Modelling breeding season foraging and tracking autumn migrations to fill knowledge gaps in gannet ecology relating to impacts of offshore wind farms

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The candidate confirms that the work submitted is his own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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Abstract

Plans for a four-fold increase in the capacity of offshore wind farms (OWFs) in the UK pose a threat to birds that interact with the footprints of such developments. Environmental impact assessments (EIAs), required by law for new renewable developments, typically adopt top-down population projection models to understand how scenarios of collision mortality, displacement and barrier effects impact on a population. Risks outside the breeding season are often only very crudely assessed, and standard techniques used within the breeding season lack the sophistication to capture important processes such as individual specialisation, which may have its own implications for risk. These are the two knowledge gaps that are addressed in this thesis.

To investigate risk to different age classes and populations of northern gannets *Morus bassanus* in the southern North Sea, which holds the world's highest concentration of OWFs, I tracked adult and juvenile gannets from the world's largest colony (Bass Rock) and reviewed two types of survey data (Chapter 2). I found that juveniles face less risk than adults from OWFs during migration, and an autumn peak of birds in the southern North Sea is likely made up of birds from colonies further north than Bass Rock.

To address the need for more sophisticated modelling I used an individual-based model (IBM) approach, which has been used extensively to interpret management scenarios such as the impacts of OWFs. Over the last 20 years individual foraging site fidelity (IFSF) has become a prominent area of research, has been attributed many drivers and consequences, but has yet to be incorporated in IBMs or EIAs. Addressing this required building a model capable of reproducing the movements and behaviour of an individual foraging trip from first principles (Chapter 3), before advancing this model to more behavioural complexity and population-level patterns (Chapter 4). For this purpose I ran simulation experiments to decipher which resource localisation mechanisms, harnessing different levels of public and/or private information, were the best at reproducing empirical patterns of individual foraging site fidelity. The results indicated that memory of several departure angles, learned in previous exploration, plus the ability to react to conspecifics in both an attractive and repulsive manner were key mechanisms required to reproduce IFSF patterns. This finding provides ecological insight into IFSF while also creating a robust behavioural model of foraging gannets that could be applied to understanding the impacts of OWFs in the future. Alongside the potential for more reliable prediction of potential population-level impacts through effects on body condition and breeding success, I argue that this approach could also be useful in forecasting shifting population distributions through its ability to model adaptive populations.

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Chapter 1: General Introduction

1.1 Threats to seabirds

Over 90% of seabird species are colonial (Coulson, 2002) and breed on land. The ability to count and manipulate seabirds relatively easily has led to their prominence as a study system and has yielded many ecological insights. Long-term monitoring schemes give insights into population dynamics. Consequently, they can provide an indicator of the health of the marine system they occupy (Parsons et al., 2008) that is difficult to acquire from more aquatic clades like fish and marine mammals. With the advent of relatively small tracking devices in the 21st Century we have gained untold insights into, previously elusive, seabirds' movements and their consequent interaction with the ocean (Wakefield et al., 2009; Bernard et al., 2021). One major lesson has been that our biased perception of the ocean as a "featureless" environment has been invalidated by observations of how seabirds relate to this space, not only in a species-specific manner but with individuals within a population often showing preference to certain localities (Piper, 2011, Phillips et al. 2017).

This flourishing knowledge coincides with a 70% decrease in global seabird populations since 1950, making them the most threatened of all bird groups (Grémillet et al., 2018). This decline has been partially attributed to competition from commercial fisheries; a threat that persists today. However, others persist, including the threat from bycatch, climate change or severe weather, and invasive alien species which comprise the three major threats to seabirds globally in terms of the number of species affected and size of impact (Dias et al., 2019). Although it should be recognised that most of our seabird populations increased in the 1960s-1990s (Mitchell et al., 2004), recent trends in seabird breeding numbers in the UK are similar to global trends, with over one third of species experiencing significant declines (20-30% or more) in the last 30 years (Mitchell 2018) with climate change being cited as a primary cause for declines (Mitchell et al., 2020).

