Environmental drivers of variability in population and individual foraging strategies



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# Abstract

Efficient foraging can offer individuals a key opportunity to maximise fitness, with important consequences for population dynamics, species distributions, and ecosystem processes. The constant quest to minimise costs and maximise resource gains has given rise to a diverse range of movement behaviours among animals, the complexities of which we are continually uncovering as we accumulate more data, advance technology and develop methods. We know that animals typically forage on patchy resources that seldom stay constant in space or time. However, it remains unknown whether the degree of resource patchiness, or resource heterogeneity, can shape the costs and benefits of foraging, thus affecting foraging movements and population dynamics of animals. The overall aims of this study were therefore to use environmental, movement, and reproductive success data to understand how resource heterogeneity can drive individual and population foraging behaviour. We focus on the ecology of black-legged kittiwakes, Rissa tridactyla, which are a model species for such questions. As central place breeders that feed solely at the surface, kittiwakes are sensitive to changes in prey availability within the environment around their colony. Furthermore, kittiwakes have been widely studied as an ecosystem indicator species, and so we can build upon prior knowledge and benefit from a large body of existing data. To determine foraging behaviour I use GPS tracking data from 15 colonies around the UK and Ireland collected during the breeding seasons between 2010 and 2017; totalling 415 individuals and 1567 foraging trips. These tracking data were combined with environmental data to determine foraging habitat selection and variability over a predictable cycle, and to characterise environmental heterogeneity, as a proxy for resource heterogeneity, within the foraging range of kittiwakes at each colony. I compare environmental heterogeneity to foraging dynamics and reproductive success to understand the potential fitness costs and benefits of foraging in heterogeneous environments. Finally, I extend habitat selection functions to quantify individual specialisation in habitat selection between colonies, and to

understand whether environmental heterogeneity could shape the diversity of movement behaviours. Studies revealed that habitat selection differed over the 12.4-h tidal cycle; and that environmental heterogeneity was associated with amplified changes in habitat selection, most likely because of greater spatial variability in temporal resource changes. In more heterogeneous environments, kittiwakes undertook longer foraging trips, overlapped more with other individuals, and had lower breeding success, which suggests that there is greater competition between individuals where resources are clustered into patches, at a cost to reproduction. Potentially as a mechanism to reduce competition, individual specialisations in habitat selection were more prevalent in heterogeneous environments. Together, results highlight the importance of local environmental processes in governing behavioural adaptations of predators. Chapters provide novel advances into the ecology of kittiwakes, but also into the drivers of optimal foraging trade-offs and the origins of individual differences in behaviour that are relevant well beyond this species. Overall, the work presented in this thesis demonstrates that environmental heterogeneity can play a key role in shaping foraging movements of individuals, population dynamics, and potentially the diversity of animal behaviour.

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# Chapter 1

# General Introduction



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### Animal movement and optimal foraging

Movement is fundamental to animals, and is central to the rich biodiversity of life on earth (Jeltsch *et al.* 2013). Animals move to find food, mates, knowledge, new territories and shelter. These movements decide the fate of individuals, which ultimately determines population dynamics, species distributions, and the evolution of traits, communities and ecosystems (Hanski *et al.* 1994; Armsworth & Roughgarden 2005; Cushman & Lewis 2010; Morales *et al.* 2010). Therefore, understanding the causes and consequences of animal movement has wide-ranging implications for our knowledge of ecology and evolution, as well as effective management and conservation (Nathan *et al.* 2008).

A primary driver of movement is the need to obtain food, which is essential for survival and reproduction. Over broad scales, this search for food gives rise to some of the most spectacular animal movements on earth, as animals migrate across hemispheres, ocean basins, and mountain ranges to track foraging opportunities (Shaffer et al. 2006; Egevang et al. 2010; Hawkes et al. 2011). At finer scales, the diversity of daily foraging movements reflects complex adaptations along a plethora of ecological gradients; for example, from sit-and-wait tactics of ambush predators (Uetz 1992; Reed & Shine 2002; Villanueva et al. 2017), to the searching movements of many active predators (Perry & Pianka 1997). Solitary foragers aim to avoid competition with conspecifics (Tamò et al. 2006; Dammhahn & Kappeler 2009) or steal from other individuals (Brockmann & Barnard 1979), whereas social foragers can benefit from skilful group strategies (Macdonald 1983; Wiley et al. 2011). Herbivores graze, and opportunists scavenge on static prey (Jones et al. 1998; Bischof et al. 2012), while predators hunt mobile prey using adapted physiology (e.g. Dial et al. 2008), sensory abilities (e.g. Villanueva et al. 2017), morphology (e.g. Luck & Pietsch 2008) and tooluse (e.g. Hunt 1996).

As we gather more data on animal movements, and technological and statistical methods continue to advance, we are learning more about the complexities of animal foraging behaviour (Hussey *et al.* 2015; Kays *et al.* 2015). Analyses of high resolution movement trajectory data are revealing more detailed estimates of animal behavioural states (Michelot *et al.* 2016; Williams *et al.* 2017; Bennison *et al.* 2018), energy expenditure (Halsey 2016; Hicks *et al.* 2017), and interactions with both the physical environment (McClintock & Michelot 2018; Scacco *et al.* 2019) and other individuals (Jones *et al.* 2018; Westley *et al.* 2018). An increasing number of animal tracking studies are contributing to our knowledge of behavioural differences among species, populations and individuals (Phillips *et al.* 2017). Meanwhile, collaborative projects using large data sets have shed light on some of the unifying patterns driving animal movement over wide geographic ranges (Rodríguez *et al.* 2017; Sequeira *et al.* 2018).

Different foraging movements are united by the ultimate goal of net energy gain. This therefore leads to a constant trade-off between maximising energy gain from resource acquisition, and minimising energy allocation to foraging movements; an ecological mechanism regularly studied under the umbrella of optimal foraging theory (Stephens & Krebs 1986). The concept of optimal foraging derives from natural selection favouring 'optimal' phenotypes, which have higher fitness relative to the remainder of the population because of more efficient resource acquisition. Over time, natural selection acts on the reproductive fitness of individuals to favour optimal phenotypes, and change the gene pool of a population.

Optimal foraging theory can often explain the foraging movements of animals across taxa. For example, animals typically forage in habitat patches rich in resources, and switch to new patches when the profitability of the current patch drops below another (Werner & Mittelbach 1981; Godin & Keenleyside 1984). Herbivores typically feed more intensely in areas of high patch density to concentrate foraging effort where

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reward is high and minimise travel distance between patches (de Knegt *et al.* 2007). Marine megafauna such as humpback whales, *Megaptera novaeangliae*, and bigeye tuna, *Thunnus obesus*, employ different vertical dive strategies in order to minimise the energetic costs of underwater travel and maximise the proportion of time spent actively foraging (Thygesen *et al.* 2016; Tyson *et al.* 2016). Optimal foraging decisions can even describe human behaviour, such as hunter-gatherers who switch foraging patches when concentrations of resources in the current patch become depleted (Wolfe 2013); and similarly, humans searching for information switch sources as reward rates decrease in the current source – strings of letters, memories, library shelves, or web pages (Sandstrom 1994; Pirolli 2007; Wilke *et al.* 2009).

As animals constantly seek to balance costs and rewards, the availability and distribution of resources is therefore integral to decisions about optimality (Nathan *et al.* 2008). Individuals ought to make decisions about where and when to forage based on a balance between patch quality and the costs of travel between patches (Bell 1990; Fauchald 1999; Fauchald & Tveraa 2006). For that reason, not only the amount of available resources but crucially the nature of resource patchiness, namely the degree of resource heterogeneity, is essential to understanding foraging decisions of individuals. By extension, variability in resource distributions could therefore be an important ecological gradient contributing to the diversity of foraging behaviours between animals.

### Resource heterogeneity

The absence of uniformity within nature, and adaptations to 'scale', 'variability', 'patchiness' and 'heterogeneity', have long been considered central to ecology (Levin 1992; Sparrow 1999). Heterogeneity in both resources and risk has led individual organism to adapt their morphology, physiology and behaviour. For example, plants modify their roots, proliferating and enhancing physiological ion-uptake in nutrientrich soil patches relative to elsewhere (Hodge 2004), resulting in higher growth rates (Hutchings *et al.* 2003). Grazers respond to heterogeneity in predation risk and fear landscapes in grasslands, influencing survival rates (Atuo & O'Connell 2017) and the risk of disease transmission (Fox *et al.* 2013). And as predicted by optimal foraging theory, foragers invest more effort where resources are concentrated (Hart 1981; Thompson *et al.* 2001; Seymour *et al.* 2009), with positive consequences for resource intake rates (Klaassen *et al.* 2006). Indeed, areas of concentrated resources in patchy environments support foraging opportunities for a diverse array of taxa (Worm *et al.* 2005), sufficient to warrant conservation of resource 'hotspots' (Lascelles *et al.* 2012) and management action to increase the diversity of available habitat types in human-modified landscapes (Tews *et al.* 2004).

At the population and ecosystem levels, heterogeneity in resources and the physical structure of the environment supports diverse communities of birds (MacArthur & MacArthur 1961), reptiles (Pianka 1967), plants (Johnson & Simberloff 1974), insects (Haslett 1997), mammals (Williams *et al.* 2002), and fish (Massicotte *et al.* 2015). Such species diversity is thought to arise in more heterogeneous environments because spatially complex habitats can offer greater available niche space (Tews *et al.* 2004), provide opportunity for niche diversification (Temunović *et al.* 2012; Huang *et al.* 2017), facilitate species coexistence (Waugh & Weimerskirch 2003) and buffer the effects of environmental change (Oliver *et al.* 2010).

However, it is unlikely that all environments are comprised of equally patchy resources (Anderson *et al.* 1982; Mueller & Fagan 2008). Resource patches are likely to differ in size, shape, prey types, spatial density, and temporal predictability because of variability in the underlying physical environment (Mueller & Fagan 2008). Such factors are likely to influence the fitness costs and benefits of foraging in different areas. Therefore, we could expect the nature and degree of resource heterogeneity to influence fine-scale foraging trade-offs and decisions made by individual foragers. Different characteristics of resource heterogeneity may favour alternative stable strategies by individuals, with potential consequences for population dynamics.

### The importance of individuals

Individual differences are increasingly being documented across the majority of animal behaviours (Bolnick *et al.* 2003; Araújo *et al.* 2011), and are important when considering optimal foraging behaviour because decisions about optimality are principally made by individuals. Individuals from the same populations have been found to consistently forage in unique areas (Beverly *et al.* 2009; Lowther *et al.* 2011), at different distances from their breeding site (Patrick *et al.* 2014), use different habitats (Leclerc *et al.* 2016), and feed on different prey species (Svanbäck *et al.* 2011).

Such individual differences are the currency of natural selection, and are therefore key to population level processes (Dall *et al.* 2012). Individual foraging specialisation can influence foraging efficiency, individual fitness and reproductive success (Bernays *et al.* 2004; Cucherousset *et al.* 2011; Daunt *et al.* 2014; Patrick & Weimerskirch 2014), and can also determine vulnerability to predators and parasites (Cresswell 1994; Darimont *et al.* 2007; Knudsen *et al.* 2011). Selection on individual strategies that offer fitness benefits will presumably influence the composition of behavioural strategies among a population (Bolnick *et al.* 2003). In turn, high variability between individual phenotypes can affect the potential for adaptive speciation, and the ability of a population to respond to change (Bolnick *et al.* 2003; Phillips *et al.* 2017).

However, the composition of individual differences varies between species and populations (Araújo *et al.* 2011). For example, the frequency of individual dietary specialisations in perch, *Perca fluviatiils L.*, can fluctuate over time (Svanbäck & Persson 2004). A population of northern gannets, *Morus bassanus*, breeding in the Channel Islands exhibited very little individual site fidelity (Soanes *et al.* 2013), whereas a population in the North Sea were highly individually site faithful (Wakefield *et al.* 2015). There is evidence to suggest that individual differences can arise because of ecological opportunity (Darimont *et al.* 2009), or as a mechanism to avoid competition (Svanbäck *et al.* 2007). However, the generality of these mechanisms remains uncertain (Araújo *et al.* 2011). Furthermore, whether resource heterogeneity can shape individual behavioural differences between populations is unclear, despite the importance of resource distributions for individual foraging decisions.

### Seabirds and the marine environment

Seabirds offer an ideal system to study foraging behaviour in light of heterogeneous resource distributions. Marine ecosystems are highly dynamic, typically governed by a combination of spatial and temporal features that can exert bottom up control. As top predators, seabirds are therefore dependent on resources that are considered patchy and unpredictable (Weimerskirch 2007; Fauchald 2009), and so optimising foraging efficiency and maximising resource gains are key to seabird survival and reproduction. Studies of seabird behaviour and fitness have paved the way in marine ecology because we are able to monitor success as an indicator of fitness at terrestrial breeding sites, and many species are large enough to carry bio-logging devices (Hussey *et al.* 2015). As such, there is now a growing body of seabird tracking data (e.g. Wakefield *et al.* 2017) that can facilitate new comparative studies of environmental drivers of individual and population foraging movements and reproductive success along environmental gradients.

Seabird foraging behaviour and fitness have been linked to a suite of environmental factors that can influence resource distributions (e.g. Carroll *et al.* 2015; Wakefield *et al.* 2017; Cox *et al.* 2018). Interactions of bathymetric features, such as seamounts, islands, headlands and bays, with the tidal cycle can interrupt and change the flow of tidal currents, which in turn drives predictable changes in zooplankton abundance

and distribution (Johnston & Read 2007; Benjamins et al. 2015). These changes can increase prey accessibility and vulnerability, and hence marine predators are often found foraging in areas of high tidal activity (Johnston et al. 2005; Bailey & Thompson 2010), or around sub-sea bathymetric features (Genin 2004; Yen et al. 2004). Sea surface temperature can be a proxy for oceanographic processes that influence nutrient availability, for example upwelling of cold nutrient rich water (Benazzouz et al. 2014), and has been linked to the at-sea distribution and breeding success of seabirds (Frederiksen et al. 2007; Carroll et al. 2015; Johnston et al. 2015; Wakefield et al. 2017). Vertical stratification occurs when temperature and salinity differ with depth sufficiently to create distinct layers of different densities, and is a key driver of marine ecosystem dynamics (Carroll et al. 2015), prey fish distribution (Waggitt et al. 2018) and seabird distribution (Wakefield et al. 2017). Horizontal boundaries between different water masses, referred to as fronts, generate physical processes that can cause upwelling of deeper, nutrient rich water and entrain plankton at the surface (Franks 1992a, b). Fronts are known to be an important feature of marine environments, shaping resource distribution and thus marine vertebrate behaviour (Scales et al. 2014; Waggitt et al. 2018).

However, a key pattern emerging from studies to date is that links between seabird ecology and the physical environment are complex, and vary between species and populations (Frederiksen *et al.* 2007; Lauria *et al.* 2012; Carroll *et al.* 2015). Some seabird populations show clear responses to sea surface temperature changes (Frederiksen *et al.* 2004), whereas such trends are weak or absent elsewhere (Frederiksen *et al.* 2007; Grémillet *et al.* 2008; Lauria *et al.* 2012). Geographic variability in the predominant environmental drivers of seabird behaviour and fitness highlights the importance of considering local conditions, fine scale processes and simultaneously analysing multiple environmental variables (Sydeman *et al.* 2012; Carroll *et al.* 2015). The importance of the degree of resource heterogeneity to seabird

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ecology remains unknown, and so too whether resource heterogeneity could be an underlying driver of patterns governing foraging behaviour and success between individuals and populations.

Seabirds are the most threatened marine taxonomic group, and are more threatened than all other groups of birds with similar numbers of species, with nearly 30% of species recorded by the IUCN as globally threatened (Croxall et al. 2012). Furthermore, many seabird species are valuable indicators in environmental legislation (ICES 2001). As measures of at-sea marine litter, oil and contaminant pollution, targets have been set to reduce the incidence of plastic waste in stomachs of northern fulmars, Fulmarus glacialis; the proportion of common guillemots, Uria aalge, with oiled plumage; and the concentrations of mercury and organic pollutants in eggs of common terns, Sterna hirundo, and Eurasian oystercatchers, Haematopus ostralegus (Heslenfeld & Enserink 2008). Reproductive success of black-legged kittiwakes, Rissa tridactyla, is used as a proxy for the state of the North Sea sandeel fishery, whereby fishing is halted if reproductive success falls below 0.6 chicks per nest per year over a 3-year period (Heslenfeld & Enserink 2008). Such measures acknowledge the ongoing rapid global declines of both seabird populations and marine biodiversity, and the value of terrestrial breeding seabirds to indicate processes at lower trophic levels (Sydeman et al. 2015). Therefore, to understand whether there is a universal pattern driving variability in behaviour of seabird populations and individuals, as well as population trends, would offer a valuable advance towards the conservation and management of this group and the ecosystems that support them.

### Study Species: the kittiwake

This thesis explores the movement ecology of black-legged kittiwakes (*Rissa tridactyla*; hereafter kittiwake), a small gull species abundant in the northern hemisphere that

breeds on sea cliffs, and forages solely at sea. Kittiwakes are surface feeders that typically prey on small shoaling fish; primarily sandeel, *Ammodytes spp* (Lewis *et al.* 2001) and sometimes gadids and clupeids (Chivers *et al.* 2012a). Kittiwakes seldom switch prey species and therefore sandeel availability is a key driver of energy gain and foraging success (Lewis *et al.* 2001). Furthermore, as surface feeders, kittiwakes are unable to access prey deeper in the water column, and therefore must compensate for lower food availability by spending more time foraging, and/or increasing their foraging range (Kotzerka *et al.* 2010). The flapping flight style of kittiwakes is energetically expensive compared to gliding species (Gabrielsen *et al.* 1987; Elliott *et al.* 2014). In response to adverse wind and weather kittiwakes typically do not adjust their foraging behaviour (location or duration), but expend extra energy on flight (Gabrielsen *et al.* 1987; Collins 2017). These restricted foraging abilities make kittiwakes one of the most sensitive seabird species to environmental change via differences in prey availability (Furness & Tasker 2000; Burthe *et al.* 2012).

During the breeding season, as with many terrestrial-breeding marine predators, kittiwakes are central place foragers. This places an additional constraint on behaviour, limiting kittiwakes to foraging within the vicinity of their breeding colony (Chivers *et al.* 2012b), and restricting behaviour to co-ordinate with their partner (Boersma & Rebstock 2009). Breeding colonies span a range of environmental conditions within the species' range, and thus in combination with their sensitivity to environmental conditions, kittiwakes are well suited to studies of how the environment can shape foraging behaviour. Indeed, previous studies have reported stark differences in foraging dynamics of kittiwakes across their range. For example, Wakefield *et al.* (2017) reported a mean foraging range of 11.9 km (IQR 4.2-30.9) at colonies around the UK. In contrast, Paredes *et al.* (2014) found that kittiwakes travelled on average 206.7  $\pm$  6.7 km from the colony in the Bering Sea, Alaska, to reach oceanic waters, and similarly Christensen-Dalsgaard *et al.* (2017) found that

kittiwakes breeding at Sør-Gjæslingan, Norway, travelled on average  $303.7 \pm 6.1$  km to reach the continental shelf edge.

Not only does the foraging behaviour of kittiwakes vary between populations, but long-term monitoring data have recorded varying trends in breeding success and population demographics geographically. Across the UK, kittiwake reproductive success has declined by 0.02 chicks per nest per year since 2000, and the number of breeding pairs has declined by 44% (JNCC 2016). These declines have been largely attributed to changes in food availability, namely declines in sandeel driven by fisheries impacts and climate regime shifts (Furness & Tasker 2000; Frederiksen et al. 2004, 2007; Carroll et al. 2015). However, these negative trends have not occurred uniformly across the UK range of kittiwakes (Mitchell et al. 2004). Populations on the east coast have shown the steepest population declines, whereas along the north coast of Scotland and around the Irish Sea some populations are stable or even increasing (Mitchell et al. 2004). Furthermore, demographic trends of some populations are linked to environmental metrics, such as temperature driven recruitment of sandeel, however these links are absent elsewhere (Carroll et al. 2015). Understanding whether geographic variation in breeding success is linked to foraging behaviour of kittiwakes, and in turn environmental conditions surrounding the breeding colony, will be a valuable advance in our understanding of the ecology of this species. This is particularly pertinent given kittiwakes' status as valuable sentinels of ecological processes (Grémillet & Charmantier 2010), and therefore results could offer insight for other taxa and trophic levels.

#### Study Sites

This study focusses on the movement behaviour of kittiwakes around the UK and Ireland (Figure 1.1A). The marine ecology of the UK and Ireland is well studied, from the physical processes governing the oceanography of the region to the ecology of top predators. Underlying this temperate ecosystem is a dynamic physical environment characterised by undulating bathymetry, some of the largest tidal ranges on Earth, seasonal changes in temperature and stratification, and oceanic fronts that persist from days to months. Broadly speaking, the UK and Ireland's coastal ecosystems are located on the shelf sea where depths range up to 200 m, although the coasts of northwest Scotland are close to the continental shelf edge, where depths exceed 1,000 m (Figure 1.1B). At finer scales, bathymetry surrounding seabird colonies varies from shallow sand banks within 10-20 m of the sea surface, such as the Dogger bank off the coast of East Anglia (1-4°E & 54-55°N), to channels over 200 m deep, such as between Northern Ireland and W Scotland (Figure 1.1B).

As with many shelf seas, the tidal cycle exerts strong control on the physical dynamics here (Polton et al. 2011), in particular the semidiurnal lunar tide. Spring tidal ranges exceed 10 m where tidal energy is high (Figure 1.1C), which in combination with undulating bathymetry result in complex currents and geographic differences in water column structure (Figure 1.1D). Much of the shelf region is vertically mixed over winter, however seasonal changes in sea surface temperature promote the onset of vertical stratification during spring and summer depending on water depth and the degree of tidal mixing (Simpson & Bowers 1981). Shallow waters with high tidal energy will likely remain well mixed, whereas deeper areas with less tidal energy are more likely to become stratified as the surface layer warms. Sea surface temperature therefore varies not only seasonally, but also geographically because of latitudinal gradients and local oceanographic processes (Figure 1.1E). As with many regions globally, long-term mean sea surface temperatures are rising in UK coastal waters, from 11.1 °C between 1961-90 up to 11.7 °C during 2008-17, the most recent period covered by the annual UK climate review and the study period of this thesis (Kendon et al. 2018). Whereas tidal mixing can homogenise the water column and, conversely, temperature can create vertical stratification, geographic variation in all these physical features, both within and between sites, creates a tapestry of ocean fronts within the study region, which vary in strength, persistence, and distance from the shore (Figure 1.1D), and contribute to spatial heterogeneity of environmental conditions.

The physical dynamics of the study region and seasonal temperature fluctuations exert bottom up control on biotic communities, typically characterised by spring phytoplankton blooms (Sharples et al. 2006) and high species richness at basal trophic levels, but comparatively low diversity at intermediate trophic levels (Fauchald et al. 2011; Burthe et al. 2012). Sandeel, Ammodytes spp, and clupeid fish dominate intermediate trophic levels that link zooplankton to top predators around the UK and Ireland (Daan et al. 1990), and as such are the main prey fish of kittiwakes and other seabirds in the region (Lewis et al. 2001; Swann & Harris 2008; Chivers et al. 2012a). Lesser sandeel, Ammodytes marinus, are the most abundant sandeel species and the predominant prey fish of kittiwakes in the North Sea, where kittiwakes seldom switch to other prey species even when sandeel are scarce (Lewis et al. 2001). Elsewhere around the UK, sandeel remain the primary prey of kittiwakes, however they may also forage on gadids and clupeids, such as herring and sprat (Chivers et al. 2012a). Sandeel are highly dependent on sandy sediment to burrow over winter and overnight, thought to be a mechanism to both conserve energy and avoid predation (van Deurs et al. 2010). Foraging distributions and behaviour of sandeel are hard to measure because fisheries data are often sparse, and only available at coarse resolutions (van der Kooij et al. 2008). Nevertheless, some studies using acoustic data have revealed that daytime sandeel distributions can be driven by a complex suite of environmental factors that are likely location specific, including the availability of substrate habitat, seafloor temperature and current speed, but not linked to the distribution of zooplankton, their primary prey (van der Kooij et al. 2008). Swimming is energetically expensive for sandeel, and therefore tidal currents may facilitate energy-saving
movement (van der Kooij *et al.* 2008), or conversely cause unwanted travel away from burrowing sites (Wright *et al.* 2000). Either way, potentially cyclic changes in the presence of sandeel within the water column could offer a chance for sandeel predators to learn the location and timing of predictable foraging sites (Zamon 2003).

The UK and Ireland support large and diverse seabird colonies of global ecological importance (Mitchell *et al.* 2004). The most recent census of breeding seabirds in the region revealed a steady rise in numbers over the preceding 30 years, from around 5 million in 1969-70 to over 8 million in 1998-2002 (Mitchell *et al.* 2004), although this increase was not common to all species. The current breeding seabird census (2015-2019) will be a much-needed update to reveal whether recent and widespread declines in productivity have impacted the status of populations.

The first study presented in this thesis uses kittiwake tracking data collected by the Seabird Ecology Group at the University of Liverpool and specifically for this thesis at Puffin Island, NW Wales; Skomer Island, SW Wales; and Rathlin Island, N Ireland (Figure 1.2). These three islands support colonies of 571, 2257 and 9917 breeding pairs of kittiwakes, respectively (Mitchell *et al.* 2004), and vary in surrounding water depths and tidal regime (Figure 1.1). The remaining studies use data from Puffin, Skomer and Rathlin Islands, as well as data for 12 other colonies where kittiwake tracking data were collected during the RSPB and Bird Watch Ireland's FAME and STAR projects: Bardsey, NW Wales; Bempton Cliffs, E England; Copinsay, Orkney Islands; Coquet, NE England; Colonsay, W Scotland; Filey, E England; Fowlsheugh, E Scotland; Isle of May, E Scotland; Lambay, E Ireland; Muckle Skerry, Orkney Islands; St Martins, Isles of Scilly; and Whinnyfold, E Scotland (Figure 1.2).



Figure 1.1. Study area showing: (A) study colony locations; (B) bathymetry; (C) tidal stress; (D) potential tidal stratification; (E) sea surface temperature, averaged over all study years (2010-17); and (F) frontal strength, averaged over all years studied within this thesis (2010-2017). All figures show environment data presented and analysed within this thesis.



Figure 1.2. Foraging tracks of all kittiwakes that feature within this thesis. All individuals were tracked between 2010 and 2017 during chick rearing, using GPS loggers. Chapter 2 focuses on data from Rathlin, Skomer and Puffin Islands. Chapters 3 & 4 include data from all 15 colonies.

#### Thesis aims and outline

The central aim of this thesis is to understand the effect of the environment on the foraging ecology of kittiwakes. By using multi-colony comparisons, this thesis seeks to understand the physical and biological processes that determine movement strategies of populations and individuals. Whilst focused on kittiwakes, the results presented here extend beyond seabirds to contribute to a broader understanding of how animals make foraging decisions in response to heterogeneous resource distributions, and how this in turn can shape variability and diversity of movement behaviours. The chapters have been written to stand alone, tied by a common thread of kittiwake foraging behaviour in the context of their local physical environment. Therefore, some information may be repeated. The specific aims of the following chapters are as follows:

**Chapter 2:** Environmental heterogeneity amplifies behavioural response to a temporal cycle

This study explores the fine-scale interaction between spatial and temporal processes in governing foraging behaviour of kittiwakes. The main aims are to explore how habitat selection changes over a predictable temporal cycle, the tide, and how temporal changes in foraging behaviour are influenced by the degree of variability in the physical environment. The focus is on three colonies of differing tidal dynamics and environmental heterogeneity – Puffin Island (NW Wales), Skomer Island (SW Wales) and Rathlin Island (N Ireland).

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**Chapter 3:** Environmental heterogeneity decreases reproductive success via effects on foraging behaviour

This study builds on the fine-scale analyses in *Chapter 2* to explore potential fitness costs and benefits of foraging in heterogeneous environments. The main aims are to quantify environmental heterogeneity across colonies, indicative of resource distribution, and to test the effects of environmental heterogeneity on the foraging behaviour, movement dynamics, intraspecific competition and reproductive success of kittiwakes. This study uses data from 15 colonies around the UK and Ireland along a gradient of environmental heterogeneity.

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Daunt, F., Owen, E., Bolton, M., Colhoun, K., Newton, S., Robertson, G. & Patrick, S.
C. (2019). Proceedings of the Royal Society B, 286 (1904): 20190795, DOI: 10.1098/rspb.2019.0795

**Chapter 4:** Environmental heterogeneity promotes individual specialisation in habitat selection

This study builds on population-level analyses in *Chapter 2* and *Chapter 3* to explore the environmental drivers of individual behaviour. The main aims are to determine appropriate model structure for quantifying individual specialisations in habitat selection, to establish kittiwake habitat selection at the species, population and individual levels, and to determine whether environmental heterogeneity influences the prevalence of individual specialisations in habitat selection among populations. This study, again, uses data from 15 colonies around the UK and Ireland along a gradient of environmental heterogeneity. Chapter in preparation for submission: Trevail, A. M., Green, J. A., Bolton, M., Colhoun, K., Daunt, F., Miller, P. I., Newton, S., Owen, E., Polton, J. A., Robertson, G., Sharples, J. & Patrick, S. C. (In prep).

#### Chapter 5: General discussion

This chapter aims to summarise and discuss the key findings of the above chapters in the broader context of animal movement and seabird ecology. Potential implications of results are discussed, as well as ideas for future research.

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# Chapter 2

# Environmental heterogeneity amplifies behavioural response to a temporal cycle



Tidal currents near Rathlin Island in the distance

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#### Environmental heterogeneity amplifies behavioural response to a temporal cycle

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#### Abstract

Resource acquisition is integral to maximise fitness, however in many ecosystems this requires adaptation to resource abundance and distributions that seldom stay constant. For predators, prey availability can vary at fine spatial and temporal scales as a result of changes in the physical environment, and therefore selection should favour individuals that can adapt their foraging behaviour accordingly. The tidal cycle is a short, yet predictable, temporal cycle, which can influence prey availability at temporal scales relevant to movement decisions. Here, we ask whether black-legged kittiwakes (Rissa tridactyla) can adjust their foraging habitat selection according to the tidal cycle using GPS tracking studies at three sites of differing environmental heterogeneity. We used a hidden Markov model to classify kittiwake behaviour, and analysed habitat selection during foraging. As expected for a central-place forager, we found that kittiwakes preferred to forage nearer to the breeding colony. However, we also show that habitat selection changed over the 12.4-hour tidal cycle, most likely because of changes in resource availability. Furthermore, we observed that environmental heterogeneity was associated with amplified changes in kittiwake habitat selection over the tidal cycle, potentially because environmental heterogeneity drives greater resource variation. Both predictable cycles and environmental heterogeneity are ubiquitous. Our results therefore suggest that, together, predictable cycles and environmental heterogeneity may shape predator behaviour across ecosystems.

#### Key words

Foraging behaviour; Tide; Seabird; Habitat Selection; Predictability

#### Introduction

The need to acquire resources to survive and reproduce is fundamental to all animals. Searching for resources is costly, and therefore selection favours individuals that can maximise foraging efficiency by matching the distribution of their target resources (Stephens & Krebs 1986). When prey distribution is stable, consistent area use is adaptive (Weimerskirch et al. 2005). However, resources typically vary both in space and time (Weimerskirch et al. 2005). For example, the physical environment can concentrate prey into patches (Genin 2004) and predictable cycles can alter prey abundance (Yamamoto et al. 2008; Brierley 2014). Furthermore, temporal changes in resource distribution may be explicitly linked to the structure of the physical landscape (Boulinier et al. 2001). In physically less variable environments, a temporal change may have a spatially uniform effect on resources. In contrast, where physical features enhance or interrupt temporal changes, the response of resources will vary in space (Benjamins et al. 2015). In combination, both temporal and spatial variation in the physical environment can shape when and where animals can find resources. An animal's ability to learn and adapt to such changes will offer a vital opportunity to increase fitness, and hence should be under selection.

Adaptive foraging behaviour is a key link between environmental variability, resources and fitness (Matthiopoulos *et al.* 2015). Animals can adapt to resource differences by using a profitable subset of habitat types within the landscape available to them. Habitat preferences have been widely demonstrated for spatial landscape features (e.g. Leclerc et al. 2016, Christensen-Dalsgaard et al. 2017), and can change over time in response to factors such as predictable, long-term, seasonal resource cycles (Guyot *et al.* 2017) or changing predation risk (Godvik *et al.* 2009; Lone *et al.* 2017). However, while resources are known to change at very fine temporal scales (Zamon 2003), associated fine-scale changes in habitat selection, and whether environmental heterogeneity can influence behavioural responses, are less

understood. Such adaptive responses to predictable resource changes would increase foraging efficiency, and therefore likely enhance an individual's fitness.

Resource distribution in the marine environment is both spatially and temporally variable (Pinaud et al. 2005; Weimerskirch et al. 2005), and so marine ecosystems are a model system to study changes in habitat selection with temporal cycles and environmental heterogeneity. In coastal seas, the tidal cycle has an important influence on ecosystem dynamics (Embling et al. 2012; Cox et al. 2018). The tidal coupling hypothesis (Zamon 2003) suggests that interactions between tidal currents and variation in bathymetry (the depths of the sea floor) create predictable changes in resource availability. It considers that physical features, such as islands or channels, interrupt and change the flow of currents, which in turn drives predictable changes in zooplankton abundance and distribution (Johnston & Read 2007; Benjamins et al. 2015). These changes can increase prey accessibility and vulnerability, and hence marine predators are often found foraging in areas of high tidal activity (Johnston et al. 2005; Bailey & Thompson 2010). For example, in tidal channels, studies have observed that tidal cycles lead to fluctuating numbers of diving seabirds (Holm & Burger 2002) and marine mammals (Johnston et al. 2005; Hastie et al. 2016). There is also evidence that seabird numbers fluctuate with the tide further offshore (Zamon 2003; Embling et al. 2012; Cox et al. 2013), although the nature of these relationships varies between locations (Zamon 2003; Embling et al. 2012; Cox et al. 2013). Such geographic differences in behavioural responses to the tidal cycle may arise because of location-specific interactions between bathymetry and tidal currents (Scott et al. 2013; Waggitt et al. 2016b; Cox et al. 2018), and therefore associated variability in forage fish abundance and distribution (Couperus et al. 2016). The surrounding environment may also play a key role in shaping behavioural responses, and therefore warrants further study (Benjamins et al. 2015).

In this study, we explore changes in foraging habitat preferences of black-legged kittiwakes (Rissa tridactyla, hereafter "kittiwakes") over the predictable semi-diurnal (~12.4-hour) tidal cycle. Kittiwakes feed at the surface, predominately on shoaling fish such as lesser sandeel, Ammodytes marinus (Daunt et al. 2002). Kittiwakes forage opportunistically throughout their trips away from the colony, in contrast to the commuting behaviour of some other seabird species, such as gannets (Soanes et al. 2013). Breeding kittiwakes are constrained in the timing of their foraging trips by the behaviour of their partner (Coulson & Wooller 1984). Furthermore, whilst provisioning chicks, kittiwakes are relatively short-ranging central-place foragers (Daunt et al. 2002), and are thus constrained to the physical environment surrounding their colony. As with many other central place foragers, kittiwakes live within finely balanced energy budgets (Collins et al. 2016). As such, distance to the colony is known to be a primary driver of foraging behaviour, as animals seek to minimise energy expenditure from flight costs during travel to foraging areas (Chivers et al. 2013; Collins et al. 2016). A decision, therefore, to forage further from the colony may signify an important adaptation to maximise foraging gains.

In order to study foraging adaptations of kittiwakes to the physical environment and the tidal cycle, we first consider behaviour in relation to distance to the colony, and then explore fine-scale adaptations of habitat selection to the environment and predictable temporal changes. We predict that kittiwakes will preferentially remain close to the colony, and therefore will selectively forage in water depths that are found close to the colony. Because tidal currents interact with bathymetry to change prey availability to predators, we expect that preference for different water depths within the bathymetric landscape will change over the 12.4 hour tidal cycle. Furthermore, in more heterogeneous environments where changes in bathymetry are more common and tidal changes are more pronounced, potentially causing greater spatial and temporal variability in prey fish abundance and distribution, we hypothesise that

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kittiwakes will adjust their habitat selection more over the tidal cycle than in homogeneous environments.

#### Material and Methods

GPS tracking

To determine fine-scale movement behaviour of kittiwakes, we attached GPS loggers (Mobile Action<sup>®</sup> IgotU GT-120; weighing 15.3g in 2010 & 2011; and subsequently 10.3g with modified battery in 2015-17) to the back feathers between the wings using 3g of TESA® waterproof tape. We deployed loggers at three UK kittiwake colonies (Figure 2.1a): Puffin Island (NW Wales; 53.32 N 4.03 W); Skomer Island (SW Wales; 51.74 N 5.30 W); and Rathlin Island (Northern Ireland; 55.30 N 6.27 W), during chick rearing (June-July) and retrieved them after an average of  $2.7 \pm 1.25$  days ( $\pm$  sd). GPS tracks were obtained for a total of 457 trips from 80 individuals: 341 trips from 49 individuals at Puffin Island (14 individuals in 2010, 20 in 2011, 9 in 2015 and 10 in 2016), 33 trips from 14 individuals at Skomer Island (11 individuals in 2016 and 6 in 2017) and 83 trips from 17 individuals at Rathlin Island (2017 only). At Puffin Island, two individuals were tracked in two different study years, and one individual was tracked in three different study years. At Skomer Island, three birds were tracked in both study years. Full sample sizes are given in Supplementary material (Appendix S2.A, Table S2.A1). The loggers recorded a GPS location every two minutes, between the hours of 03:00 and 23:00 to reduce battery consumption overnight when kittiwakes exhibit minimal foraging activity (Daunt et al. 2002). GPS data were not interpolated. To eliminate departures from the colony because of disturbance (Collins et al. 2016; Warwick-Evans et al. 2016a), we excluded points closer than 300 m to the colony, and attributed sequential points to a foraging trip if the total trip duration was over 14 minutes (based on a frequency distribution of trip duration; Warwick-Evans et al. 2016b). Hereafter we refer to fixes recorded by GPS loggers as locations used by kittiwakes. All data manipulation and analyses were conducted in R version 3.2.2 (R Core Team 2016).

#### Environmental data

Bathymetry data were collated from the UK Hydrographic Office (UKHO) Data Archive Centre for bathymetric surveys and integrated with the General Bathymetric Chart of the Oceans (GEBCO). UKHO data contains public sector information, available under the Open Government Licence as part of the INSPIRE initiative. UKHO data, collected from boat surveys, covered a subset of the study areas at between 2 and 4 m resolution. Bathymetry from UKHO data were available for 66.8% of the locations used by kittiwakes. Depths for the remaining locations were extracted from GEBCO data, which is a global bathymetric grid with 30" resolution (approximately 1 km), updated in 2014. However, because both UKHO and GEBCO bathymetry follow a relatively coarse grid for the coastline, 7% of locations used by kittiwakes fell outside the gridded bathymetry data. For these locations, we used the mean bathymetry from all GEBCO grid cells within a 1.1 km radius. This buffer slightly exceeds the resolution of GEBCO data and was sufficient to capture bathymetry data for all locations used by kittiwakes. Percentage coverage of each type of bathymetry data at each colony are given in supplementary material (Appendix S2.A, Figure S2.A1).

Times during the tidal cycle for each kittiwake location were generated using POLTIPS tidal software (v.3.9.0/16; National Oceanography Centre UK, 2013). The Irish Sea and surrounding areas (Figure 2.1) are strongly influenced by tidal processes, having significant tidal ranges (exceeding 10m in the Bristol Channel) and extreme tidal races (exceeding 2.5 m/s around NW Anglesey) (Polton et al. (2011), see also for a dynamical review of the region). Data were extracted from the nearest secondary port to the study colony (Trywn Dinmor 1 km from Puffin Island, Skomer Island for Skomer Island, and Ballycastle Bay 10 km from Rathlin Island). Tide times may vary across the kittiwake foraging range by up to 20 minutes at Puffin Island, and up to an hour at Skomer Island. At Rathlin Island tide times may be more variable, however there are few nearby secondary ports for tidal calculations and tidal amplitudes are small. We therefore derived tide times at all colonies from a single location to maintain consistency between study sites. We split the ~12.4-hr tidal cycle into four sections relative to the time of local high water (Waggitt *et al.* 2016b), since flow characteristics are known to affect prey behaviour and distribution (Zamon 2002; Embling *et al.* 2012): 1) slack low: >5 hours either side of high water to correspond to low flow rate either side of low tide; 2) flood: between 5 and 1 hours before high water, high flow rate during the rising tide; 3) slack high: 1 hour either side of high water, high flow rate during the falling tide (Waggitt *et al.* 2016a). Each kittiwake location was assigned to a section of the tidal cycle according to the time before or after high water that the GPS fix was recorded.

