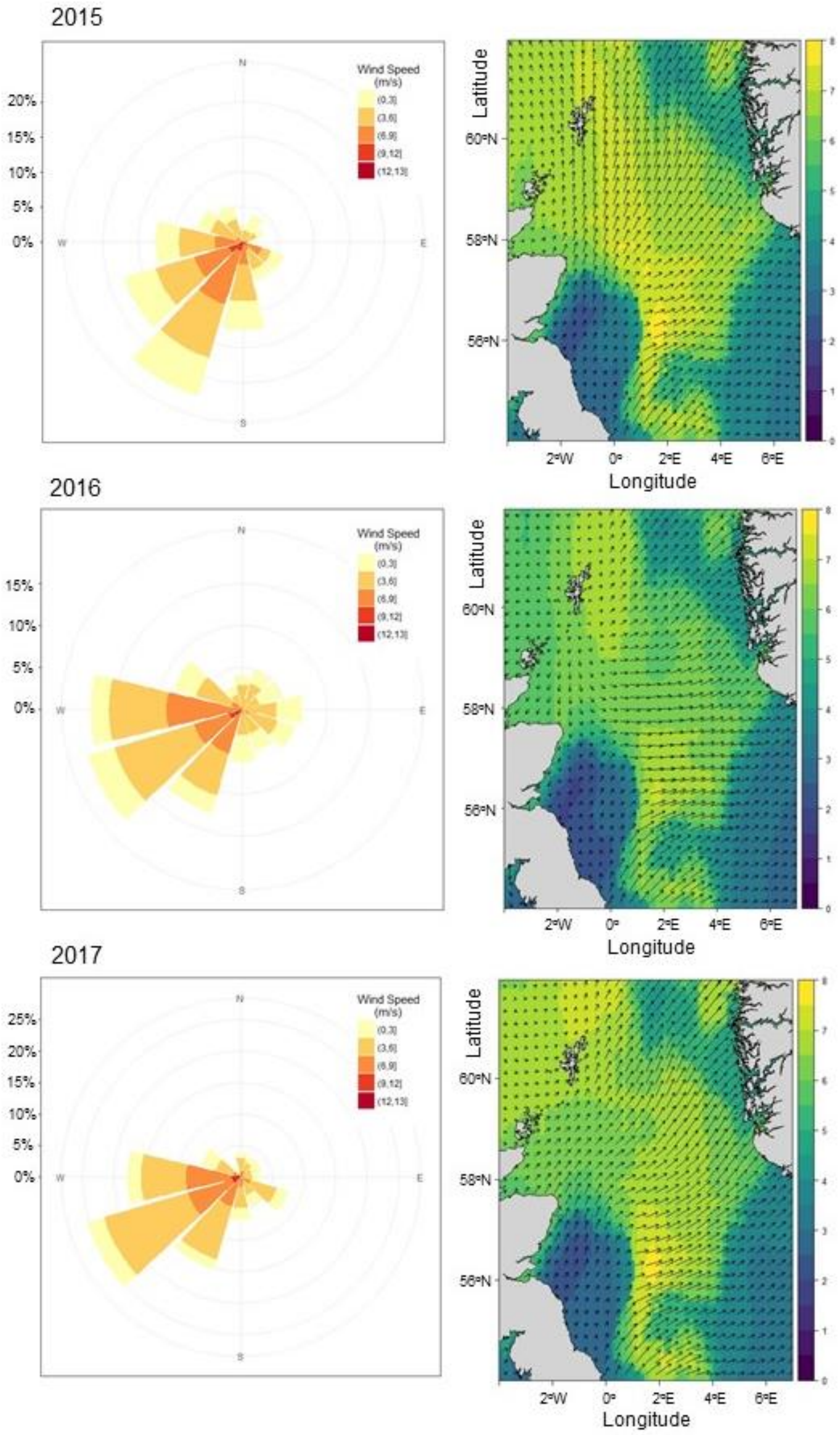

Figure 4.3. Wind speed and direction (wind origin) at Bass Rock (left column) and across the northern and central North Sea (right column) during the breeding seasons (June-August) of 2015, 2016 and 2017. Wind data are represented on a 0.125 × 0.125° grid. Shading represents wind speed (ms^{-1}) from 0 (dark blue) to 8 (yellow). Black arrows represent wind direction and their length is proportional to wind speed.

4.3.1 Effects of weather conditions on behaviour at sea

When commuting away from the colony, birds spent 28 % of their time in flight with a tail wind and 15 % with a head wind, compared with 12 % with a tail wind and 41 % with a headwind when returning to the colony (Figure 4.4a & c). When actively foraging, birds spent significantly more time flying into the wind (33 %) and less with the wind behind them (18 %) than expected by chance (Figure 4.4b; $\chi^2_2 = 511.0$, $P < 0.0001$).

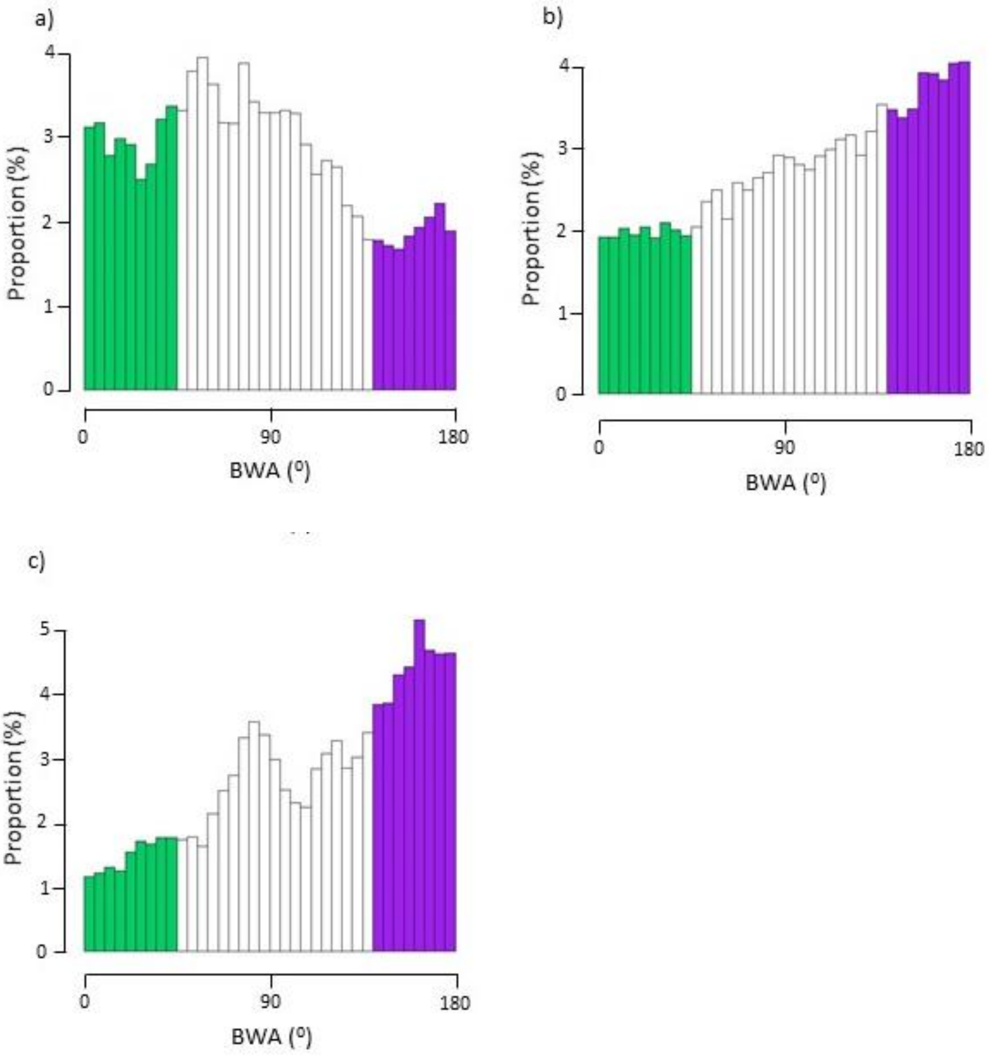

Figure 4.4. Frequency distribution of bird-wind angles for GPS locations during **(a)** outbound commuting (n = 19,238 locations), **(b)** active foraging (n = 20,446) and **(c)** inbound commuting (n = 21,233). Green shading represents tail winds; white, cross winds; purple, head winds.

Linear mixed effects models allowed evaluation of how different weather variables affected trip durations and the proportions of each trip spent travelling, actively foraging and sitting on the water. Increases in the distance travelled per trip resulted in significant increases in both trip duration (Figure 4.5a; $F_{1,140} = 522.7$, $P < 0.001$) and the proportion of each trip spent commuting (Figure 4.5b; $F_{1,140} = 45.1$, $P < 0.001$) but no other predictor variable meaningfully improved either model (ΔAIC > 2 in each case; AICc weight dropped from 0.80 to 0.05 and from 0.50 to 0.11, respectively; Appendix B1). The proportion of time spent actively foraging per trip increased significantly with increasing wind speed (Figure 4.6; $F_{1,140} = 18.4$, $P < 0.001$) but the model was not meaningfully improved by including any other variable (Appendix B1).

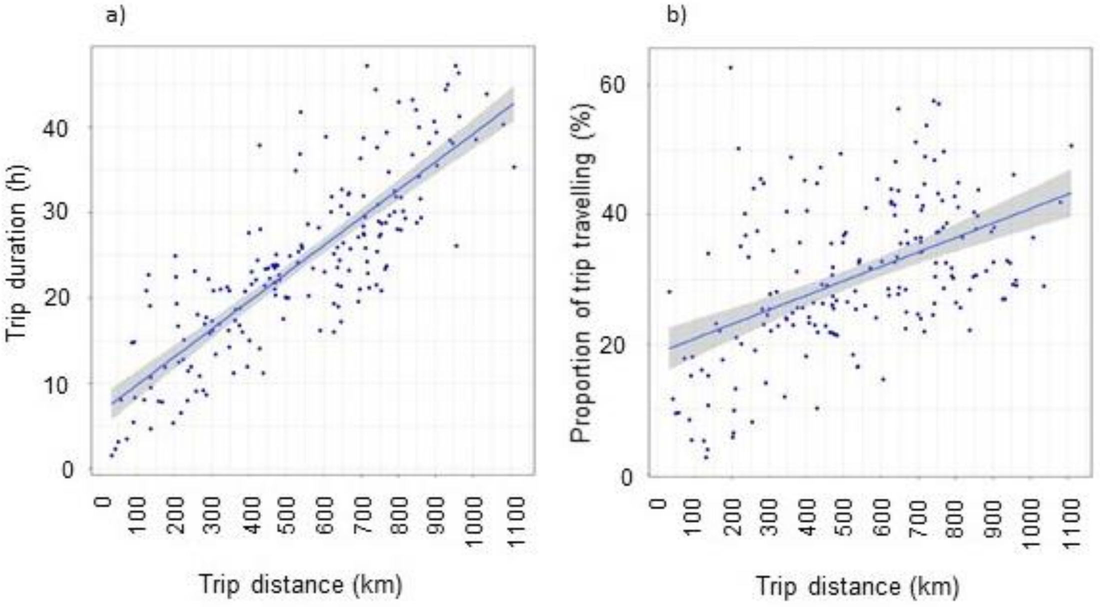

Figure 4.5. Trip distance in relation to **(a)** trip duration and **(b)** proportion of the trip spent travelling. Lines show linear model predictions with 95% confidence region.