The two processes through which climate change may impact on seabirds are direct effects such as mortality from extreme weather, and indirect effects via changes in food supply. Storms during the breeding season have been shown to impact reproductive success in several UK species (Newell et al., 2015). In winter, extreme weather which results in heightened wave activity, such as that in 2013/2014 (Masselink et al., 2016), can be linked to wrecks of seabirds attributed to starvation, exhaustion and drowning (Morley et al., 2016). In cases not severe enough to result in mortality, there may be future implications of poor body condition sustained in one season influencing future survival and breeding success (Harrison et al., 2011). Seabirds' prey supplies can be affected in several ways including change in abundance (Howells et al., 2017), distribution (Reygondeau & Beaugrand, 2011), and nutritional value (Harris et al., 2008) but can be hard to disentangle from the effects of commercial fisheries. Species that can exploit food throughout the water column (such as auks) appear to be buffered to some of the negative impacts that surface feeders experience (Furness & Tasker, 2000; OSPAR 2017). An indicator of climate change is rising sea-surface temperatures (SST) and this has been linked to changing demographic rates in many of the UK's seabird species (Burthe et al., 2014), exemplified by the decline in breeding abundance of black-legged kittiwake (*Rissa tridactyla*, Frederiksen 2014; Wanless et al., 2018) which may be explained by abundance of their main prey, the lesser sandeel (*Ammodytes marinus,* Daunt et al., 2008). Finally, climate change may cause temporal mismatch of trophic levels, a mechanism whereby the peak energy demand of predators is out of sync with the peak availability of prey, which has been displayed in both the North Sea (Burthe et al., 2012) and at the global level (Keogan et al., 2018).

Through continued investment in developing renewable energy resources, many countries are attempting to slow anthropogenic climate change by reducing the emission of greenhouse gases. Offshore renewable developments (ORD) contribute a significant portion of this effort, including tidal, wave, and wind energy developments. Offshore wind farms (OWF) comprise the majority of proposals for development in the marine environment. Europe and China are currently the largest producers of wind energy (GWEC 2019), with the UK currently being the world leader in offshore wind, owing in part to its topographical situation as an island nation in an area with sustained moderate to high wind. Despite the prospects of such developments alleviating the magnitude of climate change, the footprints of such developments can be large, bringing about their own set of challenges for marine life in our waters.

1.2 Offshore wind farms and their impacts

The development of relatively high concentrations of OWF sites has not been without controversy in the UK. For instance, one high-profile case between an NGO and developers regarding OWF developments in the Firth of Forth and Tay in Scotland was taken to the Supreme Court. The appeal against the development was eventually overturned in the favour of the developments going ahead, but progress for the developers was curtailed (see Marsden, 2018 for details on this case). Moreover, there are plans for a four-fold expansion to 40GW by 2030 (8GW installed capacity in 2020, BEIS, 2020). Considering that empirical evidence for the population-level consequences of such developments is still lacking, the outlook for the UK's seabird populations and wider marine life is a cause for concern.

Potential positive impacts of offshore wind farms include increased productivity around the base of turbines due to acting as artificial reefs (Inger et al., 2009). Both grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) use these structures for foraging (Russell et al., 2014), indicating that they either concentrate or increase prey (Pickering & Whitmarsh, 1997). How such modifications to the environment may benefit, or indeed disadvantage seabirds, is yet to be determined. In contrast, the potential negative impacts of operating OWFs can been assigned to the three categories; collision mortality, displacement and barrier effects. Collision mortality due to animals colliding with the sweeping turbine blades of OWFs is a direct demographic impact and has been documented well onshore (Thaxter et al., 2017), but is more challenging to assess offshore. Displacement is thought to occur when birds avoid OWFs, displacing them from previously accessible habitat (Drewitt & Langston, 2006). Barrier effects occur when a development obstructs the journey of a bird requiring more time and energy to fly around it. Displacement and barrier effects are indirect demographic impacts, because their impacts are mediated through energetic costs, which may in turn adversely affect individual survival or breeding success. As such effects are delayed, assessing their population impacts can be challenging.

Owing to their respective behaviours and distributions vulnerability to the impacts of OWFs is species-specific (Furness et al., 2013). Empirical studies indicate that red-throated divers (*Gavia stellata*) show strong avoidance of OWFs (Heinänen et al., 2020), resulting in a risk of displacement for this species. Other species may be at a greater risk of collision with turbines, such as the northern gannet (*Morus bassanus*, hereafter gannet) due to their flight heights often being within the range of turbine blades (Cleasby et al., 2015; Lane et al., 2019). Seabird populations which are at risk from the negative impacts of OWFs may be subject to cumulative exposure, where they may encounter multiple OWFs. Cumulative effects can also refer to the, potentially additive, effects of drivers such as climate change alongside OWF impacts (Crain et al., 2008). This requires simultaneous quantification (Masden et al., 2010) and is part of stipulations from EU legislation [EU Birds Directive 2009/147/EC], with a UK equivalent, as part of the statutory environmental impact assessment (EIA) required of those planning to build a new development. In lieu of empirical data, which are often difficult and costly to obtain, there is a suite of modelling techniques available to aid scientists and practitioners in estimating the potential effects of a proposed development on nearby seabird populations.