#### Assessing environmental heterogeneity of colonies

To investigate how the degree of environmental heterogeneity influenced kittiwake foraging behaviour, we compared the physical environment surrounding each breeding colony by characterising depth and tidal regime within the maximum foraging range of kittiwakes, defined as the maximum linear distance from each colony from kittiwake tracking data. To do this, following Verney et al. (2006), we compared bathymetry and tidal shear stress. Tidal shear stress is a measure of the amount of turbulence caused by the friction between tidal flow and the seafloor, and is used as a proxy for the extent to which tidal flow alters the foraging environment over the tidal cycle. Tidal shear stress is simulated numerically at 1.8km resolution over the North West European shelf (Guihou *et al.* 2018), further details given in Supplementary materials, Appendix S2.B. We used ANOVA and post-hoc Tukey tests to determine whether the environment differed between colonies. We compared mean values, standard deviation and the range of values as an indication of spatial environmental heterogeneity at each colony.

#### Behavioural classification

To study habitat selection whilst foraging, we used a hidden Markov model to classify behaviour from GPS tracking data using the package moveHMM (Michelot *et al.* 2016). Behaviour of an individual during trips away from the colony was classified as either foraging, resting or transiting (Chivers *et al.* 2012) based on distributions of step lengths and turning angles between consecutive locations. Standard deviation of time steps of the data are small (around 2 seconds), and so we assume that our time steps are sufficiently regular for this approach, which also allowed us to model real locations rather than interpolated locations in the habitat selection analysis described below. We used a gamma distribution to describe step lengths and a von Mises distribution to describe turning angles. We used the Viterbi algorithm to estimate the most likely sequence of movement states based on the fitted hidden Markov model (Supplementary materials, Appendix S2.C). Hidden Markov models use prior estimates of step length and turning angle distributions, and therefore we ran 25 models with different distribution starting parameters to test model sensitivity (Grecian *et al.* 2018).

#### Habitat Selection Analysis

To determine whether kittiwake foraging behaviour is influenced by a predictable cycle and the degree of environmental heterogeneity, we tested whether spatial habitat selection by kittiwakes varied temporally over the tidal cycle, and between study colonies with different degrees of environmental heterogeneity. Firstly, because of the importance of colony location to foraging behaviour of breeding kittiwakes (Chivers *et al.* 2013), we considered differences in habitat selection by distance to the colony. Secondly, because the tidal coupling hypothesis suggests that tidal currents

and bathymetry interact to change the foraging environment over the tidal cycle, we considered differences in habitat selection of water depth.

Habitat selection functions were performed using generalised linear mixed effects models to compare the habitat used by the birds with the habitat available to them (Aarts et al. 2012). A dataset of available habitat was generated for 10 random geographic points (Northrup et al. 2013) per foraging location used by kittiwakes from within the foraging range of the colony in the given study year to reflect second-order habitat selection, i.e. broad-scale habitat choice within the range of habitats accessible to a population (Johnson 1980; Boyce 2006; Christensen-Dalsgaard et al. 2017). Random points were selected using the sampleRandom function of the R package raster (Hijmans & Etten 2018). Habitat use (binomial response variable: y; available = 0 or used = 1) was modelled in response to three explanatory variables: (1)the physical environment (either colony distance or depth in two separate models, standardised to mean = 0, sd = 1), (2) tidal state (four-level factor), and (3) colony (threelevel factor). Colony distance or depth were included in a three-way interaction with tidal state and colony to explore how the degree of environmental heterogeneity influences the interaction between constant landscape characteristics and temporal cycles.

Models were implemented using a binomial error structure with a logit link using the *glmer* function of the R package lme4 (Bates *et al.* 2015). We selected the random effects structure based on pseudo-replication in the sampling design, in all cases including trip ID nested within individual ID as random intercepts in the model. We also included a colony-specific factor for year as a random effect to allow for year differences specific to each colony. We selected the most suitable fixed effects structure based on AIC values in backward stepwise selection (Zuur *et al.* 2009), and checked model fit by calculating the area under the receiving operator characteristic

curve (AUC) (Zweig & Campbell 1993), predictive power, sensitivity and specificity (Warwick-Evans *et al.* 2016b) (Supplementary Material, Table S2.D3).

Testing by inspection of Moran's I of model residuals at each colony revealed that there was no influence of spatial autocorrelation in any of our findings (Moran's I < 1, p = 1) (Diniz-Filho *et al.* 2003). Variance explained, R<sup>2</sup>, was calculated using the *sem.model.fits* function of the R package *piecewiseSEM* (Lefcheck 2016) following methods in Nakagawa & Schielzeth (2013). To ensure accurate characterisation of habitat preference of kittiwakes, we assessed model sensitivity to the maximum foraging range used to select available habitat, and including all GPS locations, rather than just foraging points (Northrup *et al.* 2013). Results of sensitivity analyses (Supplementary material, Appendix S2.C) are consistent with those presented in the results, and thus we believe our analyses are robust to available habitat selection methods.

In addition to the two models described above, to further understand how the degree of environmental heterogeneity can change the effect of a predictable cycle on behaviour, we ran habitat selection models at each colony separately. We explored differences between colonies in the variance explained by the two-way interaction of tide and the environmental variable in question (distance to the colony or depth) to determine the effect of the tidal cycle on kittiwake spatial behaviour. In addition, we extracted parameter estimates for habitat selection at different tidal states to compare the probability of habitat use at different tidal states at each colony. Models were structured as above, however without colony as a factor in the fixed effects structure.

#### Results

Foraging trip metrics
Foraging trips from Puffin Island and Rathlin Island were comparable in mean duration, mean distance travelled and mean maximum distance reached from the colony (Table 2.1, Figure 2.1b). At Skomer Island, foraging trips were, on average, longer in duration, distance travelled, and reached furthest from the colony (Table 2.1, Figure 2.1b). Summaries of trip durations and distances for each year at each colony are given in Supplementary material (Appendix S2.A, Table S2.A2). GPS tracking spanned across the spring-neap cycle at Puffin Island, and was between springs and neaps at both Skomer and Rathlin (Supplementary material, Appendix S2.A, Figure S2.A2), thus reducing the potential influence of the spring-neap cycle on our findings.

#### Differences in proximal environment and heterogeneity between colonies

To assess the degree of local environmental heterogeneity, we compared local bathymetry (Figure 2.1c) and tidal shear stress (Figure 2.1d). Within the foraging range of GPS tracked kittiwakes, at Puffin Island bathymetry was shallower and more homogeneous (mean ± sd = 35.9 m + 20.9) compared to Skomer Island (65.3 m ± 27.1) and Rathlin Island (76.5 m ± 42.4). Furthermore, at Puffin Island, tidal flow caused the least amount of change in the foraging environment over the tidal cycle (maximum shear stress = 401 mN m<sup>-3</sup>), compared to Skomer Island (448 mN m<sup>-3</sup>) and Rathlin Island (523 mN m<sup>-3</sup>). At both Puffin Island and Skomer Island the water adjacent to the colony was shallow, whereas at Rathlin Island, the deepest waters within the foraging range (over 200 m) were found within 10 km of the colony (Figure 2.1c). Based on the differences in bathymetry and tidal shear stress (further details in Supplementary material, Appendix S2.B) we identified different degrees of environmental heterogeneity between the study colonies, both in terms of spatial (bathymetry) and temporal (tide) variability; Puffin Island: low heterogeneity, Skomer Island: medium heterogeneity and Rathlin Island: high heterogeneity.

Habitat selection

Habitat selection by distance to the colony and depth were analysed separately, and in both cases the most parsimonious models according to AIC values (Supplementary material, Appendix S2.D, Tables S2.D1 and S2.D2) were the 'full models' that retained the three-way interaction between the environment variable in question (distance to the colony or depth), tidal state and colony. This means that habitat selection by kittiwakes was influenced by distance to the colony and local bathymetry, varied over the tidal cycle, and that the response to the tidal cycle was different between environments. Depth also influenced kittiwake habitat selection, which also varied according to the tidal cycle and with environmental heterogeneity. Model parameter estimates are given for habitat selection by colony distance in Table 2.2, and for habitat selection by depth in Table 2.3.

Distance to the colony was a significant driver of kittiwake foraging behaviour; the full model accounted for over two thirds of the total variance (marginal  $R^2 = 65\%$ ). At all colonies, kittiwakes had higher probability of using habitat closer to the colony (Figure 2.2). The probability of remaining closer to the colony was strongest at Rathlin Island (high heterogeneity) (parameter estimate on logit scale ± standard error: -3.41 ± 0.34), weakest at Skomer Island (medium heterogeneity) (-1.94 ± 0.28) and intermediate at Puffin Island (low heterogeneity) (-2.87 ± 0.17).

Bathymetry at locations used by kittiwakes corresponded to water depths close to the study colony (Figure 2.3). The full model showed that bathymetry affected kittiwake habitat choice (marginal  $R^2 = 19.8\%$ ). However, as expected, this model explained less variance than the full model of habitat selection by colony distance. The effect of bathymetry on habitat selection was strongest at Puffin Island (low heterogeneity) (parameter estimate on logit scale ± standard error: -11.28 ± 0.07), weakest at Rathlin Island (high heterogeneity) (2.90 ± 0.08) and intermediate at Skomer Island (medium heterogeneity) (-6.70 ± 0.11). At Puffin Island and Skomer Island, where bathymetry close to the colony was shallower (Figure 2.1), kittiwakes had higher probability of

using shallow water (Figure 2.3), whereas at Rathlin Island, which was adjacent to very deep water (Figure 2.1), kittiwakes had higher probability of using deeper water (Figure 2.3).

Kittiwake habitat selection changed during the predictable 12.4-hour tidal cycle (Tables 2.2 and 2.3), and the change in kittiwake habitat selection over the tidal cycle differed in magnitude between the colonies (Tables 2.2 and 2.3). The most parsimonious habitat selection models for each colony separately according to AIC values (Supplementary material, Appendix S2.F, Tables S2.F3 and S2.F4) were the models including the two-way interaction between the environmental variable in question (distance to the colony or depth) and tidal state. Based on these models, the interaction between tide and the environmental variable (distance to colony or depth) explained more additional variation in the model at Rathlin Island, where environmental heterogeneity was greatest (13.2% for colony distance, and 3.1% for depth; Table 2.4), and least variation at Puffin Island, where environmental heterogeneity was lowest (1.6% for colony distance, and 0.4% for depth; Table 2.4).

The probability of habitat selection of different water depths changed during the tidal cycle following a similar pattern between Skomer Island (medium heterogeneity) and Rathlin Island (high heterogeneity), with some overlap at Puffin Island (low heterogeneity). At all colonies, during slack low water kittiwakes had a higher probability of selecting deeper water and a lower probability of selecting shallow water (Figure 2.4). At Skomer Island and Rathlin Island (medium and high heterogeneity), during the flood tide kittiwakes had the highest probability of selecting shallow water and the lowest probability of selecting deep water, whereas this was the case during high water (the subsequent tidal stage) at Puffin Island (low heterogeneity) (Figure 2.4).

The probability of remaining close to the colony changed during the tidal cycle (Figures 2.3 & 2.4) depending on habitat preference by bathymetry. During low water,

the bathymetry model showed that individuals had the lowest probability of being in shallower waters at all colonies (Figures 2.3 & 2.4), and accordingly kittiwakes had lower probability of remaining close to the colony where adjacent waters were shallow (Puffin Island and Skomer Island). In contrast, kittiwakes had highest probability of remaining close to the colony where adjacent waters were deep (Rathlin Island) (Figure 2.4). Table 2.1. Summary of kittiwake foraging trip characteristics at each colony over all study years (Puffin island: 2010-11 & 2015-16; Skomer Island: 2016-17; and Rathlin Island: 2017). Full details of sample sizes and trip characteristics for each year are given in Supplementary material (Appendix S2.A).

| Colony  | Mean Trip duration | Mean total distance | Mean maximum distance         |
|---------|--------------------|---------------------|-------------------------------|
|         | (hours ± se)       | travelled (km ± se) | from the colony (km $\pm$ se) |
| Puffin  | $3.8 \pm 0.3$      | 39.4 ± 2.5          | 11.9 ± 0.7                    |
| Skomer  | 9.7 ± 1.5          | 90.0 ± 13.3         | 22.0 ± 2.6                    |
| Rathlin | $3.4 \pm 0.3$      | 39.7 ± 3.7          | 13.5 ± 1.3                    |



Figure 2.1. Colony locations around the UK (a) and areas around Puffin Island (left), Skomer Island (middle) and Rathlin Island (right) showing (b): GPS tracks of kittiwakes (Puffin island: 2010-11 & 2015-16, n = 49; Skomer Island: 2016-17, n = 14; and Rathlin Island: 2017, n = 17), (c) water depths and (d) depth-standardised tidal shear stress. In all plots, the study kittiwake colony is marked with a point.



Figure 2.2. Density curves of available habitat (sampled for 10 random points per foraging GPS point) and habitat used by kittiwakes whilst foraging (GPS points classed as foraging from HMM model) with increasing distance from the colony (left) and water depths (right) at the three study colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Greater density of used than available habitat indicates selection of that particular habitat. At all colonies, habitat close to the colony was used at a greater frequency density than available, indicating preference for remaining close to the colony. At Puffin Island and Skomer Island, shallower waters were used at a greater frequency density than available, indicating preference for shallower waters, whereas at Rathlin Island, deeper waters were used at a greater frequency density than available, indicating preference for deeper waters.



Figure 2.3. Probability of habitat use whilst foraging at different distances to the colony (left) and at varying water depths (right) for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Curves from full models of all colonies together (Tables 2 & 3). At all colonies, kittiwakes preferentially remain close to the colony. At Puffin Island and Skomer Island, where water depth close to the colony is shallower, kittiwakes preferentially forage in shallow water, whereas at Rathlin Island, which is adjacent to very deep water, kittiwakes preferentially forage in deep water

Table 2.2. Parameter estimates (slope  $\pm$  95% confidence intervals) for the most parsimonious model of kittiwake habitat selection by distance to the colony. All values are below zero (dashed line), indicating a general preference for remaining closer to the colony. Lower negative values, indicate stronger preference for habitat closer to the colony. Model is a generalised linear mixed effects model with a binomial response of habitat use (used = 1, available = 0), with Year (specific to colony), BirdID and TripID included as random effects. Tidal states are defined as slack low: >5 hours either side of high water; flood: 1 – 5 hours before high water; slack high: 1 hour either side of high water; and ebb: 1 – 5 hours after high water. Environmental heterogeneity is low at Puffin Island, medium at Skomer Island and high at Rathlin Island.

Table 2.3. (Overleaf) Parameter estimates (slope  $\pm$  95% confidence intervals) for the most parsimonious model of kittiwake habitat selection by depth, where values below zero (dashed line) indicate preference for shallower water, and values above zero indicate preference for deeper water.

| Colony  | Tidal state | Colony dist | ance selection | estimate (slop | e & 95% confide | nce intervals) | No. of<br>individuals | No. of<br>trips |
|---------|-------------|-------------|----------------|----------------|-----------------|----------------|-----------------------|-----------------|
| Puffin  | Overall     |             |                | ł              | -2.87 [-3       | .21, -2.55]    | 49                    | 341             |
|         | Slack Low   |             |                | ł              | -2.46 [-2       | 79, -2.12]     | 45                    | 147             |
|         | Flood       |             |                | +              | -2.64 [-2       | .97, -2.31]    | 49                    | 206             |
|         | Slack High  |             |                | Ŧ              | -3.75 [-4       | .08, -3.41]    | 46                    | 141             |
|         | Ebb         |             |                | ł              | -2.84 [-3       | .18, -2.51]    | 49                    | 215             |
| Skomer  | Overall     |             |                | ł              | -1.94 [-2       | 50, -1.39]     | 14                    | 33              |
|         | Slack Low   |             |                | ł              | -1.62 [-2       |                | 13                    | 22              |
|         | Flood       |             |                | ł              | -2.46 [-3       | :02, -1.91]    | 14                    | 30              |
|         | Slack High  |             |                | ł              | -1.84 [-2       | .40, -1.28]    | 13                    | 20              |
|         | Ebb         |             |                | ł              | -1.65 [-2       | .21, -1.09]    | 14                    | 22              |
| Rathlin | Overall     |             | •              | ł              | -3.41 [-4       | .07, -2.75]    | 17                    | 83              |
|         | Slack Low   | ł           |                |                | -8.60 [-9       | .61, -7.59]    | 15                    | 28              |
|         | Flood       |             |                | ł              | -2.14 [-2       | 78, -1.49]     | 16                    | 40              |
|         | Slack High  |             |                | ł              | -2.32 [-2       | .97, -1.67]    | 17                    | 39              |
|         | Ebb         |             |                | ł              | -2.34 [-2       | 99, -1.69]     | 17                    | 53              |
|         |             | -10.0 -7.5  | -5.0           | -2.5           | - 0.0           |                |                       |                 |
|         |             |             |                | Odds ratio     |                 |                |                       |                 |

|         |              |                              |                    |                 | ,           |        |
|---------|--------------|------------------------------|--------------------|-----------------|-------------|--------|
| Colony  | Tidal state  | Denth selection estimate (sl | one & 95% confider | nce intervals)  | No. of      | No. of |
|         |              |                              |                    |                 | individuals | trips  |
| Puffin  | Overall      | •                            | -11.28 [-          | -11.41, -11.15] | 49          | 341    |
|         | Slack Low    | •                            | -10.24 [-          | -10.48, -10.00] | 45          | 147    |
|         | Flood        | •                            | -11.40 [-          | -11.60, -11.21] | 49          | 206    |
|         | Slack High ● |                              | -13.55 [-          | -13.81, -13.29] | 46          | 141    |
|         | Ebb          | •                            | -10.38 [-          | -10.58, -10.19] | 49          | 215    |
| Skomer  | Overall      | •                            | -6.70 [-6          | 5.91, -6.48]    | 14          | 33     |
|         | Slack Low    | •                            | -4.90 [-5          | 5.18, -4.62]    | 13          | 22     |
|         | Flood        | •                            | -8.55 [-8          | 3.86, -8.23]    | 14          | 30     |
|         | Slack High   | +                            | -5.98 [-6          | 5.39, -5.57]    | 13          | 20     |
|         | Ebb          | •                            | -6.27 [-6          | 6.57, -5.96]    | 14          | 22     |
| Rathlin | Overall      |                              | • 2.90 [2.7        | 74, 3.06]       | 17          | 83     |
|         | Slack Low    |                              | • 3.62 [3.3        | 35, 3.90]       | 15          | 28     |
|         | Flood        | •                            | 1.25 [1.0          | )6, 1.43]       | 16          | 40     |
|         | Slack High   |                              | • 3.27 [3.0        | )7, 3.48]       | 17          | 39     |
|         | Ebb          |                              | • 3.97 [3.7        | 79, 4.15]       | 17          | 53     |
|         |              | -10 -5 0                     | 2                  |                 |             |        |
|         |              | Odds ratio                   |                    |                 |             |        |



Figure 2.4. Kittiwake habitat preferences for greater distances from the colony (left) and greater water depths (right) from models of habitat selection ran separately at each colony and including the effect of tidal state (see methods text for details). All slope values for colony distance (left) are negative, which indicates a general preference for foraging closer to the colony. Lower slope values (or more negative) indicate a stronger preference for areas closer to the colony compared to other tidal states. At Puffin Island and Skomer Island, slope values for bathymetry (right) are negative, indicating an overall preference for shallower water, whereas slope values at Rathlin Island are positive, indicating an overall preference for shallow waters compared to other tidal states. Tidal states are defined as slack low: >5 hours either side of high water; flood: 1 – 5 hours before high water; slack high: 1 hour either side of high water; and ebb: 1 – 5 hours after high water. Environmental heterogeneity is low at Puffin Island and high at Rathlin Island.

Table 2.4. Variance explained by models of each environment variable (distance to colony or depth) separately for each of the three study colonies, both with and without the two way interaction between the environment (distance to colony or depth) variable and tidal state. Models are generalised linear mixed effects models with a binomial response of habitat use (used = 1, available = 0), with Bird ID and Trip ID included as random effects. Environmental heterogeneity is low at Puffin Island, medium at Skomer Island and high at Rathlin Island.

|               |         |              | Marginal R <sup>2</sup> (%) |                              |
|---------------|---------|--------------|-----------------------------|------------------------------|
| Two-way       | -       | With two-way | Without two-way             | Difference in R <sup>2</sup> |
| interaction   | Colony  | interaction  | interaction                 | (%)                          |
| Distance to   | Puffin  | 65.1         | 63.5                        | -1.6                         |
| colonv x tide | Skomer  | 34.6         | 32.8                        | -1.8                         |
| ,             | Rathlin | 63.0         | 49.9                        | -13.2                        |
|               | Puffin  | 19.7         | 19.3                        | -0.4                         |
| Depth x tide  | Skomer  | 17.5         | 15.7                        | -1.8                         |
|               | Rathlin | 22.2         | 19.0                        | -3.1                         |

#### Discussion

Our study demonstrates that, in addition to the previously documented effect of proximity to the colony, habitat selection by kittiwakes was influenced by depth and tidal state, and that this latter effect was greater in a more heterogeneous local environment. This means that kittiwakes showed temporal variation in spatial habitat selection over a predictable cycle that alters the foraging environment at time scales relevant to single foraging trips. Furthermore, we show that environmental heterogeneity increased temporal variability in habitat selection, suggesting that adaptations to the local environment and short-term cycles could maximise foraging efficiency, and therefore fitness gains.

Foraging theory predicts that animals should adapt to the distribution of their target resources (Stephens & Krebs 1986), and temporal changes in habitat preference have been demonstrated in response to long-term resource changes, such as seasonal cycles (Guyot et al. 2017). In this study, we provide evidence supportive of short-term changes in habitat selection that are most likely an adaptation to cyclic changes in resource availability. We found that kittiwake habitat selection of different bathymetries varied temporally during the tidal cycle, a ubiquitous process in the coastal marine environment that can shape resource distribution because of interactions between tidal currents and the bathymetric landscape (Zamon 2003). This behavioural response is therefore most likely an adaptation to enhanced resource availability or accessibility (Ladd et al. 2005). For example, we found a lower probability of kittiwake presence in deep water during the flood tide, when elsewhere fish have been found to be more dispersed throughout a deep channel (Zamon 2003), and therefore less accessible to surface-feeding kittiwakes. We also found lower probability of kittiwake presence in shallow water during low tide, which concurs with when previous studies in the North Sea have found lowest numbers of pelagic fish in shallow waters (Couperus et al. 2016). Kittiwakes may be selecting to forage in shallower waters during flood tides because currents improve prey accessibility for surface feeders, in contrast to diving seabirds that may be hindered by high energetic costs of swimming in strong currents (Waggitt *et al.* 2016a). When rearing small chicks, kittiwakes are unable to time their departure from the colony with the tide because they are constrained by their partner's behaviour, which highlights the importance of adapting their spatial behaviour to match temporal conditions. Such behavioural adaptation may be possible because of the predictability and regular repetition of the 12.4-hr tidal cycle. Whilst tide-driven resource changes are unique to the marine environment, predictable diurnal cycles are commonplace, and alter both the physical environment (e.g. light intensity, thermal wind speed (Deser 1994) and precipitation (Dai 2001)) with knock-on effects for the biological environment (e.g. prey availability and predation risk (Rydell *et al.* 1996; Timewell & Mac Nally 2004; Brierley 2014)). Our results suggest that predictable cycles may therefore have significant effects on where and when foraging animals can locate resources in many ecosystems.

As well as the influence of a predictable temporal cycle on behaviour, here we find that environmental heterogeneity increases behavioural adaptation to resource changes. Kittiwakes in the more heterogeneous environments modified their spatial foraging behaviour over the tidal cycle more than those in the more homogeneous environment, showing greater variation in habitat preference between tidal stages both in respect to distance to the colony and depth. We suggest that this occurs because environmental heterogeneity drives the effect of a temporal cycle on resource changes, and therefore also causes spatial variability in temporal resource changes. In contrast, in more homogeneous environments, the features that cause tidal resource changes are reduced or absent, and therefore behaviour changes less over the tidal cycle. This location-specific mechanism could also explain why previous studies of prey fish and seabirds find varying magnitudes of responses to different stages of the tidal cycle (Irons 1998; Embling *et al.* 2012; Cox *et al.* 2013), as

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observations in a single site may not reveal the full extent of behaviour in relation to the surrounding physical environment. Research has shown that behavioural adaptations to environmental heterogeneity can prove profitable to individual foragers (Klaassen *et al.* 2006) and whole communities (Waugh & Weimerskirch 2003) by increasing prey encounter rates and enabling species coexistence through resource specialisation. Our results support these studies, and provide additional evidence that behavioural adaptation to environmental heterogeneity is likely beneficial, potentially through maximising prey location.

When travelling away from their breeding site, central place foragers experience a trade-off between distance from the colony and habitat quality (Olsson & Bolin 2014). Individuals can be constrained to remain close to the colony unless limited resources require them to seek prey further away (Burke & Montevecchi 2009; Elliott et al. 2009), potentially at the cost of breeding success (Boersma & Rebstock 2009; Chivers et al. 2012). Here, we confirm that distance to the colony is a major driver of habitat selection; at all study sites kittiwakes had a higher probability of remaining close to the colony. The effect of distance to the colony on habitat selection was greater than that of bathymetry, likely because of energetic constraints. Nevertheless, we observed changes in the probability of remaining close to the colony over the tidal cycle, which importantly reflect bathymetry influences on kittiwakes that are consistent between study sites. Not only does this add weight to the theory that resource availability drives habitat selection changes, but it stresses the importance of apparently finescale environmental differences on behaviour. The interactions between the tidal cycle and distance to the colony or depth might appear to explain relatively small amounts of model variance. However, they are comparable to the variance explained by oceanic fronts (Cox et al. 2016), which are now widely accepted to be important features enhancing prey availability to marine top predators (Scales et al. 2014; Cox et al. 2016). Furthermore, for animals with such finely balanced energy budgets (Collins *et al.* 2016), the fact that these behavioural changes occur repeatedly within centralplace foraging suggests that the ability to adapt to predictable resource changes in otherwise variable environments could make all the difference between breeding success and failure.

## Conclusions

In this study, we demonstrate that a predictable temporal cycle can influence spatial movement behaviour at time scales not previously demonstrated, and that environmental heterogeneity can enhance the magnitude of this effect. Such shifts in behaviour across multiple environments show a key adaptation of animals to maximise foraging efficiency by matching their own distribution to that of their resources at hourly time scales. We have studied this process in the marine environment, and provide new evidence in support of the tidal coupling hypothesis using direct measurements of seabird behaviour in contrasting environments, highlighting the complex nature of interactions between predators, prey, and their surrounding physical features. Kittiwakes are an environmental indicator species (Wanless et al. 2007), and thus results may have applied relevance for marine management. For example, in the context of tidal energy installations, which have the potential to significantly reduce tidal flow dynamics in surrounding areas (Pérez-Ortiz et al. 2017), the loss of predictable prey fluctuations could have negative consequences for animals that are adapted to tidal changes. Furthermore, as temporal cycles and environmental variability are ubiquitous in nature, the results of this study highlight that interactions between fine-scale resource distribution changes and the physical environment may shape predator behaviour across many ecosystems.

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Supplementary material to: Environmental heterogeneity amplifies behavioural response to a temporal cycle

Appendix S2.A: GPS tracking sample sizes, summary trip metrics & bathymetry data coverage

Appendix S2.B: Assessing colony environmental heterogeneity

Appendix S2.C: Hidden Markov models for behavioural classification

Appendix S2.D: Model Selection

Appendix S2.E: Sensitivity analysis of resource selection model to available habitat selection.

Appendix S2.F: Habitat selection models for colonies separately

References

Appendix S2.A. GPS tracking sample sizes, summary trip metrics & bathymetry data coverage

|         |      |             |        | Mean       | Unique   | First      | Last       | Individuals | Individuals | Individuals |
|---------|------|-------------|--------|------------|----------|------------|------------|-------------|-------------|-------------|
|         |      | No. of      | No. of | trips per  | tracking | tracking   | tracking   | with one    | with 2-3    | with >4     |
| Colony  | Year | Individuals | trips  | individual | days     | date       | date       | trip        | trips       | trips       |
| ALL     | ALL  | 80          | 457    | 5.71       | 41       | 28/06/2010 | 09/07/2017 | œ           | 26          | 53          |
| Puffin  | ALL  | 49          | 341    | 6.96       | 33       | 28/06/2010 | 02/07/2016 | 2           | 12          | 39          |
| Puffin  | 2010 | 14          | 133    | 9.50       | 11       | 28/06/2010 | 14/07/2010 | 0           | 0           | 14          |
| Puffin  | 2011 | 20          | 116    | 5.80       | 15       | 27/06/2011 | 11/07/2011 | -           | 4           | 15          |
| Puffin  | 2015 | 6           | 41     | 4.56       | с<br>С   | 10/07/2015 | 12/07/2015 | 0           | 4           | Ŋ           |
| Puffin  | 2016 | 10          | 51     | 5.10       | 4        | 28/06/2016 | 02/07/2016 | 7           | 4           | Ω           |
| Skomer  | ALL  | 14          | 33     | 2.35       | ъ        | 27/06/2016 | 29/06/2017 | 9           | 10          | 1           |
| Skomer  | 2016 | 11          | 20     | 1.82       | 5        | 27/06/2016 | 28/06/2016 | 4           | 7           | 0           |
| Skomer  | 2017 | 9           | 13     | 2.17       | ŝ        | 27/06/2017 | 29/06/2017 | 2           | 3           | 1           |
| Rathlin | ALL  | 17          | 83     | 4.88       | 4        | 06/07/2017 | 09/07/2017 | 0           | 4           | 13          |
| Rathlin | 2017 | 17          | 83     | 4.88       | 4        | 06/07/2017 | 09/07/2017 | 0           | 4           | 13          |

Table S2.A1. Sample sizes of individuals, trips and tracking dates at all colonies and years.

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| Colony  | Year | Mean trip | ± se | Trip        | Mean total     | ± se  | Total distance | Mean Max    | ± se | Max distance |
|---------|------|-----------|------|-------------|----------------|-------|----------------|-------------|------|--------------|
|         |      | duration  |      | duration    | distance       |       | travelled      | distance to |      | to colony    |
|         |      | (hrs)     |      | range (hrs) | travelled (km) |       | range (km)     | colony (km) |      | range (km)   |
| ALL     | ALL  | 4.14      | 0.24 | 0.1 - 40.7  | 43.1           | 2.25  | 0.1 - 273.7    | 13.0        | 0.63 | 0.3 - 71.0   |
| Puffin  | ALL  | 3.77      | 0.27 | 0.1 - 40.7  | 39.4           | 2.45  | 0.1 - 245.2    | 11.9        | 0.73 | 0.3 - 71.0   |
| Puffin  | 2010 | 2.58      | 0.22 | 0.2 - 12.8  | 29.1           | 2.70  | 0.7 - 182.1    | 9.1         | 0.95 | 0.3 - 71.0   |
| Puffin  | 2011 | 5.00      | 0.44 | 0.2 - 23.6  | 58.2           | 4.58  | 0.7 - 245.2    | 17.8        | 1.25 | 0.3 - 61.6   |
| Puffin  | 2015 | 5.48      | 1.50 | 0.2 - 40.7  | 40.2           | 9.60  | 0.5 - 219.4    | 10.6        | 2.71 | 0.4 - 68.3   |
| Puffin  | 2016 | 2.69      | 0.49 | 0.1 - 13.2  | 22.5           | 5.00  | 0.1 - 169.0    | 7.3         | 1.73 | 0.3 - 53.7   |
| Skomer  | ALL  | 9.68      | 1.52 | 0.3 - 32.5  | 90.06          | 13.27 | 0.6 - 273.7    | 22.0        | 2.58 | 0.4 - 49.2   |
| Skomer  | 2016 | 9.91      | 1.93 | 0.3 - 24.2  | 87.5           | 17.60 | 0.6 - 243.3    | 20.0        | 3.28 | 0.4 - 44.9   |
| Skomer  | 2017 | 9.31      | 2.54 | 0.5 - 32.5  | 93.8           | 20.88 | 2.4 - 273.7    | 25.0        | 4.20 | 1.1 - 49.2   |
| Rathlin | ALL  | 3.44      | 0.31 | 0.2 - 14.7  | 39.7           | 3.70  | 0.4 - 167.1    | 13.5        | 1.29 | 0.3 - 57.1   |
| Rathlin | 2017 | 3.44      | 0.31 | 0.2 - 14.7  | 39.7           | 3.70  | 0.4 - 167.1    | 13.5        | 1.29 | 0.3 - 57.1   |

Table S2.A2. Summary trip characteristics

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Supplementary Material



Figure S2.A1: Percentage coverage of kittiwake GPS tracking points at each colony of combined, GEBCO and UKHO bathymetry data.



Figure S2.A2. Heights of all high and low tides during June and July for each year of tracking at Puffin Island, Skomer Island and Rathlin Island. Boxes show periods of kittiwake GPS tracking.

Appendix S2.B. Assessing colony environmental heterogeneity

## Methods

To understand the effect of the physical marine environment surrounding the breeding colony on kittiwake foraging behaviour, we characterised the proximal environment at each colony by comparing depth and tidal regime within the maximum foraging area of kittiwakes. In this case, maximum foraging area was determined from all years of kittiwake tracking data at each study site.

To characterise spatial heterogeneity in the physical environment, we studied the bathymetric landscape using UKHO bathymetry data, in combination with GEBCO data outside the gridded area of UKHO data (sources of data detailed in paper methods). We also characterised spatial differences in the depth scaled shear stress ( $\tau$ ) caused by tidal velocity as a proxy for the extent to which tidal flow alters the foraging environment over the tidal cycle. Tidal shear stress is a measure of force caused by the friction between tidal flow and the seafloor. High tidal stress values indicate high tide-driven turbulence at the maximum tidal velocities during the tidal cycle, which in turn indicates a bigger alteration to the physical foraging environment. Depth scaled tidal shear stress (in Newtons per m<sup>3</sup>) is given as:

$$\frac{\tau}{h} = \frac{\rho C_d U^2}{h}$$

Where  $\tau$  is the shear stress driven by tidal velocity,  $\rho$  is water density (assumed constant, 1025 kg m<sup>-3</sup>),  $C_d$  is the drag coefficient, here taken as 0.0025 (Pérez-Ortiz *et al.* 2017). *U* is depth-averaged maximum tidal velocities from the 12.4 hr tidal cycle (M2 tidal constituent). Tidal velocities were generated from a 3D hydrostatic simulation of the North West European shelf using the NEMO AMM60 configuration (Guihou *et al.* 2018). The simulation has 51 stretched layers in the vertical and a resolution of 1.8km in the horizontal. A barotropic harmonic analysis was performed on the simulation and the M2 constituent is processed here (as the most energetic

constituent). The M2 tidal speeds are defined as the amplitude of maximum barotropic M2 velocity, over the tidal cycle. Values of tidal speed range from 0.001 to 1.99 m s<sup>-1</sup>.*h* is water depth, from bathymetry data described above. Between the three study colonies, we compared mean values of depth and tidal shear stress, standard deviation and range of values as an indication of heterogeneity. We conducted analyses of variance tests (ANOVA) with post-hoc Tukey tests to determine whether the environment (depth or tidal shear stress data) differed between colonies. Both depth and tidal shear stress were square root transformed to approximate to Gaussian distributions (Figures S2.B1 and S2.B2 respectively) in order to use parametric analyses of variance.

## Results

Local bathymetry within the foraging range of GPS tracked kittiwakes significantly differed between the three different study colonies ( $F_{(2, 191831)}$ = 30469, p < 0.001). A posthoc Tukey test showed that all three colonies were significantly different at pair-wise level (for all comparisons, p < 0.001). The area around Puffin Island was shallowest and least variable (based on standard deviation from the mean), although reached a maximum depth intermediate to Skomer Island and Rathlin Island (mean ± sd = 35.9 m ± 20.9, max = 167.4 m). Around Rathlin Island, the water column was deepest and most variable, and extended to the greatest maximum depths of the study colonies (mean  $\pm$  sd = 76. 5 m  $\pm$  42.4, max = 269.3 m). Around Skomer Island, average and variability in depth was intermediate to Puffin Island and Rathlin Island, and the maximum depth within the foraging range was the shallowest out of the three colonies (mean  $\pm$  sd = 65.3 m  $\pm$  27.1, max = 135.8 m). Interestingly at Rathlin Island, the deepest waters, at over 200m deep, were found within 10km of the colony, whereas at both Skomer Island and Puffin Island deeper waters were found further away from the colony (Figure S2.B1). Variability in depth from different data sources (GEBCO/UKHO/Combined) supports the above results (Figure S2.B3)

Local tidal shear stress within the foraging range of GPS tracked kittiwakes significantly differed between the three different study colonies ( $F_{12, 5573}$ = 516.7, p < 0.001). A post-hoc Tukey test showed that all three colonies were significantly different at pair-wise level (for all comparisons, p < 0.001). Tidal shear stress was highest on average around Puffin Island (mean ± sd = 44.5 mN m<sup>-3</sup> ± 29.1), however this may be because of an area of high tidal stress off the north-west tip of Anglesey. Maximum tidal shear stress was lowest out of the three study colonies at Puffin Island (401 mN m<sup>-3</sup>). Tidal shear stress was similar at Skomer Island (mean ± sd = 25.9 mN m<sup>-3</sup> ± 24.1) and Rathlin Island (mean ± sd = 26.4 mN m<sup>-3</sup> ± 35.5) although the maximum tidal shear stress at Skomer Island (448 mN m<sup>-3</sup>) was intermediate to Puffin Island and Rathlin Island, and was greatest out of the three study colonies at Rathlin Island (523 mN m<sup>-3</sup>). As with bathymetry, the proximity of areas of high tidal stress to the colony varied between the sites (Figure S2.B2). At both Rathlin Island and Skomer Island, there were areas of higher tidal stress adjacent to the colony, whereas at Puffin Island, the colony was surrounded by lower tidal stress.

Results from non-parametric analyses of variance on the original, un-transformed depth data concur with parametric tests on transformed depth data that there is a significant difference in water depth within the foraging range of kittiwakes at the three different study colonies (Kruskal-Wallis rank sum test,  $\chi^2$ = 51381, p < 0.001). Pairwise comparisons showed that there is a significant difference between all three colonies (Wilcoxon rank sum test, in all cases p < 0.001). Likewise for tidal shear stress, results from non-parametric analyses of variance on the original, un-transformed data concur with parametric tests on transformed data that there is a significant difference in tidal shear stress within the foraging range of kittiwakes at the three different study colonies (Kruskal-Wallis rank sum test,  $\chi^2$ = 1247, p < 0.001). Pairwise comparisons showed that there is a significant difference matrix sum test, in all cases p < 0.001).



Figure S2.B1. Differences in water depth with increasing distance to the colony at the three study sites, Puffin Island, Skomer Island and Rathlin Island, showing all points (grey) and GAM smoothing (blue).


Figure S2.B2. Differences in tidal stress with increasing distance to the colony at the three study sites, Puffin Island, Skomer Island and Rathlin Island, showing all points (grey) and GAM smoothing (blue).



Figure S2.B3. Water depth within the foraging radius at each colony from different bathymetry data (see paper methods for more details). Combined data, used in the paper analyses, takes UKHO data, and then GEBCO data where UKHO data is unavailable. Differences in range and variability of bathymetry values is comparable between GEBCO and UKHO datasets, and therefore differences in heterogeneity between sites are unlikely to be driven by differences in resolution of input datasets.

Appendix S2.C: Hidden Markov models for behavioural classification The hidden Markov model successfully classified kittiwake tracks into three movement types, which we use as proxies of behaviour: (1) resting: short step lengths and narrow turning angles (step:  $0.08 \pm 0.05$  km; turn:  $\mu = 0$ ,  $\kappa = 14$ ), (2) foraging: shortmedium step lengths and wide turning angles (step:  $0.27 \pm 0.31$  km; turn:  $\mu = 0$ ,  $\kappa = 0.4$ ) & (3) transiting: long step lengths and narrow turning angles (step:  $1.00 \pm 0.35$  km; turn:  $\mu = 0$ ,  $\kappa = 6.8$ ). The model was robust to different priors, each time converging on the same parameters of step lengths and turning angles (Figure S2.C1). Using the Viterbi algorithm to determine the most likely sequence of behavioural states, 21.1% of GPS locations were classified as resting, 55.1% as foraging and 24% as transiting. Examples of trips with points classified as foraging are given in Figure S2.C2. Maps of foraging points only, by each state of the tidal cycle are given in Figure S2.C3.