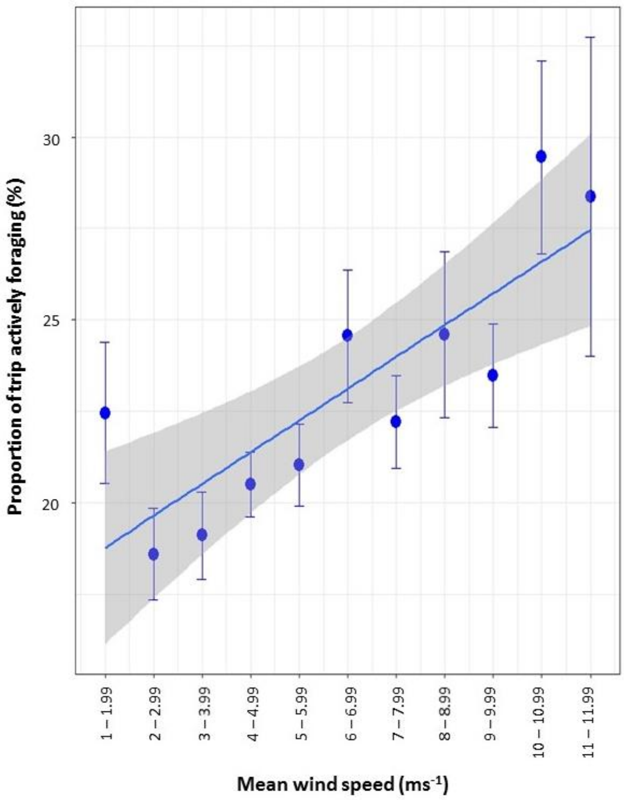

Figure 4.6. Proportion of trip spent actively foraging (mean ± SE) in relation to mean wind speed encountered at sea. Line shows linear model prediction with 95% confidence region.

There was no clear top model for the proportion of daylight hours spent on the water but all seven models with ΔAIC < 2 included distance travelled per trip and three included wind speed, including the top model (Appendix B1), indicating that the proportion of time on the water decreased as distance travelled increased and with increasing wind speed (Figure 4.7).

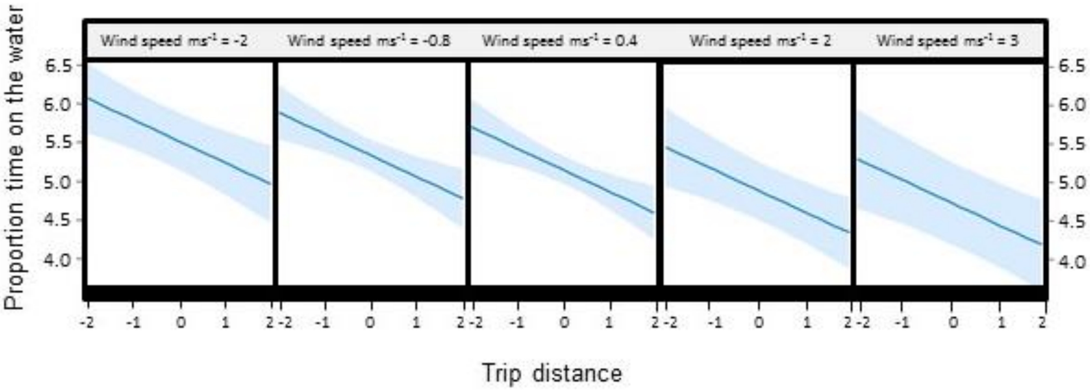

Figure 4.7. LMM predictions for the proportion of daylight hours spent on the water in relation to distance travelled per trip, for five different wind speeds.

During periods of commuting, whether outbound or inbound, ground speeds were higher during tail winds than head winds (mean ± SD = 17.5 ± 3.4 ms^{-1} and 12.6 ± 2.0 ms^{-1}, respectively; Figure 4.8). Ground speed increased by ~3 ms^{-1} for every 10 ms^{-1} increase in tail wind speed (LM; $F_{1,8} = 18.46$, $P < 0.001$, $R^2 = 0.70$, slope = 0.31) and decreased by ~ 4 ms^{-1} for every 10 ms^{-1} increase in head wind speed (LM; $F_{1,8} = 171$, $P < 0.001$, $R^2 = 0.96$, slope = -0.41).

Average travel speed over the return leg of a trip (including time on the water) was significantly related to distance from the colony (GLM; $F_{1,184} = 26.1$, $P < 0.001$) and bird-wind angle (GLM; $F_{1,182} = 5.9$, $P < 0.05$), with the best fitting GLM describing a quadratic relationship:

$$\text{Travel speed (km h}^{-1}\text{)} = 3.394 \times 10^{-2} \text{ (SE} \pm 7.68\text{) distance} - 5.9 \times 10^{-5} \text{ (SE} \pm 2.22 \times 10^{-5}\text{) distance}^2 - 1.229 \times \text{bird-wind angle}$$

Travel speed increased with increasing distance to the colony up to 100 - 200 km, beyond which the relationship levelled off, with some indication of a reduction in average speed over the longest distances (Figure 4.9a). In addition, travel speeds over distances up to ~150 km were fastest for birds returning with a tail wind and slowest for those returning into a head wind, with no clear effect of bird-wind angle over greater distances (Figure 4.9a). Time spent on the water during the return leg of a trip was also significantly related to maximum distance from the colony, distance^2 and bird-wind angle (GLM; $P < 0.001$ in each case). For return legs up to 100 - 200 km in length, time on the water decreased with increasing distance and was greatest for birds returning with a tail wind and least for those returning into a head wind (Figure 4.9b).

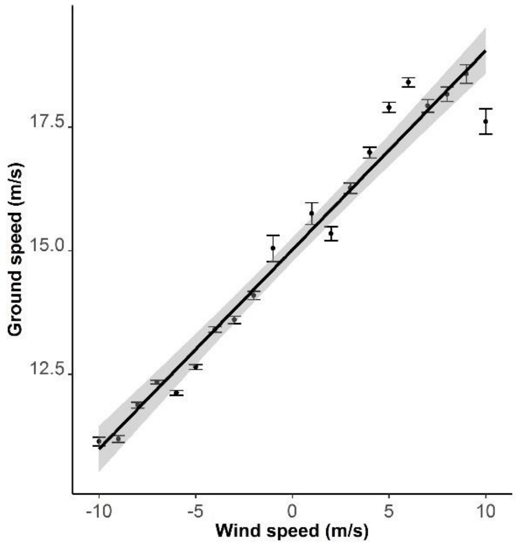

Figure 4.8. Ground speeds of commuting gannets in relation to head (- ve) and tail (+ ve) wind speed.

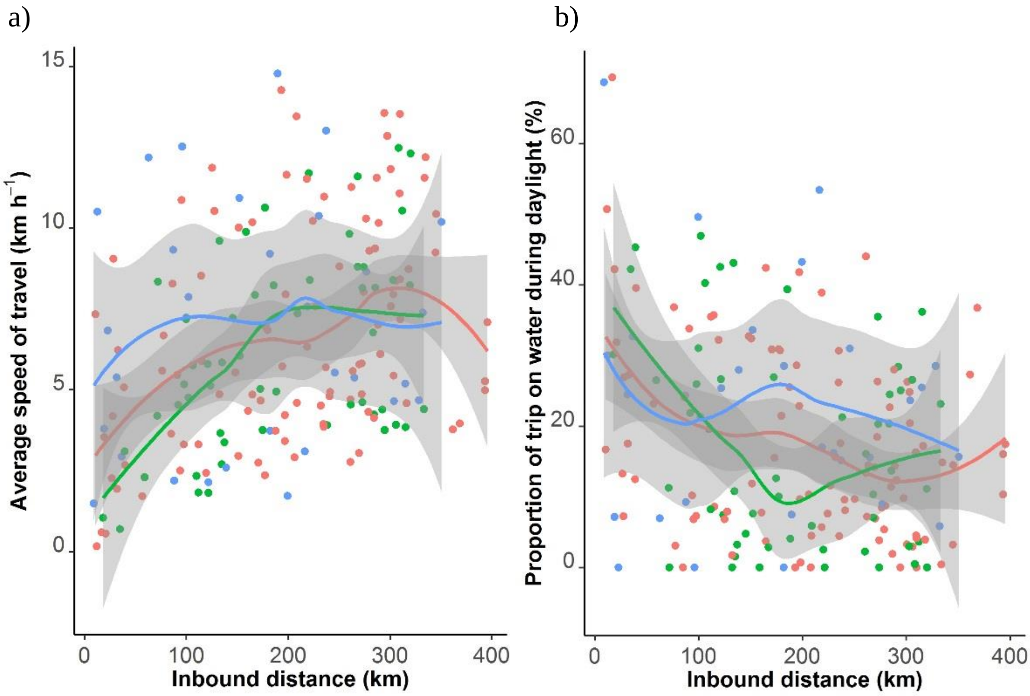

Figure 4.9. (a) Average speed of travel and **(b)** proportion of daylight hours on the water during the return leg of foraging trips in relation to distance (km) for different bird-wind angles (green, head wind; pink, cross wind; blue, tail wind). Lines show linear model predictions estimated with loess function in R. Shaded areas are 95% confidence regions. Based on data for 198 foraging trips.

4.3.2 Flight height

Gannets adjusted their flight heights depending on wind speed and direction. Flight heights were lower when commuting than when actively foraging (Chapter 2) and lower when commuting into head winds than with tail winds (LM; $\chi^2 = 761.7$, $P < 0.001$; Table 4.1). When actively foraging, flight heights were unaffected by bird-wind angle, with median heights of ~ 28 m in both head and tail winds (Table 4.1).

Table 4.1. Flight heights of gannets during commuting and active foraging with head and tail winds.

	Head wind		**Tail wind**	
	Median (m)	IQR (m)	Median (m)	IQR (m)
Commuting	12.6	3.8 – 29.2	25.6	9.6 – 46.1
Active foraging	27.8	9.4 – 47.3	28.3	7.7 – 48.7

Linear mixed effects modelling allowed evaluation of the effects of different weather variables on flight heights of males and females during active foraging and commuting. The top models, ranked according to AICc (ΔAIC < 2), indicated that wind speed and rainfall had the strongest influence on flight height during active foraging (Appendix B2) with both variables included in all six top models, whereas sex and low cloud were included in four of the top six models. Model predictions from the top model set indicated that flight height during active foraging increased as wind speed increased and as rainfall increased in both males and females. There was no difference between sexes in the slopes of these relationships but females flew higher in both cases (Figure 4.10). Wind speed and rainfall also interacted such that the relationship between wind speed and flight height became steeper as rainfall increased in both sexes (Figure 4.11). Some caution should be placed on the interpretation of the rainfall data, however, due to the small quantity of data during heavy rain.