1.3 Assessment of population-level impacts

How populations respond to new developments is inferred in a context-specific manner with various techniques, conventionally centred around population viability analysis (PVA; Beissinger & McCullough, 2002). Within this remit, techniques such as population projection through matrix multiplication (Lefkovitch, 1965) can be used to estimate the effects of different proposed management strategies on the age or life stage of the species in question (Lebreton & Clobert, 1991). They do so by deriving counterfactuals of a model with additional mortality that are then measured against a baseline model. This method is more robust than another common method, potential biological removal (PBR) which is criticised for lack of biological realism leading to oversimplification (O'Brien et al., 2017), and the potential to overestimate harvest levels (Milner-Gulland & Akçakaya, 2001). Hence, population projection models are the recommended technique to employ (Green et al., 2016), but they are not without their own caveats such as the conventional simplifying assumption of closed populations and density independence.

Precursory modelling is often required to inform PVA, of which two types are particularly relevant. One is mark-recapture/resighting studies used to estimate the survival of a species/population through marking individuals (i.e. ringed birds). The second technique is collision-risk modelling (CRM), typically using the Band model (Band, 2012), which estimates mortality from collision by providing a set of parameters on characteristics of both the bird (e.g. densities, morphology and flight behaviour) and development (e.g. turbine height and speed) being assessed. The CRM outputs can be then fed to matrix models to project populations through time based on varying potential levels of mortality. A recent study has recommended using site-specific flight speed estimates where possible (Masden et al., 2021) to increase accuracy in CRM. Large initiatives such as the Offshore Renewable Joint Industry Partnership (ORJIP) Bird Collision Avoidance study (Skov et al., 2018) also aid in our understanding, but precautionarily high mortality estimates are still observed due to remaining uncertainty.

The impact of displacement and barrier effects on survival and productivity were originally given less attention in environmental impact assessments (Green et al., 2016), but have recently become more prominent as evidence has indicated stronger collision avoidance than had been assumed in earlier precautionary assessments, and more evidence of displacement/barrier effects has been accumulated from empirical studies (e.g. Heinänen et al. 2020). Previous energetic models on the subject have indicated that such effects may be negligible in comparison to other factors such as low food abundance or severe weather (Masden et al., 2010). However, there are many indicators suggesting that some UK seabird species are already under stress. One example is the mass mortality of auk (Alcidae) species in 2021 which is likely attributed to lack of prey as indicated by poor body condition (Fullick et al., 2022). Energetic models can provide some insight, but are often too simple to capture the driving processes. Such scenarios may call for spatially-explicit (Zurell et al., 2021) tactical model assessments where complexity can be determined as required (Evans et al., 2013).

One example is a recent model developed by Searle et al. (2017) to estimate population level consequences of displacement and barrier effects on seabird populations resulting from renewable developments. By simulating the foraging decisions of individual seabirds acting in a colony during the chick-rearing period, predicted time/energy budgets for each individual can be scaled up to project annual adult survival and productivity at population level. This approach, which adopts the individual-based model (IBM, also known as agent-based model, Railsback & Grimm, 2019) technique is in contrast to the “top-down” models associated with classic population ecology. In this “bottom-up” approach, individuals are modelled as discrete entities with various properties and associated stochasticity, parameterised from the available literature. Their interaction with other individuals and their environment determine the system’s higher level properties, such as population dynamics. This approach is heralded for its potential capabilities, but applied models have yet to incorporate some pertinent behaviours. Furthermore, they have focused on the breeding season and adult age classes only, thus excluding a large part of the yearly cycle and substantial proportion of the population.

1.4 Risk during migration

The majority of seabirds are migratory with distances travelled varying both between and within species (Berthold, 2001). Migration from UK colonies to wintering grounds may be relatively local as seen in auk species (Buckingham et al., 2021), whereas birds from UK gannet colonies tend to winter further afield such as the west coast of Africa (Grecian et al., 2019). It is important to determine migration corridors that overlap with future developments to have encompassing EIAs, which is a difficult task due to their fleeting and seasonal nature. Furthermore, waters around the UK are wintering grounds for many species which should be taken into account as well.