Figure S2.C1. Histograms of observed step lengths (left) and turning angles (right) for GPS-tracked kittiwakes. Lines show fitted HMM state distributions for each behavioural state.



Figure S2.C2. An example individual from each kittiwake colony (Puffin Island top, Skomer middle & Rathlin bottom) showing the total GPS track (black), and foraging points (red) as identified from the HMM model.



Figure S2.C3. Kittiwake GPS locations classed as foraging at Puffin Island (left), Skomer Island (middle) and Rathlin Island (right) by tidal state. Tidal states are defined as slack low: >5 hours either side of high water; flood: 1 – 5 hours before high water; slack high: 1 hour either side of high water; and ebb: 1 – 5 hours after high water.

Appendix S2.D. Model Selection

| Table S2.D1. Generalise    | l linear mixed effects models testing for habitat use in relation to dist | ance to the      | colony, witl  | n different fixed           |
|----------------------------|---|------------------|---------------|-----------------------------|
| effects structures for mo  | del selection. In all cases, models include Year (specific to colony), Bi | rd ID and T      | 'rip ID as ra | ndom effects, and           |
| are run with a logit link. | N.B. BIC values favoured the same model selection.                        |                  |               |                             |
|                            |   |                  | Difference    | e compared to               |
|                            |   | Marginal         | most pars     | imonious model              |
| Model                      | Coefficients  | ${ m R}^{2}$ (%) | AIC           | Marginal R <sup>2</sup> (%) |
| Full model                 | ColonyDist:Tidal.state:Colony +   | 64.8             | 0             | 0                           |
|                            | ColonyDist:Colony + Colony:Tidal.state + ColonyDist:Tidal.state +         |                  |               |                             |
|                            | ColonyDist + Colony + Tidal.state   |                  |               |                             |
| Without 3-way              | ColonyDist:Colony + Colony:Tidal.state + ColonyDist:Tidal.flag +          | 63.5             | 2146.6        | -1.33                       |
| interaction                | ColonyDist + Colony + Tidal.state   |                  |               |                             |
| Without                    | ColonyDist:Colony + ColonyDist:Tidal.state +                              | 63.1             | 2589.9        | -1.70                       |
| Colony:Tidal.state         | ColonyDist + Colony + Tidal.state   |                  |               |                             |
| Without                    | ColonyDist:Colony + Colony:Tidal.state +                                  | 62.7             | 3350.9        | -2.13                       |
| ColonyDist:Tidal.state     | ColonyDist + Colony + Tidal.state   |                  |               |                             |
| Without                    | Colony:Tidal.state + ColonyDist:Tidal.state +                             | 60.6             | 4638.4        | -4.24                       |
| ColonyDist:Colony          | ColonyDist + Colony + Tidal.state   |                  |               |                             |
|                            |   |                  |               |                             |

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| are run with a logit lii      | ık.   |                                |                               |                             |
|-------------------------------|---|--------------------------------|-------------------------------|-----------------------------|
|                               |   | Marginal<br>R <sup>2</sup> (%) | Difference co<br>parsimonious | mpared to most<br>model     |
| Model                         | Coefficients  |                                | AIC                           | Marginal R <sup>2</sup> (%) |
| Full model                    | Depth:Tidal.state:Colony +<br>Depth:Colonv + Colonv:Tidal.state + Depth:Tidal.state +   | 19.8                           | 0                             | 0                           |
|                               | Depth + Colony + Tidal.state  |                                |                               |                             |
| Without 3-way<br>interaction  | Depth:Colony + Colony:Tidal.state + Depth:Tidal.state +<br>Depth + Colony + Tidal.state | 19.5                           | 811.3                         | -0.30                       |
| Without<br>Colony:Tidal.state | Depth:Colony + Depth:Tidal.state +<br>Depth + Colony + Tidal.state                      | 19.1                           | 1453.6                        | -0.68                       |
| Without<br>Depth:Tidal.state  | Depth:Colony + Colony:Tidal.state +<br>Depth + Colony + Tidal.state                     | 18.8                           | 2549.6                        | -0.99                       |
| Without<br>Depth:Colony       | Colony:Tidal.flag + Depth:Tidal.state +<br>Depth + Colony + Tidal.state                 | 2.1                            | 69534.0                       | -17.7                       |

Table S2.D2. Generalised linear mixed effects models testing for habitat use in relation to water depth, with different fixed effects

| Table S2.D3. Mod   | el scores from receiv         | ring operator chara    | acteristic curves of   | full models present | ted in Tables S2.D1 | and S2.D2           |
|--------------------|-------------------------------|------------------------|------------------------|---------------------|---------------------|---------------------|
| Model              | Correct<br>classification (%) | Positive<br>Predictive | Negative<br>Predictive | Sensitivity         | Specificity         | Area under<br>curve |
|                    |                               | Power (%)              | Power                  |                     |                     |                     |
| Colony<br>Distance | 83.3                          | 34.1                   | 98.8                   | 06.0                | 0.83                | 0.86                |
| Depth              | 64.6                          | 16.4                   | 95.6                   | 0.71                | 0.64                | 0.67                |

| Table S2.D4. G<br>colony separate | eneralised linear mixed effe<br>sly, with different fixed effe | ects models testing for foraging habitat use in rel<br>sets structures for model selection. In all cases, m | ation to distance to the colony for each<br>odels include Bird ID and Trip ID as |
|-----------------------------------|--|---|--|
| random effects,                   | , and are run with a logit lii                                 | nk.   |  |
| Colony                            | Model  | Coefficients  | Difference in AIC compared to most   |
|                                   |  |   | parsimonious model   |
| Puffin                            | Full model   | ColonyDist:Tidal.state + ColonyDist +   | 0  |
|                                   |  | Tidal.state   |  |
|                                   | Without interaction  | ColonyDist + Tidal.state  | 1696.3   |
| Skomer                            | Full model   | ColonyDist:Tidal.state + ColonyDist +   | 0  |
|                                   |  | Tidal.state   |  |
|                                   | Without interaction  | ColonyDist + Tidal.state  | 664.2  |
| Rathlin                           | Full model   | ColonyDist:Tidal.state + ColonyDist +   | 0  |
|                                   |  | Tidal.state   |  |
|                                   | Without interaction  | ColonyDist + Tidal.state  | 978.3  |
|                                   |  |   |  |

| Table S2.D5. G   | eneralised linear mixed eff   | ects models testing for foraging habitat use   | in relation to water depth for each colony |
|------------------|-------------------------------|--|--|
| separately, with | ו different fixed effects str | actures for model selection. In all cases, mod | lels include Bird ID and Trip ID as random |
| effects, and are | run with a logit link.        |  |  |
| Colony           | Model                         | Coefficients                                   | Difference in AIC compared to most         |
|                  |                               |  | parsimonious model                         |
| Puffin           | Full model                    | Depth:Tidal.state + Depth + Tidal.state        | 0  |
|                  | Without interaction           | Depth + Tidal.state                            | 495.6                                      |
| Skomer           | Full model                    | Depth:Tidal.state + Depth + Tidal.state        | 0  |
|                  | Without interaction           | Depth + Tidal.state                            | 419.4                                      |
| Rathlin          | Full model                    | Depth:Tidal.state + Depth + Tidal.state        | 0  |
|                  | Without interaction           | Depth + Tidal.state                            | 1655.6                                     |
|                  |                               |  |  |

Appendix S2.E. Sensitivity analysis of resource selection model to available habitat selection.

To determine habitat preference of kittiwakes, we compared habitat for foraging only GPS points to a set of random points as a proxy of available habitat. Resource selection methods can be sensitive to available habitat selection, and therefore sensitivity analyses are advisable (Northrup *et al.* 2013). Here, we consider the sensitivity of our model to varying available habitat selection in light of the ecology of our species, the black-legged kittiwake.

For the available habitat in the final model, we chose 10 random points from within the foraging radius of each colony during the given tracking year. For GPS tracking studies such as ours, sampling more individuals increases the measured foraging area of the sampled population (Soanes *et al.* 2013). We therefore chose to use foraging radius specific to each tracking year at each colony to allow for differences in the number of tracking years at each colony and maintain potential inference from results.

#### Reduced area for available habitat selection

To test sensitivity of results to the area of available habitat, we restricted the available habitat to within 90% and 75% of the maximum foraging range in a given tracking year for each colony and ran habitat selection models of water depth, and a test of the three-way interaction between depth, colony and tidal state. Results concur with those presented in the main paper, that when available habitat was selected from 90% of the maximum foraging range, the most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction:  $\Delta AIC = +3645.0$ ,  $\Delta R^2m = -2.0\%$ ) and water depth (model without 3-way interaction:  $\Delta AIC = +771.7$ ,  $\Delta R^2m = -0.3\%$ . When available habitat was selected from 75% of the

maximum foraging range, the most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction:  $\Delta AIC = +2508.3$ ,  $\Delta R^2m = -1.7\%$ ) and water depth (model without 3-way interaction:  $\Delta AIC = +733.1$ ,  $\Delta R^2m = -0.3\%$ ).

#### Full data set

To test sensitivity of results to restriction to foraging only data points, we ran identical models to the full data set, i.e. all GPS points, each with 10 random 'available' points. The most parsimonious model retained the three-way interaction between environment (distance to colony or depth), colony and tidal state for both habitat selection by distance to the colony (model without 3-way interaction:  $\Delta AIC =$  +3230.35,  $\Delta R^2m = -1.0\%$ ) and water depth (model without 3-way interaction:  $\Delta AIC =$  +530.87,  $\Delta R^2m = -0.2\%$ ). Parameter estimates are plotted in Figure S2.E1. Models for each colony separately also support results in the main paper. In all cases model selection retained the two-way interaction between environment (distance to colony or depth) and tide by AIC values. As in the main results, the interaction between tide and the environmental variable (distance to colony or depth) explained more additional variation in the model at Rathlin Island, where environmental heterogeneity was greatest (7.5% for colony distance, and 2.1% for depth), and least variation at Puffin Island, where environmental heterogeneity was lowest (1.5% for colony distance, and 0.6% for depth).



Figure S2.E1. Probability of habitat use at different distances to the colony (left) and at varying water depths (right) using all tracking points for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom). Results are from models with all GPS points, and are concurrent with findings of foraging only models presented in the main paper.

Appendix S2.F. Habitat selection models for colonies separately

To understand differences in results between colonies, we ran habitat selection models for distance to colony and depth at each colony separately, and looked at the difference in variance explained by the interaction of tide with the environmental variable in question. Parameter estimates and figures for each colony are given here for both colony distance and bathymetry.

| Table S2.F1. Paramete   | estimates,    | ± standard erro  | r, for the slope o | of the interactio | n between the    |
|-------------------------|---------------|------------------|--------------------|-------------------|------------------|
| environment variable (  | (distance to  | colony or depth) | ) and tide, deriv  | ed from models    | ran separately a |
| each colony. A positive | e parameter   | estimate indica  | tes a positive re  | lationship betw   | een kittiwake    |
| habitat use and locatio | ons further a | way from the co  | olony, or greater  | water depths.     |                  |
|                         |               | Parameter est    | timates for diff   | erent tidal stat  | es               |
| Model                   | Colony        | Slack Low        | Flood              | Slack High        | Ebb              |
| Distance to Colony      | Puffin        | -2.51 ± 0.02     | $-2.50 \pm 0.01$   | $-3.34 \pm 0.02$  | -2.83 ± 0.01     |
|                         | Skomer        | $-1.53 \pm 0.02$ | $-2.37 \pm 0.03$   | $-1.93 \pm 0.04$  | $-1.69 \pm 0.03$ |
|                         | Rathlin       | $-5.80 \pm 0.24$ | $-1.71 \pm 0.02$   | $-2.10 \pm 0.03$  | $-2.32 \pm 0.02$ |
| Bathymetry              | Puffin        | $-1.30 \pm 0.01$ | $-1.44 \pm 0.01$   | $-1.71 \pm 0.02$  | $-1.32 \pm 0.01$ |
|                         | Skomer        | $-0.70 \pm 0.02$ | $-1.22 \pm 0.02$   | $-0.86 \pm 0.03$  | $-0.89 \pm 0.02$ |
|                         | Rathlin       | $0.74 \pm 0.02$  | $0.29 \pm 0.01$    | $0.65 \pm 0.01$   | $0.78 \pm 0.01$  |
|                         |               |                  |                    |                   |                  |



Figure S2.F1. Probability of habitat use (from models of each colony separately) whilst foraging at different distances to the colony (left) and at varying water depths (right) for GPS tracked kittiwakes during different tidal states at three different colonies: Puffin Island (top), Skomer Island (middle) and Rathlin Island (bottom).

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# Chapter 3

Environmental heterogeneity decreases reproductive success via effects on foraging behaviour



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## Environmental heterogeneity decreases reproductive success via effects on foraging behaviour

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#### Abstract

Environmental heterogeneity shapes the uneven distribution of resources available to foragers, and is ubiquitous in nature. Optimal foraging theory predicts that an animal's ability to exploit resource patches is key to foraging success. However, the potential fitness costs and benefits of foraging in a heterogeneous environment are difficult to measure empirically. Heterogeneity may provide higher quality foraging opportunities, or alternatively could increase the cost of resource acquisition because of reduced patch density or increased competition. Here, we study the influence of physical environmental heterogeneity on behaviour and reproductive success of black-legged kittiwakes, Rissa tridactyla. From GPS tracking data at 15 colonies throughout their British and Irish range, we found that environments that were physically more heterogeneous were associated with longer trip duration, more time spent foraging whilst away from the colony, increased overlap of foraging areas between individuals, and lower breeding success. These results suggest that there is greater competition between individuals for finite resources in more heterogeneous environments, which comes at a cost to reproduction. Resource hotspots are often considered beneficial, as individuals can learn to exploit them if sufficiently predictable. However, we demonstrate here that such fitness gains can be countered by greater competition in more heterogeneous environments.

#### Keywords

Competition, seabird, hidden Markov model, heterogeneity gradient, optimal foraging theory, resource availability

#### Introduction

The spatial and temporal distribution of resources places a major constraint on foraging success (MacArthur & Pianka 1966; Stephens & Krebs 1986; Bell 1990).

Therefore, heterogeneity in resource distribution, which is considered a universal feature of natural environments (Tilman & Kareiva 1998; Sparrow 1999), has played a defining role in the evolution of animal foraging behaviour (MacArthur & Pianka 1966; Bell 1990). Theory predicts that key to an individual's success is the ability to maximise gains from areas with high resource density and minimise energy expenditure locating resources, and therefore optimise energy allocation to fitness (MacArthur & Pianka 1966; Stephens & Krebs 1986). This theory is supported by numerous empirical studies, e.g. (Watanabe *et al.* 2014; Thygesen *et al.* 2016; Tyson *et al.* 2016). In response to resource heterogeneity, selection will therefore favour efficient foraging behaviour, whereby individuals minimise the energetic costs of searching and transiting between high resource locations and maximise resource intake (MacArthur & Pianka 1966; Bell 1990).

However, not all heterogeneous environments are equal (Stein *et al.* 2014; Yang *et al.* 2015; Trevail *et al.* 2019), as high prey locations vary in distribution, predictability and numbers of competing individuals. Studies often present these 'prey hotspots' as beneficial resource patches (Worm *et al.* 2005; Scott *et al.* 2010; Abrahms *et al.* 2018); however, the optimality of foraging strategies in response to resource heterogeneity may be constrained by both the nature of resource heterogeneity (Bernstein *et al.* 1991; Pinaud *et al.* 2005) and the behaviour of other foragers (Lewis *et al.* 2001; López-Bao *et al.* 2011). Firstly, the travel distance to reach foraging patches in heterogeneous environments will determine the trade-off between resource intake and the additional energetic costs to the animal's own fitness (Pinaud *et al.* 2005; Barrette *et al.* 2010; Lihoreau *et al.* 2011). Secondly, higher levels of intraspecific competition at resource patches in heterogeneous environments may also limit resource acquisition from a patch (Goldberg *et al.* 2001; Lewis *et al.* 2001; López-Bao *et al.* 2011; Bonin *et al.* 2015) through competitive exclusion (López-Bao *et al.* 2011; Bonin *et al.* 2015) and prey disturbance (Lewis *et al.* 2001) and depletion (Birt *et al.* 1987). The key knowledge gap

is whether greater environmental heterogeneity has positive or negative consequences for fitness.

Underlying variability in the physical environment is a strong driver of heterogeneous resource distributions, and therefore can be used as a proxy for resource heterogeneity, particularly where resource availability to foragers is difficult to measure directly. Indeed, because of effects on resources, physical environmental heterogeneity, hereafter 'environmental heterogeneity', is known to be an important driver of community dynamics (Tews *et al.* 2004; Stein *et al.* 2014) and life history strategies (Giesel 1976; Berdahl *et al.* 2015). Marine environments provide a model study system of environmental heterogeneity, with numerous physical features (such as fronts, eddies and currents) that together define resource availability to foragers (Scott *et al.* 2010; Wakefield *et al.* 2017). Furthermore the degree to which any given marine environment is heterogeneous can vary (Trevail *et al.* 2019), and therefore offers the opportunity to study the influence of heterogeneity on behaviour and fitness.

In this study, we test the influence of environmental heterogeneity on behaviour and reproductive success using data from black-legged kittiwakes (*Rissa tridactyla*, hereafter "kittiwakes") at 15 colonies across their UK and Irish breeding range. Studying such a comprehensive data set is ideal to understand how environmental heterogeneity affects behaviour and fitness. As with many seabirds, kittiwakes are central place foragers during the breeding season, and are therefore constrained to forage within their local environment. As such, greater travel distances away from the breeding location are considered indicative of poorer resource availability nearby (Hamer *et al.* 1993; Elliott *et al.* 2009). Furthermore, as surface feeders, kittiwakes are thought to suffer from direct competition with conspecifics for prey as fish schools are forced lower down in the water column to inaccessible depths (Ainley *et al.* 2003; Fauchald 2009). We first calculate a measure of local environmental heterogeneity at

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each colony based on six environmental metrics that can all influence kittiwake prey distributions. Secondly, we consider kittiwake foraging behaviour along the gradient of environmental heterogeneity between study colonies, and then test the link between the degree of environmental heterogeneity and reproductive success. Our analyses tested the following alternative hypotheses (see schematic, Table 3.1) based on the literature reviewed above. (H1) Foraging opportunity hypothesis: greater environmental heterogeneity is associated with higher fitness because it features greater amounts of profitable habitat within the foraging range of the colony that animals can learn to exploit, which enables individuals to remain closer to the colony (Pinaud et al. 2005), provision offspring more frequently (Davoren & Montevecchi 2003) and relieve partners of nest-attendance duties (Boersma & Rebstock 2009). (H2) Reduced patch density hypothesis: greater environmental heterogeneity is detrimental to fitness because habitat patches with sufficient resources to support foraging are located further apart within the foraging range. This therefore would prompt individuals to more readily switch between patches (Stephens & Krebs 1986), requiring an increase in travel distance away from the colony, time spent commuting and foraging area size (Pinaud et al. 2005), and resulting in greater expenditure to transit between patches. (H3) Competition hypothesis: greater environmental heterogeneity is detrimental to fitness because it increases competition between individuals at relatively profitable habitats, which results in greater overlap between individuals, greater time investment in foraging behaviour and increased duration of foraging trips (Lewis et al. 2001).

| Crosses                  | indicate no expected cha<br>Dorential effect of  | pwards and downwarus ange.                            | arrows indicate an exp<br>Expected chang   | ected increase ai<br>ge in foraging met                                     | na aecrease, resj<br>trics                                | pectively, and                   |
|--------------------------|--|---|--|---|---|----------------------------------|
| sisədtoqYH               | greater environmental<br>heterogeneity on<br>resources                                 | Expected change in<br>population foraging<br>dynamics | <b>Travel distance</b><br>(maximum, total &<br>proportion of time<br>transiting) | <b>Time foraging</b><br>(trip duration &<br>proportion of<br>time foraging) | <b>Competition</b><br>(overlap<br>between<br>individuals) | Expected<br>change in<br>fitness |
| Foraging<br>Poportunity  | Resource patches<br>present higher quality<br>foraging opportunities                   | Smaller foraging<br>range                             | →  | →   | ×   | <b>←</b>                         |
| qensity<br>Reduced patch | Resource patches<br>offering sufficient<br>foraging opportunities<br>are further apart | Longer foraging<br>distance                           | ÷  | ↑ or X  | X or $\bigstar$   | <b>→</b>                         |
| Competition              | Resources concentrated<br>into smaller patches   | Increased<br>competition                              | X  | ÷   | ÷   | <b>→</b>                         |

Table 3.1. Hypotheses of the potential effects of greater environmental heterogeneity on resources, foraging dynamics, and

#### Methods

Quantifying environmental heterogeneity

To quantify environmental heterogeneity, we used a multivariate dispersion analysis (Anderson *et al.* 2006) to identify the dissimilarity of spatial environmental characteristics. Multivariate dispersion analyses have primarily been used for species diversity studies (Anderson *et al.* 2006); however, they have also been used to quantify environmental heterogeneity using multiple continuous variables in studies of freshwater ecosystems (Heino 2013; Bini *et al.* 2014), marine ecosystems (Anderson *et al.* 2006) and grasslands (Conradi & Kollmann 2016). Multivariate dispersion analysis is suitable for this study because it incorporates variance in multiple environmental parameters that can all influence resource distribution into a single metric, in contrast to measures such as standard deviation or range of a single continuous variable (Oliver *et al.* 2010; Yang *et al.* 2015), or the diversity of categorical habitat variables (Hendrickx *et al.* 2007).

We calculated environmental heterogeneity using six environmental metrics; (1) bathymetry, (2) potential tidal stratification, (3) sea surface temperature, and ocean front (4) strength, (5) distance and (6) persistence all of which have been shown to influence resource location for foraging seabirds. (1) Bathymetry, or sea floor depth, can shape the flow of horizontal water currents and control vertical water column structure (Genin 2004; Stevick *et al.* 2008), both of which are physical processes that can influence the availability and accessibility of prey fish to surface foragers such as kittiwakes (Genin 2004; Stevick *et al.* 2008; Wakefield *et al.* 2017). (2) Potential tidal stratification incorporates both depth and tidal currents (Scott *et al.* 2010), to quantify the vertical water column structure – a key physical driver of marine ecosystem dynamics (Carroll *et al.* 2015), prey fish distribution (Waggitt *et al.* 2018) and seabird distribution (Wakefield *et al.* 2017). (3) Sea surface temperature can be a proxy for oceanographic processes that influence nutrient availability, such as upwelling of cold nutrient rich water (Benazzouz *et al.* 2014), and has been linked to the at-sea

distribution and breeding success of kittiwakes (Frederiksen *et al.* 2007; Carroll *et al.* 2015; Johnston *et al.* 2015; Wakefield *et al.* 2017). (4-6) Ocean fronts are horizontal boundaries between different water masses where physical processes cause upwelling of deeper, nutrient rich water and entrain plankton at the surface (Franks 1992a, b). Fronts are known to be an important feature of marine environments, shaping resource distribution and thus marine vertebrate behaviour (Scales *et al.* 2014; Waggitt *et al.* 2018). These six variables were chosen to well represent the suite of physical variables that influence seabird foraging behaviour (Cox *et al.* 2018). Chlorophyll was not included because of common spatial and trophic mismatch between basal trophic levels and top predators, such as seabirds (Grémillet *et al.* 2008). Full details of data sources are described in supplementary material (Appendix S3.A).

We used a principal coordinate analysis (a type of multivariate dispersion analysis) (Gower 1966) to determine the heterogeneity of environmental conditions at each colony and year (hereafter 'colony-year') from within the maximum foraging range of kittiwakes. We used the overall maximum foraging range across all years as a measure of the environment available to each colony (Supplementary material Appendix S3.B). Principal coordinate analyses place values from all colonies along all axes (or principal coordinates) in unconstrained ordination space based on a Euclidean distance matrix of standardised environmental data, using the functions vegdist and betadisper in the R package vegan (Oksanen et al. 2018). Herein, we use the average distance of observations from the colony-year centroid (or spatial median) in the principal coordinate analysis ordination space (using all axes) as a continuous measure of environmental heterogeneity, with higher values indicating greater heterogeneity. As such, environmental heterogeneity can vary independently of the absolute values of the six environmental variables. Permutation tests of dispersion (PERMDISP; Anderson et al. 2006) calculate an F-statistic to compare the average distances of observations from the colony-year centroid between each colony-year in the analysis

to test for differences in heterogeneity. We used a two-way ANOVA to test whether environmental heterogeneity differed between colonies and between years (as factors), and TukeyHSD post hoc tests for pairwise differences. To understand whether environmental heterogeneity was simply associated with availability of a particular habitat type or was a proxy of overall prey abundance within the foraging range of kittiwakes (maximum foraging distance across years at each colony from tracking data, H1 & H2, Table 3.1), we used linear regression to test whether environmental heterogeneity was linked to the mean value of any of the individual environmental metrics. To determine whether environmental heterogeneity was influenced by the size of the foraging radius used to extract environmental data (maximum foraging distance across years at each colony), we compared environmental heterogeneity values to the maximum foraging range of kittiwakes at each colony across all years using linear regression.

#### Quantifying kittiwake foraging behaviour

To determine the foraging behaviour of kittiwakes around the UK, adults from multiple colonies were tracked using GPS loggers (Mobile Action i-GotU GT-120), whilst raising small chicks. Tracked individuals were selected randomly with respect to brood size and were assumed to be representative of each study population. Loggers were attached to the back feathers between the wings (or infrequently to the tail) using waterproof tape, and total instrument mass was <5% of body mass (or <3% where tail attachments were used or battery size reduced; mean  $\pm$  se body mass at Skomer, Rathlin & Puffin Island:  $327.9 \pm 5.1$  from Trevail et al. (Trevail *et al.* 2019). We do not expect differences in logger attachment weight to influence results, because changes in methods were consistent between colonies (i.e. lower device weight used across all colonies from 2016 onwards, and with no obvious link to colony heterogeneity). However, we are unable to explicitly test this, as we do not have colonies for which both types of logger were used simultaneously (in the interest of

uniformly improving study ethics), and therefore would not be able to rule out the effects of colony and year on any results. Loggers were set to record a position every 2 minutes. Full details of tracking procedures can be found in the first publications of the data: Wakefield et al. (2017) and Trevail et al. (Trevail et al. 2019). Here, we use data from a total of 1567 trips from 415 chick-rearing kittiwakes at 15 colonies in Britain and Ireland between 2010 and 2017 (Figure 3.1): Bardsey (NW Wales; 2011, n = 8), Bempton Cliffs (E England; 2010-13 & 2015, n = 59), Copinsay (Orkney Islands; 2010-12, n = 26), Coquet (NE England; 2011-12, n = 26), Colonsay (W Scotland; 2010-14, n = 69), Filey (E England; 2013 & 2015, n = 26), Fowlsheugh (E Scotland; 2012, n = 13), Isle of May (E Scotland; 2013, n = 16), Lambay (E Ireland; 2010, n = 10), Muckle Skerry (Orkney Islands; 2012-2014, n = 26), Puffin Island (NW Wales; 2010-16, n = 63), Rathlin (Northern Ireland; 2017, n = 17), Skomer (SW Wales; 2016-17, n = 14), St Martins (Isles of Scilly; 2010-11, n = 28) & Whinnyfold (E Scotland; 2012, n = 14). Full sample sizes, including colony co-ordinates, tracking dates and number of individuals per year are given in supplementary material (Appendix S3.B, Table S3.B1). For further analyses, we excluded points closer than 500 m to the colony, and attributed sequential points to a foraging trip if the total trip duration was over 14 minutes (Trevail et al. 2019) to eliminate departures from the colony due to disturbance (Warwick-Evans et al. 2016). At all colonies, we included trips where individuals were away from the colony overnight. At Rathlin, Skomer and Puffin Island, loggers did not record data between 23:00 and 03:00 to save battery power overnight whilst kittiwakes exhibit minimal foraging activity (Daunt et al. 2002; Trevail et al. 2019). At all other colonies, we excluded locations during this period.

To understand the influence of environmental heterogeneity on foraging behaviour, we calculated three different measures of behaviour, all predicted to vary with each hypothesis (Table 3.1). Firstly, for each year and at each colony, we calculated the following trip metrics: mean trip duration, mean total distance travelled during a foraging trip, and mean maximum distance from the colony, all important indicators of resource accessibility for central place foragers as they seek to remain close to the colony and minimise travel times (Hamer et al. 1993; Lewis et al. 2001; Pinaud et al. 2005). Secondly, we examined movement behaviours whilst away from the colony using a hidden Markov model to classify behaviour into rest, forage (including searching) or transit (Patterson et al. 2009). Time spent in each behaviour can signal the energetic trade-off between travel costs and resource gains from exploiting prey patches (Ropert-Coudert et al. 2004). We used the R package moveHMM (Michelot et al. 2016) for behavioural classification based on distributions of step lengths and turning angles, after interpolating GPS data to regular 2 minute time steps to fulfil HMM assumptions, using the R package adehabitatLT (Calenge 2006). We used a gamma distribution to describe step lengths and a von Mises distribution to describe turning angles, and the Viterbi algorithm to estimate the most likely sequence of movement states based on the fitted hidden Markov model (supplementary material, Appendix S3.C). We used values from previous classification of kittiwake behaviour to inform model starting parameters (Trevail et al. 2019), and found that model outputs were robust to different values of starting parameters when tested on a subset of tracking data. For each bird, we quantified the proportion of time away from the colony whilst on a foraging trip spent in each behaviour classified by the HMM (forage, transit and rest). Thirdly, we determined at-sea area use of kittiwakes by calculating the size of 50% core foraging areas of individuals from utilisation kernels on a 1km grid using the kernelUD function in the R package adehabitatHR (Calenge 2006). The appropriate smoothing parameter (h) was determined by the default, ad hoc method, which assumes a bivariate normal distribution (Calenge 2006). As a proxy for intra-specific competition, we calculated the overlap of 50% core foraging areas between all individuals tracked in the same year at each colony using Bhattacharya's affinity. Values of Bhattacharya's affinity (BA) range from zero when there is no overlap between foraging areas, to 1 when utilisation distributions are identical (Fieberg & Kochanny 2005). We verified that there was no link between the overlap of 50% core foraging areas between tracked individuals and the number of tracked individuals (linear regression, p = 0.12).

#### Quantifying kittiwake reproductive success

To test the effect of environmental heterogeneity on kittiwake reproductive success, we used colony-average reproductive success data from the Seabird Monitoring Programme, collated by the UK Joint Nature Conservation Committee (JNCC; <u>http://jncc.defra.gov.uk/smp</u>) and the Centre for Ecology & Hydrology for the Isle of May (Newell *et al.* 2016). Reproductive success data were available for 11 colonies, for 1-8 years between 2010 and 2017 (supplementary material, Appendix S3.B, Table S3.B3). Reproductive success was calculated as the total number of chicks fledged divided by the number of nests/pairs monitored at each colony in each year (supplementary material, Appendix S3.B, Table S3.B4 & Figure S3.B1).

Effect of environmental heterogeneity on kittiwake foraging behaviour & reproductive success

In all analyses described below, explanatory variables were standardised to a mean of 0 and standard deviation of 1. Model structure and effect significance were determined using ANOVA comparisons (Chi squared for linear regressions and GLMMs, and F tests for quasibinomial), for which p-values are presented.

To understand the effects of environmental heterogeneity on foraging metrics and reproductive success, we used the mean environmental heterogeneity for each colony across all years because colony and year, by definition, explained a large proportion of the variation in environmental heterogeneity (supplementary material, Figure S3.A3), and did not include colony or year as variables in regression analyses. We refer to this mean value as 'colony-mean environmental heterogeneity'. To understand the effect of environmental heterogeneity on foraging behaviour in relation to the hypotheses (Table 3.1), we undertook the following statistical tests. Firstly, we compared the colony-mean environmental heterogeneity to the annual mean of trip metrics for each colony (trip duration, total distance and maximum distance; logtransformed to meet the assumptions of Gaussian models) using linear regression. Secondly, we compared the colony-mean environmental heterogeneity to the proportion of time spent away from the colony in each behavioural state (forage, transit and rest) by each individual using linear regression with a quasibinomial logitlink to account for overdispersion. Lastly, we compared the colony-mean environmental heterogeneity to the size of 50% core foraging area of each bird using linear regression, and overlap between trips of all pairs of individuals using a GLMM with the focal BirdID as a random effect and a Gaussian distribution. To understand the effect of environmental heterogeneity to the annual reproductive success for each colony using linear regression.

To verify that observed patterns in foraging dynamics and resource success could be attributed to environmental heterogeneity, we tested for potentially confounding effects of colony size and individual environmental variables on reproductive success (supplementary material, Appendix S3.D). We used data from the most recent census of UK breeding populations, Seabird 2000 (Mitchell *et al.* 2004), to compare breeding success with colony size and the number of breeding kittiwakes within the foraging radius of each colony using linear regression. Seabird 2000 data may no longer provide currently accurate estimates of breeding numbers; however, they offer the most useful indicator of relative colony size for the purpose of this study. In support of results presented below, we found no link between reproductive success and any environmental metric in isolation (bathymetry, stratification, sea surface temperature and ocean front metrics; supplementary material, Appendix S3.D, Table S3.D1)

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#### Results

#### Environmental heterogeneity at colonies

Environmental heterogeneity varied significantly between colony and year combinations in the principal co-ordinate analysis ( $F_{(119,17880)} = 16.6$ , p < 0.001). The first two coordinate axes from the principal coordinate analysis together explained 63% of the total variation between colonies (first axis: 43.1%, all others presented in supplementary material, Table S3.A1). Environmental heterogeneity differed significantly between colonies (ANOVA:  $F_{(14,98)} = 42.8$ , p < 0.001), and between years (ANOVA:  $F_{(7,98)} = 3.0$ , p = 0.007), although the effect of year was driven by a significant difference between 2011 and 2014 (supplementary material, Appendix S3.A). Environmental heterogeneity was highest at Copinsay (mean ± standard error between years =  $2.37 \pm 0.05$ ), and was lowest at Coquet (1.16 ± 0.06), the Isle of May  $(1.17 \pm 0.04)$  and Whinnyfold  $(1.19 \pm 0.07)$ . Values of environmental heterogeneity at each colony, and pairwise comparisons between colonies and years are given in supplementary material (Appendix S3.A). Comparisons of environmental heterogeneity with individual environmental metrics showed no strong relationships (Appendix S3.E). There was no link between environmental heterogeneity from the principal coordinate analysis, and the size of the radius (maximum foraging distance from the colony across all years) used to select environmental data ( $F_{(1,118)} = 0.76$ , p = 0.386).

## Hypothesis testing: Effect of environmental heterogeneity on kittiwake foraging behaviour & reproductive success

We found most support for the competition hypothesis (H3), that environmental heterogeneity was associated with greater competition between individuals, and consequently lower fitness. We found that trip duration (time spent away from the colony) was positively correlated with environmental heterogeneity (Figure 3.2b, parameter estimate  $\pm$  se: 0.27  $\pm$  0.12,  $F_{(1,33)}$ = 5.11, p = 0.03). Furthermore, the proportion of individuals' time spent foraging was significantly higher in more heterogeneous

environments (Figure 3.2a, parameter estimate  $\pm$  se: 0.14  $\pm$  0.03  $F_{(1,415)}$ =18.8, p < 0.01), and environmental heterogeneity was positively correlated with overlap of the 50% core foraging area between individuals (Figure 3.2c; parameter estimate ± se: 0.012 ± 0.004,  $\chi^{2}_{1}$  = 9.85, p < 0.01). Reproductive success was significantly lower in colonies with greater environmental heterogeneity (Figure 3.3; parameter estimate  $\pm$  se = -0.18  $\pm$  0.05; F<sub>(1,59)</sub> = 15.44, p < 0.01), equivalent to a 63% decrease in reproductive success across the observed range of environmental heterogeneity. This relationship is robust to removal of the apparent outlier of Copinsay. We did not find support for the foraging opportunity hypothesis (H1), that environmental heterogeneity was associated with greater amounts of profitable habitat: there was no link between environmental heterogeneity and the mean maximum distance kittiwakes travelled from the colony (Table 3.2,  $F_{(1,33)} = 1.11$ , p = 0.30). Lastly, we did not find support for the reduced patch density hypothesis (H2) that environmental heterogeneity is associated with greater distances between relatively profitable foraging areas, since there was no link between environmental heterogeneity and the mean maximum distance travelled (detailed above) or the total distance travelled (Table 3.2,  $F_{(1,33)} = 2.59$ , p = 0.12). The proportion of individuals' time spent transiting was significantly lower in more heterogeneous environments (Figure 3.2a, parameter estimate  $\pm$  se: -0.17  $\pm$  0.04,  $F_{(1,415)}$ =23.5, p < 0.01), and there was no change in the time spent resting (Figure 3.2a,  $F_{(1,415)}=0.08$ , p = 0.78). There was no link between environmental heterogeneity and the size of an individual's 50% core foraging area (Table 3.2,  $F_{(1,414)}=0.34$ , p = 0.56). In support of the above results that environmental heterogeneity is an important mechanism driving fitness, reproductive success was not linked to colony size ( $F_{1,51}$  = 0.96, p = 0.33) or the number of kittiwakes breeding within the foraging radius of the colony ( $F_{1,59} = 1.64$ , p = 0.21).


Figure 3.1. (A) Map of study kittiwake colonies, coloured by mean environmental heterogeneity and (B) environment within the foraging range of two example colonies according to the position along the first axis (PCoA1) from the principal coordinate analysis used to calculate environmental heterogeneity, here for 2015 as an example. Colony environmental heterogeneity is a single measure of variance calculated as the mean distance in Euclidian space (using all PCoA axes) of all locations from the colony centroid. At the homogeneous colony (Coquet, top), values are concentrated together along the first PCoA axis. At the heterogeneous colony (Colonsay, bottom), values range along the first PCoA axis.



Figure 3.2. Comparison between environmental heterogeneity and foraging behaviour of kittiwakes: (a) the proportion of individual's time whilst away from the colony in different behavioural states varied over the observed range of heterogeneity: time spent foraging significantly increased ( $F_{(1,415)}$ =18.8, p < 0.01), time spent transiting significantly decreased ( $F_{(1,415)}$ =23.5, p < 0.01), and there was no change in time spent resting (dashed line,  $F_{(1,415)}$ =0.08, p = 0.78); (b) trip duration significantly increased over observed range of heterogeneity ( $F_{(1,33)}$ = 5.11, p = 0.031); & (c) overlap between pairs of individual's 50% core foraging areas significantly increased over observed range of heterogeneity ( $\chi^2_1$ = 9.85, p = 0.002). Colony environmental heterogeneity is a measure of variance using a principal coordinate analysis. In all cases, error bars show standard error around the mean where GPS data were collected in multiple years, and solid lines show significant regressions with standard error (dotted lines).