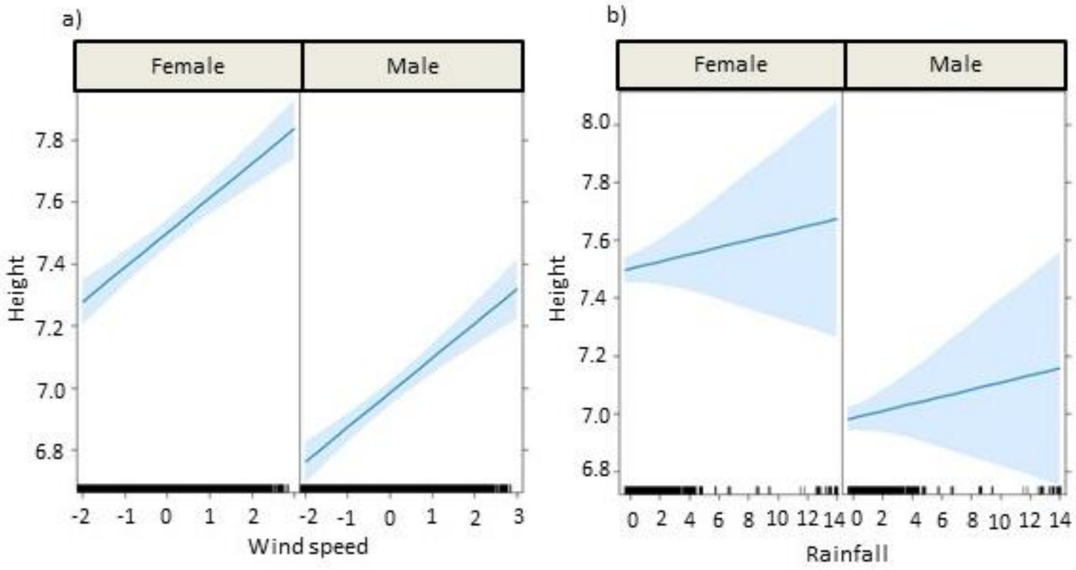

Figure 4.10. Model predictions (LMM) for the relationship between flight height during active foraging and **(a)** wind speed and **(b)** rainfall in males and females.

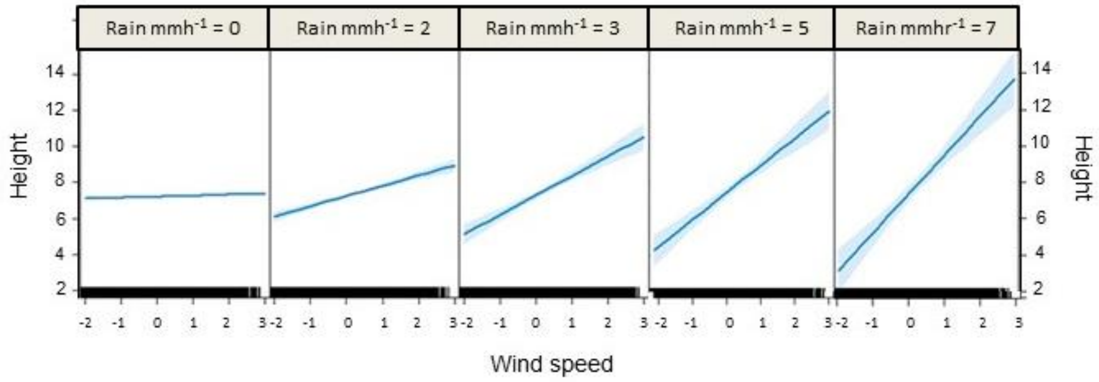

Figure 4.11. Model predictions (LMM) for the relationship between flight height during active foraging and wind speed under different rates of rainfall.

The proportion of flight in ground effect increased from 11 % in rough sea conditions to 28 % in calm sea conditions when commuting away from the colony with a tail wind and from 25 % in rough sea conditions to 42 % in calm sea conditions when returning to the colony with a head wind (Table 4.2).

Table 4.2. Proportion of time spent utilising ground effect (GE) relative to wind direction whilst commuting outbound and inbound. Wind speeds < 2 ms^{-1} produce calm sea conditions, > 2 ms^{-1} produce conditions where sea surface is rough (Met Office, 2016).

	Tail winds				**Head winds**			
Wind speed	**Outbound**		**Inbound**		**Outbound**		**Inbound**	
	GE	Non GE	GE	Non GE	GE	Non GE	GE	Non GE
< 2 ms^{-1}	0.28	0.72	0.17	0.83	0.17	0.83	0.42	0.58
> 2 ms^{-1}	0.11	0.89	0.16	0.84	0.16	0.84	0.25	0.75

4.4 Discussion

The location of the Bass Rock, 2 km off the coastline of East Lothian in the Firth of Forth, means that gannets breeding there are strongly constrained in the directions they are able to travel on foraging trips without crossing land. Nonetheless bearings of trip were bimodal, with more NE and SE of the colony and fewer due east, as also found in previous studies at this site (Hamer et al., 2000, Wakefield et al., 2015). The prevailing wind came from the south-west meaning that birds making trips to the north-east were likely to have encountered tail winds on the outbound part of the journey and head winds on the return leg whereas birds that made trips to the south-east were more likely to have encountered cross winds during both phases of the trip.

Both wind speed and direction influence energy expenditure during flight (Gabrielsen et al., 1991, Furness and Bryant, 1996, Sakamoto et al., 2013) with a greater effect for gannets during commuting than active foraging (Amelineau et al., 2014). Birds might be expected to reduce energy expenditure during trips by avoiding headwinds and making use of tailwinds but in the case of gannets breeding at Bass Rock and elsewhere (Amelineau et al., 2014) structuring a foraging trip to avoid headwinds is difficult due to the location of the colony in relation to the coastline and the prevailing wind direction. Gannets from Bass Rock spent more time flying into with head winds during active foraging than when commuting, similar to northern gannets from Rouzic (Amelineau et al., 2014). This supports the suggestion that foraging into head winds makes it easier for gannets to reduce their ground speed and spot prey (Amelineau et al., 2014, Machovsky-Capuska et al., 2012).

In support of hypothesis (1), increases in wind speed resulted in a greater proportion of each trip spent actively foraging. This suggests that lighter winds were more favourable for the location and capture of prey, possibly because as visual predators, birds could more easily target prey when there was less disruption to the water surface (Sundarabalan et al., 2016). The increase in time spent foraging did not, however, result in an increase in overall trip duration, because birds at least partly compensated for this increase by decreasing the time they spent on the water during strong winds. These results contrast to some extent with the behaviour of Cape gannets *(Morus capensis)* where mild to no wind, as well as strong winds resulted in shorter foraging trips durations (Pistorius et al., 2015). It was suggested that low rates of prey capture during strong winds could be offset by enhanced location of prey patches through wind-supported flight. However, I found no evidence that the proportion of time spent commuting during trips was affected by wind speed, and very little support for any effect of wind direction. An alternative explanation for the pattern observed in Cape gannets was that strong winds reduced the distances travelled per trip, which were not examined in that study. I found no discernible effect of rainfall on trip duration or the proportion of the trip spent actively foraging. Again, this differs from the pattern recorded in Cape gannets which shortened trip durations in response to no or heavy rainfall (Pistorius et al., 2015). However, Cape gannets experienced much heavier rainfall than the Northern gannets in this study.

Adults returned at higher speeds from more distant foraging locations up to ~200 km from the colony, presumably reflecting a benefit in returning quickly to feed dependent offspring and relieve the partner at the nest. A similar pattern was recorded by (Hamer et al., 2007), who also found that speeds decreased for the furthest destinations (beyond ~400 km), probably due to constraints on energy expenditure during flight. In keeping with this notion, I found that the increase in speed of travel for distances up to ~200 km was due at least in part to a decrease in the proportion of time on the water, with the asymptote in speed of travel corresponding with a levelling off in time on water beyond this distance, particularly for birds flying into headwinds. Over the longest return distances, birds encountering headwinds spent less time on the water and so were able to attain similar speeds of travel on average to those encountering crosswinds or tailwinds. These data suggest that by adjusting time spent on the water, birds were able to buffer trip durations to some extent against adverse weather conditions encountered at sea.

In support of hypothesis (2), wind speed significantly affected flight heights during both commuting and active foraging. The higher proportion of commuting flight at low elevations into head winds compared with tail winds supports the notion that individuals can reduce energy expenditure by avoiding headwinds (through wind shear effect) or by taking advantage of additional lift provided by ground effect. Wind speed and its interaction with rainfall had a significant but complex effect on flight height during active foraging. Flight height of both males and females during active foraging increased as wind speed increased with its influence amplified in the presence of higher rainfall. The response to the combination of these two variables, which disrupt the sea surface in different ways, could be linked to changes in the visibility or behaviour of prey (Kowalczyk et al., 2015, Albert et al., 2016). For instance, herring larvae approach the sea surface in calm conditions but move deeper when wind speed increases (Gallego et al., 1999). Mackerel are visual predators of herring larvae (Skaret et al., 2015) and so may track their vertical distribution, resulting in turn in changes in the heights from which gannets preying on mackerel commence their dives. In more challenging conditions it may also be more energetically efficient to perform multiple V-shaped dives (linked to flight height - Chapter 3) during which momentum is used to dive rather than actively pursuing prey under water.

Climate-induced changes in weather patterns and oceanic wind regimes could strongly affect both the foraging and migration strategies of seabirds as they adapt to changes in environmental conditions encountered at sea as well as in prey distribution, abundance and behaviour (Weimerskirch et al., 2012, Fayet et al., 2017). Gannets are very flexible in the distances they can travel and the range of prey they are able to capture (Hamer et al., 2007) but how they and their prey respond to weather conditions is a key aspect of their continued success. The influence of weather and particularly wind strength and direction on flight height is also something that is currently lacking from assessments of potential collision risk from offshore wind farms (Cook et al. 2018) and so more analysis of how seabirds respond to different weather conditions is recommended, particularly at proposed wind farm sites.

4.5 Literature cited

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Chapter 5 : Collision risk from offshore wind farms and potential population consequences

Abstract

Marine habitats around the coast of the UK are coming under increasing pressure from renewable energy developments leading to concerns about potential impacts on wildlife, including seabirds. Mortality from collision with turbine blades could have significant negative effects on some seabird populations but estimates of potential mortality are often based on partial or subjective data, with key knowledge gaps including temporal and age-specific variation in movements and behaviour at sea. Northern gannets are a species of key concern in this respect and in this chapter I compare the foraging movements and behaviour of adult and immature gannets at Bass Rock, including data for adults during two different periods of the breeding season (pre-laying and chick-rearing). I examine how differences in the distribution and behaviour of birds at sea affect the potential collision risk from planned and operating wind farms within the overall foraging ranges of birds and I assess the likely consequences of predicted mortality levels for future population growth. I found that birds spent > 70 % of their flight time within the wind farm sites commuting, mainly below the minimum height swept by turbine blades. However, the proportion of time spent flying at risk height varied between sexes, resulting in a higher collision risk for females than males. Collision risk was also higher for adults during chick-rearing than for immature birds or adults in spring. Adjusting vital rates to account for this predicted additional mortality reduced the predicted population growth rate but the population was still predicted to increase by > 2.5 % per annum, and increasing or decreasing predicted collisions by 10 % yielded a range of estimates that all predicted sustained population growth. Nonetheless, in view of the uncertainty in different elements of these estimates, I advocate caution including continued monitoring of adult survival and population size following installation of turbines at proposed wind farm sites.