Various data sources have provided insight into migration routes, whether their original intended purpose or not. Surveys which are used to monitor the distribution of marine life before and throughout the operation of an ORD (“before-after-control-impact”/BACI), may take the form of boat or aerial surveys, with digital aerial surveys now becoming commonplace (Buckland et al., 2012). When conducted in a standardised manner at regular intervals throughout the year, these surveys can provide insight into seasonal movements and the distribution and densities of seabirds that occupy habitat that is going to become a renewable development with cues into the amount of birds displaced. There are two main drawbacks with these data; that it is difficult to define what behaviour the bird may be doing as they are snapshots, and the birds cannot be apportioned to a particular colony. Other long-term monitoring schemes not tied to a particular ORD project may last decades, such as the European Seabirds at Sea (ESAS) project (Stone et al., 1995), which was undertaken largely by boat surveys. They can often have the same pitfalls but with longer term data comes the possibility for more robust inference on differences in interannual patterns, and such surveys often cover wider areas to inspect any changes in distributions and abundances. Tracking individual seabirds helps overcome some of these pitfalls, in that if temporal and spatial resolution is great enough behaviour can be inferred, and the breeding colony the bird belongs to is determined, allowing apportionment of colony-specific risk. However, to obtain a sample size large enough for robust inference can be demanding of both time and money. By contrasting species-specific survey and tracking datasets (e.g. Carroll et al., 2019) it would be possible to achieve new perspectives on seasonality and the migratory movements of birds from different colonies.

As a result of seabirds being relatively long-lived and slow breeding (Pianka, 1970), adults may prioritise their own survival over that of dependent offspring in the face of unfavourable conditions (Ponchon et al., 2014). This contributes to adults being the most important age class for sustaining populations (Cairns, 1988), and as a consequence little attention is given to other age groups in PVA. However, as more than 50% of a breeding colony may comprise non-breeding birds in increasing populations of long-lived birds with deferred maturity (Klomp & Furness, 1992), a large proportion of which are immatures, they are probably important as a buffer to adult mortality by being a source for recruitment into the breeding population (Potts et al., 1980; Klomp & Furness, 1992; Votier et al., 2008). From this perspective, if ORDs disproportionately affect immature birds, this may diminish buffering abilities in the face of multiple stressors. Immatures may occupy different space (Daunt et al., 2007; Pettex et al., 2019) and are often more exploratory than adults (Votier et al., 2017). When combined with their relative inexperience, they could be more readily exposed than adults to the risks OWFs present and should be afforded more attention than currently given in EIAs.

As vulnerability to OWF impact differs between age classes and populations, so might it vary between individuals within a population. Upon recruitment and initial breeding attempts, the constraints of centrally placed foraging and finding resources for a chick can be demanding. This is especially the case in large colonies where intraspecific competition for resources is high (Lewis et al., 2001), exemplified by depletion of prey around the colony (Furness & Birkhead, 1984; Weber et al., 2021). As a consequence of foraging strategies developed to deal with competition for resources, individuals of the same colony often engage with their environment in contrasting ways.

1.5 Individual foraging consistency

A seabird’s prey distribution is often characterised by small patches of higher prey densities within broad-scale lower densities. This non-uniform and hierarchically clustered environment drives complex foraging movements in seabirds (Fauchald & Erikstad, 2002). Nested searching behaviour known as area-restricted searching (ARS) is thought to occur in response to patches with higher density of prey (Fauchald & Tveraa, 2006). In tracking data, these patches of ARS are often connected by faster, more linear movements which are categorised as travelling or commuting. Central place foragers are expected to employ the strategy which minimises time spent travelling and searching for prey (Bell, 2012), so beyond this nested searching behaviour which stems from sensorial abilities (be it visual, olfactory or auditory) if there are other sources of information providing cues on the potential location of prey it is probable that they will be taken into account.