Figure 3.3. Kittiwake reproductive success compared to standardised environmental heterogeneity. Solid line shows a significant regressions  $\pm$  standard error (dashed lines) between environmental heterogeneity and reproductive success ( $F_{(1,59)}$ = 15.44, p < 0.001, R<sup>2</sup>=0.21). Colony environmental heterogeneity is a measure of variance using a principal coordinate analysis. Error bars show standard error around the mean reproductive success from multiple years.

|                               | Relationship with        | Parameter                  |                     |                            |                  |
|-------------------------------|--------------------------|----------------------------|---------------------|----------------------------|------------------|
| Response variable             | increasing heterogeneity | estimate                   | Units               | Test statistic             | p-value          |
| Proportion of time foraging   | Increase                 | $0.09 \pm 0.04$            | Proportion          | $F_{(1,415)}=$ <b>18.8</b> | p = 0.029        |
| Proportion of time transiting | Decrease                 | <b>-0.17</b> ± <b>0.04</b> | Proportion          | $F_{(1,415)}{=}\ 23.5$     | p < 0.001        |
| Proportion of time resting    | No difference            | $0.04 \pm 0.05$            | Proportion          | $F_{(1,415)}{=}\;0.08$     | p = 0.479        |
| Mean trip duration            | Increase                 | $0.27 \pm 0.12$            | Hours (log-scale)   | $F_{(1,33)}{=}\;5.11$      | p = 0.031        |
| Mean total distance           | No difference            | $0.19 \pm 0.12$            | Km (log-scale)      | $F_{(1,33)}=2.59$          | p = 0.117        |
| Mean maximum distance         | No difference            | $0.12 \pm 0.11$            | Km (log-scale)      | $F_{(1,33)}=1.11$          | p = 0.299        |
| Foraging area: overlap        | Increase                 | $0.01 \pm 0.00$            | BA index            | $\chi^{2}_{1} = 9.85$      | <b>p</b> = 0.002 |
| Foraging area: size           | No difference            | 42.2 ± 71.7                | Km²                 | $F_{(1,414)}$ =0.34        | p = 0.561        |
| Breeding success              | Decrease                 | <b>-0.18 ± 0.05</b>        | Fledglings per nest | $F_{(1,59)}=15.4$          | p < 0.001        |
|                               |                          |                            |                     |                            |                  |

Table 3.2. Changes in kittiwake behaviour and reproductive success over the range of environmental heterogeneity observed in this

## Discussion

Heterogeneous resources are inherent within nature (Chesson & Case 1986; Tilman & Kareiva 1998; Sparrow 1999), and are typically assumed to be beneficial to foragers (Worm *et al.* 2005; Scott *et al.* 2010; Lascelles *et al.* 2012). However, our study demonstrates that in areas of higher environmental heterogeneity (or greater patchiness), kittiwakes undertook longer foraging trips, spent proportionally more time foraging whilst away from the colony, overlapped more with other individuals, and had reduced breeding success. Together, these results are consistent with our hypothesis that environmental heterogeneity may have concentrated resources into relatively more profitable patches; however, that this resulted in greater intraspecific competition, with negative consequences for fitness.

Heterogeneous environments can concentrate resources into patches that animals can adapt their behaviour to, in theory to optimise foraging efficiency (Bell 1990; Barton et al. 1992). Indeed, here we show differences in foraging behaviour with environmental heterogeneity; specifically, in more heterogeneous environments kittiwakes undertook longer foraging trips, and whilst away from the colony spent more time foraging. If overall resource availability was higher in heterogeneous environments, such changes in foraging behaviour could be an adaption to increase resource acquisition. However, in contrast, we found that reproductive success was lower in heterogeneous environments, suggesting that greater time investment in foraging behaviour was not compensated for by higher energetic returns (Ballance et al. 2009). Furthermore, we show that in colonies with more heterogeneous local environments, pairs of individuals overlapped more in their core foraging areas, despite no difference in individual foraging area size. These results suggest that in more heterogeneous environments there is more competition between individuals for finite resources, with costs for reproductive success. Whilst this may be balanced by lower competition elsewhere, lower resource availability away from resource patches will limit resource gains, and where resources are concentrated, resource density may still not be sufficient to benefit all competing individuals. Such findings align with the assumptions of Ideal Free Distribution theory, in that that competition between individuals at resource patches decreases the value to potential resource gain (Fretwell & Lucas 1969). Increased competition between individuals also explains extended foraging trip duration, as acquiring sufficient resources takes more time (Lewis *et al.* 2001; Ainley *et al.* 2003), which could incur additional energetic costs on adults, reduce offspring provisioning rates, and increase the risk of offspring predation during brood neglect (Lewis *et al.* 2001; López-Bao *et al.* 2011). Bio-logging devices can cause a slight increase in trip duration (Bodey *et al.* 2018); however, we would expect such effects to be equal across colonies. As such, fitness gains from resource patches may in fact be limited by the degree of environmental heterogeneity, because of the potential cost of competition.

Environmental heterogeneity may also decrease reproductive success if a greater variability of habitat types reduces the amount of productive habitat and/or is associated with generally lower primary productivity. If that were the case, we would expect foragers in heterogeneous environments to have to travel further from the colony in order to access high quality habitat (Pinaud *et al.* 2005; Burke & Montevecchi 2009; Elliott *et al.* 2009; Jovani *et al.* 2016). However, we found no difference in how far kittiwakes travelled away from the colony in heterogeneous environments, even accounting for the size of breeding populations. Maximum foraging distances recorded here (mean maximum distance:  $23.3 \pm 0.8$  km) were within both empirical and observed ranges of the species (e.g. empirical based on Isle of May data and kittiwake flight speeds:  $73 \pm 9$  km (Daunt *et al.* 2002; Wakefield *et al.* 2017), observed at Sør-Gjæslingan, Norway:  $303.7 \pm 6.1$  km (Christensen-Dalsgaard *et al.* 2017)). We can therefore assume that individuals were not foraging at, or near, their maximum physiological capability, but rather that sufficient resource availability facilitated

individuals to remain within relative proximity of the colony. Alternatively, heterogeneity may decrease reproductive success if profitable resource patches are more dispersed in space (López-Bao *et al.* 2011), requiring greater travel distances to reach sufficient resource patches (Pinaud *et al.* 2005). However, we found no difference with environmental heterogeneity in the total distance travelled during a foraging trip, and no increase in the proportion of a trip spent transiting or the size of an individual's 50% core foraging area, suggesting no increase in space use to acquire resources. Heterogeneous environments may however require behavioural adaptations that, if not compensated for by energetic gains, could contribute to the reduced breeding success observed in this study (Gils *et al.* 2006). For example, environmental heterogeneity can drive the magnitude of temporal variability in resources, which in turn prompts a greater behavioural response to temporal cycles in heterogeneous environments (Trevail *et al.* 2019).

Foraging behaviour, in particular foraging range, is typically linked to colony size in central place breeders. Density dependent prey depletion can increase the colony foraging radius (Burke & Montevecchi 2009; Elliott *et al.* 2009), up to the physiological constraints of a species, which can then limit the carrying capacity (Jovani *et al.* 2016). As such, when considering foraging adaptations and reproductive consequences of environmental heterogeneity here, it is important to recognise the potential effect of colony size. However, we found no link between reproductive success and colony size, nor the number of kittiwakes breeding within the foraging range of the colony, in contrast to previous studies of seabird population dynamics (Ainley *et al.* 2003). Our results therefore suggest that the spatial distribution of resources, as shaped by environmental heterogeneity, could be the predominant mechanism driving differences in levels of intraspecific competition, and therefore reproductive success, between kittiwake colonies in the UK and Ireland. Colony size data were from the most recent full census of the UK and Ireland seabird breeding colonies in 2000

(Mitchell *et al.* 2004). Many sites have documented population declines both before and after the Seabird 2000 survey, and kittiwakes have been reclassified as vulnerable on the IUCN Red List of threatened species (BirdLife International 2017). It is therefore likely that during the years of this study, population numbers were well below historic carrying capacity, however the Seabird 2000 data provide a useful indication of population numbers for this study.

The degree of environmental heterogeneity at each colony remained relatively consistent over time, which may favour an individual to switch breeding colony in favour of homogeneous sites where reproductive success was higher (Doligez *et al.* 2003; Danchin *et al.* 2013). Reproductive success was, however, generally low; at all but one colony in this study (Coquet) kittiwakes reared less than one fledgling per nest on average. This may mean that the potential increase in reproductive success in more homogeneous environments is not worth the risk of switching breeding site, but instead is outweighed by other factors driving strong site fidelity common among seabirds such as pair bonds (Rebke *et al.* 2017), familiarity with conspecifics (Grabowska-Zhang *et al.* 2012) and natal philopatry (Coulson & Coulson 2008). Future study could however shed light on of the effect of environmental heterogeneity on recruitment of prospecting breeders, as well as long-term population trends (Suryan & Irons 1991).

## Conclusions

In this study, we demonstrate that, in contrast to common assumptions, environmental heterogeneity is detrimental to breeding success in this species. Environmental heterogeneity can concentrate resources into hotspots, which could offer foraging opportunities; however, it may also increase competition between individuals. Reproductive success is an important driver of population dynamics across taxa (Jenouvrier *et al.* 2005; Sandvik *et al.* 2012), including adult recruitment in kittiwakes (Suryan & Irons 1991), and therefore the results of this study highlight the potential importance of environmental heterogeneity for driving population success and species distributions. Furthermore, environmental heterogeneity may be a key consideration in future studies of species resilience to environmental stressors, particularly given that many species, including kittiwakes, are undergoing population declines.

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Supplementary material to: Environmental heterogeneity decreases reproductive success via effects on foraging behaviour

Appendix S3.A. Environmental heterogeneity at study colonies and between years

Appendix S3.B: GPS tracking sample sizes & summary trip metrics

Appendix S3.C: Hidden Markov models for behavioural classification

Appendix S3.D: Other environmental variables

Appendix S3.E: Comparison of environmental heterogeneity with foraging range and environmental variables

References

Appendix S3.A. Environmental heterogeneity at study colonies and between years

In order to calculate environmental heterogeneity, we used the six environmental variables described below, (1) bathymetry, (2) potential tidal stratification, (3) sea surface temperature, and ocean front (4) strength, (5) distance and (6) persistence. We averaged all dynamic spatial variables (sst, front density, front persistence and front distance) over June and July at each colony for each year to incorporate all tracking dates and match the temporal resolution of foraging metrics and reproductive success. We found good covariance between environmental heterogeneity calculated using seasonally averaged environmental data and environmental heterogeneity calculated using weekly measures of environment variables (Figure S3.A1). To format spatial environmental data for analyses, we first resampled all environment data to the same resolution, and then randomly selected 150 points using the sampleRandom function of the R package raster (Hijmans & Etten 2018) from within the maximum foraging range of kittiwakes (linear distance from the colony) at each colony in order to achieve a balanced design for post hoc analyses. We extracted environment data from within the maximum foraging range of kittiwakes at each colony across all years to represent the available environment at each colony. Considering the potential effect of sample size to affect the observed foraging range (Soanes et al. 2013), we only included years with six or more individuals tracked at a colony in all analyses in this study. In support of using the colony-maximum foraging radius to calculate environmental heterogeneity, we found no effect of the number of GPS tracking data years on the size of the colony-maximum foraging radius ( $F_{(1,13)}$ =2.73, p = 0.123).

(1) Bathymetry, or depths of the sea floor, can shape water currents and control the vertical structure of the water column, and is known to influence kittiwake behaviour (Trevail *et al.* 2019). Bathymetric data were collated from high resolution UK

Hydrographic Office (UKHO) Data Archive Centre for bathymetric surveys and integrated with the 2014 General Bathymetric Chart of the Oceans (GEBCO). UKHO data contains public sector information, available under the Open Government Licence as part of the INSPIRE initiative. UKHO data, collected from boat surveys, covered a subset of the study areas at between 2 and 4 m resolution.

(2) Potential tidal stratification is an index for vertical water column structure in areas shallower than 200 m (Guihou et al. 2018). Low values of potential tidal stratification indicate a typically well-mixed water column. High values indicate a typically more stratified water column, comprised of vertically distinct layers with reduced transfer of abiotic and biotic matter between layers. Potential tidal stratification is calculated as  $\log_{10}(h/U^3)$ , where h is water column depth, described above, and U is the sum of tidal amplitude from both the M2 (semidiurnal lunar tide) and S2 (semidiurnal solar tide) tidal constituents (Simpson & Hunter 1974). Tidal amplitudes were generated from a 3D hydrostatic simulation of the North West European shelf using the NEMO AMM60 configuration (Guihou et al. 2018). The simulation has 51 stretched layers in the vertical and a resolution of 1.8 km in the horizontal. A barotropic harmonic analysis was performed on the simulation and the M2 constituent is processed here (as the most energetic constituent). The M2 tidal speeds are defined as the amplitude of maximum barotropic M2 velocity, over the tidal cycle. Potential tidal stratification performs well as a predictor of seasonal thermal stratification in shelf sea areas, although interpretation of absolute values requires caution in regions where stratification is influenced by salinity as a result of freshwater riverine inputs (Polton et al. 2011).

(3) Sea surface temperature (SST) can both indicate oceanographic processes that influence water column structure, such as upwelling of colder water (Benazzouz *et al.* 2014), and can be a proxy for the quality of prey availability (Carroll *et al.* 2016). SST

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data were derived from seven-day composites of advanced very high-resolution radiometer data, at a resolution of approximately 1.2 km (AVHRR).

(4-6) Oceanic fronts are horizontal boundaries between different water masses where resource availability is typically enhanced because of physical processes that cause upwelling of deeper, nutrient rich water. Fronts are therefore known to be an important feature of marine environments, shaping resource distribution and thus marine vertebrate behaviour (Scales et al. 2014; Waggitt et al. 2018). Frontal contours were detected using local regional statistics on daily SST scenes from AVHRR satellite data, at a resolution of approximately 1.2 km, and then combined into 8-day composite front maps (Miller 2009). Here we include three parameters related to ocean fronts, all of which will influence resource availability to a central place forager: (1) Front density gives the mean thermal gradient magnitude of detected fronts, i.e. the strength of fronts, spatially smoothed to give a continuous distribution of frontal activity. (2) Front distance indicates the distance at each pixel to the closest major front, determined using a simplified version of the frontal strength map. (3) Front persistence indicates the fraction of cloud-free observations of a pixel for which a front was detected, i.e. whether fronts are temporally persistent or only short-lasting, spatially smoothed to give a continuous distribution.

Table S3.A1. Eigenvalues from Principal Coordinate analyses of environmental variables used to calculate environmental heterogeneity, and cumulative explained variance. All axes are used to calculate environmental heterogeneity as the average distance of each observation from the colony-year centroid in ordination space.

| Axis  | Eigenvalue | Cumulative variance explained (%) |
|-------|------------|-----------------------------------|
| PCoA1 | 46540      | 43.1                              |
| PCoA2 | 21538      | 63.0                              |
| PCoA3 | 17282      | 79.0                              |
| PCoA4 | 11658      | 89.8                              |
| PCoA5 | 8988       | 98.2                              |
| PCoA6 | 1987       | 100.0                             |

Table S3.A2. Environmental heterogeneity, calculated using a principal coordinate analysis of six environmental variables (bathymetry, potential tidal stratification, sea surface temperature, and ocean front strength, distance and persistence) as the average distance in unconstrained ordination space of points within the foraging range of kittiwakes from the colony centroid.

| Colony        | Mean Heterogeneity | ± Standard Error |
|---------------|--------------------|------------------|
| Bardsey       | 1.93               | 0.08             |
| Bempton       | 1.73               | 0.06             |
| Colonsay      | 2.10               | 0.03             |
| Copinsay      | 2.37               | 0.05             |
| Coquet        | 1.16               | 0.06             |
| Filey         | 1.73               | 0.03             |
| Fowlsheugh    | 1.42               | 0.06             |
| Isle Of May   | 1.17               | 0.04             |
| Lambay        | 1.78               | 0.08             |
| Muckle Skerry | 1.36               | 0.04             |
| Puffin Island | 1.79               | 0.05             |
| Rathlin       | 1.98               | 0.05             |
| Skomer        | 1.68               | 0.09             |
| St Martins    | 1.39               | 0.05             |
| Whinnyfold    | 1.19               | 0.07             |



Figure S3.A1. Mean value of environmental heterogeneity from Principal coordinate analysis at all study colonies according to the temporal resolution of calculation: Colony = colony-mean environmental heterogeneity used in all analyses presented in the main paper, Year = annual measure of environmental heterogeneity for 2017 used alongside other study years (2010-6) to calculate colony-mean heterogeneity, and Week = environmental heterogeneity calculated for a single week (June 18-26, 2017) at all colonies. Colonies ordered by increasing colony-mean heterogeneity from left to right on the x axis, error bars show standard error. We found no effect of the temporal resolution of the environmental heterogeneity measure (colony-mean/year/week) on the value of environmental heterogeneity, using a linear regression with colony as a random effect ( $\chi$  <sup>2</sup><sub>2</sub>= 2.09, p = 0.352).



Figure S3.A2. Value of environmental heterogeneity across study years at each colony, indicating that individual colonies were relatively consistent in their degree of environmental heterogeneity between years.



Figure S3.A3. Residuals vs. predicted values from an ANOVA of environmental heterogeneity with colony and year. Residuals show no directional pattern, suggesting that colony and year explain the a large amount of the variance in environmental heterogeneity, and thus a single value of heterogeneity for each colony is more appropriate for analyses of the effect of heterogeneity on foraging behaviour and reproductive success.



Figure S3.A4. Environment within the foraging range of all colonies according to the position along the first axis (PCoA1) from the principal coordinate analysis used to calculate environmental heterogeneity, here for 2015 as an example. The value of environmental heterogeneity is given in each plot title, calculated as the mean distance in Euclidian space (using all PCoA axes) of all locations from the colony centroid. In all plots, the black scale bar shows 50 km.

| Table S<br>confide | 3.A3. P-v;<br>nce interv | alues for<br>vals. Valu | pairwise<br>ıes in bla | compari<br>ck type s | sons of e<br>how a się | nvironme<br>gnificant | ental het<br>differen | erogenei<br>ce in envi | ty at diffé<br>ironment | erent colo<br>al hetero | onies, bas<br>geneity a | ed on Tı<br>t p < 0.05 | ıkeyHSD<br>5. | 95%   |
|--------------------|--------------------------|-------------------------|------------------------|----------------------|------------------------|-----------------------|-----------------------|------------------------|-------------------------|-------------------------|-------------------------|------------------------|---------------|-------|
|                    | BAR                      | BEM                     | COP                    | coq                  | CSY                    | FIL                   | FOW                   | IOM                    | LAM                     | MKS                     | PUF                     | RAT                    | SKO           | STM   |
| BEM                | 0.424                    |                         |                        |                      |                        |                       |                       |                        |                         |                         |                         |                        |               |       |
| COP                | <0.001                   | <0.001                  |                        |                      |                        |                       |                       |                        |                         |                         |                         |                        |               |       |
| coq                | <0.001                   | <0.001                  | <0.001                 |                      |                        |                       |                       |                        |                         |                         |                         |                        |               |       |
| CSY                | 0.679                    | 0.001                   | 0.050                  | <0.001               |                        |                       |                       |                        |                         |                         |                         |                        |               |       |
| FIL                | 0.426                    | 1.000                   | <0.001                 | <0.001               | 0.001                  |                       |                       |                        |                         |                         |                         |                        |               |       |
| FOW                | <0.001                   | 0.015                   | <0.001                 | 0.071                | <0.001                 | 0.015                 |                       |                        |                         |                         |                         |                        |               |       |
| IOM                | <0.001                   | <0.001                  | <0.001                 | 1.000                | <0.001                 | <0.001                | 0.092                 |                        |                         |                         |                         |                        |               |       |
| LAM                | 0.871                    | 1.000                   | <0.001                 | <0.001               | 0.009                  | 1.000                 | 0.001                 | <0.001                 |                         |                         |                         |                        |               |       |
| MKS                | <0.001                   | 0.001                   | <0.001                 | 0.468                | <0.001                 | 0.001                 | 1.000                 | 0.538                  | <0.001                  |                         |                         |                        |               |       |
| PUF                | 0.932                    | 1.000                   | <0.001                 | <0.001               | 0.015                  | 1.000                 | 0.001                 | <0.001                 | 1.000                   | <0.001                  |                         |                        |               |       |
| RAT                | 1.000                    | 0.091                   | <0.001                 | <0.001               | 0.979                  | 0.092                 | <0.001                | <0.001                 | 0.402                   | <0.001                  | 0.515                   |                        |               |       |
| SKO                | 0.121                    | 1.000                   | <0.001                 | <0.001               | <0.001                 | 1.000                 | 0.092                 | <0.001                 | 0.993                   | 0.006                   | 0.979                   | 0.015                  |               |       |
| STM                | <0.001                   | 0.003                   | <0.001                 | 0.224                | <0.001                 | 0.003                 | 1.000                 | 0.274                  | <0.001                  | 1.000                   | <0.001                  | <0.001                 | 0.024         |       |
| MIN                | <0.001                   | <0.001                  | <0.001                 | 1.000                | <0.001                 | <0.001                | 0.193                 | 1.000                  | <0.001                  | 0.750                   | <0.001                  | <0.001                 | <0.001        | 0.466 |
|                    |                          |                         |                        |                      |                        |                       |                       |                        |                         |                         |                         |                        |               |       |

Table S3.A4. P-values for pairwise comparisons of environmental heterogeneity during different years, based on TukeyHSD 95% confidence intervals. Values in black type show a significant difference in environmental heterogeneity at p < 0.05.

|      | 2010  | 2011  | 2012  | 2013  | 2014  | 2015  | 2016  |
|------|-------|-------|-------|-------|-------|-------|-------|
| 2011 | 0.928 |       |       |       |       |       |       |
| 2012 | 0.976 | 1.000 |       |       |       |       |       |
| 2013 | 0.762 | 0.111 | 0.182 |       |       |       |       |
| 2014 | 0.546 | 0.047 | 0.084 | 1.000 |       |       |       |
| 2015 | 0.998 | 0.999 | 1.000 | 0.354 | 0.189 |       |       |
| 2016 | 1.000 | 0.980 | 0.996 | 0.600 | 0.381 | 1.000 |       |
| 2017 | 0.937 | 1.000 | 1.000 | 0.119 | 0.051 | 0.999 | 0.983 |

Appendix S3.B. GPS tracking sample sizes & summary trip metrics

| Table S3.B1. | Sample | sizes of i | individ | uals, trips and | trackii | ng dates at a | all colonies | and years. |            |             |             |             |
|--------------|--------|------------|---------|-----------------|---------|---------------|--------------|------------|------------|-------------|-------------|-------------|
| Colony       | Long   | Lat        | Year    | No. of          | No.     | Mean          | Unique       | First      | Last       | Individuals | Individuals | Individuals |
|              |        |            |         | Individuals     | of      | trips per     | tracking     | tracking   | tracking   | with one    | with 2-3    | with >4     |
|              |        |            |         |                 | trips   | individual    | days         | date       | date       | trip        | trips       | trips       |
| ALL          |        |            | ALL     | 415             | 1567    | 3.78          | 176          | 12/06/2010 | 09/07/2017 | 82          | 170         | 168         |
| Bardsey      | -4.870 | 52.758     | 2011    | 8               | 24      | 3.00          | 8            | 04/07/2011 | 11/07/2011 | 0           | 7           | -           |
|              |        |            | ALL     | 8               | 24      | 3.00          | 8            | 04/07/2011 | 11/07/2011 | 0           | 7           | Ч           |
| Bempton      | -0.077 | 54.114     | 2010    | 15              | 28      | 1.87          | 7            | 12/06/2010 | 04/07/2010 | 8           | 9           | 1           |
| Cliffs       |        |            | 2011    | 7               | 16      | 2.29          | 8            | 07/06/2011 | 23/06/2011 | 4           | 1           | 2           |
|              |        |            | 2012    | 8               | 24      | 3.00          | 8            | 27/06/2012 | 04/07/2012 | 1           | 4           | 3           |
|              |        |            | 2013    | 15              | 55      | 3.67          | Ω            | 29/06/2013 | 03/07/2013 | 2           | 4           | 6           |
|              |        |            | 2015    | 14              | 51      | 3.64          | 8            | 22/06/2015 | 29/06/2015 | 0           | 7           | 7           |
|              |        |            | ALL     | 59              | 174     | 2.95          | 36           | 12/06/2010 | 29/06/2015 | 15          | 22          | 22          |
| Copinsay     | -2.666 | 58.900     | 2010    | 12              | 32      | 2.67          | 8            | 13/06/2010 | 13/07/2010 | Ω           | 4           | 3           |
|              |        |            | 2011    | 7               | 21      | 3.00          | Ω            | 02/07/2011 | 06/07/2011 | 2           | 3           | 2           |
|              |        |            | 2012    | 7               | 34      | 4.86          | 9            | 26/06/2012 | 17/07/2012 | 1           | 1           | ß           |
|              |        |            | ALL     | 26              | 87      | 3.35          | 19           | 13/06/2010 | 17/07/2012 | 8           | 8           | 10          |
| Coquet       | -1.537 | 55.307     | 2011    | 13              | 32      | 2.46          | 4            | 14/06/2011 | 17/06/2011 | 3           | 8           | 2           |
|              |        |            | 2012    | 13              | 60      | 4.62          | 12           | 17/06/2012 | 06/07/2012 | 1           | 2           | 10          |
|              |        |            | ALL     | 26              | 92      | 3.54          | 16           | 14/06/2011 | 06/07/2012 | 4           | 10          | 12          |
| Colonsay     | -6.238 | 56.089     | 2010    | 8               | 21      | 2.63          | 11           | 26/06/2010 | 14/07/2010 | 3           | 2           | 3           |
|              |        |            | 2011    | 21              | 30      | 1.43          | 24           | 27/06/2011 | 24/07/2011 | 15          | Ω           | 1           |
|              |        |            | 2012    | 20              | 37      | 1.85          | 17           | 02/07/2012 | 21/07/2012 | 13          | 4           | 33          |

Supplementary Material

| ndividuals    | with >4     | trips      | 2          | Ω          | 14         | 4          | 4          | 8          | 1          | 1          | 2           | 2          | 1          | 1          | 6          | Ω          | 11         | 22         | 13         | 15         | 10         |
|---------------|-------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|-------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| Individuals I | with 2-3    | trips      | 4          | 9          | 21         | 8          | 8          | 16         | 8          | 8          | 11          | 11         | 6          | 6          | 1          | 1          | 0          | 2          | 0          | 4          | 4          |
| Individuals   | with one    | trip       | 2          | 1          | 34         | 2          | 0          | 2          | 4          | 4          | ŝ           | 3          | 0          | 0          | 0          | 1          | 0          | 1          | 0          | 1          | 0          |
| Last          | tracking    | date       | 21/07/2013 | 21/07/2014 | 21/07/2014 | 04/07/2013 | 29/06/2015 | 29/06/2015 | 26/06/2012 | 26/06/2012 | 14/07/2013  | 14/07/2013 | 19/07/2010 | 19/07/2010 | 05/07/2012 | 15/07/2013 | 04/07/2014 | 04/07/2014 | 14/07/2010 | 11/07/2011 | 12/07/2012 |
| First         | tracking    | date       | 04/07/2013 | 30/06/2014 | 26/06/2010 | 30/06/2013 | 22/06/2015 | 30/06/2013 | 19/06/2012 | 19/06/2012 | 25/06/2013  | 25/06/2013 | 14/07/2010 | 14/07/2010 | 19/06/2012 | 12/07/2013 | 02/07/2014 | 19/06/2012 | 28/06/2010 | 27/06/2011 | 26/06/2012 |
| Unique        | tracking    | days       | 15         | 15         | 82         | Ω          | 8          | 13         | 8          | 8          | 6           | 6          | 4          | 4          | 6          | 4          | 33         | 13         | 11         | 15         | 12         |
| Mean          | trips per   | individual | 2.75       | 3.17       | 2.14       | 3.14       | 3.67       | 3.38       | 2.00       | 2.00       | 2.63        | 2.63       | 2.50       | 2.50       | 5.71       | 5.71       | 9.58       | 7.50       | 9.50       | 5.80       | 5.00       |
| No.           | of          | trips      | 22         | 38         | 148        | 44         | 44         | 88         | 26         | 26         | 42          | 42         | 25         | 25         | 40         | 40         | 115        | 195        | 133        | 116        | 70         |
| No. of        | Individuals |            | 8          | 12         | 69         | 14         | 12         | 26         | 13         | 13         | 16          | 16         | 10         | 10         | 7          | 7          | 12         | 26         | 14         | 20         | 14         |
| Year          |             |            | 2013       | 2014       | ALL        | 2013       | 2015       | ALL        | 2012       | ALL        | 2013        | ALL        | 2010       | ALL        | 2012       | 2013       | 2014       | ALL        | 2010       | 2011       | 2012       |
| Lat           |             |            |            |            |            | 54.219     |            |            | 56.925     |            | 56.181      |            | 53.495     |            | 58.689     |            |            |            | 53.321     |            |            |
| Long          |             |            |            |            |            | -0.272     |            |            | -2.197     |            | -2.553      |            | -5.997     |            | -2.917     |            |            |            | -4.026     |            |            |
| Colony        |             |            |            |            |            | Filey      |            |            | Fowlsheugh |            | Isle of May |            | Lambay     |            | Muckle     | Skerry     |            |            | Puffin     | Island     |            |

Table S3.B1 (cont.)

| dividuals      | with >4     | trips      | Ω          | Ω          | 48         | 13         | 13         | 0          | 1          | 1          | 4          | 3          | 7          | 9          | 6          |
|----------------|-------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| ndividuals In  | with 2-3    | trips      | 4          | 4          | 16         | 4          | 4          | 2          | 3          | 10         | 11         | 6          | 20         | 6          | 9          |
| Individuals I1 | with one    | trip       | 0          | 1          | 2          | 0          | 0          | 4          | 2          | 9          | 0          | 1          | 1          | 2          | 2          |
| Last           | tracking    | date       | 12/07/2015 | 01/07/2016 | 01/07/2016 | 09/07/2017 | 09/07/2017 | 28/06/2016 | 29/06/2017 | 29/06/2017 | 18/07/2010 | 29/06/2011 | 29/06/2011 | 08/07/2012 | 08/07/2012 |
| First          | tracking    | date       | 10/07/2015 | 28/06/2016 | 28/06/2010 | 06/07/2017 | 06/07/2017 | 27/06/2016 | 27/06/2017 | 27/06/2016 | 19/06/2010 | 16/06/2011 | 19/06/2010 | 11/06/2012 | 11/06/2012 |
| Unique         | tracking    | days       | 3<br>C     | 4          | 45         | 4          | 4          | 2          | 3          | S          | 10         | 10         | 20         | 14         | 14         |
| Mean           | trips per   | individual | 4.56       | 5.10       | 6.52       | 4.88       | 4.88       | 1.82       | 2.17       | 2.36       | 3.27       | 2.77       | 3.04       | 3.86       | 3.86       |
| No.            | of          | trips      | 41         | 51         | 411        | 83         | 83         | 20         | 13         | 33         | 49         | 36         | 85         | 54         | 54         |
| No. of         | Individuals |            | 6          | 10         | 63         | 17         | 17         | 11         | 9          | 14         | 15         | 13         | 28         | 14         | 14         |
| Year           |             |            | 2015       | 2016       | ALL        | 2017       | ALL        | 2016       | 2017       | ALL        | 2010       | 2011       | ALL        | 2012       | ALL        |
| Lat            |             |            |            |            |            | 55.307     |            | 51.738     |            |            | 49.966     |            |            | 57.430     |            |
| Long           |             |            |            |            |            | -6.265     |            | -5.275     |            |            | -6.262     |            |            | -1.869     |            |
| Colony         |             |            |            |            |            | Rathlin    |            | Skomer     |            |            | St Martins |            |            | Whinnyfold |            |

Table S3.B1 (cont.)

| Colony   | Voar | Mean trin | 400<br>+ | T           | Mean total     | 400   | Total distance  | Maan May    | 4<br>4 | May distance to |
|----------|------|-----------|----------|-------------|----------------|-------|-----------------|-------------|--------|-----------------|
|          |      | duration  |          | duration    | distance       |       | travelled range | distance to |        | colony range    |
|          |      | (hrs)     |          | range (hrs) | travelled (km) |       | ( <b>km</b> )   | colony (km) |        | ( <b>km</b> )   |
| ALL      | ALL  | 6.49      | 0.26     | 0 - 96.3    | 76.85          | 2.96  | 0.1 - 1189.4    | 23.34       | 0.84   | 0.3 - 229.7     |
| Bardsey  | 2011 | 4.38      | 0.64     | 0.3 - 12.9  | 69.04          | 9.44  | 1.1 - 188.6     | 18.99       | 2.16   | 0.6 - 37.7      |
|          | ALL  | 4.38      | 0.64     | 0.3 - 12.9  | 69.04          | 9.44  | 1.1 - 188.6     | 18.99       | 2.16   | 0.6 - 37.7      |
| Bempton  | 2010 | 4.55      | 0.84     | 0.1 - 18.8  | 82.06          | 15.35 | 0.6 - 284.6     | 35.25       | 6.78   | 0.5 - 121.4     |
| Cliffs   | 2011 | 11.29     | 3.23     | 0.4 - 46.8  | 99.49          | 31.48 | 1.8 - 382.4     | 32.04       | 10.03  | 0.8 - 137.6     |
|          | 2012 | 14.89     | 3.05     | 0.3 - 58.4  | 214.49         | 42.01 | 1.1 - 695.9     | 82.39       | 15.14  | 0.9 - 220.7     |
|          | 2013 | 2.72      | 0.44     | 0 - 14.7    | 43.22          | 7.83  | 0.1 - 240.8     | 17.01       | 2.84   | 0.5 - 94.4      |
|          | 2015 | 10.68     | 2.21     | 0.2 - 88.1  | 162.59         | 29.39 | 1.3 - 899.5     | 53.61       | 8.54   | 0.5 - 195.4     |
|          | ALL  | 7.81      | 0.91     | 0 - 88.1    | 113.26         | 12.15 | 0.1 - 899.5     | 41.07       | 3.99   | 0.5 - 220.7     |
| Copinsay | 2010 | 9.19      | 1.64     | 0.2 - 30.1  | 104.27         | 33.62 | 1 - 689         | 32.37       | 10.64  | 0.6 - 229.7     |
|          | 2011 | 5.52      | 1.41     | 0.3 - 18.6  | 48.07          | 12.87 | 1.7 - 217.3     | 14.96       | 4.48   | 0.8 - 86.6      |
|          | 2012 | 4.95      | 0.78     | 0.2 - 15.7  | 68.54          | 13.01 | 1.7 - 341.8     | 24.36       | 4.92   | 0.9 - 129.9     |
|          | ALL  | 6.65      | 0.78     | 0.2 - 30.1  | 76.74          | 13.80 | 1 - 689         | 25.04       | 4.50   | 0.6 - 229.7     |
| Coquet   | 2011 | 5.04      | 0.73     | 0.3 - 14.2  | 83.32          | 11.65 | 1.1 - 221.3     | 26.98       | 3.87   | 0.7 - 77.5      |
|          | 2012 | 2.76      | 0.37     | 0.4 - 17.9  | 30.30          | 4.68  | 4.7 - 244.7     | 9.03        | 1.17   | 2.3 - 47.6      |
|          | ALL  | 3.55      | 0.37     | 0.3 - 17.9  | 48.74          | 5.69  | 1.1 - 244.7     | 15.27       | 1.78   | 0.7 - 77.5      |
| Colonsay | 2010 | 10.98     | 3.64     | 0.3 - 76.1  | 126.63         | 30.02 | 0.6 - 434.7     | 34.09       | 7.14   | 0.7 - 124.6     |
|          | 2011 | 28.05     | 4.45     | 0.9 - 96.3  | 201.18         | 33.76 | 1.7 - 806.2     | 35.78       | 4.03   | 1.1 - 76.2      |
|          | 2012 | 25.30     | 3.50     | 0.3 - 80.1  | 223.17         | 31.45 | 1.9 - 740.5     | 36.71       | 3.87   | 0.9 - 124.9     |

Table S3.B2. Summary trip characteristics

| Colony      | Year | Mean trip | + Se | Trip        | Mean total     | ± Se  | Total distance  | Mean Max    | + se  | Max distance to |
|-------------|------|-----------|------|-------------|----------------|-------|-----------------|-------------|-------|-----------------|
|             |      | duration  |      | duration    | distance       |       | travelled range | distance to |       | colony range    |
|             |      | (hrs)     |      | range (hrs) | travelled (km) |       | ( <b>km</b> )   | colony (km) |       | (km)            |
|             | 2013 | 16.48     | 3.50 | 0.5 - 53.3  | 136.59         | 29.59 | 1.5 - 513       | 30.02       | 5.68  | 1 - 73.7        |
|             | 2014 | 12.35     | 2.46 | 0 - 78.7    | 141.97         | 34.38 | 0.4 - 1189.4    | 32.11       | 4.68  | 0.5 - 97.3      |
|             | ALL  | 19.19     | 1.67 | 0 - 96.3    | 171.29         | 15.13 | 0.4 - 1189.4    | 33.97       | 2.17  | 0.5 - 124.9     |
| Filey       | 2013 | 7.92      | 1.36 | 0.2 - 41.6  | 146.99         | 25.91 | 0.5 - 682.9     | 51.90       | 8.39  | 0.6 - 172.9     |
|             | 2015 | 10.34     | 2.42 | 0.2 - 66.4  | 161.36         | 34.60 | 1.6 - 885.1     | 53.99       | 10.34 | 0.8 - 200.6     |
|             | ALL  | 9.13      | 1.39 | 0.2 - 66.4  | 154.17         | 21.50 | 0.5 - 885.1     | 52.95       | 6.62  | 0.6 - 200.6     |
| Fowlsheugh  | 2012 | 11.89     | 1.63 | 0.4 - 31    | 200.96         | 24.23 | 6.1 - 448.6     | 74.40       | 8.31  | 3.1 - 173       |
|             | ALL  | 11.89     | 1.63 | 0.4 - 31    | 200.96         | 24.23 | 6.1 - 448.6     | 74.40       | 8.31  | 3.1 - 173       |
| Isle of May | 2013 | 9.13      | 1.36 | 0.3 - 52    | 89.68          | 12.29 | 0.6 - 386.3     | 29.50       | 3.64  | 0.7 - 78.7      |
|             | ALL  | 9.13      | 1.36 | 0.3 - 52    | 89.68          | 12.29 | 0.6 - 386.3     | 29.50       | 3.64  | 0.7 - 78.7      |
| Lambay      | 2010 | 4.05      | 0.64 | 0.3 - 12.9  | 50.03          | 6.56  | 1 - 122.8       | 19.22       | 2.29  | 0.7 - 39.6      |
|             | ALL  | 4.05      | 0.64 | 0.3 - 12.9  | 50.03          | 6.56  | 1 - 122.8       | 19.22       | 2.29  | 0.7 - 39.6      |
| Muckle      | 2012 | 3.16      | 0.58 | 0.3 - 21.4  | 50.94          | 10.11 | 3.3 - 323       | 14.44       | 3.60  | 1.5 - 121.7     |
| Skerry      | 2013 | 1.98      | 0.32 | 0.3 - 7.7   | 23.28          | 4.13  | 1 - 91.7        | 7.73        | 1.28  | 0.7 - 31.1      |
|             | 2014 | 1.17      | 0.12 | 0.2 - 7.6   | 13.79          | 1.63  | 1.2 - 120.3     | 4.84        | 0.63  | 0.7 - 47.3      |
|             | ALL  | 1.74      | 0.16 | 0.2 - 21.4  | 23.35          | 2.63  | 1 - 323         | 7.40        | 06.0  | 0.7 - 121.7     |
| Puffin      | 2010 | 2.58      | 0.22 | 0.2 - 12.8  | 29.14          | 2.70  | 0.7 - 182.1     | 9.07        | 0.95  | 0.3 - 71        |
| Island      | 2011 | 5.00      | 0.44 | 0.2 - 23.6  | 58.23          | 4.58  | 0.7 - 245.2     | 17.78       | 1.25  | 0.3 - 61.6      |
|             | 2012 | 4.94      | 0.86 | 0.2 - 52    | 67.41          | 8.32  | 0.7 - 331.6     | 21.44       | 2.50  | 0.8 - 78.1      |

Table S3.B2 (cont.)
| Colony     | Year | Mean trip | + Se | Trip        | Mean total     | + Se  | Total distance  | Mean Max    | ± Se | Max distance to |
|------------|------|-----------|------|-------------|----------------|-------|-----------------|-------------|------|-----------------|
|            |      | duration  |      | duration    | distance       |       | travelled range | distance to |      | colony range    |
|            |      | (hrs)     |      | range (hrs) | travelled (km) |       | ( <b>km</b> )   | colony (km) |      | ( <b>km</b> )   |
|            | 2015 | 5.48      | 1.50 | 0.2 - 40.7  | 40.15          | 9.60  | 0.5 - 219.4     | 10.56       | 2.71 | 0.4 - 68.3      |
|            | 2016 | 2.69      | 0.49 | 0.1 - 13.2  | 22.46          | 5.00  | 0.1 - 169       | 7.27        | 1.73 | 0.3 - 53.7      |
|            | ALL  | 3.97      | 0.27 | 0.1 - 52    | 44.14          | 2.52  | 0.1 - 331.6     | 13.56       | 0.76 | 0.3 - 78.1      |
| Rathlin    | 2017 | 3.44      | 0.31 | 0.2 - 14.7  | 39.67          | 3.70  | 0.4 - 167.1     | 13.49       | 1.29 | 0.3 - 57.1      |
|            | ALL  | 3.44      | 0.31 | 0.2 - 14.7  | 39.67          | 3.70  | 0.4 - 167.1     | 13.49       | 1.29 | 0.3 - 57.1      |
| Skomer     | 2016 | 9.91      | 1.93 | 0.3 - 24.2  | 87.54          | 17.60 | 0.6 - 243.3     | 19.95       | 3.28 | 0.4 - 44.9      |
|            | 2017 | 9.31      | 2.54 | 0.5 - 32.5  | 93.80          | 20.88 | 2.4 - 273.7     | 25.02       | 4.20 | 1.1 - 49.2      |
|            | ALL  | 9.68      | 1.52 | 0.3 - 32.5  | 00.06          | 13.27 | 0.6 - 273.7     | 21.95       | 2.58 | 0.4 - 49.2      |
| St Martins | 2010 | 3.78      | 0.39 | 0.2 - 13.6  | 61.77          | 7.64  | 0.8 - 193.6     | 20.40       | 3.04 | 0.7 - 69        |
|            | 2011 | 6.09      | 0.89 | 0.3 - 23.7  | 74.38          | 16.53 | 0.9 - 332.9     | 23.02       | 5.25 | 0.7 - 110.5     |
|            | ALL  | 4.76      | 0.45 | 0.2 - 23.7  | 67.11          | 8.24  | 0.8 - 332.9     | 21.51       | 2.82 | 0.7 - 110.5     |
| Whinnyfold | 2012 | 7.00      | 0.97 | 0.3 - 32.6  | 75.53          | 11.56 | 0.5 - 320.9     | 25.28       | 3.48 | 0.6 - 88.9      |
|            | ALL  | 7.00      | 0.97 | 0.3 - 32.6  | 75.53          | 11.56 | 0.5 - 320.9     | 25.28       | 3.48 | 0.6 - 88.9      |

Table S3.B2 (cont.)