5.1 Introduction

Commitments made by the UK Government aimed at reducing reliance on fossil fuel energy have driven a large increase in the number of operational and proposed wind farms off the coasts of the UK (H.M. Government, 2017). Consequently, concerns have been raised over the potential ecological impacts of this industrialisation of marine habitats (Garthe and Huppop, 2004, European Commission, 2010, Certain et al., 2015), with particular concern over impacts on the internationally important populations of seabirds that forage in the seas around the UK (Masden et al., 2015, Thaxter et al., 2018).

Both direct mortality from collision with turbine blades and indirect displacement and barrier effects could have significant negative effects on some seabird populations (Cook et al., 2018). However, estimates of potential mortality are often based on partial or subjective data (Green et al., 2016), with key knowledge gaps including temporal and age-specific variation in movements and behaviour (Furness et al., 2013, Borkenhagen et al., 2018, Cook et al., 2018).

Northern gannets have been identified as potentially at risk from offshore wind farms (Furness et al., 2013, Bradbury et al., 2014) due to their long foraging ranges (Hamer et al., 2007, Wakefield et al., 2013) the heights at which they fly (Cleasby et al., 2015a) and the proximity of several consented offshore wind developments to large breeding colonies of international importance for this species (Furness and Wanless, 2014). Estimation of potential collision risks requires data on the movements and behaviour of birds at sea, which have been derived from several sources including ship-based surveys, land-based radar and bird-borne data loggers (Johnston et al., 2014a, Cleasby et al., 2015a). These different sources are to some extent complementary (Camphuysen et al., 2012) but while survey and radar data provide only limited coverage and do not allow the provenance or breeding status of birds to be determined, currently available tracking data are almost entirely for breeding adults during the chick-rearing stage of the season, with very limited or no data for birds of known sex, or for other age-classes or times of year. For instance, immature birds, which can comprise > 50 % of the total population (Klomp and Furness, 1992), are known to range more widely than adults during the breeding season (Votier et al., 2017, Grecian et al., 2018) and males and females differ in their foraging distributions and behaviour (Chapter 3) but the consequences for potential collision risk have not previously been examined. Similarly, calculations of collision risk across the year have relied on the assumption that the foraging behaviour of adults during chick-rearing is representative of the entire breeding season, although this is unlikely to be the case.

Previous data have indicated that adult gannets spend more time flying at collision risk height (i.e. within the range of heights swept by turbines' blades) when actively foraging than when commuting to or from the colony (Cleasby et al. 2015, and Chapter 3). Therefore the time spent actively foraging within offshore wind farm sites is a key determinant of potential collision risk. In this chapter I compare the foraging movements and behaviour of immature and adult gannets at Bass Rock, including data for adults during two distinct periods of the breeding season (pre-laying and chick-rearing). I examine how differences in the distribution and behaviour of birds at sea affect the potential collision risk from wind farms within the overall foraging ranges of birds at Bass Rock.

5.2 Methods

5.2.1 Fieldwork

Fieldwork took place at Bass Rock, UK (6º 6' N, 2° 36' W) between mid-April and mid-August over three consecutive years (2015 - 2017). Using a 6-meter telescopic pole fitted with a metal noose or hook, 63 adult gannets (age ≥ 5 years) were caught at the nest site while attending chicks or, in 2017, before the commencement of egg-laying (the latter had all bred at least once previously). These birds (39 males, 24 females) were sexed from observations of sex-specific behaviour or in some cases, DNA analysis (as described in Chapter 3). In addition, 21 immature birds (ages 2 - 4 years, determined from plumage characteristics; (Nelson, 2002, Votier et al., 2011) were caught in June - July 2015 at club sites (areas of the colony frequented by pre-breeding individuals) or while attempting to hold territories around the colony.

Unless already ringed, birds were fitted with a metal British Trust for Ornithology ring and an individually numbered colour ring (Wakefield et al., 2013). Each adult bird was equipped with a GPS logger (i-gotU GT600, Mobile Action Technology Inc., Taipei, Taiwan) weighing 37 g and, during chick-rearing, a pressure logger (MSR-145W, MSR Electronics, Seuzach, Switzerland) weighing 18 g. Immature birds were fitted with a GPS Radio Frequency logger (GPS-RF, e-obs GmbH, Munich, Germany) weighing 45 g, as recapture was unlikely but remote download of the data was possible within 2 km of the colony. All loggers were attached using Tesa© tape: GPS loggers were attached to the upper side of the central trail feathers and programmed to record locations every 2 minutes; pressure loggers were attached to the underside of the central tail feathers and programmed to record pressure and temperature at 1 Hz. Adults were recaptured after 7 - 14 days to retrieve the loggers. Handling time of birds at both deployment and recapture was no longer than 15 minutes. Maximum device weight per bird (55 g) was less than 2 % of body mass (3.2 ± 0.3 kg) and below the maximum recommended for bio-logging studies (Phillips et al., 2003) while the difference in device weights for adults and immature birds was at most only 0.3 % of body mass. Previous studies have shown that such deployments have no discernible impact on trip durations or body masses of birds (Hamer et al., 2007, Cleasby et al., 2015b).

5.2.2 Trip metrics

I interpolated all location data to 2 min intervals and classified behaviours at sea as described in Chapter 2 and determined trip metrics as described in Chapter 3. I then compared trip metrics between age-classes and stages of the season by fitting linear mixed models (LMM) using residual maximum-likelihood (REML) in the R package lme4 (Bates et al., 2015).

5.2.3 Population size of immature birds

Gannets have a stage-structured life history (Figure 5.1). To estimate the number of immature birds (age 2 - 4) acting as central place foragers from the Bass Rock, I used R version 3.5.1 (R Development Core Team, 2016a) to construct a Lefkovitch (stage-structured) population matrix model, A, with the following form:

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & F \\ \varphi 0-1 & 0 & 0 & 0 & 0 & 0 \\ 0 & \varphi 1-2 & 0 & 0 & 0 & 0 \\ 0 & 0 & \varphi 2-3 & 0 & 0 & 0 \\ 0 & 0 & 0 & \varphi 3-4 & 0 & 0 \\ 0 & 0 & 0 & 0 & \varphi 4-5 & \varphi a \end{bmatrix}$$

Fecundity (*F)* was set at 0.36 estimated as $P \times f \times R \times \phi_{a,}$ where P = breeding probability (assumed to be 1); f = proportion of females in the population (assumed to be 0.5), $R = E \times B \times \phi_c$ where E is clutch size (assumed to be 1), B is breeding frequency (assumed to be 1 attempt per annum) and ϕ_c is probability of the chick fledging (0.720 (Wanless et al., 2006, Sherley et al., 2015)). Annual adult survival (*φa)* was set at 0.949 (based on annual sightings of colour-ringed birds at the colony; Deakin et al. submitted), juvenile survival from age 0 – 1 (*φ0-1)* was set at 0.542 and survival of immature birds (*φ1-2* to *φ4-5)* was 0.779, 0.859, 0.863 and 0.863, respectively, based on BTO ring recovery data; (Wanless et al. 2006).

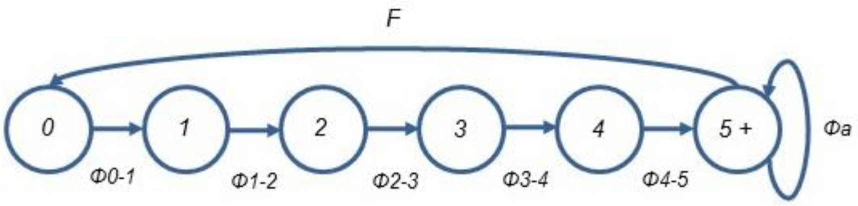

Figure 5.1. Life history model for gannets. Each life-history stage (age) is represented by a circle. The arrows represent transitions between stages and indicate survival (ϕ) and transitioning from one stage to the next. The curved arrow at the top represents fecundity (*F*) or the number of young fledging per female.

The population growth rate estimated from this model ($\lambda = 1.036$) was very similar to the observed growth of the population at Bass Rock between 2004 and 2014 (Murray et al., 2015). Hence, I used this matrix to calculate the stable age distribution, giving the numbers of individuals in each age-class for a breeding population of 150,000 adults (Murray et al., 2015).

5.2.4 Spatial distribution and density at sea

For each identified group within the population (age-class plus, for adults, sex and stage of season) I determined the 50, 75 and 95 % utilisation distribution (UD) over a 1 km^2 grid for those locations where birds were in flight, using a smoothing parameter of 10 km in the R package adehabitatHR (Calenge, 2006). I estimated the number of birds at sea at any time using mean trip duration and mean time spent at the colony between trips. I next estimated the density, d, of birds from each group in flight at sea following (Wakefield et al., 2013) using the equation:

$$d = \hat{u}_{i,x} N Z$$

where $\hat{u}_{i,x}$ is the empirical probability density of use of cell x by bird i, N is the number of birds within each group predicted to be sea at any time and Z is the proportion of time spent in flight.

5.2.5 Modelling collision risk

The foraging distribution of gannets from Bass Rock covers the footprints of six proposed, consented and operational wind farms (hereafter, wind farm sites). Within each wind farm site, I calculated the proportion of time in flight spent commuting and actively foraging. For adults in summer I then used flight heights estimated every 2 minutes (see Chapters 2 and 3) to calculate the proportion of time spent at risk height during each of these activities. For each wind farm site the total proportion of flight at risk height was therefore:

$$P_F R_F + P_C R_C$$

where P = proportion of time spent foraging (F) or commuting (C) and R = proportion of flight at risk height during each activity.

Flight height data were not obtained for immature birds or adults pre-laying so rather than calculate collision risk at individual wind farm sites I assumed that the proportion of commuting and active foraging flight at risk height (R_F and R_C above) across all sites was the same as that estimated for adults during the summer.

I then used the basic collision risk model (Band, 2012) to assess the potential impact across six wind farm sites within the foraging distribution of adult and immature gannets from Bass Rock. Locations and parameters of wind farm sites (numbers and sizes of turbines, etc) were obtained from an online database (www.4coffshore.com) with additional information from individual developers. Shape files of wind farm sites were downloaded from the Crown Estate (The Crown Estate, 2017). For each wind farm site the proportion of locations where birds were flying within the height envelope swept by the turbines was estimated using the parameters given in Appendix C. The density of birds in flight within each wind farm site was estimated from the map of estimated densities in flight at sea calculated using the method described above (1.3.5). The monthly collision risk estimates for males, females and immatures during summer (June, July and August) and adults during spring (April) for each wind farm site were estimated using an assumed avoidance rate of 98.9 % (Cook et al., 2018). Details of the bird data and the time the turbines were assumed to be operational are given in Appendix C.