If prey distributions are temporally persistent to some degree, using memory to recall a previously visited site could be advantageous. In the marine environment, the predictability of areas with enhanced productivity, such as frontal zones, shelf edges and upwellings, often persists at large and meso-scales at various timescales (Weimerskirch, 2007). Theory suggests that environments which have moderate levels of spatiotemporal complexity, i.e. prey is more dense in certain patches, are where memory provides the biggest benefits to fitness (Fagan et al., 2013). The environment many seabirds experience is typified by this patchiness, which is corroborated by many studies indicating the role of memory in seabirds through individuals returning to previously used foraging areas in successive trips (Weimerskirch, 2007; Regular et al., 2013; Wakefield et al., 2015).

Recalling a previous foraging area and orientating towards it will shape foraging trips to some degree, but it is likely that information from conspecifics will also influence a trip's trajectory (Ward & Zahavi, 1973) and cues from others may help reduce time spent searching for prey. When this occurs while out at sea on a foraging trip (i.e. information is not derived while at the colony), it is known as local enhancement (Wittenberger, 1985) and its ability to influence an individual's trajectory has been revealed by bird borne cameras (Tremblay et al., 2014). Ecological theory suggests local enhancement is only beneficial when competition is relatively low (Beauchamp, 2008, 2013), so that the benefits outweigh the costs. Therefore, in highly competitive environments, such as large seabird colonies, there may be complex foraging decisions required of individuals in order to obtain the required resources given the constraints.

The way information accrued through private (i.e. memory) and public (i.e. local enhancement) sources is implemented alongside a predator's own sensorial abilities in the pursuit of prey is hypothetically a key driver in characterising an individual's movements. Individual foraging site fidelity (IFSF) is a form of individual specialisation (Bolnick et al., 2003) which can be characterised by consistent use of foraging areas by an individual which is significantly narrower than the population's foraging area. This phenomenon has been found to persist over long time periods in a range of species (Bradshaw et al., 2004; Wakefield et al., 2015; Patrick & Weimerskirch, 2017) and is thought to be important in reducing intra-specific competition. Fidelity to a particular site may not be absolute (Hamer et al., 2001; Wakefield et al. 2015), and this flexibility is suggested to be indicative of a "win-stay/lose-switch" scenario (Kamil, 1983).

Does specialisation provide any advantages for individuals in the species which exhibit it? The repeatability of particular foraging strategies predicted foraging efficiency in great cormorants (*Phalacrocorax carbo*, (Potier et al., 2015) and higher fidelity has been shown to influence reproductive success in black-browed albatrosses (*Thalassarche melanophris*, Patrick & Weimerskirch, 2017). Hence, these specialisations may have implications for population dynamics (Phillips et al., 2017) although that is difficult to ascertain in field studies. However, the phenomenon of IFSF has received little attention in the context of OWFs which could conceivably have disproportionate impacts on birds which show fidelity to foraging areas in the footprint or proximity of renewable developments.

When considering the impacts of OWFs on seabird populations, the importance of IFSF has been previously suggested, but it has hitherto been afforded little attention in such assessments (although see Searle et al., 2015). Reasons for omission of this phenomenon to date are the incapability of standard EIA techniques to incorporate IFSF, and the lack of understanding of the characteristic patterns in the species being modelled. Among the species in which this phenomenon is well characterised is the northern gannet (*Morus bassanus*), where associated patterns are “strong” (Grimm & Railsback, 2012) thus providing the constituents required to develop theory in this regard. In previous studies where IFSF has been included in relevant models (Searle et al., 2015), it has been programmed in deterministically i.e. birds revisit the same spot consistently with no flexibility in decision making. Therefore, any adaptive qualities which may be inherent with such behaviour are ignored. An alternative to directly specifying the properties of this behaviour, would be to decipher which resource localisation mechanisms are being used by individuals so that we can have such patterns emerge from models in a natural fashion.

It is possible that IBMs predicting high mortality estimates from displacement (Searle et al. 2017) and collision (Van Bemmelen et al. 2021) from OWFs on seabirds are the result of individuals which cannot learn and adapt to their environment i.e. if there are foraging areas which take less time to reach due to not having to fly around the footprint of an OWF, a bird would potentially select those to regulate energy requirements. It may be that some of the resource localisation mechanisms which drive IFSF infer adaptive qualities in that they permit behavioural plasticity when faced with a changing landscape. Phillips et al. (2017) noted that until relatively recently, variation among individual seabirds was overlooked in ecological studies, in favour of testing for the effects of factors such as species, colony, year or sex. The consequences of individual variation and specialisation in seabirds is now well studied (Phillips et al. 2017) but has been given little to no consideration in EIAs, and this needs to be addressed.