Chapter 3 – Foraging dynamics & fitness

|                               | ז טו אוננואמו |          | uutu (01 0) o | זוות וכלו החת |      |          | 100) ac1033 C |      | alla years       |                 | o or and y.  |
|-------------------------------|---------------|----------|---------------|---------------|------|----------|---------------|------|------------------|-----------------|--------------|
|                               | Year          |          |               |               |      |          |               |      | Years            | Years           | Years        |
| Colony                        | 2010          | 2011     | 2012          | 2013          | 2014 | 2015     | 2016          | 2017 | with<br>GPS data | with RS<br>data | with<br>both |
| Bardsey                       |               | GPS + RS | RS            | RS            | RS   | RS       | RS            |      | 1                | 6               | 1            |
| Bempton cliffs                | GPS + RS      | GPS + RS | GPS + RS      | GPS + RS      | RS   | GPS + RS | RS            | RS   | Ω                | 8               | Ω            |
| Copinsay                      | GPS + RS      | GPS + RS | GPS + RS      |               | RS   |          |               |      | 33               | 3               | 3            |
| Coquet                        | RS            | GPS + RS | GPS + RS      | RS            | RS   | RS       |               |      | 2                | 6               | 2            |
| Colonsay                      | GPS           | GPS      | GPS           | GPS           | GPS  |          |               |      | Ω                | 0               | 0            |
| Filey                         |               |          | RS            | GPS + RS      | RS   | GPS + RS | RS            |      | 2                | Ω               | 2            |
| Fowlsheugh                    | RS            | RS       | GPS + RS      | RS            | RS   | RS       | RS            |      | 1                | 7               | 1            |
| Isle of may                   | RS            | RS       | RS            | GPS + RS      | RS   | RS       | RS            |      | 1                | 7               | 1            |
| Lambay                        | GPS + RS      | RS       |               |               |      |          |               |      | 1                | 2               | 1            |
| <b>Muckle Skerry</b>          |               |          | GPS           | GPS           | GPS  |          |               |      | 3                | 0               | 0            |
| Puffin island                 | GPS + RS      | GPS + RS | GPS + RS      | RS            | RS   | GPS + RS | GPS + RS      |      | Ω                | 7               | ъ            |
| Rathlin                       |               |          |               |               |      |          |               | GPS  | 1                | 0               | 0            |
| Skomer                        | RS            | RS       | RS            | RS            | RS   | RS       | GPS + RS      | GPS  | 2                | 7               | 1            |
| St martins                    | GPS + RS      | GPS + RS |               |               |      |          |               |      | 2                | 2               | 2            |
| Whinnyfold                    |               |          | GPS           |               |      |          |               |      | 1                | 0               | 0            |
| <b>Colonies with GPS data</b> | 9             | 7        | 8             | 5             | 2    | 3        | 2             | 2    |                  |                 |              |
| Colonies with RS data         | 6             | 10       | 6             | 8             | 6    | 8        | 7             | 1    |                  |                 |              |
| Colonies with both            | Ω             | 6        | Ω             | 3             | 0    | 3        | 2             | 0    |                  |                 |              |

Table S3.B4. Colony reproductive success from JNCC monitoring data, as well as colony size and number of breeding pairs within the maximum foraging range of each colony from Seabird 2000 monitoring counts.

| Colony      | Year | Nests     | Fledged | Breeding | Colony | No pairs within |
|-------------|------|-----------|---------|----------|--------|-----------------|
|             |      | monitored | chicks  | success  | Size   | foraging range  |
| Bardsey     | 2011 | 31        | 16      | 0.52     | 288    | 1637            |
| Bardsey     | 2012 | 44        | 23      | 0.52     |        |                 |
| Bardsey     | 2013 | 38        | 27      | 0.71     |        |                 |
| Bardsey     | 2014 | 67        | 14      | 0.21     |        |                 |
| Bardsey     | 2015 | 62        | 52      | 0.84     |        |                 |
| Bardsey     | 2016 | 66        | 27      | 0.41     |        |                 |
| Bempton     | 2010 | 1142      | 1332    | 1.17     | NA     | 67560           |
| Bempton     | 2011 | 1001      | 863     | 0.86     |        |                 |
| Bempton     | 2012 | 898       | 710     | 0.79     |        |                 |
| Bempton     | 2013 | 895       | 458     | 0.51     |        |                 |
| Bempton     | 2014 | 906       | 709     | 0.78     |        |                 |
| Bempton     | 2015 | 1058      | 774     | 0.73     |        |                 |
| Bempton     | 2016 | 1019      | 546     | 0.54     |        |                 |
| Bempton     | 2017 | 900       | 527     | 0.59     |        |                 |
| Colonsay    | NA   | NA        | NA      | NA       | 6485   | 29843           |
| Copinsay    | 2010 | 229       | 85      | 0.37     |        |                 |
| Copinsay    | 2011 | 64        | 12      | 0.19     |        |                 |
| Copinsay    | 2012 | 32        | 20      | 0.63     |        |                 |
| Copinsay    | 2014 | 7         | 5       | 0.71     |        |                 |
| Coquet      | 2010 | 30        | 39      | 1.30     | 51     | 28149           |
| Coquet      | 2011 | 30        | 45      | 1.50     |        |                 |
| Coquet      | 2012 | 215       | 235     | 1.09     |        |                 |
| Coquet      | 2013 | 30        | 36      | 1.20     |        |                 |
| Coquet      | 2014 | 30        | 38      | 1.27     |        |                 |
| Coquet      | 2015 | 30        | 38      | 1.27     |        |                 |
| Filey       | 2012 | 241       | 55      | 0.23     | 5120   | 67410           |
| Filey       | 2013 | 223       | 58      | 0.26     |        |                 |
| Filey       | 2014 | 255       | 114     | 0.45     |        |                 |
| Filey       | 2015 | 257       | 119     | 0.46     |        |                 |
| Filey       | 2016 | 231       | 55      | 0.24     |        |                 |
| Fowlsheugh  | 2010 | 328       | 304     | 0.93     | 18377  | 148714          |
| Fowlsheugh  | 2011 | 423       | 567     | 1.34     |        |                 |
| Fowlsheugh  | 2012 | 379       | 277     | 0.73     |        |                 |
| Fowlsheugh  | 2013 | 370       | 241     | 0.65     |        |                 |
| Fowlsheugh  | 2014 | 432       | 360     | 0.83     |        |                 |
| Fowlsheugh  | 2015 | 394       | 545     | 1.38     |        |                 |
| Fowlsheugh  | 2016 | 427       | 419     | 0.98     |        |                 |
| Isle of May | 2010 | 494       | 143     | 0.29     | 3639   | 31505           |

| Colony            | Year | Nests     | Fledged | Breeding | Colony | No pairs within |
|-------------------|------|-----------|---------|----------|--------|-----------------|
|                   |      | monitored | chicks  | success  | Size   | foraging range  |
| Isle of May       | 2011 | 449       | 391     | 0.87     |        |                 |
| Isle of May       | 2012 | 470       | 461     | 0.98     |        |                 |
| Isle of May       | 2013 | 351       | 144     | 0.41     |        |                 |
| Isle of May       | 2014 | 403       | 472     | 1.17     |        |                 |
| Isle of May       | 2015 | 569       | 609     | 1.07     |        |                 |
| Isle of May       | 2016 | 497       | 388     | 0.78     |        |                 |
| Lambay            | 2010 | 390       | 363     | 0.93     | 4091   | 7925            |
| Lambay            | 2011 | 462       | 476     | 1.03     |        |                 |
| Muckle            | NA   | NA        | NA      | NA       | 219    | 149985          |
| Skerry            |      |           |         |          |        |                 |
| Puffin            | 2010 | 117       | 106     | 0.91     | 571    | 3614            |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2011 | 57        | 79      | 1.39     |        |                 |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2012 | 61        | 47      | 0.77     |        |                 |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2013 | 65        | 0       | 0.00     |        |                 |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2014 | 71        | 5       | 0.07     |        |                 |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2015 | 67        | 61      | 0.91     |        |                 |
| Island            |      |           |         |          |        |                 |
| Puffin            | 2016 | 55        | 54      | 0.98     |        |                 |
| Island            |      |           |         |          |        |                 |
| Rathlin           | NA   | NA        | NA      | NA       | 9917   | 12126           |
| Skomer            | 2010 | 662       | 467     | 0.71     | 2257   | 2813            |
| Skomer            | 2011 | 702       | 380     | 0.54     |        |                 |
| Skomer            | 2012 | 591       | 194     | 0.33     |        |                 |
| Skomer            | 2013 | 394       | 160     | 0.41     |        |                 |
| Skomer            | 2014 | 491       | 345     | 0.70     |        |                 |
| Skomer            | 2015 | 416       | 319     | 0.77     |        |                 |
| Skomer            | 2016 | 380       | 260     | 0.68     |        |                 |
| St Martins        | 2010 | 76        | 54      | 0.71     | 27     | 2024            |
| <b>St Martins</b> | 2011 | 74        | 9       | 0.12     |        |                 |
| Winnyfold         | NA   | NA        | NA      | NA       | NA     | 70843           |



Figure S3.B1. Map of study kittiwake colonies, for which we have reproductive success data, coloured by mean reproductive success across all years. There was no link between reproductive success and colony longitude (linear regression;  $F_{(1,59)}$ =1.14, p=0.29) or latitude ( $F_{(1,59)}$ =3.51, p=0.07).

Appendix S3.C: Hidden Markov models for behavioural classification

We used the R package moveHMM (Michelot *et al.* 2016) for behavioural classification based on distributions of step lengths and turning angles. We used a gamma distribution to describe step lengths and a von Mises distribution to describe turning angles, and the Viterbi algorithm to estimate the most likely sequence of movement states based on the fitted hidden Markov model. We used distributions of step lengths and turning angles from previous classification of kittiwake behavioural classification to inform model starting parameters (Trevail *et al.* 2019).

The hidden Markov model successfully classified kittiwake tracks into three movement types, which we use as proxies of behaviour: (1) resting: short step lengths and narrow turning angles (step:  $0.09 \pm 0.08$  km; turn:  $\mu = 0$ ,  $\kappa = 26.36$ ), (2) foraging: short-medium step lengths and wide turning angles (step:  $0.20 \pm 0.26$  km; turn:  $\mu = -0.02$ ,  $\kappa = 0.34$ ) & (3) transiting: long step lengths and narrow turning angles (step:  $1.12 \pm 0.37$  km; turn:  $\mu = 0$ ,  $\kappa = 13.24$ ). Distributions of step lengths and turning angles are given in Figure S3.C1. Using the Viterbi algorithm to determine the most likely sequence of behavioural states, 16.9% of all GPS locations were classified as resting, 54.3% as foraging and 28.8% as transiting.



Figure S3.C1. Histograms of observed step lengths (left) and turning angles (right) for GPS-tracked kittiwakes. Lines show fitted HMM state distributions for each behavioural state.

#### Appendix S3.D: Other environmental variables

To verify that observed patterns were driven by environmental heterogeneity, we considered the potentially confounding effects of alternative environmental variables on foraging trip metrics and breeding success (Ashmole 1963). For bathymetry and stratification, which remain constant between years, we took an average value of the environment variable within the foraging range of kittiwakes at each colony. For SST and front variables, which vary temporally, we took an average of the environment variables at each colony and for each year during June-July to encompass the GPS tracking period. We used GLMMs for each trip metric in turn as the response variable, initially including year and colony as random effects to account for the nested data structure. We ran separate models for each environmental variable.

In support of results presented in the main paper, that observed changes in foraging dynamics and reproductive success can be attributed to environmental heterogeneity, we found that reproductive success was not correlated with any of the environmental variables when considered separately (Table S3.D1). Trip duration was negatively correlated with front density (parameter estimate: -0.34,  $\chi^2_1 = 4.79$ , p = 0.03) and front persistence (parameter estimate: -0.28,  $\chi^2_1 = 4.30$ , p = 0.04), and total distance travelled during a foraging trip was negatively correlated with front density (parameter estimate: -0.29,  $\chi^2_1 = 4.06$ , p = 0.04). There were no links between trip metrics and bathymetry, stratification, SST or front distance (Table S3.D1).

| Table S3.D1. The re   | lationship betwe | en both foragin         | ig trip metrics an    | d reproductiv         | e success with in     | idividual environme   | ntal metrics.         |
|-----------------------|------------------|-------------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Significant results a | re shown in blac | k type. Estimat         | es are from GLM       | Ms with colo          | ny as a random e      | ffect.                |                       |
| Response variable     | Model output     | Bathymetry              | Stratification        | SST                   | Front Density         | Front persistence     | Front distance        |
| Trip Duration         | Test statistic   | $\chi^{2}{}_{1} = 0.00$ | $\chi^{\ 2}{}_1=1.28$ | $\chi^{2}{}_{1}=1.60$ | $\chi^{2}_{1} = 4.79$ | $\chi^{2}_{1} = 4.30$ | $\chi^{2}{}_{1}=0.12$ |
|                       | p-value          | p = 0.995               | p = 0.258             | p = 0.205             | p = 0.029             | p = 0.038             | p = 0.729             |
|                       | Estimate ± se    | $0.00 \pm 0.17$         | $0.15 \pm 0.14$       | $-0.21 \pm 0.15$      | $-0.34 \pm 0.13$      | $-0.28 \pm 0.12$      | $0.06 \pm 0.15$       |
|                       | (logged scale)   |                         |                       |                       | $R^{2} = 0.15$        | $R^{2} = 0.13$        |                       |
| Total Distance        | Test statistic   | $\chi^{2}_{1} = 0.112$  | $\chi^{2}{}_{1}=1.00$ | $\chi^{2}_{1} = 0.66$ | $\chi^{2}_{1} = 4.06$ | $\chi^{2}_{1} = 3.66$ | $\chi^{2}_{1} = 0.20$ |
|                       | p-value          | p = 0.736               | p = 0.316             | p = 0.417             | p = 0.044             | p = 0.056             | p = 0.658             |
|                       | Estimate ± se    | $-0.06 \pm 0.16$        | $0.13 \pm 0.14$       | $-0.14 \pm 0.15$      | $-0.29 \pm 0.13$      | $-0.24 \pm 0.12$      | $0.07 \pm 0.14$       |
|                       | (logged scale)   |                         |                       |                       | $R^{2} = 0.12$        |                       |                       |
| Maximum Distance      | Test statistic   | $\chi^{2}_{1} = 0.26$   | $\chi^{2}{}_{1}=0.64$ | $\chi^{2}_{1} = 0.40$ | $\chi^{2}_{1} = 3.33$ | $\chi^{2}_{1} = 3.20$ | $\chi^{2}_{1} = 0.63$ |
|                       | p-value          | p = 0.611               | p = 0.425             | p = 0.525             | p = 0.068             | p = 0.074             | p = 0.46              |
|                       | Estimate ± se    | $-0.08 \pm 0.16$        | $0.10 \pm 0.14$       | $-0.10 \pm 0.14$      | $-0.24 \pm 0.13$      | $-0.21 \pm 0.12$      | $0.11 \pm 0.14$       |
|                       | (logged scale)   |                         |                       |                       |                       |                       |                       |
| Reproductive          | Test statistic   | $\chi^{2}_{1} = 0.46$   | $\chi^{2}{}_{1}=0.17$ | $\chi^{2}_{1} = 0.29$ | $\chi^{2}_{1} = 0.04$ | $\chi^{2}_{1} = 1.07$ | $\chi^{2}_{1} = 1.29$ |
| Success               | p-value          | p = 0.498               | p = 0.680             | p = 0.589             | p = 0.834             | p = 0.301             | p = 0.256             |
|                       | Estimate ± se    | $-0.05 \pm 0.08$        | $0.03 \pm 0.09$       | $0.08 \pm 0.06$       | $0.01 \pm 0.05$       | $0.06 \pm 0.06$       | $-0.07 \pm 0.06$      |

Appendix S3.E: Comparison of environmental heterogeneity with environmental variables

There was a significant, positive correlation between bathymetry and environmental heterogeneity ( $F_{(1,118)} = 19.17$ , p < 0.001,  $R^2 = 0.14$ , Figure S3.E1), however this relationship was driven by high environmental heterogeneity and deep waters at Copinsay. When all years of data at Copinsay were excluded, there was no significant correlation between bathymetry and heterogeneity ( $F_{(1,110)} = 1.49$ , p = 0.225, Figure S3.E2). There was also a significant, positive correlation between front density and heterogeneity ( $F_{(1,118)}$  = 8.49, p = 0.004), Figure S3.E1), however the correlation explained very little variation in the data:  $R^2 = 0.06$ . There was no correlation between environmental heterogeneity and stratification ( $F_{(1,118)} = 0.73$ , p = 0.393), sea surface temperature ( $F_{(1,118)} = 0.0044$ , p = 0.947), front persistence ( $F_{(1,118)} = 0.62$ , p = 0.433) or front distance ( $F_{(1,118)} = 1.30$ , p = 0.257). There was no relationship between environmental heterogeneity and either of the first two principal components from a PCA of mean values of environmental variables at each colony and year (PC1:  $F_{(1,118)} = 0.13$ , p = 0.719; PC2:  $F_{(1,118)} = 0.05$ , p = 0.829). In the principal component analysis, the first two principal components explained 78.1% of the total variation in mean environmental variables.



Figure S3.E1. Comparison of environmental heterogeneity with mean values of each variable used in the principal coordinate analysis from within the foraging range of kittiwakes. Regression lines show significant correlations ( $\pm$  standard error) between environmental heterogeneity and bathymetry ( $F_{(1,118)} = 19.17$ , p < 0.001, R<sup>2</sup> = 0.14), and front density ( $F_{(1,118)} = 8.49$ , p = 0.004, R<sup>2</sup> = 0.06).



Figure S3.E2. Comparison between environmental heterogeneity and bathymetry at all colonies, excluding Copinsay. When Copinsay is removed from the regression between bathymetry and environmental heterogeneity, there is no significant correlation ( $F_{(1,110)} = 1.489$ , p < 0.225).

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# Chapter 4

## Environmental heterogeneity promotes individual specialisation in habitat selection



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## Environmental heterogeneity decreases reproductive success via effects on foraging behaviour

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#### Abstract

Individual specialisations in habitat selection are predicted to arise where mean population fitness increases as a result of divergent habitat selection behaviour. In theory, specialisation is more likely in heterogeneous environments, facilitated both by frequency dependent selection and ecological opportunity. Such a relationship, which remains untested, could explain differences in rates of individual specialisation among species and populations. Here, we successfully extend habitat selection functions to quantify individual specialisations in habitat selection by black-legged kittiwakes (*Rissa tridactyla*) at 15 colonies around the UK and Ireland, along a gradient of environmental heterogeneity. We find the first support for the hypothesis that individual specialisations in habitat selection are more prevalent in heterogeneous environments. This trend was significant across multiple dynamic habitat variables, which highlights the importance of environmental processes in facilitating behavioural adaptation by predators. Furthermore, results are an important advance in understanding the origins of individual differences, which are an essential component of biodiversity.

#### Keywords

Behavioural consistency, resource selection, seabird, foraging behaviour, movement ecology

#### Introduction

Habitat choice is a behavioural response to the environment to increase fitness (Rosenzweig 1981; Morris & Davidson 2000). This process acts at the individual level, whereby an individual can ideally select the most optimal habitat for the survival and/or reproduction of its phenotype. Scaled up to the population level, natural

selection will shape population behaviour when many individuals profit from a shared habitat (Edelaar & Bolnick 2019). Indeed, at a broad scale, this process explains selection for foraging, breeding and refuge habitats, for example, that lead to speciation (Webster *et al.* 2012). However, at a finer scale, mean population fitness may in fact be compromised by identical behaviour of all individuals (Bolnick *et al.* 2003; Araújo *et al.* 2011; Dall *et al.* 2012). For example, if all individuals in a population share the same optimal habitat, frequency-dependent effects could limit fitness gains, and therefore favour divergent phenotypic change (Araújo *et al.* 2011; Riotte-Lambert *et al.* 2015; Navarro *et al.* 2017). Alternatively, individual phenotypes may differ such that they require different habitats for fitness gain (Polis 1984). In either case, where animals occupy an environment that comprises a wider range of habitat types, i.e. greater environmental heterogeneity, we predict that individual habitat specialisations are more likely to evolve (Edelaar *et al.* 2017; Courbin *et al.* 2018; Jacob *et al.* 2018).

The degree of environmental heterogeneity characterises the range of available habitats to a given population, and is a key ecosystem trait underlying population level processes (Sparrow 1999; Weimerskirch 2007). Environmental heterogeneity is often shown to shape resources into patches, whereby the physical environment can cause areas of concentrated resource density that can provide profitable and/or predictable foraging grounds to predators (Morris & Davidson 2000; Scott *et al.* 2010), yet potentially at the cost of greater competition (Goldberg *et al.* 2001; López-Bao *et al.* 2011; Trevail *et al.* 2019b). Resource distributions and intraspecific competition can both favour individual behavioural specialisations (Araújo *et al.* 2011; Svanbäck *et al.* 2011). Therefore, in heterogeneous environments, we could expect individual level specialisations in habitat selection to provide individuals the opportunity to select habitat that offers a trade-off between resource gain and lower competition risk.

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Individual specialisations across studied foraging behaviours range from widespread (reviewed by Bell et al. 2009; Dall et al. 2012; Ceia & Ramos 2015) to absent (Carneiro et al. 2014; Granadeiro et al. 2014), and vary in prevalence both within and between species (Matich et al. 2011; Ceia & Ramos 2015). Although individual specialisations in habitat selection in particular have only recently been quantified in brown bears, Ursus arctos (Leclerc et al. 2016), they were almost absent in a study of Scopoli's shearwaters, Calonectris diomedea (Courbin et al. 2018). It remains unknown whether the prevalence of individual specialisation in habitat selection is caused by environmental heterogeneity, thus potentially explaining observed differences between populations and species. We propose a framework (Figure 4.1), by which the degree of environmental heterogeneity could shape the prevalence of individual specialisations in habitat selection within populations. In more homogeneous environments, natural selection should favour a common phenotype that is well matched to the available environment (Edelaar et al. 2017). In contrast, in more heterogeneous environments, natural selection ought to favour a diverse range of individual phenotypes, as individuals are able to access a diversity of optimal habitats, i.e. opportunity, (Edelaar & Bolnick 2019) and minimise competition .

In this study, we test the proposed framework (Figure 4.1) using a large data set of individual foraging habitat selections of a temperate seabird species, the black-legged kittiwake (*Rissa tridactyla*, hereafter 'kittiwakes'). We tracked kittiwakes from 15 populations along a gradient of environmental heterogeneity during the breeding season, when they are central place foragers. Resource acquisition, intraspecific competition and environmental heterogeneity are all important drivers of animal behaviour in marine ecosystems (Lewis *et al.* 2001; Weimerskirch 2007; Wakefield *et al.* 2017). For central place foragers in particular, optimal habitat selection is particularly key during the breeding season, when individuals are constrained by the energetic requirements of offspring and partners to forage within the vicinity of

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breeding sites (Davoren & Montevecchi 2003; Pinaud *et al.* 2005). Indeed, kittiwakes can adjust their habitat selection, most likely to maximise resource acquisition (Trevail *et al.* 2019a), and experience greater levels of intraspecific competition in populations that occupy more heterogeneous environments (Trevail *et al.* 2019b). Firstly, to confirm the appropriate variables for testing individual specialisation in habitat selection, we establish whether, at the species, population and individual levels, kittiwakes select habitat according to a set of environmental variables that can influence prey accessibility. Secondly, we test the proposed framework (Figure 4.1) to determine whether the degree of environmental heterogeneity influences the prevalence of individual specialisations in habitat selection between populations. Specifically, we hypothesise that at populations with more heterogeneous local environments, individual kittiwakes will be more specialised in their selection over a suite of environmental variables; i.e. that individuals use different subsets of the available habitat relative to other individuals.



Figure 4.1. Framework by which we would expect selection to favour populations comprised of common phenotypes that share an optimal environment where environmental heterogeneity is low, compared to populations comprised of individuals with unique habitat specialisations where environmental heterogeneity is high.

#### Methods

Kittiwake GPS tracking

To determine habitat selection of kittiwakes whilst foraging, we tracked adults from multiple colonies around the UK and Ireland using GPS loggers (Mobile Action i-GotU GT-120) attached to the back or tail feathers that in all cases weighed < 5% of individual's body mass. Individuals were selected at random with respect to brood size, which can range from 1-3 chicks per clutch. Full details of tracking procedures can be found in the original publications of the data (Wakefield et al. 2017; Trevail et al. 2019a). Here, we use data from 415 chick-rearing kittiwakes at 15 colonies between 2010 and 2017: Bardsey (NW Wales; 2011, n individuals = 8), Bempton Cliffs (E England; 2010-13 & 2015, n = 59), Copinsay (Orkney Islands; 2010-12, n = 26), Coquet (NE England; 2011-12, n = 26), Colonsay (W Scotland; 2010-14, n = 69), Filey (E England; 2013 & 2015, n = 26), Fowlsheugh (E Scotland; 2012, n = 13), Isle of May (E Scotland; 2013, n = 16), Lambay (E Ireland; 2010, n = 10), Muckle Skerry (Orkney Islands; 2012-2014, n = 26), Puffin Island (NW Wales; 2010-16, n = 63), Rathlin (Northern Ireland; 2017, n = 17), Skomer (SW Wales; 2016-17, n = 14), St Martins (Isles of Scilly; 2010-11, n = 28) & Winnyfold (E Scotland; 2012, n = 14). Full sample sizes, tracking dates and colony locations are given in supplementary material (Appendix S4.A).

#### Identification of foraging locations

We considered departures from the colony as foraging trips when tracking points were greater than 500m from the colony, and when the total time spent away from the colony was over 14 minutes (based on a frequency distribution of trip duration; as per Trevail *et al.* 2019a), to eliminate departures because of disturbance (Collins *et al.* 2016; Warwick-Evans *et al.* 2016a). We used a hidden Markov model to classify behaviour into rest, forage or transit based on distributions of step lengths and turning angles of interpolated tracking data using the R package *moveHMM* (supplementary material, Appendix S4.B). We used values from previous classification of kittiwake behaviour to inform model starting parameters (Trevail *et al.* 2019a), and found that model outputs were robust to different values of starting parameters when tested on a subset of tracking data. Herein, we undertake all analyses on kittiwake locations classed as foraging, only.

#### Environmental metrics

To understand habitat selection of kittiwakes, and environmental drivers thereof, we used six environmental metrics, all known to influence resource distributions relevant to foragers in coastal seas: (1) bathymetry, (2) potential tidal stratification, (3) sea surface temperature, (4) ocean front strength, (5) persistence and (6) distance. Bathymetry and potential tidal stratification explain the vertical structure of the water column and hence prey accessibility to surface foragers (Scott *et al.* 2013), and are static over time. Sea surface temperature and ocean front metrics describe the horizontal structure and indicate the presence of processes that can enhance local productivity (Benazzouz *et al.* 2014; Scales *et al.* 2014), and are dynamic variables that can fluctuate from days to months. We extracted values of the above variables for every kittiwake foraging location, described in full in the supplementary material (Appendix S4.C).

We used values of environmental heterogeneity calculated specifically for kittiwakes foraging at these study colonies in Trevail *et al.* (2019b). Environmental heterogeneity is a single value for each colony, which indicates the dissimilarity of spatial environmental characteristics within the foraging area of kittiwakes at each colony (Anderson *et al.* 2006). It is calculated using a principal coordinate analysis of all six environmental variables detailed above. This places values of a set of points randomly selected from within foraging ranges around all colonies along principal coordinate axes in unconstrained ordination space, based on a Euclidean distance matrix of standardised environmental data, using the functions *vegdist* and *betadisper* in the R package *vegan* (Oksanen *et al.* 2018). Specifically, we refer to environmental

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heterogeneity as the mean distance of points at each colony from the colony centroid along all principle coordinate axes, with higher values indicating greater heterogeneity.

#### Determining habitat selection model structure

Resource selection models are commonly used to understand animal habitat selection in the context of their surrounding environment (Manly et al. 2002). However, only twice have they been developed to quantify individual specialisations in habitat selection (Leclerc et al. 2016; Courbin et al. 2018), to our knowledge, and never before to quantify individual specialisations in habitat selection between multiple populations. In both cases, random effects are used to account for differences in habitat selection by individuals (Lesmerises & St-Laurent 2017); however, studies of resource selection model structure alternatively refer to random effects to account for differences in sample sizes between individuals (Gillies et al. 2006), or for differences in habitat availability for free-roaming animals that may prompt individual-specific functional responses in habitat selection (Fieberg et al. 2009; Matthiopoulos et al. 2011; Aarts et al. 2013). Furthermore, foraging locations are either compared to an equal number of available locations per individual (e.g. 1000 available locations per individual (Gillies et al. 2006)), or a constant ratio of used locations to available locations for all individuals (e.g. 10 available locations per used location (Leclerc et al. 2016; Trevail et al. 2019a)). To accurately quantify individual differences in habitat selection, and furthermore to extend models of habitat selection to multiple populations simultaneously in our case, requires appropriate consideration of random effects. Therefore, prior to analyses of kittiwake data, we created simulated data to understand how sampling of available locations and the random effect structure can influence habitat selection model outputs.

Firstly, we tested the difference between sampling an equal number of points per individual (e.g. Gillies *et al.* 2006) and a constant ratio of available points per used

point (e.g. Leclerc *et al.* 2016; Trevail *et al.* 2019). We simulated two populations comprised of five individuals, each with the same distributions for used and available habitats, i.e. the same habitat selection; differing numbers of used points per individual; and either an equal number of available points per individual, or a constant ratio of used to available points. Results from habitat selection models (detailed in Supplementary material Appendix S4.D) only showed correct representation of habitat selection for the population with a constant ratio of used to available points. For the population with an equal number of used points per individual, the model calculated different resource selection slopes and intercepts for each individual, despite all individuals having the same distributions for used and available habitats. Therefore, for analyses of kittiwake habitat selection described below, we sampled a constant ratio of used to available points, and so can confidently use random effects to account for differences in habitat selection between individuals, rather than sample size. Comprehensive details and R code for data simulations are given in supplementary material (Appendix S4.D).

Secondly, we tested how the structure of random intercepts and slopes affects quantification of differences in habitat selection, both for simulated populations of individuals foraging within the same available environment (equivalent to individual level analyses in our study), and of individuals foraging within different available environments (equivalent to population level analyses in our study). We simulated multiple populations comprised of five individuals, in each case with varying habitat selection, individual differences, and available environments. We quantified habitat selection using three different models for each population with differing random effect structures for individual ID: a random intercept, a random slope, and both a random intercept and slope. Habitat selection results (detailed in Supplementary material Appendix S4.E) showed that where the available environment was the same between individuals, a random intercept captured variability in habitat selection

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between individuals for the benefit of model simplicity. Where the available environment varied between individuals, including both a random slope and intercept were favoured by model selection to accurately represent variability in habitat selection between individuals. Therefore, for analyses of kittiwake habitat selection described below, we accounted for differences in habitat selection at the population level by including both a random intercept and slope for colony-year, because the available environment differed between populations (Figure 4.2). To account for differences in habitat selection at the individual level we included a random intercept only for each foraging trip, because within a population all individuals were foraging within the same available environment (Figure 4.2). Again, comprehensive details and R code for data simulations are given in supplementary material (Appendix S4.E).

#### Kittiwake habitat selection

To understand habitat selection of kittiwakes at the species, population and individual levels, we ran resource selection models to compare available habitat to the habitat at kittiwake foraging locations, i.e. used habitat (Manly *et al.* 2002). Habitat selection (binomial response variable: y; available = 0 or used = 1) was modelled in response to each environment variable in turn. As with many central place foragers, kittiwakes preferentially forage closer to the colony (Chivers *et al.* 2013; Trevail *et al.* 2019a), and therefore we included distance to the colony as a fixed effect in all models (Matthiopoulos 2003; Patenaude-Monette *et al.* 2014). Colony distance, bathymetry, front strength, and front persistence were square-root transformed to approach the assumption of a Gaussian distribution, and all variables were standardised prior to analyses (Supplementary Material, Appendix S4.F).

As a measure of the available habitat, we selected two random points for each used point from within the maximum foraging range of kittiwakes specific to each colony and year (Supplementary Material Appendix S4.D). To ensure that our quantification of habitat selection was not biased where remote sensing data (SST and ocean fronts) were obscured by e.g. cloud cover, and against coastal regions outside of gridded modelled tide data (for stratification), we retained only kittiwake foraging locations as used points where environment data were available for the used point and both available data points. This meant that different numbers of kittiwake foraging locations were retained for each environment variable (Supplementary Material Appendix S4.D); at a minimum models included 75311 used points from 1270 trips and 378 individuals (max = 137774 used points, 1534 trips & 410 individuals).

Models were implemented using a binomial error structure with a logit link using the *glmer* function of the R package lme4 (Bates *et al.* 2015). Based on the analyses of data simulations detailed above and further in Supplementary Material Appendix S4.E, we included a random intercept and slope for colony-year and a random intercept for each foraging trip ID (Figure 4.2). Each trip ID number was unique to the individual bird and colony. We selected the most suitable fixed effects structure based on Akaike information criterion (AIC) values in backward stepwise selection, in all cases retaining both the environmental variable in question and colony distance in the model (Supplementary Material, Tables S4.G1 & S4.G2). We ensured model fit by calculating the area under the receiving operator characteristic curve (AUC; Supplementary Material, Table S4.G3) (Zweig & Campbell 1993), predictive power, sensitivity and specificity (Warwick-Evans *et al.* 2016b) (Supplementary Material, Table S4.G3).

To interpret habitat selection at the species level, i.e. across all populations, we took the global intercept and slope from models of each environmental variable (Figure 4.2). Negative slope values indicate preference for lower than average values compared to the available environment, and conversely, positive slope values indicate preference for higher than average available values. To understand how populations varied in habitat selection, we extracted slope coefficients from the habitat selection models for each colony-year (Figure 4.2). We verified that, in accordance with previous studies of this data set (Wakefield *et al.* 2019), there was no functional habitat selection at the population level (Gillies *et al.* 2006). To quantify individual habitat specialisations we extracted parameter estimates for each individual trip as random intercepts from the models described above (Figure 4.2). Parameter estimates are presented on the log-odds scale, and for colony distance, bathymetry, front strength and front persistence as square-root transformed.

#### Quantifying individual habitat specialisations

To test whether environmental heterogeneity influenced the prevalence of individual habitat specialisations, we first calculated the degree of individual specialisations in habitat selection at each colony as the adjusted repeatability index of trip intercepts (Courbin et al. 2018), using the R package rptR (Nakagawa & Schielzeth 2013) for each variable, and for each colony and year, based on the hierarchical nature of the data. Repeatability ranges from 0 to 1; where high values (approaching 1) indicate high prevalence of individual habitat specialisations within the local population, whereby individual ID explains a large amount of model variance (Figure 4.2). Conversely, low values of repeatability (approaching 0) indicate low prevalence of individual specialisations in habitat selection within the local population, whereby individual ID explains a small amount of model variance. We then compared the value of repeatability of habitat selection calculated for each colony and year to the colonymean value environmental heterogeneity (from Trevail et al. 2019b) using linear regression for habitat selection of each environmental variable in turn. To verify that any differences in individual specialisation in habitat selection were not an artefact of variability in the duration of kittiwake tracking time, we compared the mean value of repeatability for habitat selection to the mean number of foraging trips recorded per individual across colonies, using linear regression for each environmental variable.

(A) Species level: positive habitat selection



**(B) Population level:** different used & available habitats modelled with random slope & intercept



(C) Individual level: different used habitats modelled with random intercept

High individual specialisation in habitat selection





Variance can be explained by ind. ID

Low individual specialisation in habitat selection



Figure 4.2. Schematic to show how resource selection functions modelled habitat selection using linear mixed effects models at (A) the species level; and using random slopes and intercepts to quantify differences in habitat selection (B) between populations and (C) between and within individuals undertaking multiple trips. Frequency density plots show available habitat in dashed lines, and used habitat in solid lines. Individual specialisation in habitat selection was quantified using repeatability analyses to calculate the model variance explained by individual ID, at each population.

#### Results

Kittiwake foraging metrics

Tracking data yielded a total of 1567 foraging trips, on average  $3.78 \pm 0.13$  trips per individual (mean across colonies  $\pm$  se; ranging from 1 to 19, Supplementary material Table S4.A1). Trips were on average  $6.5 \pm 0.3$  hours duration,  $76.9 \pm 3.0$  km long, and reached a maximum of  $23.3 \pm 0.8$  km from the colony (Supplementary material Table S4.A2).

#### Kittiwake habitat selection

At the species level, as expected, kittiwakes preferentially foraged closer to the colony (in all models slope coefficients for colony distance were below zero, Table 4.1). Given the likelihood to remain closer to the colony, results showed that probability of kittiwake habitat selection varied according to all environmental variables (Figure 4.3). On average, kittiwakes preferentially foraged in areas of shallower water (parameter estimate  $\pm$  s.e. = -0.23  $\pm$  0.14), areas where the water column was likely to be more well mixed, i.e. weaker stratification (-0.63  $\pm$  0.26), areas of cooler water (-0.51  $\pm$  0.27), areas of weaker fronts (-0.32  $\pm$  0.09), areas that were further away from fronts (0.19  $\pm$  0.13) and lower front persistence (-0.22  $\pm$  0.0) (Figure 4.3). There was variation in habitat selection preferences of kittiwakes between colonies (Figure 4.3, Table 4.1).

#### Individual habitat specialisations

At the individual level, results show that habitat selection was individually repeatable with respect to all environmental variables (Table 4.2), although repeatability values were low. Mean repeatability among all populations varied between 0.13  $\pm$  0.03 (bathymetry) and 0.21  $\pm$  0.05 (sea surface temperature). Individual specialisations in habitat selection were more prevalent in colonies with more heterogeneous environments for all ocean front variables (Figure 4.4): front strength (parameter estimate  $\pm$  se = 0.10  $\pm$  0.03, test statistic from linear regression: F<sub>1,33</sub> = 10.01, p = 0.003); front distance (0.10 ± 0.05,  $F_{1,33}$  = 5.20, p = 0.029); and front persistence (0.11 ± 0.03,  $F_{1,33}$  = 10.32, p = 0.003). Individual specialisations in habitat selection were slightly higher in heterogeneous environments for bathymetry, stratification and SST, however the differences were not statistically significant (Table 4.2). There was no link between individual habitat specialisations and the number of foraging trips recorded per individual indicative of tracking duration (linear regressions were not significant for any environmental variable; p > 0.05).



Figure 4.3. Probability of habitat selection by kittiwakes whilst foraging along six environmental variables: bathymetry (m), potential tidal stratification  $(\log_{10} (m^{-2} s^3))$ , sea surface temperature (°C), front strength (°C/1.2 km), front distance (km) and front persistence (fraction of cloud-free observations of a pixel for which a front was detected). Habitat selection curves are shown for the whole data set (solid black lines  $\pm$  standard error; dashed black lines) and from each of the 15 study colonies (grey lines) to give an indication of variability between colonies (parameter estimates given in Table 4.1). Considering the propensity of kittiwakes to forage closer to the colony, in general kittiwakes preferentially foraged in areas characterised by shallower depths, weaker stratification, cooler temperatures, weaker fronts, further away from fronts and less persistent fronts (Table 4.1).