5.2.6 Estimating potential population impact

To assess the potential impact of mortality from wind farms on population growth, I first used the predicted additional mortality from collision with wind turbines to adjust the survival estimates for each age class in the population projection matrix A above (assuming that wind farm mortality was entirely additive, and dividing additional mortality of immature birds evenly across age-classes). I then recalculated λ and applied 10 % confidence intervals to this estimate by recalculating survival rates of each age-class assuming mortality due to wind farms was ± 10 % of estimates from collision risk models.

5.3 Results

5.3.1 Foraging trip destinations and metrics

I obtained 265 tracks (189 with altitude data) from 58 adults during chick-rearing in 2015 - 17, 16 tracks from 9 adults prior to egg-laying in 2017 and 118 tracks from 15 immature birds in 2015. Active foraging areas of adults were mainly SE and NE of the colony, extending as far as Dogger Bank to the SE and Little Halibut Bank and the Fladen Ground to the NE, with no marked difference in areas used pre-laying and during chick-rearing (Figure 5.2b-d). In contrast, immature birds ranged widely across the North Sea with core foraging areas encompassing the Norwegian Trench and Danish, Dutch and German waters (Figure

5.2a). Consequently, active foraging locations of immature gannets overlapped with more wind farm sites than those of adults (Figure 5.3).

Trip durations of adults in 2017 differed significantly between pre-laying and chick-rearing (Table 5.1; LMM using sqrt hours $\chi^2_1 = 5.0$, $P < 0.05$). This was partly because adults spent significantly longer on the water overnight during pre-laying trips (median = 13.6 h, IQR 7.6 – 14.7) than during chick-rearing (median = 4.8 h, IQR 3.7 – 6.1) ($\chi^2 = 41.8$, $P < 0.001$).

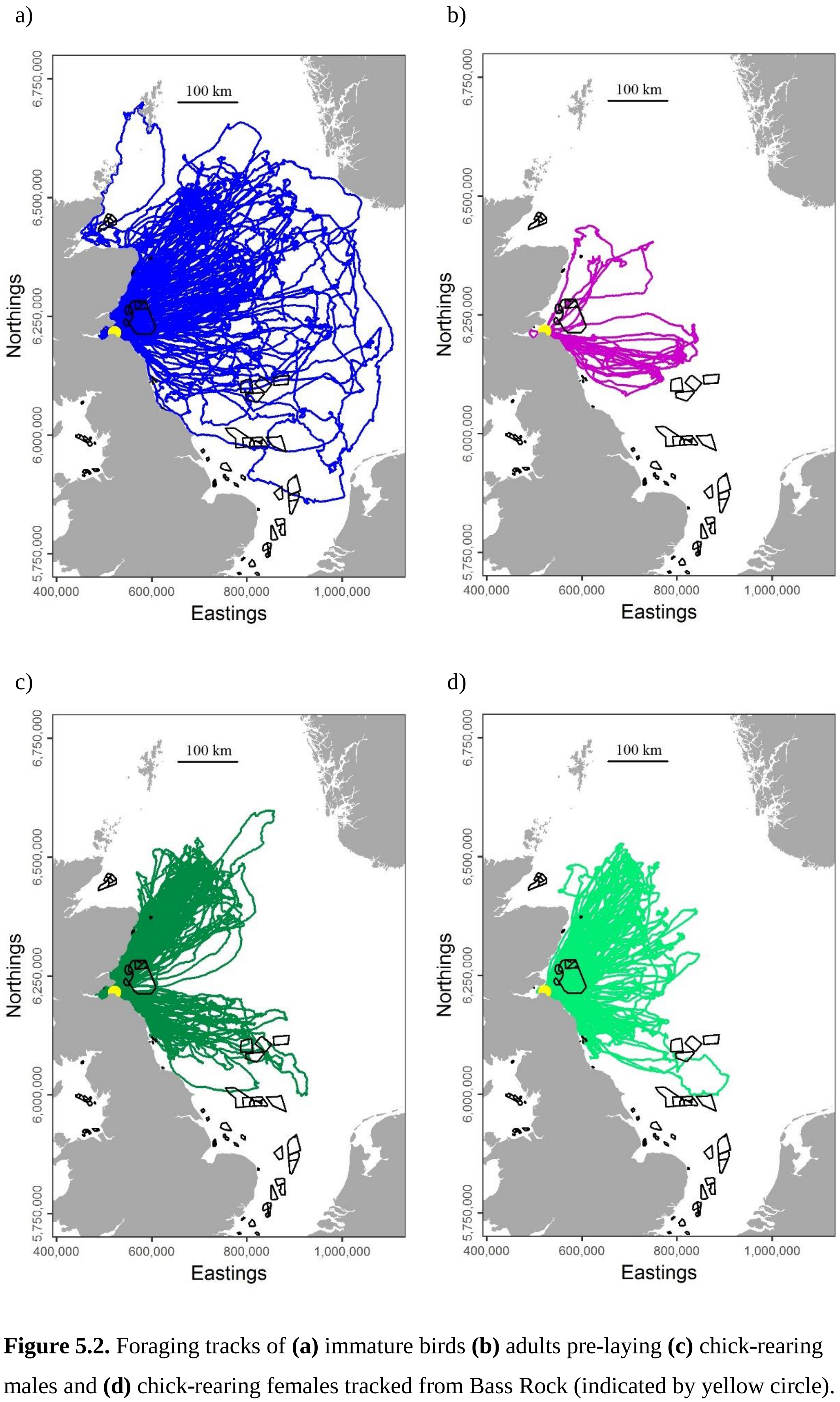

Figure 5.2. Foraging tracks of **(a)** immature birds **(b)** adults pre-laying **(c)** chick-rearing males and **(d)** chick-rearing females tracked from Bass Rock (indicated by yellow circle). Wind farm sites are outlined in black.

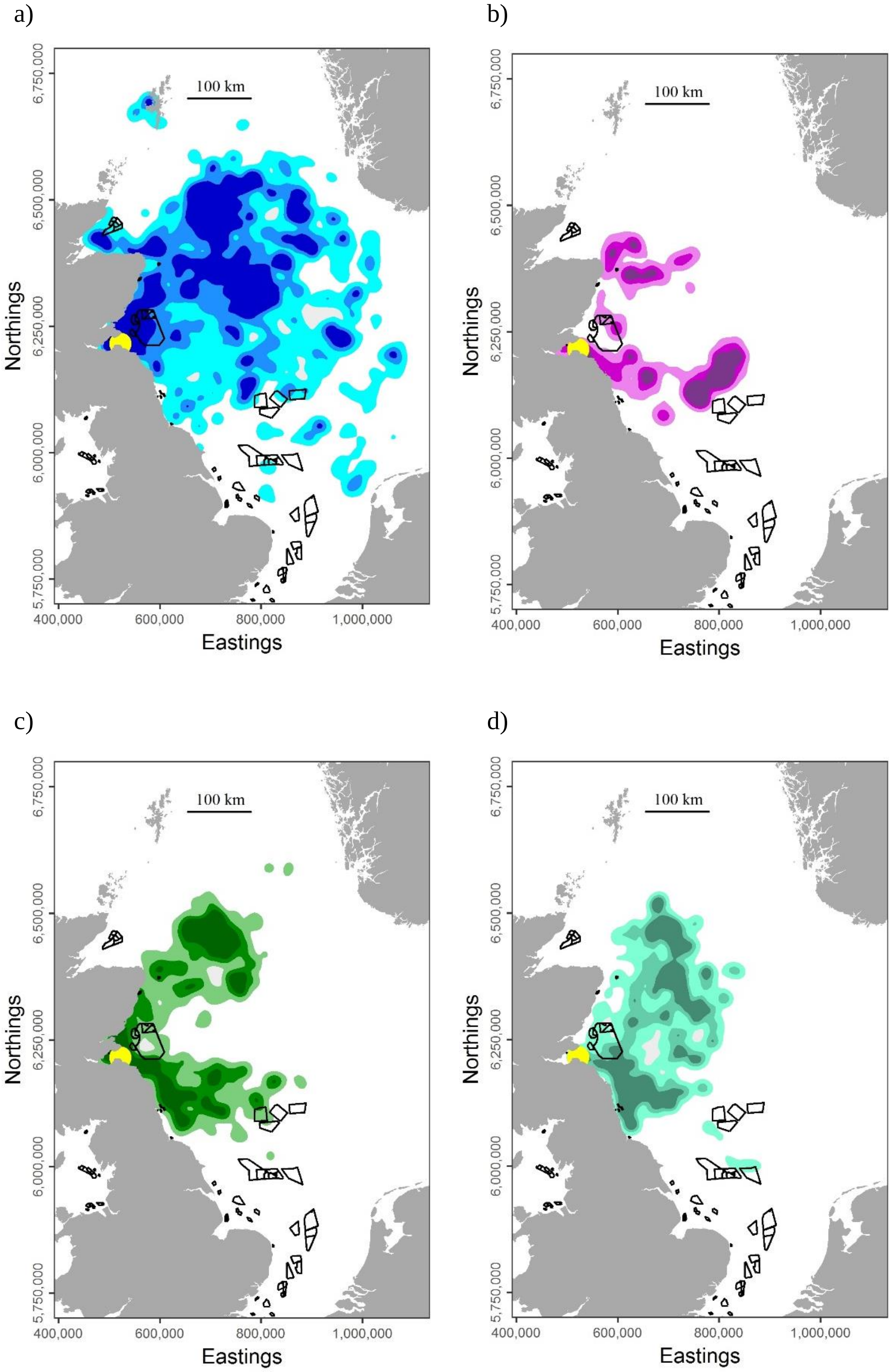

Figure 5.3. Utilisation distributions (UDs) of **(a)** immature birds **(b)** adults pre-laying **(c)** chick-rearing males and **(d)** chick-rearing females tracked from Bass Rock (indicated by yellow circle). UDs are based on active foraging locations, shading denotes UD contours (darker, 50%; lighter, 95%). Wind farm sites are outlined in black.

However, the difference in trip durations (18.2 h, calculated from Table 5.1) far exceeded the difference in time on the water overnight (8.8 h). Departure angles from the colony also differed between time-periods (Table 5.1; $\chi^2_1 = 6.8$, $P < 0.05$) but there was no significant difference in total distance travelled at sea ($\chi^2_1 = 1.57$, $P = 0.2$) or maximum displacement from the colony ($\chi^2_1 = 0.43$, $P = 0.5$). Trip durations of immature birds in 2015 were significantly longer than those of adults rearing chicks at the same time (Table 5.1; LMM using data only for 2015, with log-transformed hours, $\chi^2_1 = 4.8$, $P < 0.05$). However there was no difference between age-classes in departure angle ($\chi^2_1 = 0.00$, $P = 0.96$), total distance travelled per trip (square root of distance, $\chi^2_1 = 1.3$, $P = 0.26$) or maximum displacement ($\chi^2_1 = 0.01$, $P = 0.92$). Despite adults making trips of significantly longer duration pre-laying than when providing for chicks, there was no significant difference between time-periods in the proportion of each trip spent foraging ($\chi^2_1 = 1.68$, $P = 0.19$) or travelling to and from the colony during daylight hours ($\chi^2_1 = 0.72$, $P = 0.4$) (Figure 5.4). During June to August, immature and chick-rearing gannets spent similar proportions of each trip foraging ($\chi^2_1 = 1.68$, $P = 0.19$). However, chick-rearing adults spent a greater proportion of daylight hours travelling than immature birds ($\chi^2_1 = 21.46$, $P < 0.001$).