1.6 Individual-based models

The potential of IBMs to estimate the impacts of ORDs has not been ignored, as indicated by studies on different species in the past decade (Topping & Petersen, 2011; McDonald et al., 2012; Langton et al., 2014; Warwick-Evans et al., 2017). Section 1.3 above refers to an IBM which has been designed to assess the effects of displacement and barrier effects. This has been incorporated into a tool called "SeabORD" (Searle et al., 2017), which is designed to be used by practitioners and is beginning to be adopted as an alternative to standard EIA techniques such as population projection through matrix models. Besides IBMs being a useful tool to inform managements decisions, they can also be used to develop ecological theory and synthesise empirical findings to identify broad and wide-spread phenomena in so-called "demonstration" models (Evans et al., 2013).

Such an approach has been applied in all ecology related fields including genetics, energetics, behaviour, foraging and movement (reviewed in Gallagher et al. 2021). For example, through modelling individual soil mites with rules for genetics and phenotypic variation (Benton, 2012), their mediating effect on population dynamics was linked by altering resource availability. By extracting multiple patterns from a real system on insectivorous birds feeding on pest species in a coffee plantation, Railsback and Johnson (Railsback & Johnson, 2011) challenged foraging theory and were able to show that the marginal value theory's rules (Charnov, 1976) were not the best at reproducing the system dynamics. Models have been used to develop theory on the use of memory of previously visited areas in reproducing realistic home ranges (Nabe-Nielsen et al., 2013). Inspecting interaction between individuals in the form of social cues, Urmy (2021) used simulations to investigate theory on colonies serving as information centres for location of food (Ward & Zahavi, 1973). The results indicated that visual trail following would be beneficial in several scenarios, which they then validated with radar field studies to inspect a tern colony interacting with prey. The latter example highlights the potential for IBMs and field studies in informing each other iteratively to drive forward theory and understanding of natural systems.

Patterns, defined as anything going beyond random variation gleaned from observations of nature, are a valuable currency for all IBMs. They are fingerprints which provide insight into processes which often underpin interacting systems. Pattern-orientated modelling (POM) is defined as the explicit use of empirical patterns throughout the modelling cycle (formulating, development, implementation, evaluation) in attempt to reproduce the system's essential dynamics while balancing complexity in addressing the model's intended purpose (Grimm & Railsback, 2012; Gallagher et al., 2021). POM can aid in developing theory for individual-level mechanisms that explain patterns at population-level, providing a so-called "bridge" between bottom-up and top-down processes (Gallagher et al., 2021) and with the resultant emergent properties of the model providing insight into underpinning processes.

Given their complex and often cumbersome nature, IBMs have been subject to criticism for lack of formal structure and transparency due to communication of the models being inconsistent. With the adoption of standard protocols for publication and communication (the "ODD" protocol, Grimm et al., 2005; Grimm & Railsback, 2012), and the previously mentioned methodology for the modelling process, POM, this has been somewhat addressed. However, progress can still be slow and as such it is often the case that models are completed in stages (Stillman et al., 2015). An initially postulated question may require sufficient modelling of the underlying systems before proceeding with more complex models. Herein, a model must be evaluated properly and be shown to be fit for purpose, thus indicating that it is representing the generative properties in a robust manner, before imposing more processes and submodels. For examples of this see Stillman's series of models looking at management of inshore waders (Stillman et al., 2000; Stillman, 2008; Bowgen et al., 2015) or a lineage of models inspecting seal movements which are often applied to similar species with increasing complexity at each iteration (Nabe-Nielsen et al., 2013; Liukkonen et al., 2018; Chudzinska et al., 2021). In this thesis I have not used an IBM to assess the impacts of OWFs on gannet survival and breeding success at Bass Rock, as I first saw it necessary to develop a model which can reproduce IFSF patterns effectively as a precursor to having more behaviourally realistic models of gannet movements in future applications.

1.7 Thesis aims and structure

This thesis aims to address some pressing issues regarding our ability to effectively assess how anthropogenic developments, namely OWFs, will impact upon seabirds. The study species used is gannets with a focus on the colony at Bass Rock. It holds significance as the world's largest colony (Murray et al., 2015) and the imminent construction of OWFs within its home range makes this a pivotal time. I have omitted further description of the study site and biological background here to avoid repetition, as it is covered sufficiently within the coming chapters. Based on the limited empirical evidence available up to the 2000s, gannets were considered to be one of the UK's seabird species most at risk of collision with offshore wind farm turbines, but were thought unlikely to be affected greatly by displacement or barrier effects (Furness et al., 2013). More recent data show high avoidance of offshore wind farms by gannets, suggesting that displacement and barrier effects might be greater than had been thought, but that collision risk may be less (Dierschke et al. 2016, Garthe et al. 2017, Skov et al. 2018). However, the magnitudes of these impacts remain highly uncertain.