Figure 4.4. Individual repeatability of kittiwake habitat selection of different environmental variables whilst foraging between populations of differing environmental heterogeneity. Error bars show standard error between years. Significant relationships between individual repeatability and environmental heterogeneity (Table 4.2) are shown as linear regressions (solid lines) and standard error (dashed lines). Higher repeatability values indicate higher mean prevalence of individual habitat specialisations. Individual habitat specialisations were more prevalent in colonies with more heterogeneous environments for bathymetry, potential tidal stratification, front strength, front distance, and front persistence.

Table 4.1 (overleaf). Kittiwake habitat selection of environmental variables. Results are from models of habitat selection in response to each environmental variable in turn, in all cases including colony distance as a fixed effect, a nested random intercept structure (colony-year/trip) and a random slope for colony-year. For colonies with multiple years of tracking data, indicated with an asterisk (\*), selection and slope values are averaged across the years. Colony selection shows whether the slope of habitat selection was strongly positive (+ +, slope > 1), positive (+, 1 > slope > 0), not significant (ns, standard error overlapped with zero), negative (-, 0 > slope > -1) or strongly negative (- -, slope < -1).
|                        |                                   |                  | Potential t               | idal             | Sea surfac                        | a                                 |                           |                  | Distance to                       | o closest                               |                                |                  |
|------------------------|-----------------------------------|------------------|---------------------------|------------------|-----------------------------------|-----------------------------------|---------------------------|------------------|-----------------------------------|---|--------------------------------|------------------|
|                        | Bathymetr                         | y                | stratificati              | uo               | temperatu                         | re                                | Front strei               | ngth             | front                             |   | Front pers                     | stence           |
| All populations        | Negative so                       | election         | Negative so               | election         | Negative se                       | election                          | Negative se               | election         | Positive sel                      | ection                                  | Negative se                    | ection           |
|                        | $-0.23 \pm 0.14$                  |                  | $-0.63 \pm 0.26$          |                  | $-0.51 \pm 0.27$                  |                                   | $-0.32 \pm 0.09$          |                  | $0.19 \pm 0.13$                   |   | $-0.22 \pm -0.0$               | •                |
|                        | $R^{2}_{(m)} = 56.6$              | %                | $R^{2}_{(m)}\!=45.3$      | %                | $R^{2}_{(m)} = 47.9^{\circ}$      | %                                 | $R^{2}_{(m)} = 52.1^{-6}$ | %                | $R^{2}_{(m)} = 46.8$ <sup>9</sup> | ~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~~ | $R^{2}_{(m)} = 52.9^{\circ}$   | %                |
|                        | $R^{2}_{(c)} = 77.3$ <sup>9</sup> | %                | $R^{2}_{(c)}\!=80.6~^{0}$ | 0                | $R^{2}_{(c)} = 81.8$ <sup>9</sup> | 0                                 | $R^{2}_{(c)} = 72.4^{-0}$ | 0                | $R^{2}_{(c)} = 71.5 \ \%$         | ,0                                      | $R^{2}_{(c)} = 72.8 \ ^{0}{9}$ |                  |
|                        | Selection                         | Slope            | Selection                 | Slope            | Selection                         | Slope                             | Selection                 | Slope            | Selection                         | Slope                                   | Selection                      | Slope            |
| Bardsey                | +                                 | $0.49 \pm 0.22$  | +                         | $0.25 \pm 0.22$  | +                                 | $0.71 \pm 0.23$                   | +                         | $0.70\pm0.19$    |                                   | $-0.42 \pm 0.19$                        | +                              | $0.51 \pm 0.19$  |
| Bempton Cliffs *       | ı                                 | $-0.89 \pm 0.35$ | I                         | $-0.56 \pm 0.47$ | su                                | $-0.26 \pm 0.89$                  | +                         | $0.44 \pm 0.21$  | ns                                | $-0.03 \pm 0.41$                        | +                              | $0.49 \pm 0.28$  |
| Copinsay *             | su                                | $0.25\pm0.35$    | +                         | $0.90\pm0.82$    | +++                               | $1.84 \pm 1.09$                   | ns                        | $0.07\pm0.22$    | us                                | $-0.19 \pm 0.54$                        | su                             | $-0.01 \pm 0.29$ |
| Coquet *               | su                                | $0.44\pm0.60$    | +<br>+                    | $1.18 \pm 1.61$  | +                                 | $\textbf{0.59} \pm \textbf{0.19}$ | ns                        | $-0.10 \pm 0.40$ | ns                                | $0.59\pm0.80$                           | su                             | $-0.06 \pm 0.30$ |
| Colonsay *             | su                                | $0.10\pm0.17$    | +<br>+                    | $1.36 \pm 0.21$  | su                                | $-0.57 \pm 0.89$                  | I                         | $-0.28 \pm 0.27$ | +                                 | $0.42\pm0.14$                           | I                              | $-0.43 \pm 0.19$ |
| Filey *                | ;                                 | $-1.70 \pm 0.41$ | +<br>+                    | $1.63 \pm 0.91$  | su                                | $1.92 \pm 2.56$                   | su                        | $0.25\pm0.35$    |                                   | $-0.47 \pm 0.06$                        | +                              | $0.39 \pm 0.33$  |
| Fowlsheugh             | +                                 | $0.62\pm0.21$    | 1                         | $-1.39 \pm 0.21$ | I                                 | $-0.37 \pm 0.22$                  | +                         | $0.98\pm0.18$    | ı                                 | $-0.60 \pm 0.17$                        | +                              | $0.87\pm0.18$    |
| Isle Of May            | +<br>+                            | $1.41 \pm 0.17$  | ;                         | $-2.92 \pm 0.16$ | +                                 | $0.78\pm0.17$                     | +                         | $0.65\pm0.14$    |                                   | $-0.76 \pm 0.14$                        | +                              | $0.69 \pm 0.14$  |
| Lambay                 | +<br>+                            | $1.15 \pm 0.21$  | :                         | $-3.30 \pm 0.22$ | 1                                 | $-1.89 \pm 0.26$                  | ns                        | $-0.09 \pm 0.18$ | 1                                 | $-1.84 \pm 0.29$                        | I                              | $-0.30 \pm 0.18$ |
| Muckle Skerry *        | +                                 | $0.54\pm0.38$    | ;                         | $-1.93 \pm 0.16$ | su                                | $-0.14 \pm 0.71$                  | su                        | $-0.21 \pm 0.53$ | ns                                | $0.16\pm0.27$                           | su                             | $-0.29 \pm 0.44$ |
| Puffin Island *        | +                                 | $0.37 \pm 0.21$  | +                         | $0.51\pm0.37$    | su                                | $-0.60 \pm 0.51$                  | I                         | $-0.28 \pm 0.20$ | su                                | $0.09 \pm 0.30$                         | su                             | $-0.02 \pm 0.20$ |
| Rathlin                | +                                 | $0.39 \pm 0.12$  | +<br>+                    | $1.18\pm0.12$    | ;                                 | $-1.25 \pm 0.12$                  | ı                         | $-0.21 \pm 0.10$ | ++++                              | $1.36 \pm 0.14$                         | 1                              | $-0.11 \pm 0.10$ |
| Skomer *               | su                                | $-0.13 \pm 0.13$ | ns                        | $-0.30 \pm 0.68$ | ı                                 | $-0.17 \pm 0.73$                  | su                        | $-0.33 \pm 0.45$ | ns                                | $0.03 \pm 0.97$                         | su                             | $-0.44 \pm 0.45$ |
| St Martins *           | 1                                 | $-1.01 \pm 0.26$ | 1                         | $-1.47 \pm 0.78$ | 1                                 | $-0.63 \pm 0.22$                  | su                        | $-0.30 \pm 0.39$ | ns                                | $0.01 \pm 0.37$                         | ı                              | $-0.33 \pm 0.02$ |
| Whinnyfold             | +                                 | $0.68\pm0.15$    | +                         | $0.98\pm0.15$    | +                                 | $0.92\pm0.20$                     | su                        | $-0.01 \pm 0.13$ |                                   | $-0.22 \pm 0.16$                        | su                             | $0.03\pm0.13$    |
| <b>Colony distance</b> | Negative so                       | election         | Negative so               | election         | Negative se                       | election                          | Negative se               | election         | Negative se                       | election                                | Negative se                    | ection           |
|                        | -2.77 ± 0.01                      |                  | $-2.65 \pm 0.01$          |                  | $-2.78 \pm 0.01$                  |                                   | $-2.48 \pm 0.01$          |                  | $-2.37 \pm 0.01$                  |   | $-2.53 \pm 0.01$               |                  |

| Variable                       | Individual repeatability    |                   | Effect of e               | environmental hete | rogeneity |
|--------------------------------|-----------------------------|-------------------|---------------------------|--------------------|-----------|
|                                | in habitat selection (± se) | Relationship      | Parameter estimate (± se) | Test statistic     | p-value   |
| Bathymetry                     | $0.13 \pm 0.03$             | Marginal increase | $0.06 \pm 0.03$           | $F_{1,33} = 4.09$  | 0.051     |
| Potential tidal stratification | $0.18\pm0.04$               | Marginal increase | $0.05 \pm 0.03$           | $F_{1,33} = 2.71$  | 0.109     |
| Sea surface temperature        | $0.21 \pm 0.05$             | Marginal increase | $0.07 \pm 0.04$           | $F_{1,33} = 3.01$  | 0.092     |
| Front strength                 | $0.18\pm0.04$               | Increase          | $0.10 \pm 0.03$           | $F_{1,33}=10.01$   | 0.003     |
| Front distance                 | $0.19 \pm 0.05$             | Increase          | $0.10 \pm 0.05$           | $F_{1,33}=5.20$    | 0.029     |
| Front persistence              | $0.18\pm0.04$               | Increase          | $0.11 \pm 0.03$           | $F_{1,33}=10.32$   | 0.003     |
|                                |                             |                   |                           |                    |           |

Table 4.2. Individual habitat specialisations of kittiwakes whilst foraging, here showing the mean repeatability values among all populations, and the effect of environmental heterogeneity on repeatability, where parameter estimates and test statistics are from linear regressions.

## Discussion

As predicted by our theoretical framework, we demonstrate that kittiwakes showed greater individual specialisation in habitat selection in more heterogeneous environments. This pattern was evident across multiple environmental variables, which we also show influence kittiwake habitat selection, most likely because of effects on resource distribution and availability. These results are among early evidence of individual specialisations in habitat selection (Leclerc *et al.* 2016), and provide the first evidence that environmental heterogeneity, a known driver of resource distributions and intraspecific competition (Trevail *et al.* 2019b), may also give rise to individual specialisations in behaviour.

Differences between individuals are at the heart of biodiversity (Dall et al. 2012). In theory, individual specialisation in habitat selection will arise where it leads to favourable fitness (Estes et al. 2003). Such a situation is particularly likely in heterogeneous environments, where competition between phenotypes for a shared habitat and/or the opportunity to exploit a range of habitat types will allow scope for a diverse range of phenotypes (Figure 4.1). Whilst testing the exact origin of specialisation is beyond the scope of our study and data, we demonstrate that, in line with this prediction, individual specialisations in habitat selection are more likely to occur in heterogeneous environments. Environmental heterogeneity is a known driver of heterogeneous resource distributions, and can lead to enhanced intraspecific competition with negative consequences for fitness (Trevail et al. 2019b). Individual specialisations in habitat selection may therefore offer a key mechanism to reduce the detrimental effects of intraspecific competition (Svanbäck et al. 2007), and could contribute to maintaining spatial segregation between individuals and neighbouring populations (Bogdanova et al. 2014; Riotte-Lambert et al. 2015). Furthermore, our results support longstanding theory and empirical studies that ecological opportunity can facilitate individual specialisation (Roughgarden 1974; Herrera et al. 2008; Darimont et al. 2009).

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Individual specialisations in diet and foraging strategies have been extensively documented among animals (Bolnick et al. 2003; Bell et al. 2009; Araújo et al. 2011), across a range of seabird species (e.g. Bearhop et al. 2006; Patrick et al. 2014; Patrick & Weimerskirch 2014b). The repeatability of animal behaviour is on average 0.37 (Bell et al. 2009), which is within the range of values of individual specialisations in habitat selection that we find here (Table 4.2). Previous studies have found support for intrinsic drivers of variation in foraging behavioural consistency, including personality-mediated differences in behaviour (Harris et al. 2019), sex specific dimorphism (Nakagawa et al. 2007; Patrick & Weimerskirch 2014a) and ontogenetic shifts in behaviours and requirements (Polis 1984; Grecian et al. 2018). However, extrinsic drivers are more difficult to determine because of the need for data across multiple environments. For this reason, the large dataset that we study here offers a unique opportunity to test the extrinsic drivers of variation in individual specialisations. Our result, that environmental heterogeneity can drive differences in individual specialisation in habitat selection, therefore leads to the question of whether we need further research into the incidence of animal behavioural specialisations, taking into consideration differences between populations and their proximal environment.

Local adaptations are a key process in ecology and evolution, by which particular traits are favoured in the local environment regardless of their consequences for fitness elsewhere (Kawecki & Ebert 2004). Local adaptations are thought to be maintained by natural selection, however gene flow and temporal variability in the environment can both act as limiting factors. Here, we find variability between populations in the strength and direction of habitat selection (Table 4.1). These differences highlight the scope for local adaptations despite potential gene flow between neighbouring populations (McCoy *et al.* 2005), and therefore demonstrates

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the importance of local physical processes in governing behaviour in a highly dynamic environment (Carroll *et al.* 2015).

In dynamic systems, ephemeral environmental features can be key drivers of prey distributions to mobile predators (Weimerskirch 2007; Fernandez *et al.* 2017). In such cases, animals can optimise foraging efficiency by returning to previously productive areas, in theory to minimise the costs of searching for new resource patches (Switzer 1993; Wolf *et al.* 2009). Indeed, many mobile predators exhibit site fidelity to foraging and wintering grounds that may offer predictable or familiar prey types (Gonzalez-Gomez & Vasquez 2006; Abrahms *et al.* 2018; Carroll *et al.* 2018). Here, we found greater prevalence in heterogeneous environments of individual specialisations in habitat selection of ocean fronts, which can move between days and months and are often visible at the surface as changes in surface roughness and ocean colour (Miller 2009; Rascle *et al.* 2016). This result builds on previous findings that dynamic habitat characteristics can offer a key advantage to foragers (Beerens *et al.* 2011; Scales *et al.* 2014; Sunde *et al.* 2014); specifically that fine-scale tracking of mobile prey patches may be particularly important to individuals where resources are more heterogeneous.

In the marine environment, a suite of habitat characteristics are thought to shape prey distributions and therefore foraging behaviour of oceanic predators (Wakefield *et al.* 2017; Cox *et al.* 2018). In support we found that, at the species level, kittiwake habitat selection was influenced by bathymetry, potential tidal stratification, sea surface temperature, and ocean fronts. We found that, on average, kittiwakes preferentially foraged in shallower, well mixed waters, even considering the propensity for kittiwakes to remain close to the colony in analyses. This may be because in such areas, the interaction between bathymetry and tidal currents can enhance local prey availability (Zamon 2003; Trevail *et al.* 2019a). Furthermore, in deep waters, vertical mixing can restrict access to prey for surface foraging seabirds (Carroll *et al.* 2015), and seasonal depletion of surface waters in stratified areas could reduce foraging opportunities (Behrenfeld & Boss 2014). Kittiwakes also exhibited strong habitat selection for cooler sea surface temperatures, typically beneficial to many seabird species at a seasonal time scales (Carroll et al. 2015) and indicative of physical processes that can enhance local productivity (Benazzouz et al. 2014). This link between kittiwake habitat selection and sea surface temperature contrasts with commonly observed spatial mismatches between sea surface temperature and animal behaviour at higher trophic levels (Grémillet et al. 2008). Lastly, kittiwakes selected foraging areas characterised by weaker fronts, greater distances from fronts, and areas of less persistent fronts. This is in contrast to common assumptions that ocean fronts are important physical processes offering predictably enhanced prey 'hotspots' to all marine taxa (Scales et al. 2014; Cox et al. 2016). This result could therefore suggest that fronts are less important to foraging kittiwakes, relative to other environmental features; that kittiwakes are outcompeted at fronts by larger marine predators such as large diving birds, mammals and turtles (Scales et al. 2014); or that kittiwakes are able to exploit ephemeral fronts (Belkin et al. 2009), which, because of their transient nature, may still offer enhanced prey but with less interspecific competition (Scales et al. 2014).

## Conclusions

Our study demonstrates the importance of environmental heterogeneity in shaping the degree of individual specialisations in behaviour between populations. In homogeneous environments, all individuals have presumably evolved to match their phenotype to the environment. In contrast, in heterogeneous environments, frequency dependent effects and ecological opportunity likely facilitate selection of divergent habitat specialisations between individuals (Figure 4.1). The behavioural systems that enable individuals, within a population, to adjust their phenotype to select the optimal habitat for fitness have presumably evolved through the past action of natural selection (Edelaar & Bolnick 2019). Our results therefore suggest that environmental heterogeneity could be an important driver of the degree of variation in individual phenotypes within populations, and hence the potential scope of populations to respond to environmental change (Sih *et al.* 2012). Intra-individual variation forms the foundation of diversity, and therefore both individual specialisations in habitat selection and environmental heterogeneity could be of major importance for speciation and biodiversity over evolutionary timescales (Sih *et al.* 2004).

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Supplementary material to: Environmental heterogeneity promotes individual specialisation in habitat selection

Appendix S4.A - GPS tracking sample sizes & summary trip metrics

Appendix S4.B – Hidden Markov models for behavioural classification

Appendix S4.C – Environmental data

Appendix S4.D - Available point selection for resource selection models

Appendix S4.E - Intercepts and slopes in resource selection models

Appendix S4.F - Model selection and validation

References

Appendix S4.A. GPS tracking sample sizes & summary trip metrics

|          | 4      |        |      | •           |       | )          |          | ×          |            |             |             |             |
|----------|--------|--------|------|-------------|-------|------------|----------|------------|------------|-------------|-------------|-------------|
| Colony   | Long   | Lat    | Year | No. of      | No.   | Mean       | Unique   | First      | Last       | Individuals | Individuals | Individuals |
|          |        |        |      | Individuals | of    | trips per  | tracking | tracking   | tracking   | with one    | with 2-3    | with >4     |
|          |        |        |      |             | trips | individual | days     | date       | date       | trip        | trips       | trips       |
| ALL      |        |        | ALL  | 415         | 1567  | 3.78       | 176      | 12/06/2010 | 09/07/2017 | 82          | 170         | 168         |
| Bardsey  | -4.870 | 52.758 | 2011 | 8           | 24    | 3.00       | 8        | 04/07/2011 | 11/07/2011 | 0           | 7           | -           |
|          |        |        | ALL  | 8           | 24    | 3.00       | ∞        | 04/07/2011 | 11/07/2011 | 0           | 7           | 4           |
| Bempton  | -0.077 | 54.114 | 2010 | 15          | 28    | 1.87       | 7        | 12/06/2010 | 04/07/2010 | 8           | 9           | 1           |
| Cliffs   |        |        | 2011 | 7           | 16    | 2.29       | 8        | 07/06/2011 | 23/06/2011 | 4           | 1           | 2           |
|          |        |        | 2012 | 8           | 24    | 3.00       | 8        | 27/06/2012 | 04/07/2012 | 1           | 4           | ŝ           |
|          |        |        | 2013 | 15          | 55    | 3.67       | Ω        | 29/06/2013 | 03/07/2013 | 2           | 4           | 6           |
|          |        |        | 2015 | 14          | 51    | 3.64       | 8        | 22/06/2015 | 29/06/2015 | 0           | 7           | 7           |
|          |        |        | ALL  | 59          | 174   | 2.95       | 36       | 12/06/2010 | 29/06/2015 | 15          | 22          | 22          |
| Copinsay | -2.666 | 58.900 | 2010 | 12          | 32    | 2.67       | 8        | 13/06/2010 | 13/07/2010 | 5           | 4           | 3           |
|          |        |        | 2011 | 7           | 21    | 3.00       | Ω        | 02/07/2011 | 06/07/2011 | 2           | 3           | 2           |
|          |        |        | 2012 | 7           | 34    | 4.86       | 9        | 26/06/2012 | 17/07/2012 | 1           | 1           | Ω           |
|          |        |        | ALL  | 26          | 87    | 3.35       | 19       | 13/06/2010 | 17/07/2012 | 8           | 8           | 10          |
| Coquet   | -1.537 | 55.307 | 2011 | 13          | 32    | 2.46       | 4        | 14/06/2011 | 17/06/2011 | 3           | 8           | 2           |
|          |        |        | 2012 | 13          | 60    | 4.62       | 12       | 17/06/2012 | 06/07/2012 | 1           | 2           | 10          |
|          |        |        | ALL  | 26          | 92    | 3.54       | 16       | 14/06/2011 | 06/07/2012 | 4           | 10          | 12          |
| Colonsay | -6.238 | 56.089 | 2010 | 8           | 21    | 2.63       | 11       | 26/06/2010 | 14/07/2010 | 3           | 2           | 3           |
|          |        |        | 2011 | 21          | 30    | 1.43       | 24       | 27/06/2011 | 24/07/2011 | 15          | Ω           | 1           |
|          |        |        | 2012 | 20          | 37    | 1.85       | 17       | 02/07/2012 | 21/07/2012 | 13          | 4           | ĉ           |

Table S4.A1. Sample sizes of individuals, trips and tracking dates at all colonies and years.

| Colony      | Long   | Lat    | Year | No. of      | No.   | Mean       | Unique   | First      | Last       | Individuals | Individuals | Individuals |
|-------------|--------|--------|------|-------------|-------|------------|----------|------------|------------|-------------|-------------|-------------|
|             |        |        |      | Individuals | of    | trips per  | tracking | tracking   | tracking   | with one    | with 2-3    | with >4     |
|             |        |        |      |             | trips | individual | days     | date       | date       | trip        | trips       | trips       |
|             |        |        | 2013 | 8           | 22    | 2.75       | 15       | 04/07/2013 | 21/07/2013 | 2           | 4           | 2           |
|             |        |        | 2014 | 12          | 38    | 3.17       | 15       | 30/06/2014 | 21/07/2014 | 1           | 9           | Ω           |
|             |        |        | ALL  | 69          | 148   | 2.14       | 82       | 26/06/2010 | 21/07/2014 | 34          | 21          | 14          |
| Filey       | -0.272 | 54.219 | 2013 | 14          | 44    | 3.14       | Ω        | 30/06/2013 | 04/07/2013 | 2           | 8           | 4           |
|             |        |        | 2015 | 12          | 44    | 3.67       | 8        | 22/06/2015 | 29/06/2015 | 0           | 8           | 4           |
|             |        |        | ALL  | 26          | 88    | 3.38       | 13       | 30/06/2013 | 29/06/2015 | 2           | 16          | 8           |
| Fowlsheugh  | -2.197 | 56.925 | 2012 | 13          | 26    | 2.00       | 8        | 19/06/2012 | 26/06/2012 | 4           | 8           | 1           |
|             |        |        | ALL  | 13          | 26    | 2.00       | 8        | 19/06/2012 | 26/06/2012 | 4           | 8           | 1           |
| Isle of May | -2.553 | 56.181 | 2013 | 16          | 42    | 2.63       | 6        | 25/06/2013 | 14/07/2013 | 3           | 11          | 2           |
|             |        |        | ALL  | 16          | 42    | 2.63       | 6        | 25/06/2013 | 14/07/2013 | 3           | 11          | 2           |
| Lambay      | -5.997 | 53.495 | 2010 | 10          | 25    | 2.50       | 4        | 14/07/2010 | 19/07/2010 | 0           | 6           | -           |
|             |        |        | ALL  | 10          | 25    | 2.50       | 4        | 14/07/2010 | 19/07/2010 | 0           | 6           | 1           |
| Muckle      | -2.917 | 58.689 | 2012 | 2           | 40    | 5.71       | 6        | 19/06/2012 | 05/07/2012 | 0           | -           | 6           |
| Skerry      |        |        | 2013 | 7           | 40    | 5.71       | 4        | 12/07/2013 | 15/07/2013 | 1           | 1           | Ω           |
|             |        |        | 2014 | 12          | 115   | 9.58       | 3        | 02/07/2014 | 04/07/2014 | 0           | 0           | 11          |
|             |        |        | ALL  | 26          | 195   | 7.50       | 13       | 19/06/2012 | 04/07/2014 | 1           | 2           | 22          |
| Puffin      | -4.026 | 53.321 | 2010 | 14          | 133   | 9.50       | 11       | 28/06/2010 | 14/07/2010 | 0           | 0           | 13          |
| Island      |        |        | 2011 | 20          | 116   | 5.80       | 15       | 27/06/2011 | 11/07/2011 | 1           | 4           | 15          |
|             |        |        | 2012 | 14          | 70    | 5.00       | 12       | 26/06/2012 | 12/07/2012 | 0           | 4           | 10          |

Table S4.A1 (cont.)

| Individuals | with >4     | trips      | S          | Ω          | 48         | 13         | 13         | 0          | 1          | 1          | 4          | 3          | 7          | 9          | 9          |
|-------------|-------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|
| Individuals | with 2-3    | trips      | 4          | 4          | 16         | 4          | 4          | 7          | 3          | 10         | 11         | 6          | 20         | 9          | 9          |
| Individuals | with one    | trip       | 0          | 1          | 2          | 0          | 0          | 4          | 2          | 9          | 0          | 1          | 1          | 2          | 2          |
| Last        | tracking    | date       | 12/07/2015 | 01/07/2016 | 01/07/2016 | 09/07/2017 | 09/07/2017 | 28/06/2016 | 29/06/2017 | 29/06/2017 | 18/07/2010 | 29/06/2011 | 29/06/2011 | 08/07/2012 | 08/07/2012 |
| First       | tracking    | date       | 10/07/2015 | 28/06/2016 | 28/06/2010 | 06/07/2017 | 06/07/2017 | 27/06/2016 | 27/06/2017 | 27/06/2016 | 19/06/2010 | 16/06/2011 | 19/06/2010 | 11/06/2012 | 11/06/2012 |
| Unique      | tracking    | days       | 3          | 4          | 45         | 4          | 4          | 2          | 3          | S          | 10         | 10         | 20         | 14         | 14         |
| Mean        | trips per   | individual | 4.56       | 5.10       | 6.52       | 4.88       | 4.88       | 1.82       | 2.17       | 2.36       | 3.27       | 2.77       | 3.04       | 3.86       | 3.86       |
| No.         | of          | trips      | 41         | 51         | 411        | 83         | 83         | 20         | 13         | 33         | 49         | 36         | 85         | 54         | 54         |
| No. of      | Individuals |            | 6          | 10         | 63         | 17         | 17         | 11         | 9          | 14         | 15         | 13         | 28         | 14         | 14         |
| Year        |             |            | 2015       | 2016       | ALL        | 2017       | ALL        | 2016       | 2017       | ALL        | 2010       | 2011       | ALL        | 2012       | ALL        |
| Lat         |             |            |            |            |            | 55.307     |            | 51.738     |            |            | 49.966     |            |            | 57.430     |            |
| Long        |             |            |            |            |            | -6.265     |            | -5.275     |            |            | -6.262     |            |            | -1.869     |            |
| Colony      |             |            |            |            |            | Rathlin    |            | Skomer     |            |            | St Martins |            |            | Whinnyfold |            |

Table S4.A1 (cont.)

Chapter 4 – Individual habitat selection

| Colony   | Year | Mean trip | ± Se | Trip        | Mean total     | ÷ Se  | Total distance  | Mean Max    | ± Se  | Max distance to |
|----------|------|-----------|------|-------------|----------------|-------|-----------------|-------------|-------|-----------------|
|          |      | duration  |      | duration    | distance       |       | travelled range | distance to |       | colony range    |
|          |      | (hrs)     |      | range (hrs) | travelled (km) |       | ( <b>km</b> )   | colony (km) |       | ( <b>km</b> )   |
| ALL      | ALL  | 6.49      | 0.26 | 0 - 96.3    | 76.85          | 2.96  | 0.1 - 1189.4    | 23.34       | 0.84  | 0.3 - 229.7     |
| Bardsey  | 2011 | 4.38      | 0.64 | 0.3 - 12.9  | 69.04          | 9.44  | 1.1 - 188.6     | 18.99       | 2.16  | 0.6 - 37.7      |
|          | ALL  | 4.38      | 0.64 | 0.3 - 12.9  | 69.04          | 9.44  | 1.1 - 188.6     | 18.99       | 2.16  | 0.6 - 37.7      |
| Bempton  | 2010 | 4.55      | 0.84 | 0.1 - 18.8  | 82.06          | 15.35 | 0.6 - 284.6     | 35.25       | 6.78  | 0.5 - 121.4     |
| Cliffs   | 2011 | 11.29     | 3.23 | 0.4 - 46.8  | 99.49          | 31.48 | 1.8 - 382.4     | 32.04       | 10.03 | 0.8 - 137.6     |
|          | 2012 | 14.89     | 3.05 | 0.3 - 58.4  | 214.49         | 42.01 | 1.1 - 695.9     | 82.39       | 15.14 | 0.9 - 220.7     |
|          | 2013 | 2.72      | 0.44 | 0 - 14.7    | 43.22          | 7.83  | 0.1 - 240.8     | 17.01       | 2.84  | 0.5 - 94.4      |
|          | 2015 | 10.68     | 2.21 | 0.2 - 88.1  | 162.59         | 29.39 | 1.3 - 899.5     | 53.61       | 8.54  | 0.5 - 195.4     |
|          | ALL  | 7.81      | 0.91 | 0 - 88.1    | 113.26         | 12.15 | 0.1 - 899.5     | 41.07       | 3.99  | 0.5 - 220.7     |
| Copinsay | 2010 | 9.19      | 1.64 | 0.2 - 30.1  | 104.27         | 33.62 | 1 - 689         | 32.37       | 10.64 | 0.6 - 229.7     |
|          | 2011 | 5.52      | 1.41 | 0.3 - 18.6  | 48.07          | 12.87 | 1.7 - 217.3     | 14.96       | 4.48  | 0.8 - 86.6      |
|          | 2012 | 4.95      | 0.78 | 0.2 - 15.7  | 68.54          | 13.01 | 1.7 - 341.8     | 24.36       | 4.92  | 0.9 - 129.9     |
|          | ALL  | 6.65      | 0.78 | 0.2 - 30.1  | 76.74          | 13.80 | 1 - 689         | 25.04       | 4.50  | 0.6 - 229.7     |
| Coquet   | 2011 | 5.04      | 0.73 | 0.3 - 14.2  | 83.32          | 11.65 | 1.1 - 221.3     | 26.98       | 3.87  | 0.7 - 77.5      |
|          | 2012 | 2.76      | 0.37 | 0.4 - 17.9  | 30.30          | 4.68  | 4.7 - 244.7     | 9.03        | 1.17  | 2.3 - 47.6      |
|          | ALL  | 3.55      | 0.37 | 0.3 - 17.9  | 48.74          | 5.69  | 1.1 - 244.7     | 15.27       | 1.78  | 0.7 - 77.5      |
| Colonsay | 2010 | 10.98     | 3.64 | 0.3 - 76.1  | 126.63         | 30.02 | 0.6 - 434.7     | 34.09       | 7.14  | 0.7 - 124.6     |
|          | 2011 | 28.05     | 4.45 | 0.9 - 96.3  | 201.18         | 33.76 | 1.7 - 806.2     | 35.78       | 4.03  | 1.1 - 76.2      |
|          | 2012 | 25.30     | 3.50 | 0.3 - 80.1  | 223.17         | 31.45 | 1.9 - 740.5     | 36.71       | 3.87  | 0.9 - 124.9     |

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| Colony      | Year | Mean trip | + Se | Trip        | Mean total     | + se  | Total distance  | Mean Max    | + Se  | Max distance to |
|-------------|------|-----------|------|-------------|----------------|-------|-----------------|-------------|-------|-----------------|
|             |      | duration  |      | duration    | distance       |       | travelled range | distance to |       | colony range    |
|             |      | (hrs)     |      | range (hrs) | travelled (km) |       | ( <b>km</b> )   | colony (km) |       | ( <b>km</b> )   |
|             | 2013 | 16.48     | 3.50 | 0.5 - 53.3  | 136.59         | 29.59 | 1.5 - 513       | 30.02       | 5.68  | 1 - 73.7        |
|             | 2014 | 12.35     | 2.46 | 0 - 78.7    | 141.97         | 34.38 | 0.4 - 1189.4    | 32.11       | 4.68  | 0.5 - 97.3      |
|             | ALL  | 19.19     | 1.67 | 0 - 96.3    | 171.29         | 15.13 | 0.4 - 1189.4    | 33.97       | 2.17  | 0.5 - 124.9     |
| Filey       | 2013 | 7.92      | 1.36 | 0.2 - 41.6  | 146.99         | 25.91 | 0.5 - 682.9     | 51.90       | 8.39  | 0.6 - 172.9     |
|             | 2015 | 10.34     | 2.42 | 0.2 - 66.4  | 161.36         | 34.60 | 1.6 - 885.1     | 53.99       | 10.34 | 0.8 - 200.6     |
|             | ALL  | 9.13      | 1.39 | 0.2 - 66.4  | 154.17         | 21.50 | 0.5 - 885.1     | 52.95       | 6.62  | 0.6 - 200.6     |
| Fowlsheugh  | 2012 | 11.89     | 1.63 | 0.4 - 31    | 200.96         | 24.23 | 6.1 - 448.6     | 74.40       | 8.31  | 3.1 - 173       |
|             | ALL  | 11.89     | 1.63 | 0.4 - 31    | 200.96         | 24.23 | 6.1 - 448.6     | 74.40       | 8.31  | 3.1 - 173       |
| Isle of May | 2013 | 9.13      | 1.36 | 0.3 - 52    | 89.68          | 12.29 | 0.6 - 386.3     | 29.50       | 3.64  | 0.7 - 78.7      |
|             | ALL  | 9.13      | 1.36 | 0.3 - 52    | 89.68          | 12.29 | 0.6 - 386.3     | 29.50       | 3.64  | 0.7 - 78.7      |
| Lambay      | 2010 | 4.05      | 0.64 | 0.3 - 12.9  | 50.03          | 6.56  | 1 - 122.8       | 19.22       | 2.29  | 0.7 - 39.6      |
|             | ALL  | 4.05      | 0.64 | 0.3 - 12.9  | 50.03          | 6.56  | 1 - 122.8       | 19.22       | 2.29  | 0.7 - 39.6      |
| Muckle      | 2012 | 3.16      | 0.58 | 0.3 - 21.4  | 50.94          | 10.11 | 3.3 - 323       | 14.44       | 3.60  | 1.5 - 121.7     |
| Skerry      | 2013 | 1.98      | 0.32 | 0.3 - 7.7   | 23.28          | 4.13  | 1 - 91.7        | 7.73        | 1.28  | 0.7 - 31.1      |
|             | 2014 | 1.17      | 0.12 | 0.2 - 7.6   | 13.79          | 1.63  | 1.2 - 120.3     | 4.84        | 0.63  | 0.7 - 47.3      |
|             | ALL  | 1.74      | 0.16 | 0.2 - 21.4  | 23.35          | 2.63  | 1 - 323         | 7.40        | 06.0  | 0.7 - 121.7     |
| Puffin      | 2010 | 2.58      | 0.22 | 0.2 - 12.8  | 29.14          | 2.70  | 0.7 - 182.1     | 9.07        | 0.95  | 0.3 - 71        |
| Island      | 2011 | 5.00      | 0.44 | 0.2 - 23.6  | 58.23          | 4.58  | 0.7 - 245.2     | 17.78       | 1.25  | 0.3 - 61.6      |
|             | 2012 | 4.94      | 0.86 | 0.2 - 52    | 67.41          | 8.32  | 0.7 - 331.6     | 21.44       | 2.50  | 0.8 - 78.1      |

Table S4.A2 (cont.)

| Colony     | Year | Mean trip         | + Se | Trip                    | Mean total                 | + Se  | Total distance          | Mean Max                   | + Se | Max distance to      |
|------------|------|-------------------|------|-------------------------|----------------------------|-------|-------------------------|----------------------------|------|----------------------|
|            |      | auration<br>(hrs) |      | auration<br>range (hrs) | aistance<br>travelled (km) |       | travelled range<br>(km) | distance to<br>colony (km) |      | colony range<br>(km) |
|            | 2015 | 5.48              | 1.50 | 0.2 - 40.7              | 40.15                      | 9.60  | 0.5 - 219.4             | 10.56                      | 2.71 | 0.4 - 68.3           |
|            | 2016 | 2.69              | 0.49 | 0.1 - 13.2              | 22.46                      | 5.00  | 0.1 - 169               | 7.27                       | 1.73 | 0.3 - 53.7           |
|            | ALL  | 3.97              | 0.27 | 0.1 - 52                | 44.14                      | 2.52  | 0.1 - 331.6             | 13.56                      | 0.76 | 0.3 - 78.1           |
| Rathlin    | 2017 | 3.44              | 0.31 | 0.2 - 14.7              | 39.67                      | 3.70  | 0.4 - 167.1             | 13.49                      | 1.29 | 0.3 - 57.1           |
|            | ALL  | 3.44              | 0.31 | 0.2 - 14.7              | 39.67                      | 3.70  | 0.4 - 167.1             | 13.49                      | 1.29 | 0.3 - 57.1           |
| Skomer     | 2016 | 9.91              | 1.93 | 0.3 - 24.2              | 87.54                      | 17.60 | 0.6 - 243.3             | 19.95                      | 3.28 | 0.4 - 44.9           |
|            | 2017 | 9.31              | 2.54 | 0.5 - 32.5              | 93.80                      | 20.88 | 2.4 - 273.7             | 25.02                      | 4.20 | 1.1 - 49.2           |
|            | ALL  | 9.68              | 1.52 | 0.3 - 32.5              | 90.00                      | 13.27 | 0.6 - 273.7             | 21.95                      | 2.58 | 0.4 - 49.2           |
| St Martins | 2010 | 3.78              | 0.39 | 0.2 - 13.6              | 61.77                      | 7.64  | 0.8 - 193.6             | 20.40                      | 3.04 | 0.7 - 69             |
|            | 2011 | 6.09              | 0.89 | 0.3 - 23.7              | 74.38                      | 16.53 | 0.9 - 332.9             | 23.02                      | 5.25 | 0.7 - 110.5          |
|            | ALL  | 4.76              | 0.45 | 0.2 - 23.7              | 67.11                      | 8.24  | 0.8 - 332.9             | 21.51                      | 2.82 | 0.7 - 110.5          |
| Whinnyfold | 2012 | 7.00              | 0.97 | 0.3 - 32.6              | 75.53                      | 11.56 | 0.5 - 320.9             | 25.28                      | 3.48 | 0.6 - 88.9           |
|            | ALL  | 7.00              | 0.97 | 0.3 - 32.6              | 75.53                      | 11.56 | 0.5 - 320.9             | 25.28                      | 3.48 | 0.6 - 88.9           |

Table S4.A2 (cont.)



Figure S4.A1. Foraging tracks of all kittiwakes from the 15 colonies in this study.

Appendix S4.B: Hidden Markov models for behavioural classification

We used the R package moveHMM (Michelot *et al.* 2016) for behavioural classification based on distributions of step lengths and turning angles. We used a gamma distribution to describe step lengths and a von Mises distribution to describe turning angles, and the Viterbi algorithm to estimate the most likely sequence of movement states based on the fitted hidden Markov model. We used distributions of step lengths and turning angles from previous classification of kittiwake behavioural classification to inform model starting parameters (Trevail *et al.* 2019a).

The hidden Markov model successfully classified kittiwake tracks into three movement types, which we use as proxies of behaviour: (1) resting: short step lengths and narrow turning angles (step:  $0.09 \pm 0.08$  km; turn:  $\mu = 0$ ,  $\kappa = 26.36$ ), (2) foraging: short-medium step lengths and wide turning angles (step:  $0.20 \pm 0.26$  km; turn:  $\mu = -0.02$ ,  $\kappa = 0.34$ ) & (3) transiting: long step lengths and narrow turning angles (step:  $1.12 \pm 0.37$  km; turn:  $\mu = 0$ ,  $\kappa = 13.24$ ). Distributions of step lengths and turning angles are given in Figure S4.B1. Using the Viterbi algorithm to determine the most likely sequence of behavioural states, 16.9% of all GPS locations were classified as resting, 54.3% as foraging and 28.8% as transiting.