Table 5.1. Characteristics of foraging trips by immature gannets (2015), and by adult gannets prior to laying (2017) and during chick-rearing (2015-2017).

	Immatures		**Pre-laying**		**Chick-rearing**	
	Median	IQR	Median	IQR	Median	IQR
Duration (h)	42.9	12.1 – 71.0	41.6	28.0 – 50.4	23.4	17.0 – 29.5
Distance (km)	695.5	122.0 – 1063.0	717.8	555.5 – 800.6	536.6	309.6 – 724.0
Maximum displacement (km)	283.9	40.7 – 364.3	267.6	185.2 – 295.5	218.3	121.1 – 303.6
Departure angle (deg)	30.9	-6.5 – 70	-18.3	-27.4 – -2.9	37.2	-16.9 – 62.6

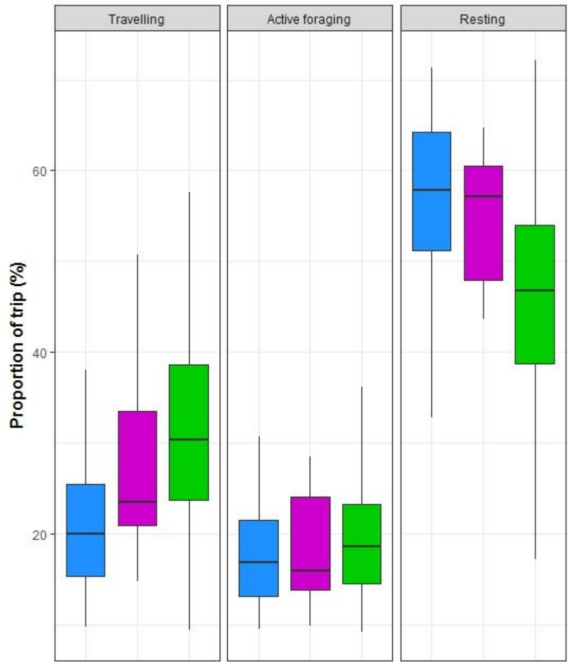

Figure 5.4. Activity budgets as the proportion of the total trip time (medians, IQRs and ranges) for trips made by immature birds (blue) and adult foraging trips during pre-laying (purple) and chick-rearing (green).

5.3.2 Collision risk

The population of immatures (ages 2 - 4 yrs) acting as central-place foragers from Bass Rock was estimated at 49,814 birds. Immatures spent approximately 68 % of their time at sea giving an estimated 33,874 at sea at any one time. Adults spent approximately 65 % of time at sea pre-laying and 50 % of time at sea during chick-rearing, giving estimates of 97,500 and 75,000, respectively, at sea at any one time.

During the summer, adult females spent 7.6 % and adult males spent 4.5 % of their total time in flight within wind farm sites, compared with 4.0 % spent by immatures. In spring, adults spent 3.2 % of their total flight time within wind farm sites. Across all groups, the majority of flight time within wind farm sites was spent commuting (adults pre-laying, 71.3 %; adult males during chick-rearing, 70.8 %; adult females during chick-rearing, 77.2 %; immatures, 79.6 %).

The estimated combined density of adults and immatures in wind farm sites during the summer varied between 0.08 and 2.31 birds km^{-2} with higher densities at sites in the Firth of Forth than elsewhere. The proportion of time spent flying at collision risk height varied between sites and sexes, resulting in a total of 457 predicted collisions by males and 853 predicted collisions by females for the months of June, July and August combined. A total of 353 collisions by immature birds were predicted during the months of June, July and August and 142 collisions by adults during the month of April (Table 5.2). Combining the monthly totals for males and females and conservatively assuming the same number of collisions in May as in April, an estimated 1,593 collisions of adults would be predicted to occur between April and August. Assuming immatures behaved the same way during April and May as they did in June would give a total of 440 predicted collisions between April and August.

Table 5.2. Predicted number of collisions per month for adults and immature gannets from Bass Rock, summed across six wind farm areas in the North Sea.

	April	**June**	**July**	**August**
Adults				
Unknown sex	142	-	-	-
Male	-	155	157	145
Female	-	289	292	271
Immatures	-	89	90	83

5.3.3 Potential population impacts

Including the predicted additional mortality from collisions with turbine blades reduced the predicted population growth rate (λ) from 1.036 to 1.026. However the population was still predicted to increase by > 2.5 % per annum (Figure 5.5) and increasing or decreasing predicted collisions by 10 % yielded a range of estimates that were all > 1 (λ =1.35 – 1.017), predicting sustained population growth.

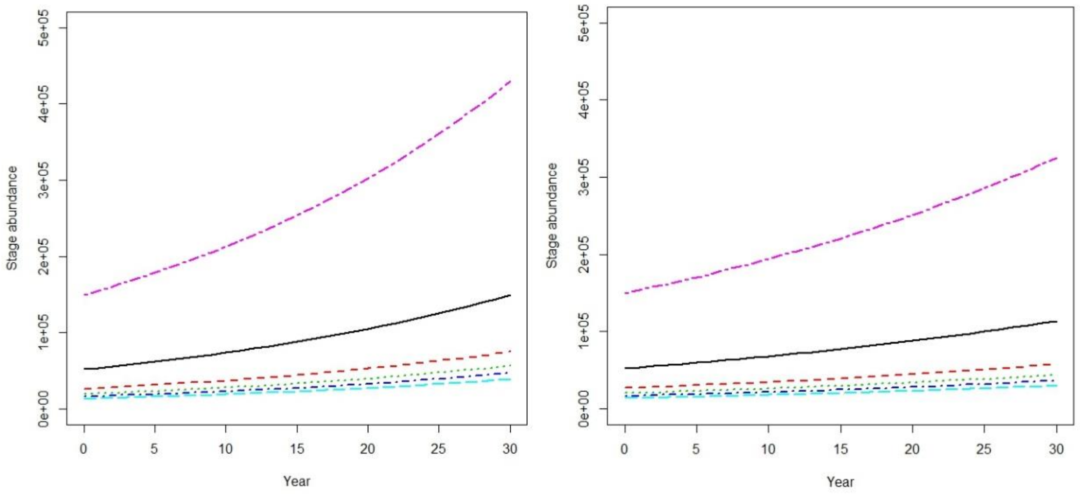

Figure 5.5. Predicted age-structured population growth for the Bass Rock gannet colony under conditions **(a)** without mortality from wind turbines and **(b)** with mortality from wind turbines. Line colour identifies age class; adults (purple), age 4 (light blue), age 3 (dark blue), age 2 (green), age 1 (red), age 0 (black).

5.4 Discussion

5.4.1 Collision risk

When travelling between the colony and active foraging sites, gannets had a mean flight height below the minimum height swept by wind turbine blades, as shown in Chapter 3 and previously (Cleasby et al., 2015a). Differences in time spent travelling between sexes, age-classes or time-periods within or among years were therefore unlikely to greatly alter potential collision risk. Flight heights within the collision risk envelope were more likely to occur during active foraging (Cleasby et al. 2015a; Chapter 3) although there was some overlap in flight heights during the two behaviours and birds sometimes commuted at collision risk height.

Cleasby et al. (2015a) estimated that ~300 adults from Bass Rock could be killed each month of the breeding season at two wind farm sites in the Firth of Forth. They suggested that if behaviour earlier in the season was similar to during the summer there was potential for ~1500 adults to be killed each year between mid-April and mid-September. By tracking birds in April I have shown that the behaviour of adults early in the breeding season differs from that later in the summer. In April adults spent longer at sea than at the colony and when at sea they spent more time on the water than when they were feeding chicks. Despite spending more time at sea, the densities of adults and the proportion of time they spent actively foraging in the wind farm sites was lower in spring than in summer, resulting in a lower number of predicted collisions. Had I assumed the same behaviour in April and May as in June, the total number of predicted collisions across all six wind farm sites would have been ~ 2200 between April and August compared with the estimate of ~1600. However, the predictions for adults in spring should be viewed with caution due to the small sample size and short tracking period. Collision risk also differed between males and females. Despite females occurring at lower densities than males within wind farm sites they spent a greater proportion of time actively foraging, resulting in a greater number of predicted collisions.

The predicted number of collisions for immature birds holds considerable uncertainty, including a lack of information on movements between colonies, flight heights and turbine avoidance behaviour, but was less than half that of adults during the summer months. This was partly a consequence of the smaller number of immature birds than adults, but the predicted number of collisions per bird during the summer months was much higher for adults (1310/150,000 = 0.87 %) than for immatures (262/47,800 = 0.58 %). Coupled with the low elasticity of immature survival compared to adult survival in long-lived species such as gannets (Crone, 2001), this lower per capita probability of mortality suggests that impacts of turbines on immature birds are likely to be of less consequence than those on adults.

5.4.2 Potential population-level effects

A previous population model based on a population of 48,000 breeding pairs at Bass Rock in 2004, suggested that additional mortality of 1400 adults and 600 immature birds would be sufficient to cause a sustained decrease in the breeding population size (WWT Consulting

2012). The estimated predictions of additional mortality in this study of 1593 adults and 593 immatures are therefore large enough to cause concern. Cleasby et al. (2015a) suggest that this threshold may have been underestimated, since the breeding population at Bass Rock has apparently increased by an average of 2700 pairs per year since then (Murray et al., 2015). Green et al. (2016) drew attention to inadequacies in approaches based on thresholds and suggested that predicted changes in population sizes based on projection models would provide much more robust assessments of impact. Here I have used a stage-structured matrix model to suggest that predicted mortality from wind farms would reduce the growth rate of the gannet population at Bass Rock but would be insufficient to drive the population into decline. Moreover, my model assumes that mortality from wind farms is entirely additive and takes no account of density-dependent population regulation or compensatory mechanisms such as recruitment from other colonies, which might off-set losses from collisions (Horswill et al., 2017). Nonetheless, in view of the uncertainty in different parameter estimates and the potential population consequences of both sexed-biased mortality and stochastic variation in different model parameters (Donald, 2007, Szekely et al., 2014) I advocate continued caution including further collection of foraging data during different stages of the breeding season and continued monitoring of adult survival and population size following installation of turbines at proposed wind farm sites.