The first part of the thesis gathers empirical data from different sources, especially tracking of migrating gannets, to gain novel insights into how risks from OWFs may be colony and age specific. The second part develops a movement model in breeding gannets to be used in developing understanding of IFSF in seabirds, with a view to this being used in future applications of IBMs to questions like OWF impacts so that complex behaviours are reproduced in a robust manner. More specifically:

Chapter 2 aims to assess which age classes and populations of gannets may be most at risk from the high concentration of offshore wind farms in the southern North Sea. We question whether it is juveniles or adults of the population which have more interaction with offshore wind farm areas during migration, therefore inferring the potential risk of collision mortality, and if risk varies seasonally for populations coming from different colonies. This was achieved by comparing tracking data from different age classes at Bass Rock with two types of survey data. This chapter has been published in Marine Environmental Research (Pollock et al., 2021).

Chapter 3 aims to develop an individual-based model which represents a typical foraging trip of an adult gannet at Bass Rock during the chick-rearing period. This required a model with fine scale movements and time steps, so that we could compare it directly to GPS data. The goal was to develop a robust and suitably parameterised framework on which to develop more behaviourally realistic models.

Chapter 4 aims to further develop the IBM detailed in chapter 3 to incorporate a memory components and interaction between individuals in order to question which behaviours could be driving the characteristic patterns of IFSF, such as repeatability in an individual's use of foraging areas. Hypotheses based on different resource localization mechanisms deriving combinations of public and/or private information were then used as simulation experiments to decipher which hypothesis reproduces the empirical patterns of IFSF the best. The hypotheses tested included different memory timescales (short-/long-term) derived from recalling the departure angle to previously successful foraging areas, and whether interaction with conspecifics works on through attraction ("local enhancement"), repulsion, or a combination of these two. The goal was to build a foraging model which is capable of having realistic IFSF patterns emerge to advance realism for future application in conservation and management scenarios.

Chapter 5 aims to synthesise the lessons learned from these studies and suggest ideas for future work, including the prospects for using the model to examine the impacts of OWFs.

1.8 Literature cited

Band, B. (2012). Using a collision risk model to assess bird collision risks for offshore windfarms. *SOSS Steering Group*. https://www.bto.org/sites/default/files/u28/downloads/Projects/Final_Report_SOSS02_Band1ModelGuidance.pdf

Beauchamp, G. (2008). A spatial model of producing and scrounging. *Animal Behaviour*, *76*(6), 1935–1942.

Beauchamp, G. (2013). *Social Predation: How Group Living Benefits Predators and Prey*. Elsevier.

BEIS. 2020. *Energy White Paper: Powering our Net Zero Future*. Page Prime Minister’s Office Brunei Darussalam. HM Government, London UK. http://www.ret.gov.au/energy/facts/white_paper/Pages/energy_white_paper.aspx.

Beissinger, S. R., & McCullough, D. R. (2002). *Population Viability Analysis*. University of Chicago Press.

Bell, W. J. (2012). *Searching Behaviour: The behavioural ecology of finding resources*. Springer Science & Business Media.

Benton, T. G. (2012). Individual variation and population dynamics: lessons from a simple system. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1586), 200–210.

Bernard, A., Rodrigues, A. S. L., Cazalis, V., & Grémillet, D. (2021). Toward a global strategy for seabird tracking. *Conservation Letters*, *14*(3).

Berthold, P. (2001). *Bird Migration: A General Survey*. Oxford University Press.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28.

Bowgen, K. M., Stillman, R. A., & Herbert, R. J. H. (2015). Predicting the effect of invertebrate regime shifts on wading birds: Insights from Poole Harbour, UK. *Biological Conservation*, *186*, 60–68.

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, *68*(6), 1349–1360.