Figure S4.B1. Histograms of observed step lengths (left) and turning angles (right) for GPS-tracked kittiwakes. Lines show fitted HMM state distributions for each behavioural state.



Figure S4.B2. Histogram of kittiwake locations classified as foraging only, according to distance away from the colony.

# Appendix S4.C: Environmental data

To understand the habitat preferences of kittiwakes, and environmental drivers thereof, we studied kittiwake foraging behaviour in the context of seven environmental metrics, all known to influence resource distributions relevant to foragers: (1) bathymetry, (2) potential tidal stratification, (3) sea surface temperature, (4) ocean front strength, (5) persistence and (6) distance, and (7) environmental heterogeneity. Here, we describe the relevance of each variable as well as methods of collation and calculation.

(1) Bathymetry, or sea floor depth, can influence both the movement of horizontal water currents and the vertical structure of the water column (e.g. Genin 2004, Stevick et al. 2008). Such physical features can drive the distributions and behaviours of prey species, with knock on effects for prey availability and accessibility to higher trophic levels (e.g. Genin 2004, Stevick et al. 2008, Embling et al. 2013, Jones et al. 2014). Bathymetry data were collated from the UK Hydrographic Office (UKHO) Data Archive Centre for bathymetric surveys (high resolution boat survey data between 2 and 4 m resolution) and integrated with the 2014 General Bathymetric Chart of the Oceans (GEBCO). UKHO data contains public sector information, available under the Open Government Licence as part of the INSPIRE initiative.

(2) Potential tidal stratification is an index for vertical water column structure in areas shallower than 200 m (Simpson & Hunter 1974; Scott *et al.* 2010). It is a useful static variable since it incorporates both depth and tidal current values (Scott *et al.* 2010), both of which are individually important (Embling *et al.* 2013), but together control the degree of vertical mixing – a key physical driver of marine ecosystem dynamics. Low values of potential tidal stratification indicate a typically well-mixed water column, often characterised by a spread of resources throughout the water column. In deep waters, vertical mixing can restrict access to prey for surface foraging seabirds (Carroll et al. 2015). High values indicate a typically more stratified water column, comprised of vertically distinct layers with reduced transfer of abiotic and biotic matter between layers (Carroll et al. 2015). Stratification is often associated with nutrient blooms that are caused by the entrainment of nutrients into shallow waters, which in turn facilitates primary production and again a cascading effect up the trophic web (Embling et al. 2012). Potential tidal stratification is calculated as  $\log_{10}(h/U^3)$ , where h is water column depth, described above, and U is the sum of tidal amplitude from both the M2 (semidiurnal lunar tide) and S2 (semidiurnal solar tide) tidal constituents (Simpson & Hunter 1974). This represents a spring tide scenario that would have the most potential to erode stratification, if present. Tidal amplitudes were generated from a 3D hydrostatic simulation of the North West European shelf using the NEMO AMM60 configuration (Guihou et al. 2018). The simulation has 51 stretched layers in the vertical and a resolution of 1.8 km in the horizontal. A barotropic harmonic analysis was performed on the simulation and the M2 and S2 constituents are processed here (as the most energetic constituents). The tidal speeds are defined as the barotropic velocity maxima, over the tidal cycle. Potential tidal stratification performs well as a predictor of seasonal thermal stratification in shelf sea areas, although interpretation of absolute values requires caution in regions where stratification is influenced by salinity as a result of freshwater riverine inputs (Polton et al. 2011), or in seasons where there is no thermal stratification.

(3) Sea surface temperature (SST) can both indicate oceanographic processes that influence water column structure and nutrient availability, such as upwelling of cold nutrient rich water (Benazzouz *et al.* 2014), and can be a proxy for the quality of prey availability (Carroll *et al.* 2016). SST data were derived from seven-day composites of advanced very high-resolution radiometer data, at a resolution of approximately 1.2 km.

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(4-6) Ocean fronts are horizontal boundaries between different water masses where resource availability is typically enhanced because of physical processes that cause upwelling of deeper, nutrient rich water (Franks 1992a, b). Fronts are therefore known to be an important feature of marine environments, shaping resource distribution and thus marine vertebrate behaviour (Scales et al. 2014; Waggitt et al. 2018). Frontal contours were detected using local regional statistics on daily SST scenes from AVHRR satellite data, at a resolution of approximately 1.2 km, and then combined into 8-day composite front maps (Miller 2009). Here we include three parameters related to ocean fronts (Miller et al. 2015), all of which will influence resource availability to a central place forager: (1) Front strength gives the mean thermal gradient magnitude of detected fronts, spatially smoothed to give a continuous distribution of frontal activity. (2) Front distance indicates the distance at each pixel to the closest major front, determined using a simplified version of the frontal strength map. (3) Front persistence indicates the fraction of cloud-free observations of a pixel for which a front was detected, i.e. whether fronts are temporally persistent or only short-lasting, spatially smoothed to give a continuous distribution.

(7) Environmental heterogeneity is a measure of the diversity of environmental variables, indicative of the heterogeneity of habitat types and therefore resource distributions, and has been shown to influence seabird foraging behaviour and fitness (Trevail *et al.* 2019b). Environmental heterogeneity was calculated based on the above environmental variables as a single value for each colony (bathymetry, potential tidal stratification, SST, front strength, front distance and front persistence) using a multivariate dispersion analysis, detailed in Trevail *et al.* (2019b).



Figure S4.C1. Study area showing: (A) kittiwake colony locations; (B) bathymetry; (C) tidal stress; (D) potential tidal stratification; (E) sea surface temperature, averaged over all study years (2010-17); and (F) front strength, averaged over all study years (2010-2017).

Appendix S4.D – Available point selection for resource selection models

Quantification of an animal's habitat selection preferences using resource selection models is dependent on the data that models are based upon (Manly *et al.* 2002). In our study, we infer habitat preferences by comparing direct observations of animals from bio-logging data, namely 'used' locations, to a dataset of randomly generated pseudoavailable locations, namely 'available' locations. For bio-logging studies, the number of used locations can vary because of the animal's ecology, such as the duration of foraging trips, or because of sampling artefacts that can vary the amount of time the device was actively tracking the individual, such as field site logistics or device battery life. In contrast, the selection of available locations is decided by the researcher conducting the analyses, and varies between studies. Therefore, the selection of available locations for resource selection analyses is a key consideration to accurately quantify animal habitat preferences.

Here, we present analyses to understand how the selection of available locations can influence model outputs, both at the population and individual levels (S4.D.1) as well as the number of available points necessary for accurate model results (S4.D.2). We use analyses below of both simulated data and actual kittiwake data used to inform the generation of available data presented in the main paper. All associated R code is given at the end of this appendix.

#### S4.D.1 Ratio of used to available points in sampling design

Typically, studies of animal resource selection using bio-logging derived 'used' locations can either compare used locations to an equal number of available locations per individual, e.g. 1000 available locations per individual (Gillies *et al.* 2006); or a constant ratio of used to available locations for all individuals, e.g. 10 available locations per used location (Leclerc *et al.* 2016; Trevail *et al.* 2019a). Here, we test how model outputs vary between these two methods for selecting available locations. We present habitat selection results for two simulated populations, comprising five individuals each, with different sampling designs for available locations: *simulation A*: an equal number of available locations per individual (Table S4.D1); and *simulation B*: a constant ratio of used to available locations for all individuals (Table S4.D1).

Table S4.D1. Sample sizes of used and available locations for 5 individuals from each simulated population:

| Individual | No. used locations | No. available locations               | Ratio used : available      |
|------------|--------------------|---------------------------------------|-----------------------------|
|            | Simulation 2       | A: equal number of availabl           | e locations per individual  |
| 1          | 200                | 3000                                  | 1:15                        |
| 2          | 400                | 3000                                  | 1:7.5                       |
| 3          | 600                | 3000                                  | 1:5                         |
| 4          | 800                | 3000                                  | 1:3.75                      |
| 5          | 1000               | 3000                                  | 1:3                         |
|            | Simu               | <i>llation B:</i> constant ratio of u | used to available locations |
| 1          | 200                | 1000                                  | 1:5                         |
| 2          | 400                | 2000                                  | 1:5                         |
| 3          | 600                | 3000                                  | 1:5                         |
| 4          | 800                | 4000                                  | 1:5                         |
| 5          | 1000               | 5000                                  | 1:5                         |

To ensure that results reflect differences in sample design only, in both simulated populations all individuals had available locations derived from the same random normal distribution (mean = 100, SD = 40) and the same distribution parameters for their individual used habitats (mean = 160, SD = 5), i.e. we expect to observe the same habitat preferences between the two populations (Figure S4.D1.a). To understand the effect of available location sampling design on model outputs, we ran a mixed effects model of habitat selection for each population with individual ID as a random slope and intercept, and present outputs both as log-odds (Figure S4.D1.b) and probabilities (Figure D1.c) of habitat selection.
Model results indeed revealed positive habitat selection preferences by both populations (parameter estimates for the slope of habitat selection were >0 in both populations; Table S4.D2). However, incorporating a random slope and intercept for each individual revealed that the sampling design of available points led to differences in model results for both population and individual habitat selection preferences (Table S4.D2).

In Simulation A, where there were equal numbers of available locations for all individuals and therefore a different ratio of used to available points (Table S4.D1), habitat selection models resulted in different estimates for slope and intercept for each individual (Figure S4.D1.b). The individual with the greatest number of used points and a 1:3 ratio of used to available points, individual 5, had the highest value of intercept and the steepest slope estimate, i.e. the strongest modelled habitat selection, despite using habitat from the same distribution as all other individuals. We can understand this as follows: as the number of used points increases relative to the number of available points, this effectively increases the overall probability of observing the individual within the sampled habitat. Therefore, the intercept increases - i.e. at any given location within the sampled habitat, there is a greater probability of observing individual 5 compared to individuals 1 - 4 (Figure S4.D1.c). Furthermore, because individuals positively select habitat, we only observe the individuals within a subset of the available habitat, i.e. their preferred habitat. Therefore, as the ratio of used to available locations increases, this increases the probability of observing the individual within this subset of habitat. This is balanced (because probabilities are constrained between 0 and 1) by a resulting decrease in the probability of observing the individual outside its preferred habitat. Therefore, because of this change in probability along the environmental gradient, the slope of habitat selection also increases. For more explanation of slopes and intercepts in resource selection models, see Appendix S4.E.

In Simulation B, however, where sampling design used a constant ratio of used to available locations (Table S4.D1), habitat selection models accurately determined equal habitat preferences between all individuals (Figure S4.D1.b & c), because the overall probability of observing any individual is constant between individuals.

Based on these analyses, in the main study we used a constant ratio of used to available locations for all individuals to ensure that model results of population and individual parameter estimates accurately reflects differences in habitat preferences, rather than differences in number of observations between individuals.

Table S4.D2. Parameter estimates for population level habitat selection from resource selection models for each simulated population, with individual ID as a random effect:

|  | Simulation A:             | Simulation B:             |
|--|---------------------------|---------------------------|
|  | equal number of available | constant ratio of used to |
| Model output                           | locations per individual  | available locations       |
| Population intercept (± se)            | -3.67 ± 0.11              | $-3.73 \pm 0.07$          |
| Population slope (± se)                | $2.98 \pm 0.21$           | $3.21\pm0.06$             |
| Variance explained by random intercept | $0.03 \pm 0.11$           | $0.00\pm0.00$             |
| Variance explained by random slope     | $0.21\pm0.46$             | $0.00\pm0.00$             |



Figure S4.D1. Habitat selection by five individuals from two simulated populations: *Simulation A*: equal number of available locations for all individuals; and *Simulation B*: constant ratio of used to available locations. Habitat selection presented as: (a) frequency densities of population available habitat (black dashed line) and individual used habitat (solid lines); (b) log-odds from resource selection functions to visualise changes in intercept and slope; and (c) probabilities from resource selection functions (inverse logit link). Both populations are comprised of individuals that use habitat from the same distributions (plot a). For Simulation A, the difference in ratio of used and available points between individuals results in different intercepts and slopes of habitat selection for each individual (plots b-c). For Simulation B, the same ratio of used and available points between individuals, hence why there only appears to be a habitat selection curve for one individual (plots b-c).

S4.D.2 Number of random points for accurate measurement of individual variance

To determine the number of available points to include per used point for our data, we ran kittiwake habitat selection models for bathymetry, with between one and ten available points, and tested for differences in model parameter estimates at the species, population and individual levels. Points were weighted accordingly. We ran models with the same structure as presented in the main paper, and extracted model slopes (species level), random slope estimates for each colony-year (population level) and random intercept estimates for each trip (individual level). At the species level, we visually determined the number of points above which there was no change in slope estimate, and validated this with a linear regression to test whether, above this number of random points, there was a difference in slope estimates. At the population and individual level, we used a linear model with a random effect (colony-year or trip) to determine whether the number of random points effected model estimates.

At the species level, there were no significant differences in the slope estimates when two or more random points were included in the model ( $F_{1,5}=2.3$ , p=0.05; Figure S4.D2). At both the population level and individual level, there was no effect of the number of random points and model parameter estimates ( $\chi^{2}_{9}=2.29$ , p=1.0; and  $\chi^{2}_{9}=0$ , p=1.0, respectively).

To ensure that habitat availability was not biased where remote sensing data (sst and ocean fronts) can be obscured by e.g. cloud cover, and against coastal regions outside of gridded modelled tide data (for stratification), we used the same random points for all habitat selection models and retained foraging points of kittiwakes as used locations where points were matched with environment data at the used location and all 5 available data points. This retained all used kittiwake locations for bathymetry (137774 used points, 1534 trips & 410 individuals), 128923 used points for potential tidal stratification (1528 trips & 410 individuals), 96790 used points for front strength

and persistence (1493 trips & 405 individuals), 75311 used points for front distance (1270 trips & 378 individuals) and 86858 used points for sea surface temperature (1364 trips & 399 individuals).



Figure S4.D2. The slope of habitat selection remained statistically constant above 2 random points.

# R Code - Appendix S4.D data simulations

#### 1. Ratio of used to available points in sampling design ####

library(truncnorm)

library(ggplot2)

library(lme4)

library(boot)

#### Simulation A: Equal available locations ####

# create available data

avail=as.data.frame(cbind(indID=c(rep("1",3000),rep("2",3000),rep("3",3000), rep("4",3000),

rep("5",3000)),

y=0))

avail\$value=rnorm(15000,mean=100,sd=40)

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=200, a=min(avail\$value),

b=max(avail\$value), mean=160, sd=5)))

ind2 <- as.data.frame(cbind(value = rtruncnorm(n=400, a=min(avail\$value),

b=max(avail\$value), mean=160, sd=5)))

ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail\$value),

b=max(avail\$value), mean=160, sd=5)))

ind4 <- as.data.frame(cbind(value = rtruncnorm(n=800, a=min(avail\$value),

b=max(avail\$value), mean=160, sd=5)))

ind5 <- as.data.frame(cbind(value = rtruncnorm(n=1000, a=min(avail\$value),

b=max(avail\$value), mean=160, sd=5)))

# give individual IDs
ind1\$indID <- "1"</pre>

ind2\$indID <- "2"

ind3\$indID <- "3"

ind4\$indID <- "4" ind5\$indID <- "5" used <- rbind(ind1, ind2, ind3, ind4, ind5) used\$y <- "1"

# plot frequency density

ggplot(avail, aes(x=value))+

stat\_density(geom="line", linetype = "dashed", position = "identity")+

stat\_density(data = used, geom="line", aes(colour= indID), position = "identity")

# combine data

popA <- rbind(avail, used)</pre>

# standardise explanatory variable

popA\$value.st <- (popA\$value-mean(popA\$value))/sd(popA\$value)

# habitat selection model

m1 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popA)

# plot model outputs

popA\$fit <- predict(m1)</pre>

ggplot(popA,aes(value, fit, col= indID))+

geom\_line()

ggplot(popA,aes(value, inv.logit(fit), col= indID))+

geom\_line()

#### Simulation B: Constant ratio of used to available locations ####

# create available data

availB=as.data.frame(cbind(indID=c(rep("1",1000),rep("2",2000),rep("3",3000), rep("4",4000), rep("5",5000)),

y=0))

availB\$value=rnorm(15000,mean=100,sd=40)

# create used data

ind1B <- as.data.frame(cbind(value = rtruncnorm(n=200, a=min(availB\$value), b=max(availB\$value), mean=160, sd=5))) ind2B <- as.data.frame(cbind(value = rtruncnorm(n=400, a=min(availB\$value), b=max(availB\$value), mean=160, sd=5))) ind3B <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(availB\$value), b=max(availB\$value), mean=160, sd=5))) ind4B <- as.data.frame(cbind(value = rtruncnorm(n=800, a=min(availB\$value), b=max(availB\$value), mean=160, sd=5))) ind5B <- as.data.frame(cbind(value = rtruncnorm(n=1000, a=min(availB\$value), b=max(availB\$value), mean=160, sd=5)))

# give individual IDs ind1B\$indID <- "1" ind2B\$indID <- "2" ind3B\$indID <- "3" ind4B\$indID <- "4" ind5B\$indID <- "5" usedB <- rbind(ind1B, ind2B, ind3B, ind4B, ind5B) usedB\$y <- "1"

# plot frequency density

ggplot(availB, aes(x=value))+

stat\_density(geom="line", linetype = "dashed", position = "identity", size = 1)+

stat\_density(data = usedB, geom="line", aes(colour= indID), position = "identity", size = 1)

# combine data

popB <- rbind(availB, usedB)</pre>

# standardise explanatory variable

popB\$value.st <- (popB\$value-mean(popB\$value))/sd(popB\$value)

# habitat selection model

m2 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popB)

# plot model outputs

popB\$fit <- predict(m2)</pre>

ggplot(popB,aes(value, fit, col= indID))+

 $geom\_line()$ 

ggplot(popB,aes(value, inv.logit(fit), col= indID))+

 $geom\_line()$ 

Appendix S4.E – Intercepts and slopes in resource selection models

Resource selection functions (also known as habitat selection functions/models) approximate an animal's resource or habitat preference by comparing the subset of habitat used by the animal to the habitat that was available. In such models, behaviour is quantified on a linear scale using intercepts and slopes. In our study, we sought to quantify habitat selection of kittiwakes at the species, population, and individual levels. Published studies that discuss resource selection model structure state that random intercepts can be used to account for differences in sample sizes between individuals (Gillies et al. 2006) and/or that random effects can account for differences in habitat preferences of individuals (Lesmerises & St-Laurent 2017). To ensure appropriate model structure and accurate interpretation of kittiwake behaviour at all three group levels, we here present analyses of simulated data with the aim of understanding how the intercepts and slopes derived from resource selection models can be used to infer behaviour. We do not present these supplementary analyses as an alternative to the many detailed and mathematical explanations of resource selection models e.g. (Boyce et al. 1999; Manly et al. 2002), since knowledge of the underlying mathematical principles and assumptions are vital when applying models to animal data. Rather, we present these analyses as a tool for visualising and understanding how different ecological scenarios can be quantified and therefore interpreted in behavioural terms using resource selection models. All R code for data simulations and models described below is given at the end of this appendix.

#### Data simulation

To understand how intercepts and slopes from resource selection functions can be used to interpret behaviour, we present analyses of six populations (A - F)representing different ecological scenarios (Table S4.E1):

- A) No habitat preference at either the population or individual level
- B) Population level habitat preference, no individual habitat specialisations: all individuals with the same habitat selection (mean) and the same variance in habitat use (sd)
- C) Population level habitat preference, no individual habitat specialisations: all individuals with the same habitat selection (mean); but different variance in individual habitat use (sd)
- D) Population level habitat preference, and individual habitat specialisations:
   different habitat selection between individuals (mean)
- E) Different available habitat between individuals, population and individual level habitat preference. All individuals have a mean habitat use that is a constant value above the mean available habitat (i.e. for an individual with mean available habitat = 50, mean used habitat = 70; for an individual with mean available habitat = 60, mean used habitat = 80)
- F) Different available habitat between individuals, population level habitat preference, functional habitat selection by individuals: all individuals have the same preferred habitat (i.e. when mean available habitat = 50, mean used habitat = 70; when mean available habitat = 60, mean used habitat = 70)

Table S4.E1 (overleaf). Available and used habitat (mean  $\pm$  sd) for six simulated populations, each comprising five individuals, as well as habitat frequency density curves. Available habitat frequency densities (dashed lines in right column) are given for the population where individuals have the same available habitat (populations A – D), and for all individuals where available habitat differs (populations E – F).

| Individual     | Available habitat        | Used habitat             | Habitat frequency dens        | ity                      |
|----------------|--------------------------|--------------------------|-------------------------------|--------------------------|
| Population A   | : No habitat preferenc   | e at population or ind   | lividual level                |                          |
| 1              |                          |                          | A                             | Habitat                  |
| 2              | -                        |                          |                               | Used                     |
| 3              | 140 ± 40                 | $140 \pm 40$             |                               | Individual               |
| 4              | -                        |                          |                               | 2<br>3                   |
| 5              | -                        |                          |                               | 4<br>5                   |
| Population B   | : Population habitat p   | reference, individuals   | with the same habitat select  | ion                      |
| 1              |                          |                          | ٨                             | Habitat                  |
| 2              | -                        |                          | ň                             | Available<br>Used        |
| 3              | 140 ± 40                 | 180 ± 10                 |                               | Individual               |
| 4              | -                        |                          |                               | <u> </u>                 |
| 5              | -                        |                          |                               | <u> </u>                 |
| Population C   | : Population habitat p   | reference, individuals   | with the same mean habitat    | use but                  |
| different sd   |                          |                          |                               |                          |
| 1              |                          | 160 ± 5                  | ٨                             | Habitat                  |
| 2              | -                        | 160 ± 10                 | -                             | Used                     |
| 3              | 140 ± 40                 | 160 ± 15                 | _                             | Individual               |
| 4              | -                        | 160 ± 20                 | - A                           | 2<br>3                   |
| 5              | -                        | 160 ± 30                 |                               | 4<br>5                   |
| Population D   | P: Population level habi | itat preference, differe | ent habitat selection between | individuals              |
| 1              |                          | 160 ± 10                 | ~ ^ ^ ^ ^ ^                   | Habitat                  |
| 2              | -                        | 180 ± 10                 |                               | - Used                   |
| 3              | 140 ± 40                 | 200 ± 10                 |                               | Individual               |
| 4              | -                        | 220 ± 10                 | -++                           | 2<br>3                   |
| 5              | -                        | 240 ± 10                 |                               | 4<br>5                   |
| Population E   | : Population level habi  | tat preference, differe  | ent available habitat between | individuals,             |
| all individual | s with habitat selectior | n a constant value abo   | ove the mean available habite | at                       |
| 1              | 100 ± 40                 | 140 ± 10                 | - AN AN-                      | Habitat<br>– – Available |
| 2              | 120 ± 40                 | 160 ± 10                 |                               | Used                     |
| 3              | 140 ± 40                 | 180 ± 10                 |                               |                          |
| 4              | 160 ± 40                 | 200 ± 10                 |                               | 2<br>3                   |
| 5              | 180 ± 40                 | 220 ± 10                 |                               | 4<br>5                   |
| Population F   | : Population level habi  | tat preference, differe  | ent available habitat between | individuals,             |
| all individual | s with the same preferr  | ed habitat               |                               |                          |
| 1              | 100 ± 40                 | _                        | ٨                             | Habitat<br>Available     |
| 2              | 120 ± 40                 | _                        |                               | - Used                   |
| 3              | 140 ± 40                 | 200 ± 10                 |                               |                          |
| 4              | 160 ± 40                 | _                        | 17933                         | 2<br>3                   |
| 5              | 180 ± 40                 |                          |                               | 4<br>5                   |

# Models

To model population level habitat selection, we ran resource selection as binomial models with habitat use as the response varaiable (0 = available, 1 = used), with habitat as a fixed effect. To understand how the intercept and slope vary and co-vary with behaviours exhibited in the simulated populations (Table S4.E1), we fitted three different models for each population with individual ID as a random effect, but with different random effect structures:

- 1) Random intercept only (model structure: y ~ habitat + (1 | individual ID))
- 2) Random slope only (model structure: y ~ habitat + (-1 + habitat | individual ID))
- Random intercept and slope (model structure: y ~ habitat + (1 + habitat | individual ID))

Table S4.E2 details population level habitat selection slope and intercepts that indicate population behaviour, as well as individual model coefficients that indicate how differences in behaviour are quantified by the models. Table S4.E2 also gives model AIC values, which favours minimum complexity, to indicate which random effect structure is most appropriate.

#### Results

#### Population A: No habitat preference at population or individual level

As expected, the slope of habitat selection was not significant in all three models of habitat selection for population A (p = 0.63), confirming that there was no effect of the habit value on whether an animal was present or not. Furthermore, and again as expected, model coefficients for the five individuals were the same in all three models with different random effect structures (Table S4.E2), which reflects that all individuals had the same used habitat distributions (Table S4.E1). The models with fewer random effects (either just intercept, or just slope) are favoured by AIC values.

# Population B: Population habitat preference, individuals with the same habitat selection

As expected, a positive population level slope confirmed habitat selection at the population level, i.e. animals were more likely to be present at higher values of the habitat variable. As with population A, model coefficients for the five individuals were the same in all three models with different random effect structures (Table S4.E2), which is as we expected given that all individuals had the same used habitat distributions (Table S4.E1). Again, the models with fewer random effects (either just intercept, or just slope) are favoured by AIC values.

# Population C: Population habitat preference, individuals with the same mean habitat use but different standard deviation

As with population B, a positive population level slope confirmed selection for higher values of the habitat variable by the population. Despite the fact that all individuals had different variances of habitat use (i.e. different sd), model coefficients for the five individuals were the same in all three models with different random effect structures (Table S4.E2). This shows that both the intercept and slope are driven by differences in mean habitat values. For an individual with a wider range of used habitat values, the larger range of used habitat values above the mean will be compensated for by the larger range of used habitat values below the mean, hence the slope and intercept remain the same. The models with fewer random effects (either just intercept, or just slope) are favoured by AIC values.

Population D: Population level habitat preference, different habitat selection between individuals

Here, where individuals show specialised habitat preferences, we do find a difference between individual coefficients in all three models (Table S4.E2). Individual specialisations are quantified by the random intercept model. Here we see that individual 1, whose habitat preference is most similar to the available habitat, has the

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highest intercept. We can interpret this as a higher probability of observing individual 1 across all habitat values, which makes sense given that out of all five individuals, individual 1 preferentially selects for habitat that is closest to the mean available habitat, i.e. the most abundant. In contrast, individual 5 preferentially uses the most extreme values compared to the mean available habitat, i.e. the least common habitat values, and hence has the lowest intercept (Table S4.E2). The random slope only model indeed gives different coefficient values for each individual, however does not seem to perform well according to AIC values or the order in which individual slopes rank from lowest to highest - we would expect the steepest slope for individual 5, whose used habitat is the furthest from the mean available. Instead, the steepest slope of habitat selection is given for individual 3. The random intercept and slope model is favoured by AIC selection, and correctly shows a negative co-variance between individual intercepts and slopes. As an individual's mean used habitat increases away from the mean, the intercept decreases in line with a lower probability of presence and the slope increases reflecting an increased preference for higher habitat values (Table S4.E2).

Population E: Population level habitat preference, different available habitat between individuals, all individuals select habitat above the mean available habitat

Individual habitat selection here is accurately described by the random intercept only model. The random slope model again does not perform well by AIC selection, or the order in which individual's slopes are ranked. In the model with a random slope and intercept, the slope coefficients are almost the same for all individuals, which we would expect given that the individuals' mean used habitat values are a constant value above their own mean available habitat.

Population F: Population level habitat preference, different available habitat between individuals, all individuals with the same preferred habitat (i.e. functional response)

Here, the random intercept and slope model performs best at explaining habitat selection (Table S4.E2). All individuals have the same mean used habitat, and so the relative difference between used and available habitats drives the differences between slopes and intercepts. In contrast to populations D and E, the random slope model here performs better than the random intercept model in terms of AIC, and correctly ranks the individual slopes as we would expect. In the random intercept only model, individual one has the highest intercept despite having the biggest difference between used and available habitats, which is the opposite of what we would expect based on results from Populations D and E. The random intercept and slope model ranks the intercepts as we would expect based on the individual's own available habitat, and the slope coefficients vary in line with a functional behavioural response to the habitat variable.

Table S4.E2 (overleaf). Habitat selection by six simulated populations, each comprising of five individuals. For each simulation, we present habitat density curves from Table S4.E1., alongside model outputs from the three resource selection models with varying random effect structures: random intercept only, random slope only, and both a random intercept and slope. We present model outputs as plots of habitat use for all individuals separately (for populations A – C, parameter estimates are the same for all individuals, hence lines overlap and appear as one) both on the log-odds scale (fitting the assumptions of linear models) and probability scale (transformed model output). We also present the model parameter estimates for the intercept and slope at the population level (p value only given when non-significant, else p < 0.05), and for all five individuals. Lastly, we give model AIC values to indicate model fit.

|                                       | Intercept only              |                              | Slope only                   |                              | Intercept and slope          |                              |
|---------------------------------------|-----------------------------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
|                                       | $y \sim habitat + (1   inc$ | lividual ID)                 | $y \sim habitat + (-1 + ha)$ | bitat   individual ID)       | $y \sim habitat + (1 + hab)$ | itat   individual ID)        |
| Population A: No habitat <sub>l</sub> | rreference at populatio     | n or individual level        |                              |                              |                              |                              |
|                                       | Log-odds scale              | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>     |
|                                       |                             |                              |                              |                              |                              |                              |
| Parameter estimates                   | Intercept                   | Slope                        | Intercept                    | Slope                        | Intercept                    | Slope                        |
| Population                            | $-1.61 \pm 0.02$            | $0.01 \pm 0.02 \ (p = 0.63)$ | $-1.61 \pm 0.02$             | $0.01 \pm 0.02 \ (p = 0.63)$ | $-1.61 \pm 0.02$             | $0.01 \pm 0.02 \ (p = 0.63)$ |
| Individual 1                          |                             |                              |                              |                              |                              |                              |
| Individual 2                          | 1                           |                              |                              |                              |                              |                              |
| Individual 3                          | -1.61                       | 0.01                         | -1.61                        | 0.01                         | -1.61                        | 0.01                         |
| Individual 4                          | I                           |                              |                              |                              |                              |                              |
| Individual 5                          | I                           |                              |                              |                              |                              |                              |
| Model AIC                             | 16226                       |                              | 16226                        |                              | 16230                        |                              |
| Population B: Population I            | abitat preference, indi     | viduals with the same hab    | itat selection               |                              |                              |                              |
|                                       | Log-odds scale              | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>     |
|                                       |                             |                              |                              |                              |                              |                              |
| Parameter estimates                   | Intercept                   | Slope                        | Intercept                    | Slope                        | Intercept                    | Slope                        |

|                                   | Intercept only              |                           | Slope only                   |                          | Intercept and slope          | a                        |
|-----------------------------------|-----------------------------|---------------------------|------------------------------|--------------------------|------------------------------|--------------------------|
|                                   | $y \sim habitat + (1   ind$ | lividual ID)              | $y \sim habitat + (-1 + ha)$ | bitat   individual ID)   | $y \sim habitat + (1 + hal)$ | bitat   individual ID)   |
| Population                        | $-2.14 \pm 0.03$            | $1.41 \pm 0.03$           | $-2.14 \pm 0.03$             | $1.41 \pm 0.03$          | $-2.14 \pm 0.03$             | $1.41 \pm 0.03$          |
| Individual 1                      |                             |                           |                              |                          |                              |                          |
| Individual 2                      |                             |                           |                              |                          |                              |                          |
| Individual 3                      | -2.14                       | 1.41                      | -2.14                        | 1.41                     | -2.14                        | 1.41                     |
| Individual 4                      |                             |                           |                              |                          |                              |                          |
| Individual 5                      |                             |                           |                              |                          |                              |                          |
| Model AIC                         | 13231                       |                           | 13231                        |                          | 13235                        |                          |
| Population C: Population <i>I</i> | nabitat preference, indi    | viduals with the same mee | ın habitat use but diffe     | rent sd                  |                              |                          |
|                                   | Log-odds scale              | <b>Probability scale</b>  | Log-odds scale               | <b>Probability scale</b> | Log-odds scale               | <b>Probability scale</b> |
|                                   |                             |                           |                              |                          |                              |                          |
|                                   |                             |                           |                              |                          |                              |                          |
| Parameter estimates               | Intercept                   | Slope                     | Intercept                    | Slope                    | Intercept                    | Slope                    |
| Population                        | $-1.71 \pm 0.02$            | $0.57 \pm 0.02$           | $-1.71 \pm 0.02$             | $0.57 \pm 0.02$          | $-1.71 \pm 0.02$             | $0.57 \pm 0.02$          |
| Individual 1                      |                             |                           |                              |                          |                              |                          |
| Individual 2                      |                             |                           |                              |                          |                              |                          |
| Individual 3                      | -1.71                       | 0.57                      | -1.71                        | 0.57                     | -1.71                        | 0.57                     |
| Individual 4                      |                             |                           |                              |                          |                              |                          |
| Individual 5                      |                             |                           |                              |                          |                              |                          |
| Model AIC                         | 15483                       |                           | 15483                        |                          | 15487                        |                          |

|                          | Intercent only              |                              | Slone only                   |                           | Intercent and slone         |                          |
|--------------------------|-----------------------------|------------------------------|------------------------------|---------------------------|-----------------------------|--------------------------|
|                          | $y \sim habitat + (1   ind$ | ividual ID)                  | $y \sim habitat + (-1 + ha)$ | bitat   individual ID)    | $y \sim habitat + (1 + ha)$ | oitat   individual ID)   |
| Population D: Population | level habitat preference    | , different habitat selectio | n between individuals        |                           |                             |                          |
|                          | Log-odds scale              | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>  | Log-odds scale              | <b>Probability scale</b> |
|                          |                             |                              |                              |                           |                             |                          |
| Parameter estimates      | Intercept                   | Slope                        | Intercept                    | Slope                     | Intercept                   | Slope                    |
| Population               | $-2.81 \pm 0.26$            | $2.24 \pm 0.04$              | $-2.58 \pm 0.04$             | $1.90 \pm 0.18$           | <b>-4.68</b> ± <b>1.44</b>  | 3.25 ± 0.91              |
| Individual 1             | -2.10                       |                              |                              | 1.16                      | -1.61                       | 0.75                     |
| Individual 2             | -2.34                       |                              |                              | 2.17                      | -2.05                       | 1.71                     |
| Individual 3             | -2.76                       | 2.24                         | -2.58                        | 2.22                      | -3.18                       | 2.73                     |
| Individual 4             | -3.21                       |                              |                              | 2.07                      | -6.40                       | 4.77                     |
| Individual 5             | -3.66                       |                              |                              | 1.89                      | -10.04                      | 6.23                     |
| Model AIC                | 10480.5                     |                              | 10729.1                      |                           | 9378.5                      |                          |
| Population E: Population | evel habitat preference,    | different available habito   | at between individuals,      | all individuals select ab | ove the mean available      | e habitat                |
|                          | Log-odds scale              | <b>Probability scale</b>     | Log-odds scale               | <b>Probability scale</b>  | Log-odds scale              | <b>Probability scale</b> |
|                          |                             |                              |                              |                           |                             |                          |
| Parameter estimates      | Intercept                   | Slope                        | Intercept                    | Slope                     | Intercept                   | Slope                    |

|                          | Intercept only            |                            | Slope only                   |                          | Intercept and slope          |                          |
|--------------------------|---------------------------|----------------------------|------------------------------|--------------------------|------------------------------|--------------------------|
|                          | y ~ habitat + (1   indi   | ividual ID)                | $y \sim habitat + (-1 + ha)$ | oitat   individual ID)   | $y \sim habitat + (1 + hab)$ | itat   individual ID)    |
| Population               | $-2.15 \pm 0.44$          | $1.74 \pm 0.04$            | $-1.87 \pm 0.03$             | $1.22 \pm 0.20$          | $-2.19 \pm 0.46$             | $1.74 \pm 0.05$          |
| Individual 1             | -0.76                     |                            |                              | 0.98                     | -0.78                        | 1.66                     |
| Individual 2             | -1.46                     |                            |                              | 1.88                     | -1.45                        | 1.69                     |
| Individual 3             | -2.12                     | 1.74                       | -1.87                        | 1.54                     | -2.12                        | 1.73                     |
| Individual 4             | -2.85                     |                            |                              | 1.00                     | -2.89                        | 1.78                     |
| Individual 5             | -3.56                     |                            |                              | 0.68                     | -3.68                        | 1.82                     |
| Model AIC                | 13232                     |                            | 14107                        |                          | 13233                        |                          |
| Population F: Population | level habitat preference, | different available habite | at between individuals,      | all individuals with the | same preferred habitat       |                          |
|                          | Log-odds scale            | <b>Probability scale</b>   | Log-odds scale               | <b>Probability scale</b> | Log-odds scale               | <b>Probability scale</b> |
|                          |                           |                            |                              |                          |                              |                          |
| Parameter estimates      | Intercept                 | Slope                      | Intercept                    | Slope                    | Intercept                    | Slope                    |
| Population               | $-2.78 \pm 0.39$          | $2.48 \pm 0.04$            | $-2.88 \pm 0.05$             | $3.03 \pm 0.65$          | $-3.41 \pm 0.43$             | <b>3.70 ± 1.10</b>       |
| Individual 1             | -1.62                     |                            |                              | 5.16                     | -4.84                        | 7.46                     |
| Individual 2             | -2.09                     |                            |                              | 4.12                     | -4.10                        | 5.51                     |
| Individual 3             | -2.76                     | 2.48                       | -2.88                        | 2.73                     | -3.14                        | 2.98                     |
| Individual 4             | -3.40                     |                            |                              | 1.87                     | -2.66                        | 1.70                     |
| Individual 5             | -4.04                     |                            |                              | 1.24                     | -2.32                        | 0.84                     |
| Model AIC                | 10589.4                   |                            | 9538.1                       |                          | 9383.8                       |                          |

Implications for our understanding of slopes and intercepts

In the context of understanding resource selection function slopes and intercepts, with relevance for random effect structure in our models, we can take the following points away from these analyses:

- Slopes and intercepts in random selection models describe differences between the mean available and used habitats, and are not affected by the variance in habitat use (Populations B and C)
- 2. When comparing habitat selection between individuals that are foraging within the same available environment (Populations A-D), the intercept can incorporate variation in habitat selection between individuals.
- 3. When comparing habitat selection between individuals that are foraging in different available environments (Populations E-F), variation in the slope is key to describing behaviour, and incorporating potential functional responses to habitat selection.
- Random slope only models typically did not perform well in our simulated examples, often not ranking individual coefficients as we would expect based on behaviour (Populations D-E).

Based on these analyses, in models presented in the main paper, we accounted for differences in habitat preferences between populations that were foraging in different available habitats, we included a random intercept and slope for colony-year. To account for differences in habitat preferences between individuals foraging within the same available environment, we included a random intercept only for each foraging trip. Each trip ID number was unique to the individual bird and colony. This allowed us to extract parameter estimates for trip intercept to calculate repeatability in behaviour.