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Chapter 6 : Discussion

6.1 Introduction

At a time when there is great pressure on the environment as a result of climate change and direct anthropogenic changes there is increasing need to understand how animals use space over different temporal and spatial scales (Wikelski et al., 2007). Foraging is a fundamental component of animal behaviour and the ability to document foraging movement is key to understanding the ecology of a species (Kranstauber et al., 2011). Foraging behaviour is influenced by intrinsic factors including sex and morphology (Ginnett and Demment, 1997, Bueno and Motta-Junior, 2008). Studies of animal movement have been revolutionised by tracking devices which can provide highly accurate location data at high temporal frequency. Integrating other sensors with tracking tags and combining this information with remotely sensed or modelled environmental data is greatly improving our ability to describe movement and understand how habitats and weather influence behaviour (Kays et al., 2015). However, movement does not only occur in the horizontal dimension but also in the vertical dimension (Watts et al., 2017, Attanasi et al., 2015). Birds are a group of organisms that move within three-dimensional space yet tracking individuals in three dimensions has been the focus of relatively few studies, with even fewer focusing on the influence of weather on three-dimensional behaviour.

The aim of this thesis was to increase understanding of three-dimensional foraging behaviour in the Northern gannet. The four previous chapters explored sex-specific foraging, the influence of weather and variation between sexes and birds of different age in the context of the potential risk posed by wind farms. In this chapter I summarise my key findings from the previous four chapters and consider them in a broader context. I then discuss the wider implications of my work and recommend directions for future research.

6.2 Three-dimensional tracking

A number of methods exist for estimating the flight height of birds but very few involve the direct measurement of height using loggers attached to an individual (Cleasby et al., 2015a, Ross-Smith et al., 2016). The advantage of recording height directly from the bird is that the provenance of the bird is known and multiple measurements of height can be estimated providing greater scope for behaviour interpretation (Cleasby et al., 2015a). However, error in height estimates has always been a significant concern especially when considering the potential effects of collisions with structures and aircraft.

The error in flight height estimates becomes increasingly important for low flying birds such as many species of seabird including gannets (Johnston et al., 2014a). Gannets have also been identified as being one of those species at greatest potential risk of collision with wind turbines, making them an excellent species on which to refine methods for measuring flight height. I explored the potential for collision with wind turbines in **Chapter 5** but first, in **Chapter 2** I developed and explored a novel refinement to a published method that uses atmospheric pressure recorded on the bird to estimate flight height. My revised method tries to reduce the previously acknowledged error in height estimates over prolonged periods in flight. Cleasby et al. (2015a) showed how the error in estimates of flight height is likely to increase over time and so the durations of individual flight bouts are important for estimating the potential error in measurements. Gannets make some of the longest foraging trips of any seabird breeding in the UK and in **Chapter 2** I presented for the first time estimates of individual flight bout durations. Cleasby et al. (2015a) had already partially accounted for changes in atmospheric pressure by recalibrating sea level pressure for each individual flight bout. I then recalibrated sea level pressure throughout the time in flight using reanalysis data of sea surface pressure data. In doing so I was able to reduce the continuous drift in height estimates that can occur when atmospheric pressure changes over the spatial and or temporal extent of a period in flight. Typically environmental datasets are used to investigate how conditions influence behaviour as I did in **Chapter 4.** However, to the best of my knowledge, this is the first time a global dataset has been used to improve estimates of a behavioural parameter. I propose that this integration of reanalysis sea level pressure could be important for the estimation of flight heights in birds that spend long periods in sustained flight, especially those that fly at low elevations and at latitudes where atmospheric circulation is variable.

At present the only other method for determining flight height measurements directly from a bird is to use estimates from GPS (Ross-Smith et al., 2016, Bouten et al., 2013). The accuracy of GPS height estimates is highly dependent on the dilution of precision which varies between species and could be related to behaviour (Ross-Smith et al., 2016). For gannets, a fast-moving species that shows considerable variation in the distribution of flight heights, I suggest that using a combination of GPS and pressure is the most appropriate method for interpreting three-dimensional behaviour, especially if continuous high-resolution data are required. Such data are especially pertinent when it comes to acquiring detailed information on three-dimensional space use in locations proposed for wind farm construction; an area I explore in **Chapter 5**.

In an exciting initiative for the world of animal movement science, ICARUS (International Cooperation for Animal Research Using Space) has the potential to increase the capacity for exploring the three-dimensional space use by birds, not just short-range foraging trips but long distance migrations (Wikelski et al., 2007). Tags that combine GPS technology with other sensors including atmospheric pressure will communicate with the ICARUS satellite, installed on the International Space Station in August 2018, with the anticipation that the system will open to the scientific community in 2019 (http://www.orn.mpg.de/ICARUS). These tags, currently with a working lifespan of a year will create the potential for estimates of flight height to be obtained from individuals not only undertaking foraging trips from a central place but during long distance migrations and over winter when many species are entirely pelagic. These tags will open up new possibilities for exploring three-dimensional movement of birds and increase knowledge of how birds reduce flight costs and manage energy budgets over winter as well as during the breeding season.

Sex-specific differences in two-dimensional foraging behaviour, dive behaviour and diet occur in sexually size-monomorphic seabirds including Northern gannets. However, these differences are not found consistently between years. The aim of **Chapter 3** was to establish whether differences in foraging behaviour between male and female gannets also extended to flight height and what the possible selective advantage could be of sex-specific foraging differences in a sexually size-monomorphic seabird. By using the method I refined in **Chapter 2**, I created spatial maps of the variation in three-dimensional foraging behaviour showing for the first time that spatial segregation above the water occurs in three, not just two dimensions. Cleasby et al. (2015b) suggested that the difference could be mediated by different responses to habitat features such as tidal mixing fronts and that their dive behaviour could result from adaptations to the habitats in which they forage. I found a possible relationship between foraging trip durations of males and females and the abundance of 0-group sandeels, a species that contributes more extensively to the diet of gannets at Bass Rock in some years than in others (Hamer et al., 2007). I also found that flight height during active foraging was higher in females than in males and that females made deeper dives, consistent with the findings of Cleasby et al. (2015b). This spatial segregation has potentially important consequences which I began to explore in **Chapter 5** where I found that collision risk could potentially be biased towards females as a result of them flying higher during active foraging and spending a greater proportion of time flying within wind farm sites. Studies of sex-biased mortality at wind farms sites are limited but have been found to occur in common terns (*Sterna hirundo*) and skylarks (*Alauda arvensis*) (Morinha et al., 2014, Stienen et al., 2008) both of which were linked to behavioural differences. Sex-biased mortality could have potential consequences for minimum viable population size but has received very little focus in risk assessments and population modelling so far, and has not been identified as a key knowledge gap (Cook et al., 2018).

Foraging behaviour is influenced not only by sex but also by weather conditions. Animals, especially central place foragers, are constrained to return to the nest site to provide food for their offspring (Boyd et al., 2014). To have the best opportunity of a successful breeding attempt, foraging for prey must be undertaken as efficiently as possible meaning that behaviour has to be adjusted to compensate for environmental conditions. However, how seabirds that forage far from the colony do this has until recently been unknown. For birds that forage within a few km of the colony, data from a near-by weather station can be used to provide reliable data about conditions experienced at sea (Lewis et al., 2015). Visual observations are also used (Spear and Ainley, 1997) however establishing the weather conditions encountered at sea by mid-long range foragers has always been a challenge. We are now in an exciting phase of animal tracking where the temporal and spatial resolution of environmental reanalysis data is appropriate for integrating with animal movement data, providing opportunities for understanding three-dimensional space use, which has been impossible until now.

In **Chapter 4** I combined three-dimensional movement data with data on wind, rain and cloud cover to explore how these variables influenced the foraging behaviour of gannets at sea. The adjustments gannets made to their behaviour suggest that they are able to compensate for unfavourable conditions at sea by altering activity-time budgets and flight height. Gannets spend ~50 % of the total trip duration on the water, motivated by the need to rest, preen and by hours of darkness making prey detection difficult (Carter et al., 2016). Gannets typically spend a lower proportion of time during trips (~20 %) actively foraging (**Chapter 5**). I suggest that gannets can adjust this time on the water to buffer extended periods of time spent foraging in more challenging conditions associated with higher wind speeds. The increase in flight height during active foraging in both males and females in response to increases in wind and rainfall highlights the complex relationship between weather, prey behaviour and predator response. Under current climate projections increases in wind and rain could occur meaning that birds will be required to spend more time flying at higher elevations. This is the first time that the three-dimensional behaviour of gannets has been explored in relation to weather variables and highlights the importance of including the influence of weather on behaviour in collision risk models (Cook et al., 2018).

Assessments of potential collision risk for seabirds are required for any wind farm development proposal with flight height a critical parameter for the models (Drewitt and Langston, 2006). The majority of flight height estimates for seabirds around the UK have been measured visually or using radar in or around the locations of potential wind farm developments (Skov et al., 2018, Johnston et al., 2014a). The disadvantages and biases associated with data collected using these methods were discussed in **Chapter 5** and include the lack of data in poor weather conditions and for birds of different ages. The work in **Chapters 3, 4 and 5** of this thesis has demonstrated how three-dimensional space use varies with behaviour, sex and weather conditions. It is also known that horizontal movements of immature birds differ from adults and **Chapter 5** indicates that adult behaviour differs throughout the breeding season. When using visual or radar methods for estimating flight heights of seabirds, behaviour, sex, time in the area cannot be evaluated and with just a single estimate of height per bird can give no indication how flight height varies over time. The work in **Chapter 5** is to my knowledge the first attempt to undertake a collision risk assessment for immature gannets and to account for different behaviour in adults at different times of the year. As a consequence it has revealed the potential for variation in collision risk between males, females and immature birds. The results should be viewed with caution due to sample sizes, the lack of flight height data for immatures and adults in spring and the estimates of the number of immature birds associated with the Bass Rock colony and therefore the density of immature birds at sea. Nonetheless, by using an age-structured population model I have been able to present a population projection for the Bass Rock colony based on the potential additional mortality from wind farm collisions as recommended by Green et al. (2016).

6.3 Wider context

The research in this thesis should be viewed in the context of the colony at which the work was undertaken. The Bass Rock is the largest gannet colony in the world, having grown rapidly since the late 1970’s to the extent that there is virtually no remaining space (Murray 2015). As colonies increase in size, individuals have to travel further to find food due to depletion or disturbance of prey close to the colony (Lewis et al., 2001, Wakefield et al., 2013). Distances travelled during foraging trips by gannets from Bass Rock are amongst the longest in the UK (Wakefield et al., 2013) therefore activity budgets and the way in which they are adjusted under varying environmental conditions have the potential to differ from gannets at other colonies. In addition to this, the location of the Bass Rock on the eastern side of the UK, means gannets at the Bass Rock experience different prevailing wind conditions when at sea compared to other colonies in the UK, with the exception of the colony at Bempton Cliffs (**Chapter 1**).

6.4 Future research

Three-dimensional foraging behaviour in seabirds is an area with huge potential for future research. Here I suggest number of possible areas for further research based on the work in this thesis.

In **Chapter 2** I introduced a refinement to the method of using GPS and pressure data to estimate flight height which improves height estimates during long periods of flight. This method is especially relevant for species such as Procellariiformes that fly at low elevations and spend prolonged periods of time in flight without landing on the water. It would, for instance, allow a greater understanding of dynamic soaring.