# R Code - Appendix S4.E data simulations

library(ggplot2) library(truncnorm) library(lme4) library(effects) library(boot)

#### Population A: No habitat selection ####
#### create data ####
# create available data
avail1 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))</pre>

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value),

b=max(avail1\$value), mean=140, sd=40)))

ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value),

b=max(avail2\$value), mean=140, sd=40)))

ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value),</pre>

b=max(avail3\$value), mean=140, sd=40)))

ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value),

b=max(avail4\$value), mean=140, sd=40)))

ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail5\$value),

```
b=max(avail5$value), mean=140, sd=40)))
```

# give individual IDs

avail1\$indID <- "1"

avail2\$indID <- "2"

avail3\$indID <- "3"

avail4\$indID <- "4"

avail5\$indID <- "5"

avail <- rbind(avail1, avail2, avail3, avail4, avail5)

avail\$y <- 0

```
avail$type <- "Available"
```

ind1\$indID <- "1"

ind2\$indID <- "2"

ind3\$indID <- "3"

ind4\$indID <- "4"

ind5\$indID <- "5"

used <- rbind(ind1, ind2, ind3, ind4, ind5)

used\$y <- 1

used\$type <- "Used"

# combine populations

popA <- rbind(avail, used)</pre>

```
# density plot
ggplot(avail, aes(x=value, linetype = type))+
stat_density(geom="line", position = "identity")+
```

```
stat_density(data = used, geom="line", position = "identity", aes(colour=indID))+
scale_linetype_manual(values = c("dashed", "solid"))
```

#### resource selection models ####

# standardise explanatory variable

popA\$value.st <- (popA\$value-mean(popA\$value))/sd(popA\$value)

mA <- glmer(y~value.st+(1|indID),family="binomial",popA) popA\$fit.int <- predict(mA)

ggplot(popA,aes(value.st, fit.int, col=indID))+

geom\_line(size = 1)+

scale\_color\_viridis\_d()+

ylim(-5, 2.5)+

theme\_void()+

theme(legend.position="none")

ggplot(popA,aes(value.st, inv.logit(fit.int), col=indID))+

geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

mA2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popA) popA\$fit.slope <- predict(mA2)

ggplot(popA,aes(value.st, fit.slope, col=indID))+

geom\_line(size = 1)+
theme\_bw()+
scale\_color\_viridis\_d()+
ylim(-5, 5)

ggplot(popA,aes(value.st, inv.logit(fit.slope), col=indID))+

geom\_line(size = 1)+
theme\_bw()+

scale\_color\_viridis\_d()+

ylim(0, 1)

mA3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popA) popA\$fit.intslope <- predict(mA3)

ggplot(popA,aes(value.st, fit.intslope, col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

ylim(-5, 2.5)+

theme\_void()+

theme(legend.position="none")

ggplot(popA,aes(value.st, inv.logit(fit.intslope), col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

ylim(0, 1)+

theme\_void()+

theme(legend.position="none")

anova(mA, mA2, mA3)

#### Population B: Population habitat selection ####

#### create data ####

# create available data

avail1 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value), b=max(avail1\$value), mean=180, sd=10))) ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value), b=max(avail2\$value), mean=180, sd=10))) ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value), b=max(avail3\$value), mean=180, sd=10))) ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value), b=max(avail4\$value), mean=180, sd=10))) ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value), b=max(avail4\$value), mean=180, sd=10)))

# give individual IDs avail1\$indID <- "1" avail2\$indID <- "2"

```
avail3$indID <- "3"
avail4$indID <- "4"
avail5$indID <- "5"
avail <- rbind(avail1, avail2, avail3, avail4, avail5)
avail$y <- 0
avail$type <- "Available"
ind1$indID <- "1"
ind2$indID <- "2"
ind3$indID <- "3"
ind4$indID <- "4"
ind5$indID <- "5"
used <- rbind(ind1, ind2, ind3, ind4, ind5)
used$y <- 1
used$type <- "Used"
# combine populations
popB <- rbind(avail, used)</pre>
# density plot
ggplot(avail, aes(x=value, linetype = type))+
 stat_density(geom="line", position = "identity")+
 stat_density(data = used, geom="line", position = "identity", aes(colour=indID))+
 scale_linetype_manual(values = c("dashed", "solid"))
```

#### resource selection models ####

# standardise explanatory variable

popB\$value.st <- (popB\$value-mean(popB\$value))/sd(popB\$value)

mB <- glmer(y~value.st+(1|indID),family="binomial",popB)

summary(mB)

coef(mB)

popB\$fit.int <- predict(mB)</pre>

ggplot(popB,aes(value.st, fit.int, col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popB,aes(value.st, inv.logit(fit.int), col=indID))+

```
geom_line(size = 1)+
scale_color_viridis_d()+
ylim(0, 1)+
theme_void()+
theme(legend.position="none")
```

mB2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popB) popB\$fit.slope <- predict(mB2)

ggplot(popB,aes(value.st, fit.slope, col=indID))+
geom\_line(size = 1)+
theme\_bw()+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popB,aes(value.st, inv.logit(fit.slope), col=indID))+

geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

mB3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popB) popB\$fit.intslope <- predict(mB3)

ggplot(popB,aes(value.st, fit.intslope, col=indID))+

geom\_line(size = 1)+

scale\_color\_viridis\_d()+

theme\_void()+

theme(legend.position="none")

ggplot(popB,aes(value.st, inv.logit(fit.intslope), col=indID))+

geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

anova(mB, mB2, mB3)

#### Population C: Different individual variance ####

# #### create data #### # create available data avail1 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) # create used data ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value), b=max(avail1\$value), mean=160, sd=5))) ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value), b=max(avail2\$value), mean=160, sd=10))) ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value), b=max(avail3\$value), mean=160, sd=15))) ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value), b=max(avail4\$value), mean=160, sd=20)))

ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail5\$value),

b=max(avail5\$value), mean=160, sd=30)))

```
# give individual IDs
avail1$indID <- "1"
avail2$indID <- "2"
avail3$indID <- "3"
avail4$indID <- "4"
avail5$indID <- "5"
avail <- rbind(avail1, avail2, avail3, avail4, avail5)
avail$y <- 0</pre>
```

avail\$type <- "Available"

```
ind1$indID <- "1"
ind2$indID <- "2"
ind3$indID <- "3"
ind4$indID <- "4"
ind5$indID <- "5"
used <- rbind(ind1, ind2, ind3, ind4, ind5)
used$y <- 1
used$type <- "Used"</pre>
```

```
# combine populations
popC <- rbind(avail, used)</pre>
```

```
# density plot
```

```
ggplot(avail, aes(x=value, linetype = type))+
```

```
stat_density(geom="line", position = "identity")+
```

stat\_density(data = used, geom="line", position = "identity", aes(colour=indID))+

```
scale_linetype_manual(values = c("dashed", "solid"))
```

```
#### resource selection models ####
```

# standardise explanatory variable

```
popC$value.st <- (popC$value-mean(popC$value))/sd(popC$value)</pre>
```

mC <- glmer(y~value.st+(1|indID),family="binomial",popC)
popC\$fit.int <- predict(mC)</pre>

```
ggplot(popC,aes(value.st, fit.int, col=indID))+
```

geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popC,aes(value.st, inv.logit(fit.int), col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

ylim(0, 1)+

 $theme_void()+$ 

theme(legend.position="none")

mC2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popC) popC\$fit.slope <- predict(mC2)

ggplot(popC,aes(value.st, fit.slope, col=indID))+

```
geom_line(size = 1)+
scale_color_viridis_d()+
theme_void()+
theme(legend.position="none")
```

ggplot(popC,aes(value.st, inv.logit(fit.slope), col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

mC3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popC)

```
popC$fit.intslope <- predict(mC3)</pre>
```

ggplot(popC,aes(value.st, fit.intslope, col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

theme\_void()+

theme(legend.position="none")

```
ggplot(popC,aes(value.st, inv.logit(fit.intslope), col=indID))+
```

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

ylim(0, 1)+

theme\_void()+

```
theme(legend.position="none")
```

anova(mC, mC2, mC3)

#### Population D: Different individual habitat selection ####
##### create data ####
# create available data
avail1 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))
avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))</pre>

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value),

b=max(avail1\$value), mean=160, sd=10)))

ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value),

b=max(avail2\$value), mean=180, sd=10)))

ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value),

```
b=max(avail3$value), mean=200, sd=10)))
```

ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value),

b=max(avail4\$value), mean=220, sd=10)))

ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail5\$value),

```
b=max(avail5$value), mean=240, sd=10)))
```

# give individual IDs

```
avail1$indID <- "1"
```

```
avail2$indID <- "2"
```

```
avail3$indID <- "3"
```

avail4\$indID <- "4"

avail5\$indID <- "5"

avail <- rbind(avail1, avail2, avail3, avail4, avail5)

availy < -0

avail\$type <- "Available"

ind1\$indID <- "1"

ind2\$indID <- "2"

ind3\$indID <- "3"

ind4\$indID <- "4"

ind5\$indID <- "5"

used <- rbind(ind1, ind2, ind3, ind4, ind5)

used\$y <- 1

used\$type <- "Used"

# combine populations

popD <- rbind(avail, used)</pre>

# density plot ggplot(avail, aes(x=value, linetype = type))+ stat\_density(geom="line", position = "identity")+ stat\_density(data = used, geom="line", position = "identity", aes(colour=indID))+ scale\_linetype\_manual(values = c("dashed", "solid"))

#### resource selection models ####

# standardise explanatory variable

popD\$value.st <- (popD\$value-mean(popD\$value))/sd(popD\$value)</pre>

mD <- glmer(y~value.st+(1|indID),family="binomial",popD)
popD\$fit.int <- predict(mD)</pre>

ggplot(popD,aes(value.st, fit.int, col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popD,aes(value.st, inv.logit(fit.int), col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

```
mD2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popD)
popD$fit.slope <- predict(mD2)
```

ggplot(popD,aes(value.st, fit.slope, col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popD,aes(value.st, inv.logit(fit.slope), col=indID))+

```
geom_line(size = 1)+
scale_color_viridis_d()+
ylim(0, 1)+
theme_void()+
theme(legend.position="none")
```

mD3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popD) popD\$fit.intslope <- predict(mD3)

ggplot(popD,aes(value.st, fit.intslope, col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popD,aes(value.st, inv.logit(fit.intslope), col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

ylim(0, 1)+

theme\_void()+

theme(legend.position="none")

anova(mD, mD2, mD3)

#### Population E: Different available and used habitat ####

#### create data ####

# create available data

avail1 <- as.data.frame(cbind(value = rnorm(3000,mean=100,sd=40))) avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=120,sd=40))) avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40))) avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=160,sd=40)))

avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=180,sd=40)))

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value),

b=max(avail1\$value), mean=140, sd=10)))

ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value),

b=max(avail2\$value), mean=160, sd=10)))

ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value),

b=max(avail3\$value), mean=180, sd=10)))

ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value),

b=max(avail4\$value), mean=200, sd=10)))

ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail5\$value), b=max(avail5\$value), mean=220, sd=10)))

```
# give individual IDs
avail1$indID <- "1"
avail2$indID <- "2"
avail3$indID <- "3"
avail4$indID <- "4"
avail5$indID <- "5"
avail <- rbind(avail1, avail2, avail3, avail4, avail5)
avail$y <- 0
avail$type <- "Available"</pre>
```

```
ind1$indID <- "1"
ind2$indID <- "2"
ind3$indID <- "3"
ind4$indID <- "4"
ind5$indID <- "5"
used <- rbind(ind1, ind2, ind3, ind4, ind5)
used$y <- 1
used$type <- "Used"
```

# combine populations

popE <- rbind(avail, used)</pre>

```
# density plot
```

```
ggplot(popE, aes(x=value, colour=indID, linetype = type))+
```

```
stat_density(geom="line", position = "identity")+
```

```
stat_density(data = used, geom="line", position = "identity")+
scale_linetype_manual(values = c("dashed", "solid"))
```

#### resource selection models ####
# standardise explanatory variable
popE\$value.st <- (popE\$value-mean(popE\$value))/sd(popE\$value)</pre>

mE <- glmer(y~value.st+(1|indID),family="binomial",popE)
popE\$fit.int <- predict(mE)</pre>

ggplot(popE,aes(value.st, fit.int, col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d()+$ 

 $theme\_void() +$ 

theme(legend.position="none")

```
ggplot(popE,aes(value.st, inv.logit(fit.int), col=indID))+
geom_line(size = 1)+
scale_color_viridis_d()+
ylim(0, 1)+
```

 $theme\_void() +$ 

```
theme(legend.position="none")
```

mE2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popE)
popE\$fit.slope <- predict(mE2)</pre>

```
ggplot(popE,aes(value.st, fit.slope, col=indID))+
geom_line(size = 1)+
```

```
scale_color_viridis_d()+
theme_void()+
theme(legend.position="none")
```

ggplot(popE,aes(value.st, inv.logit(fit.slope), col=indID))+

```
geom_line(size = 1)+
scale_color_viridis_d()+
ylim(0, 1)+
theme_void()+
theme(legend.position="none")
```

```
mE3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popE)
popE$fit.intslope <- predict(mE3)
```

```
ggplot(popE,aes(value.st, fit.intslope, col=indID))+
geom_line(size = 1)+
scale_color_viridis_d()+
theme_void()+
theme(legend.position="none")
```

```
ggplot(popE,aes(value.st, inv.logit(fit.intslope), col=indID))+
geom_line(size = 1)+
scale_color_viridis_d()+
ylim(0, 1)+
theme_void()+
theme(legend.position="none")
```

anova(mE, mE2, mE3)

#### Population F: Different available and used habitat ####

#### create data ####

# create available data

 $avail 1 <- \ as. data. frame (cbind (value = rnorm (3000, mean = 100, sd = 40)))$ 

avail2 <- as.data.frame(cbind(value = rnorm(3000,mean=120,sd=40)))

avail3 <- as.data.frame(cbind(value = rnorm(3000,mean=140,sd=40)))

avail4 <- as.data.frame(cbind(value = rnorm(3000,mean=160,sd=40)))

avail5 <- as.data.frame(cbind(value = rnorm(3000,mean=180,sd=40)))

# create used data

ind1 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail1\$value), b=max(avail1\$value), mean=200, sd=10))) ind2 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail2\$value), b=max(avail2\$value), mean=200, sd=10))) ind3 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail3\$value), b=max(avail3\$value), mean=200, sd=10))) ind4 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value), b=max(avail4\$value), mean=200, sd=10))) ind5 <- as.data.frame(cbind(value = rtruncnorm(n=600, a=min(avail4\$value), b=max(avail4\$value), mean=200, sd=10)))

# give individual IDs

avail1\$indID <- "1"

avail2\$indID <- "2"

avail3\$indID <- "3"

avail4\$indID <- "4"

```
avail5$indID <- "5"
avail <- rbind(avail1, avail2, avail3, avail4, avail5)
avail$y <- 0
avail$type <- "Available"
ind1$indID <- "1"
ind2$indID <- "2"
ind3$indID <- "2"
ind4$indID <- "3"
ind4$indID <- "4"
ind5$indID <- "5"
used <- rbind(ind1, ind2, ind3, ind4, ind5)
used$y <- 1
used$type <- "Used"</pre>
```

# combine populations

popF <- rbind(avail, used)</pre>

# density plot

```
ggplot(popF, aes(x=value, colour=indID, linetype = type))+
stat_density(geom="line", position = "identity")+
stat_density(data = used, geom="line", position = "identity")+
scale_linetype_manual(values = c("dashed", "solid"))
```

#### resource selection models ####
# standardise explanatory variable
popF\$value.st <- (popF\$value-mean(popF\$value))/sd(popF\$value)</pre>

mF <- glmer(y~value.st+(1|indID),family="binomial",popF)

popF\$fit.int <- predict(mF)</pre>

ggplot(popF,aes(value.st, fit.int, col=indID))+

geom\_line(size = 1)+

scale\_color\_viridis\_d()+

theme\_void()+

theme(legend.position="none")

ggplot(popF,aes(value.st, inv.logit(fit.int), col=indID))+

geom\_line(size = 1)+

 $scale\_color\_viridis\_d() +$ 

ylim(0, 1)+

theme\_void()+

theme(legend.position="none")

mF2 <- glmer(y~value.st+(-1+value.st|indID),family="binomial",popF) popF\$fit.slope <- predict(mF2)

ggplot(popF,aes(value.st, fit.slope, col=indID))+
geom\_line(size = 1)+
scale\_color\_viridis\_d()+
theme\_void()+
theme(legend.position="none")

ggplot(popF,aes(value.st, inv.logit(fit.slope), col=indID))+

```
geom_line(size = 1)+
```

 $scale\_color\_viridis\_d() +$ 

ylim(0, 1)+

theme\_void()+

theme(legend.position="none")

mF3 <- glmer(y~value.st+(1+value.st|indID),family="binomial",popF)

popF\$fit.intslope <- predict(mF3)</pre>

ggplot(popF,aes(value.st, fit.intslope, col=indID))+

geom\_line(size = 1)+

scale\_color\_viridis\_d()+

theme\_void()+

theme(legend.position="none")

ggplot(popF,aes(value.st, inv.logit(fit.intslope), col=indID))+

geom\_line(size = 1)+
scale\_color\_viridis\_d()+
ylim(0, 1)+
theme\_void()+
theme(legend.position="none")

anova(mF, mF2, mF3)





Figure S4.F1. Histograms showing distributions of raw (left) and square-root transformed environmental data (right) at kittiwake foraging points.

| Table S4.G1. Generalise             | d linear mixed effects mo    | odels testing for habitat | use in relation to colony distance. In all cases, models |
|-------------------------------------|------------------------------|---------------------------|--|
| include random intercel             | pts for colony-year and ti   | rip ID (nested within B   | irdID), and are run with a logit link. Results show that |
| distance from the colony            | ∕ has a significant effect o | n kittiwake behaviour, a  | nd therefore for future model selection (Table S4.G2) we |
| use the model includin <sub>{</sub> | g colony distance as a ba    | ase model, by which to    | compare the additional effect of other environmental     |
| variables.                          |                              |                           |  |
|                                     |                              |                           | Difference in AIC compared to most parsimonious          |
| Model                               | Coefficients                 | AIC                       | model  |
| Full model                          | Colony distance              | 475149                    | 0  |

288838

763987

NA

Null model

| include random iı | ntercepts for colony-year a | and trip ID (nested within BirdID) a | and are run with a lo | ogit link. |                    |
|-------------------|-----------------------------|--------------------------------------|-----------------------|------------|--------------------|
|                   |                             |                                      |                       |            | Difference in AIC  |
|                   |                             |                                      |                       |            | compared to most   |
| Variable          | Model                       | Coefficients                         | Random slope          | AIC        | parsimonious model |
| Bathymetry        | Full model                  | Bathymetry + Colony distance         | Bathymetry            | 453914     | 0                  |
|                   | Without bathymetry          | Colony distance                      | NA                    | 475149     | 21235              |
| Potential tidal   | Full model                  | Stratification + Colony distance     | Stratification        | 417909     | 0                  |
| stratification    | Without Stratification      | Colony distance                      | NA                    | 448611     | 30702              |
| Sea surface       | Full model                  | SST + Colony distance                | SST                   | 295594     | 0                  |
| temperature       | Without SST                 | Colony distance                      | NA                    | 330054     | 34460              |
| Front strength    | Full model                  | Front strength + Colony              | Front strength        | 362514     | 0                  |
|                   |                             | distance                             |                       |            |                    |
|                   | Without front strength      | Colony distance                      | NA                    | 373397     | 10883              |
| Front distance    | Full model                  | Front distance + Colony              | Front distance        | 288212     | 0                  |
|                   |                             | distance                             |                       |            |                    |
|                   | Without front distance      | Colony distance                      | NA                    | 299611     | 11399              |
| Front             | Full model                  | Front persistence + Colony           | Front                 | 359450     | 0                  |
| persistence       |                             | distance                             | persistence           |            |                    |
|                   | Without front               | Colony distance                      | NA                    | 373397     | 13947              |
|                   | persistence                 |                                      |                       |            |                    |

Supplementary Material

Table S4.G2. Generalised linear mixed effects models testing for habitat use in relation to environmental variables. In all cases, models

| Table G2               |                    |                            |                     |             |             |            |
|------------------------|--------------------|----------------------------|---------------------|-------------|-------------|------------|
| Model                  | Correct            | <b>Positive Predictive</b> | Negative Predictive | Sensitivity | Specificity | Area under |
|                        | classification (%) | Power (%)                  | Power (%)           |             |             | curve      |
| <b>Colony Distance</b> | 80.8               | 67.9                       | 89.2                | 0.80        | 0.81        | 0.81       |
| Bathymetry             | 82.3               | 69.5                       | 90.8                | 0.84        | 0.82        | 0.83       |
| Stratification         | 82.1               | 69.1                       | 90.9                | 0.84        | 0.81        | 0.82       |
| SST                    | 81.2               | 67.9                       | 91.2                | 0.85        | 0.80        | 0.82       |
| Front strength         | 79.2               | 65.2                       | 89.0                | 0.81        | 0.78        | 0.80       |

Table S4.G3. Model scores from receiving operator characteristic curves of most parsimonious models by model selection, presented in

0.79

0.77 0.78

0.81 0.81

88.9 89.4

63.9 65.4

78.4 79.5

279

Front distance Front persistence

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# Chapter 5

# General Discussion



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#### General Discussion

The aim of this thesis was to understand the role of the environment in shaping optimal foraging movements. By developing novel methods and using large datasets that span numerous populations of a central place forager, the black-legged kittiwake, studies within this thesis have gained insight into the causes and consequences of foraging dynamics, and revealed universal patterns that can begin to explain the diversity of foraging strategies within and between populations. Overall, the chapters within this thesis complement each other to demonstrate that resource heterogeneity is key in shaping optimal foraging strategies. The degree of environmental heterogeneity can shape the magnitude of behavioural responses to resource fluctuations over a temporal cycle (Chapter 2), the degree of competition between individuals with consequences for fitness (Chapter 3), and the prevalence of individual specialisations within populations (Chapter 4). These results highlight the capacity of animals to adapt their behaviour to local resource distributions, and hence advance our knowledge of how heterogeneity in the physical environment can shape the diversity of animal movement behaviours. Below, I draw together the key findings and implications of earlier chapters, and suggest future directions to develop research themes from this project.

#### Key findings

Optimal foraging theory predicts that movement is shaped by the constant trade-off between maximising resource gain at resource patches, whilst minimising the costs associated with resource acquisition, such as travel between patches (Stephens & Krebs 1986). For example, for central place foragers, extended time away from the breeding site can be detrimental to breeding success, as observed in Chapter 3 and in accordance with previous studies (Davoren & Montevecchi 2003; Boersma & Rebstock 2009). Therefore, optimal foraging theory can explain why individuals minimise travel costs by preferentially using resource patches closer to the breeding location (Chapters 2 & 4; Elliott *et al.* 2009; Chivers *et al.* 2012). This also highlights the importance of fine-scale habitat selection changes observed in Chapter 2, and individual specialisations in habitat selection observed in Chapter 4, particularly of dynamic habitat variables. Whilst selection may be subtle, these behavioural adaptations most likely persist because they offer a key opportunity to maximise fitness within the local environment.

The importance of local resource heterogeneity to individual foragers is an emerging theme of this thesis. This adds to decades of studies that have considered behavioural adaptations in light of patchy resources (Levin 1992; Sparrow 1999; Weimerskirch 2007). A key advance made by this thesis, however, is the consideration of how heterogeneity can differ between locations, and therefore how the degree of heterogeneity can determine the value of resource patches and optimal foraging strategies. Previously unconsidered differences in environmental heterogeneity could therefore explain contrasting observations of behaviour and reproductive success that can be found in existing studies of other taxa. For example, kittiwake responses to the tidal cycle were amplified in heterogeneous environments, indicative of adaptations to greater spatial variability in temporal resource changes in patchy environments (Chapter 2). This could explain why previous studies of prey fish and seabirds from a range of taxa found varying magnitudes of behavioural responses to different stages of the tidal cycle (Irons 1998; Embling et al. 2012; Cox et al. 2013), and could be an important mechanism governing animal behavioural responses to numerous temporal cycles throughout ecosystems (e.g. day/night changes in light intensity and weather patterns). Secondly, kittiwakes were away from the breeding colony for longer and had reduced breeding success in more heterogeneous environments (Chapter 3), which provides insight into previous findings of geographic variability in foraging behaviour and breeding success in seabirds (Carroll et al. 2015). This relationship was most likely a result of intraspecific competition, a key interaction

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that can drive ecological processes such as site carrying capacity and population dynamics. Lastly, kittiwakes were more individually specialised in their habitat selection in more heterogeneous environments (Chapter 4), which could explain differences between previous studies in the observed prevalence of individual specialisations (Leclerc *et al.* 2016; Courbin *et al.* 2018). Environmental heterogeneity is ubiquitous across terrestrial and marine ecosystems (Sparrow 1999), and therefore findings within this thesis present a strong case for considering the degree of local environmental heterogeneity in future studies of ecological processes.

Multi-population comparisons in each chapter of this thesis have highlighted the diversity of foraging strategies between colonies. In theory, individuals in each population should have adapted advantageous traits specific to the local environment (Williams 1966). Local adaptations may be constrained by gene flow between populations, or by temporal variability in the environment. Nevertheless, the study of local adaptations offers an ideal opportunity to study ongoing selection driven by environmental conditions (Kawecki & Ebert 2004). Results in this thesis that demonstrate local adaptations, for example to the tidal cycle in Chapter 2 and varying habitat selection in Chapter 4, are therefore important documentations of how environmental heterogeneity can shape optimal foraging strategies, with broadreaching implications for the potential role of environmental heterogeneity in driving diversity of animal movements across ecosystems.

As well as the influence of resource distributions, results also implicate the relevance of conspecific behaviour to foraging strategies. The presence of conspecifics is typically detrimental to kittiwake foraging efficiency (Chapter 3; Ainley *et al.* 2003), which could contribute to promoting individual specialisations in habitat selection (Chapter 4; Araújo *et al.* 2011; Svanbäck *et al.* 2011). Indeed, the combined effect of both resource and competitor distributions in shaping foraging behaviour is central to longstanding Ideal Free Distribution (IFD) theory, which predicts that the size of foraging aggregations ought to be proportional to resource availability in any given patch (Fretwell & Lucas 1969). Together, results from this thesis support IFD assumptions; namely, that animals seek to forage within higher quality patches (Chapter 2), yet that competition between individuals at resource patches decreases the value to potential resource gain (Chapter 3). Furthermore, results from Chapter 4 align with IFD theory in that where resources are more patchy, individuals were more specialised in their habitat selection, indicative of modifying their distributions according to both resource availability and competitor density. Often, combined studies of predator and prey distributions do not find agreement with Ideal Free Distribution theory, thought to be because of predator avoidance behaviour by prey and local enhancement at fine spatial scales (Fauchald 2009). However, results within this thesis point towards the Ideal Free Distribution as a descriptor of predator distributions at a broad spatial scale.

#### Potential applied implications

We are in a 'golden age' of animal tracking studies, during which time humans have gained unprecedented insights into the environment from the perspective of animals (Hussey *et al.* 2015; Kays *et al.* 2015). Studies have revealed new intricacies about individual movement, and its many implications for ecology, biodiversity, and ecosystem function. Furthermore, tracking studies also offer a unique opportunity to quantify the threats directly faced by animals, as spatial information about animalenvironment interactions and species distributions are essential to ecosystem management (Maxwell *et al.* 2013; Hays *et al.* 2019). Consequently, there is considerable scope for animal tracking to inform management. However, more often than not the potential value of study results to conservation and management are simply stated as justification for research, rather than directly explained or implemented (Hays *et al.* 2019). All studies in this thesis were focussed on the ecology of kittiwakes, an important indicator species in marine legislation (ICES 2001). Therefore, in light of the importance of movement data for management, here I outline the applied value of results presented in this thesis.

Environmental heterogeneity as a predictor of kittiwake breeding success

Reproductive success of kittiwakes is an important measure in environmental legislation; the North Sea sandeel fishery is closed when the mean number of fledged chicks per nest drops below 0.6 over a three year period (Heslenfeld & Enserink 2008). Such declines in breeding success are attributed to warmer sea temperatures decreasing sandeel spawning rates (Arnott & Ruxton 2002) and the additive pressure of the sandeel fishery (Frederiksen et al. 2004). Fishery closures therefore allow stock recovery, with positive effects for kittiwake breeding success (Daunt et al. 2008). Given the importance of kittiwake breeding success as an indicator of sandeel stocks, the link between breeding success and environmental heterogeneity that we found in Chapter 3 could improve use of such management tools over a wider geographic area. Kittiwakes in more heterogeneous environments had lower breeding success, which results suggested was because of greater levels of intraspecific competition. Management and conservation policy could target areas of high environmental heterogeneity where breeding success was low (highest heterogeneity was found at Copinsay, Colonsay and Rathlin in the Irish Sea), and therefore populations may be more vulnerable to cumulative stress from multiple sources such as fishery pressure, climate driven changes in sandeel abundance, and other anthropogenic impacts such as pollution. Furthermore, comparisons of kittiwake breeding success around the UK for management and conservation purposes would benefit from considering environmental heterogeneity as an important influence on spatial variability in breeding success, which could otherwise be interpreted inaccurately as purely due to differences in prey fish availability.

Habitat selection and environmental heterogeneity to inform marine protected areas

Design of marine protected areas has traditionally mirrored the methods of terrestrial spatial planning where static borders are mapped and legislated (Biology *et al.* 2003; Foley *et al.* 2010). However, the dynamic nature of the marine environment is incomparable in magnitude and frequency to the terrestrial environment (Steele 1991; Reygondeau *et al.* 2013; Steele *et al.* 2019). Mobile marine features that support prey are fluid in space and time, and therefore emerging studies are recommending an equally fluid approach to marine management (Duck 2012; Maxwell *et al.* 2015). Dynamic ocean management can be defined as '*management that changes rapidly in space and time in response to the shifting nature of the ocean and its users based on the integration of new biological, oceanographic, social and/or economic data in near real-time*' (Maxwell *et al.* 2015). In all chapters of this thesis, we demonstrate integration of biological and oceanographic data that could aid management of kittiwakes, in an approach that is applicable to other marine predator species.

Analyses in chapters 2 and 4 focussed on kittiwake habitat selection, which is an approach that can inform placement of static marine protected areas as well as aiding dynamic management practices. For example, temperature-dependent habitat preferences of at-risk bycatch species can inform dynamic predictive models to prevent overfishing, currently in place to reduce by-catch of southern Bluefin tuna, *Thunnus maccoyii* (Hobday & Hartmann 2006), and loggerhead, *Caretta caretta*, and leatherback turtles, *Dermochelys coriacea* (Howell *et al.* 2008, 2015). Our results highlighted the fine-scale foraging habitat preferences of kittiwakes throughout the UK in relation to both static and dynamic features; specifically, that during the breeding season kittiwakes preferentially foraged in areas closer to the colony, characterised by shallower depths, weaker stratification, cooler temperatures, weaker fronts, more distant fronts and less persistent fronts. Therefore, marine protected areas aiming to benefit UK seabird species could focus on protecting areas that

feature these habitats. As the marine environment is likely to change with future climate shifts, dynamic marine protected areas could move to target the preferred foraging habitats of kittiwakes (such as ephemeral fronts and areas of mixed waters). In all three chapters we highlight the importance of environmental heterogeneity for driving fine scale habitat selection (Chapter 2), population foraging dynamics and reproductive success (Chapter 3), and individual specialisations in habitat selection (Chapter 4). The degree of environmental heterogeneity of a designated marine protected area could therefore be an important consideration for its value. Increased competition in more heterogeneous environments could reduce the carrying capacity of an area; meanwhile, homogenous environments may offer less competitive foraging opportunities and therefore potentially higher fitness benefits to foragers.

#### Tidal energy installations

Kittiwakes experience low vulnerability to direct mortality from sub-sea tidal turbines (Furness *et al.* 2012). However, installation of structures to harness tidal energy will substantially alter tidal flow dynamics (Pérez-Ortiz *et al.* 2017), both reducing mean flow speeds and diminishing tidal features such as jets and eddies. Behavioural adaptations to the tidal cycle described in Chapter 2 may highlight the potential risk of renewable energy installations to ecosystem function. In Chapter 2 we demonstrate behavioural adaptations to the tidal cycle at three locations (Puffin Island, Skomer Island and Rathlin Island) that are all close to sites where tidal energy production has been considered, or is in development (Fanning *et al.* 2014; Pérez-Ortiz *et al.* 2017). Kittiwakes were more likely to forage in shallow water on the flood tide than on the ebb tide at all three locations (Chapter 2), and therefore tidal energy installations in shallow areas could be timed to operate on the ebb tide to avoid conflict with kittiwake foraging. Should tidal features that enhance prey availability disappear, then this may have consequences for the predators that have adapted to this predictable flux in resources. These potential consequences are likely to be smaller than climate-driven regime shifts, should we continue relying on fossil fuels (Scott *et al.* 2017), but nevertheless are worth bearing in mind at local scales.

#### Limitations

Optimal foraging theory offers a valuable framework for understanding animal movement. In this thesis, we refer to optimal foraging theory to understand habitat choice (Chapters 2 & 4) and evaluate the potential consequences of resource heterogeneity on foraging movements (Chapter 3). However, our conclusions are limited, to a degree, by uncertainty about potential differences in prey capture rates and prey energetic value in different environments. Furthermore, animals are unlikely to ever be optimal (Pierce & Ollason 1987), but rather we assume that they strive for optimality. In support of our results, kittiwakes are unlikely to switch prey and can only access prey at the surface (Lewis *et al.* 2001), and therefore prey abundance and patchiness are likely to be a primary driver of behaviour and success. Nevertheless, further study using advanced telemetry devices to record energetics and/or prey capture success (Williams *et al.* 2019) could elaborate on trade-offs between high and low quality prey patches along a gradient of environmental heterogeneity.

Throughout this thesis, we use environmental heterogeneity as a proxy for resource heterogeneity. This assumes that heterogeneity in the physical environment leads to more patchy resources because of physical processes that exert strong control on resource distributions. Ideally, data on the distribution of prey to match the temporal and spatial scales of predator movements could confirm this assumption. However, data on the availability of the multiple prey species of seabirds are unavailable at the scale and resolution required to explicitly evaluate prey patchiness either around the UK and Ireland, or elsewhere. Spatial data on the distribution and abundance of prey are available in some locations (Greenstreet *et al.* 2006; Eerkes-Medrano *et al.* 2017), however these are unavailable across the majority of study colonies and temporal resolution is low. Therefore, we rely on the structure of the physical environment as a proxy for prey distributions, and behaviour of kittiwakes as an indicator of prey availability. In support of environmental heterogeneity as a proxy for resource heterogeneity, results presented throughout this thesis align with study hypotheses, which were drawn from expectations of how animals should optimise foraging efficiency where resources are patchy. Nevertheless, a test of how environmental heterogeneity influences fine-scale prey distributions and availability to foraging seabirds, potentially requiring new targeted surveys on prey fish, could make our interpretations more robust, and improve our understanding of the ecological mechanisms that link trophic levels.

Inferring behaviour and interactions between individuals from GPS tracking of a subset of the population also relies on assumptions, which again can limit interpretation of results. In Chapter 3, we found that in more heterogeneous environments there was greater spatial overlap between pairs of tracked individuals, which we interpret as indicative of greater competition between all individuals at the population level. In support, previous studies have found that with increasing numbers of foraging seabirds, including kittiwakes, aggregations of prey fish are forced lower down in the water column (Ainley et al. 2003; Fauchald 2009). However, these overlaps are solely spatial, in order to include data from all colonies and maximise the numbers of comparisons between individuals, and do not quantify temporal overlap (Long et al. 2014). Meanwhile, using the same dataset in Chapter 4, we found that in more heterogeneous environments, individuals were more specialised in habitat selection; that is they used a more different subset of the available environment relative to the remainder of the tracked population. This might imply that birds are less likely to overlap with each other since foraging areas are more distinct, which initially appears to be an opposing effect to Chapter 3. Numerically, results add up to indicate that these processes could occur simultaneously; along the observed range of environmental heterogeneity, according to model predictions, overlap between pairs of individuals increased from just over 10%, to just under 15% (Chapter 3, Figure 2), and repeatability of habitat selection typically increased to around 0.4 (Chapter 4, Figure 4), where 0 indicates identical habitat selection by all individuals (potentially a 100% overlap) and 1 indicates entirely unique habitat selection by each individual (potentially a 0% overlap). However, more fine scale analyses of individuals tracked over the same time period could test the link between spatial and temporal overlaps, and whether individuals dynamically select habitat of higher quality and/or habitat that offers minimal competition (Long *et al.* 2014). Ideally, these analyses would benefit from tracking data of a greater proportion of potentially competing individuals, however it is rarely possible to track all individuals from a single colony, particularly at large colonies favoured by colonial seabirds (although see Jones *et al.* 2018), and arguably impossible to track all individuals that could be foraging within a given area.

Lastly, throughout this thesis we evaluate the influence of the physical environment on kittiwake behaviour. We consider the importance of static features (bathymetry, tidal shear stress averaged over the spring-neap cycle, and potential tidal stratification), a predictable cycle (the tide), and dynamic variables measured from remote sensing (sea surface temperature and ocean fronts). However, we do not consider the effect of weather (wind or storminess) on influencing relationships between these environmental variables and kittiwake behaviour. Whilst previous studies have found that kittiwakes do not modify their foraging locations and flight directions as a result of wind (Collins 2017), a change in weather may make flight more costly (Gabrielsen *et al.* 1987). Furthermore, weather conditions can influence visibility of shoaling fish to surface foragers (Baptist & Leopold 2010). The influence of storminess on marine foragers has often been considered with regards to winter survival (Frederiksen *et al.* 2008; Tavares *et al.* 2019). However, as extreme weather

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events potentially become more commonplace (Coumou & Rahmstorf 2012), the importance of weather on foraging success throughout the year could increase. More advanced bio-loggers that can record an animal's external environment to higher precision will enable more detailed research into such relationships between weather and foraging trade-offs (Williams *et al.* 2019).

#### Future research directions

Throughout this project, research outcomes have prompted new questions that would further our understanding of animal movement behaviour and how the environment shapes ecology. In this section, I give an overview of three potential research questions that would build on earlier chapters of this thesis.

#### Success of individual foraging strategies

The work in this thesis revealed that environmental heterogeneity favoured individual specialisation in habitat selection, yet resulted in lower breeding success at a population level. These studies offer a 'snapshot' in evolutionary time, whereby we assume that observed foraging behaviours are the most optimal for the local environment. However, as we uncover the role of individuals in shaping the demography of populations, and technological advances allow more fine scale and continuous monitoring of both behaviour and reproductive success (De Pascalis *et al.* 2018; Hinke *et al.* 2018), we can monitor foraging strategies and reproductive success to the individual level at high temporal resolution (Williams *et al.* 2019). Simultaneous individual level analyses building on methods used in Chapters 3 & 4 would allow us to ask more questions about the fine scale origins and consequences of variability in behaviour. Future studies could focus on whether individual specialisations in habitat selection arise through ecological opportunity or to avoid competition (Araújo *et al.* 2011), and whether habitat specialists indeed have greater individual reproductive success in heterogeneous environments.

Fine scale features that prompt foraging

Kittiwakes, and indeed many other seabirds, use fine-scale marine features that offer foraging opportunities, as demonstrated throughout this thesis. To the human eye, the marine environment may appear featureless, especially in oceanic areas away from coastlines that can serve as a means to navigate. However, oceanographic processes can in fact manifest at the sea-surface as visible features, particularly in areas of coastal tidal currents, but also where different water bodies at ocean fronts or in upwelling regions differ in colour and surface roughness (Miller 2009; Rascle *et al.* 2016). Future studies could use new methodological advances (e.g. hidden Markov models directly incorporating environmental variables; McClintock & Michelot 2018) to uncover whether kittiwakes use visible features to prompt foraging, and to inform temporally fluctuating habitat selection of dynamic features such as ephemeral fronts (Chapter 4 Figure 3).

#### The importance of environmental heterogeneity at different life stages

As discussed, this thesis demonstrates that environmental heterogeneity can influence optimal foraging strategies, potential interactions between individuals, and reproductive success. These are all important factors throughout an individual's life, and therefore future studies could explore the role of environmental heterogeneity in determining other ecological processes. For example, future research questions could ask whether the degree of heterogeneity can influence long-term population trends through negative effects on reproductive success (Chapter 3). This would be an interesting hypothesis to test when results are completed for the ongoing UK seabird census, for instance. Furthermore, because of the importance of prospecting behaviour on reproductive habitat selection (Suryan & Irons 2001; Vasseur *et al.* 2013), environmental heterogeneity may influence dispersal and recruitment of new breeders to different sites. Lastly, the degree of environmental heterogeneity could influence the carrying capacity of a site to foragers, as potential resource gain from patches may be limited by the presence of competitive individuals (Frederiksen *et al.* 

2012). By extension, therefore, environmental heterogeneity could be hypothesised to limit the carrying capacity of stop-over sites to migrating individuals across a range of taxa, thus potentially influencing species migration routes and life history choices.

#### Conclusion

Results presented throughout this thesis offer new insights into the behavioural ecology of predators faced with the challenge of finding food in ever-changing landscapes. In more heterogeneous environments, foragers can adapt their habitat selection to greater spatial variability in temporal resource changes. Furthermore, greater competition at resource patches can potentially favour individuals to be more specialised in their habitat selection. Methodological advances offer new insight into the ecology of kittiwakes, an important indicator species, but also shed light on behavioural processes that are relevant to predators and ecosystems in general. Results challenge common assumptions that resource hotspots simply offer predictable foraging grounds; and therefore provide reason to consider the degree of environmental heterogeneity and its effects on optimal foraging strategies within future studies of ecological processes and population dynamics.

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