More work is required to establish whether behavioural differences between male and female gannets from Bass Rock, found in some years but not others, are related to the abundance of sandeels. This has potential consequences for spatial segregation in foraging areas. To continue the work investigating differences in the foraging behaviour of males and females, further three-dimensional tagging is required, firstly with the aim of linking flight height immediately prior to a dive with dive depth and secondly, to try and establish whether trip durations of male and female gannets from Bass Rock are indeed linked to the abundance of sandeels. This would also require data on diet to be collected.

Additional three-dimensional tracking of males and females would also provide the opportunity to investigate and better understand how the constraints on breeding birds change between pre-laying, incubation and chick-rearing. The work in **Chapter 5** has demonstrated that it is possible to collect high resolution tracking data from gannets prior to egg laying, and during field work in May 2018 data was obtained during incubation. Not only are behavioural constraints important to understand in the context of gannet ecology but they also have relevance for collision risk assessments.

This first use of weather data to annotate the foraging tracks of gannets from Bass Rock has introduced a number of potential avenues for future research. The first is to establish whether immature gannets adjust their behaviours in the same way as adults in response to wind conditions. The second would be to see how gannets breeding in colonies on the west coast of the UK respond to wind given that the prevailing wind will be different to that experienced by birds at Bass Rock. Thirdly, it would be possible to investigate the influence of weather on winter migration routes. By incorporating accelerometry data it would then be possible to establish how weather conditions and behavioural adaptations, including adjustments to plunge diving behaviour, influence energy expenditure during foraging trips (Ropert-Coudert et al., 2004).

6.5 Final Conclusion

Estimating flight heights of seabirds using bird-borne loggers is an area of research still in its infancy. Much of the data collected on flight height of European seabirds has been motivated by offshore wind farm developments and has relied on visual observations and radar measurements that are biased towards flight in favourable weather conditions during the breeding season (Johnston and Cook, 2016). This thesis provides evidence that the three-dimensional foraging behaviour of gannets is highly variable and dependent on activity, sex and weather conditions. With likely further changes to the marine environment resulting from climate change and energy generation infrastructure, it is more important than ever to understand three-dimensional space use by gannets and other seabirds.

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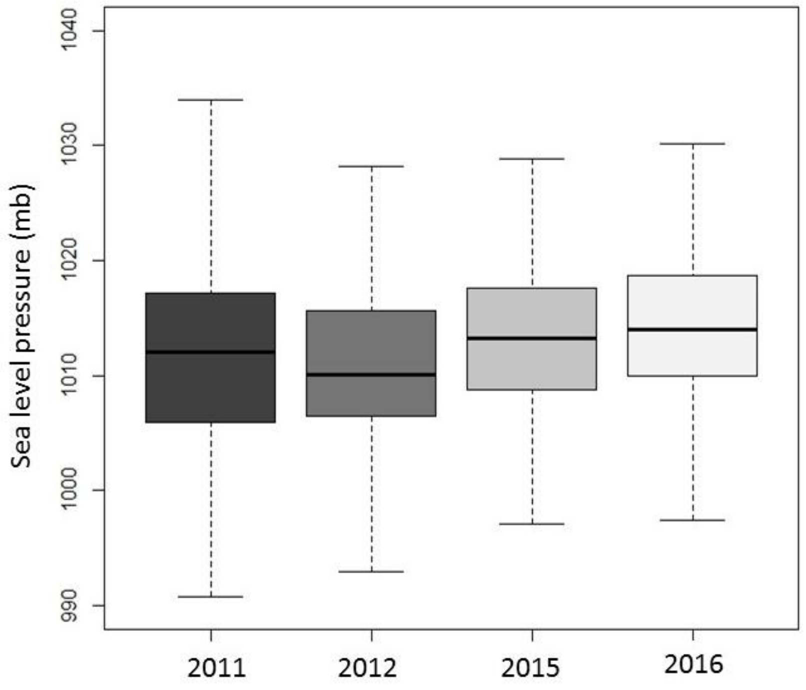
Apendices

Appendix A



A.1. Comparison of atmospheric pressure at sea level at Bass Rock during June, July and August in the years of this study (2015 and 2016) and the years (2011, 2012) studied by Cleasby et al. (2015). Calculated using ECMWF ERA-Interim reanalysis data (0.125° × 0.125°, 6-hourly product) for the closest grid cell to Bass Rock. Plot shows median, 25th and 75th percentiles and range.

Appendix B

B.1 Top models sets for estimating effects of weather parameters on trip metrics.

	Rank	Model	df	logLik	AICc	ΔAIC	AIC weight
Trip duration	1	Trip distance	4	-168.55	345.3	0	0.804
	2	Trip distance + Wind direction	5	-170.33	351.0	5.69	0.047
	3	Trip distance + Wind speed	5	-170.52	351.4	6.07	0.039
	4	Trip distance + Rainfall	5	-170.53	351.4	6.08	0.038
	5	Trip distance + Low cloud	5	-170.64	351.6	6.30	0.034
	6	Trip distance + Year	6	-170.46	353.4	8.08	0.014
Proportion of trip commuting	1	Trip distance	4	-243.61	495.5	0	0.500
	2	Trip distance + Year	6	-243.02	498.5	3.09	0.107
	3	Trip distance + Rainfall	5	-244.28	498.9	3.46	0.089
	4	Trip distance + Wind direction	5	-244.32	499.0	3.54	0.085
	5	Trip distance + Wind direction + Year	7	-242.95	500.6	5.12	0.039
	6	Trip distance + Low cloud	5	-245.27	500.9	5.44	0.033
Proportion of trip actively foraging	1	Wind speed	4	-192.21	392.7	0	0.773
	2	Wind speed + Wind direction	5	-193.75	397.9	5.2	0.057
	3	Wind speed + Rainfall	5	-194.03	398.4	5.76	0.043
	4	Wind speed + Low cloud	5	-194.16	398.7	6.02	0.038
	5	Wind speed + Trip distance	5	-194.18	398.7	6.06	0.037
	6	Wind speed + Year	6	-194.14	400.8	8.12	0.013
Proportion of trip on the water	1	Trip distance + Wind speed + Year	7	-249.82	514.3	0.00	0.143
	2	Trip distance	4	-253.11	514.5	0.15	0.133
	3	Trip distance + Wind speed	5	-252.07	514.5	0.18	0.131
	4	Trip distance + Year	6	-251.00	514.5	0.20	0.130
	5	Trip distance + Wind speed + Wind direction	8	-249.57	516.0	1.70	0.061
	6	Trip distance + Wind direction + Year	7	-250.74	516.1	1.84	0.057
	7	Trip distance + Wind direction	5	-252.97	516.3	1.98	0.053

B.2 Top models for estimating effects of weather parameters on flight height.

	Rank	Model parameters	df	logLik	AICc	ΔAIC	AICc weight
Active foraging height	1	Sex + Wind speed + Rainfall + Wind speed:Rainfall	9	-34381.12	68780.3	0	0.213
	2	Sex + Wind speed + Rainfall + Low cloud + Wind speed:Rainfall + Low cloud:Rainfall	11	-34379.49	68781.0	0.73	0.104
	3	Wind speed + Rainfall + Wind speed:Rainfall	8	-34383.2	68782.4	2.16	0.081
	4	Sex + Wind speed + Rainfall + Low cloud + Wind speed:Rainfall	10	-34381.45	68782.9	2.67	0.065
	5	Wind speed + Rainfall + Low cloud + Wind speed:Rainfall + Low cloud:Rainfall	13	-34381.67	68783.4	3.11	0.041
	6	Sex + Wind speed + Rainfall + Low cloud + Wind speed:Rainfall + Wind speed:Low cloud + Lowcloud:Rainfall	10	-34380.12	68784.3	4.01	0.041
Commuting height	1	Sex	7	-38723.3	77460.6	0	0.85
	2	Sex + Rainfall	8	-38725.46	77466.9	6.32	0.036
	5	Sex + Wind speed	8	-38725.62	77467.2	6.63	0.031
	4	Sex + Low cloud	8	-38725.7	77467.4	6.79	0.028
	5	Sex + Low cloud + Wind direction + Low coud:Wind direction	10	-38723.78	77467.6	6.96	0.026
	6	Sex + Wind direction	8	-38726.13	77468.3	7.67	0.018

Appendix C

Table C.1 Details of proposed wind farm sites within the summer (April – August) foraging distribution of gannets from Bass Rock. See Figure C.1 for map of locations of wind farm sites.

Development	Status	Number of turbines	Risk window (m)	Rotor radius (m)	Reference
Hywind	Operational	5	21 - 175	154	https://www.equinor.com/content/dam/statoil/documents/newsroom-additional-documents/news-attachments/hywind-scotland-facts.pdf
Aberdeen	Under construction	11	31 - 191	160	https://www.offshorewind.biz/2018/04/10/vattenfall-and-mhi-vestas-claim-worlds-first-with-8-8mw-eowdc-offshore-wind-turbine/ https://corporate.vattenfall.co.uk/contentassets/d3aadc7a5b1244b9b605c7715222afaa/project-overview-february-2017.pdf
Neart na Gaoithe	Consented	54	35 - 208	167	https://www.4coffshore.com/transmission/neart-na-gaoithe-gb-uk56.html
Inch Cape	Consented	72	22 - 272	250	http://www.inchcapewind.com/files/Inch_Cape_Wind_Farm_Scoping_Report_2017_Hi_Resolution.pdf
Seagreen Phase One - Alpha Bravo	Consented	150	26.1 - 193.1	167	http://www.seagreenwindenergy.com/assets/phase1-offshore-addendum1.pdf
Seagreen Phase Two & Three	Planning stage	260	26.1 - 193.1	167	http://www.seagreenwindenergy.com/offshore-scoping-phases2and3.asp
Dogger Bank Creyke Beck A & B	Consented	400	100 - 315	215	http://www.forewind.co.uk/uploads/files/Creyke_Beck/Phase_2_Consultation/Chapter_5_Project_Description.pdf

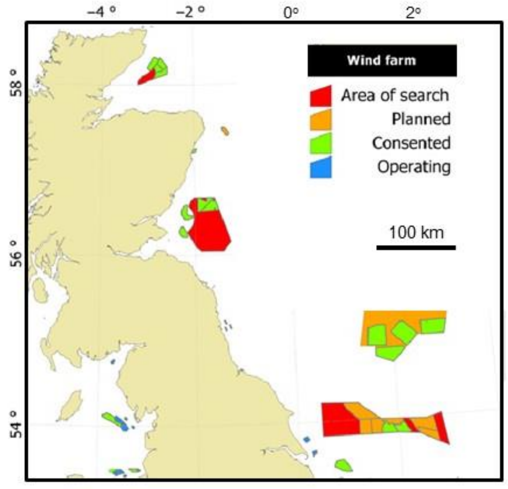


Figure C.1 Map of wind farm sites. Adapted from Russell et al. (2016).

Table C.2. Gannet data used in basic overall collision risk models.

Flight speed	14.9 m/sec
Bird length	0.94 m
Wingspan	1.72 m
Nocturnal activity score	2
Flying mode	Gliding
Proportion of flights upwind	50%

Table C.3 Proportion of time wind farms likely to be operational.

April	0.773
June, July and August	0.8