Buckingham, L., Bogdanova, M. I., Green, J. A., Dunn, R. E., Wanless, S., Bennett, S., Bevan, R. M., Call, A., Canham, M., Corse, C. J., Harris, M. P., Heward, C. J., Jardine, D. C., Lennon, J., Parnaby, D., Redfern, C. P. F., Scott, L., Swann, R. L., Ward, R. M., Weston, E. D., Furness, R. W., & Daunt, F. (2021). Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. *Marine Ecology Progress Series*, *684*, 181-197.

Buckland, S. T., Burt, M. L., Rexstad, E. A., Mellor, M., Williams, A. E., & Woodward, R. (2012). Aerial surveys of seabirds: the advent of digital methods: Assessing the effects of offshore wind farms. *The Journal of Applied Ecology*, *49*(4), 960–967.

Burthe, S., Daunt, F., Butler, A., Elston, D. A., Frederiksen, M., Johns, D., Newell, M., Thackeray, S. J., & Wanless, S. (2012). Phenological trends and trophic mismatch across multiple levels of a North Sea pelagic food web. *Marine Ecology Progress Series*, *454*, 119–133.

Burthe, S. J., Wanless, S., Newell, M. A., Butler, A., & Daunt, F. (2014). Assessing the vulnerability of the marine bird community in the western North Sea to climate change and other anthropogenic impacts. *Marine Ecology Progress Series*, *507*, 277–295.

Cairns, D. K. (1988). Seabirds as Indicators of Marine Food Supplies. *Biological Oceanography*, *5*(4), 261–271.

Carroll, M. J., Wakefield, E. D., Scragg, E. S., Owen, E., Pinder, S., Bolton, M., Waggitt, J. J., & Evans, P. G. H. (2019). Matches and Mismatches Between Seabird Distributions Estimated From At-Sea Surveys and Concurrent Individual-Level Tracking. *Frontiers in Ecology and Evolution*, *7*. https://doi.org/10.3389/fevo.2019.00333

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136.

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., & McConnell, B. (2021). AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, *440*, 109397.

Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C., & Hamer, K. C. (2015). Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. *The Journal of Applied Ecology*, *52*(6), 1474–1482.

Coulson, J. (2002). Colonial breeding in seabirds. In: Schreiber EA, Burger J (eds) Biology of Marine Birds, CRC Press, Boca Raton, FL, 87–113.

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315.

Daunt, F., Wanless, S., Greenstreet, S. P. R., Jensen, H., Hamer, K. C., & Harris, M. P. (2008). The impact of the sandeel fishery closure in the northwestern North Sea on seabird food consumption, distribution and productivity. *Canadian Journal of Fisheries and Aquatic Sciences*, *65*(3), 362–381.

Daunt, F., Wanless, S., Harris, M. P., Money, L., & Monaghan, P. (2007). Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. *Functional Ecology*, *21*(3), 561–567.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537.

Dierschke, V., Furness, R.W., & Garthe, S. (2016). Seabirds and offshore wind farms in European waters: avoidance and attraction. *Biological Conservation*, *202*, 59-68.

Drewitt, A. L., & Langston, R. H. W. (2006). Assessing the impacts of wind farms on birds. *The Ibis*, *148*, 29–42.

Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., Weisberg, M., Wilkinson, D. J., Wolkenhauer, O., & Benton, T. G. (2013). Do simple models lead to generality in ecology? *Trends in Ecology & Evolution*, *28*(10), 578–583.

Fagan, W. F., Lewis, M. A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U. E., Tang, W.-W., Papastamatiou, Y. P., Forester, J., & Mueller, T. (2013). Spatial memory and animal movement. *Ecology Letters*, *16*(10), 1316–1329.

Fauchald, P., & Erikstad, K. E. (2002). Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. *Marine Ecology Progress Series*, *231*, 279–291.

Fauchald, P., & Tveraa, T. (2006). Hierarchical patch dynamics and animal movement pattern. *Oecologia*, *149*(3), 383–395.

Frederiksen, M. (2014) *Environmental demography – Exploring the links between vital rates and a fluctuating environment*. Doctor's dissertation. Aarhus University, Department of Bioscience, Denmark, 80 pp, doi: 10.13140/2.1.2975.4569

Fullick, E., Bidewell, C. A., Duff, J. P., Holmes, J. P., Howie, F., Robinson, C., Goodman, G., Beckmann, K. M., Philbey, A. W., & Daunt, F. (2022). Mass mortality of seabirds in GB. *The Veterinary Record*, *190*(3), 129–130.

Furness, R. W., & Birkhead, T. R. (1984). Seabird colony distributions suggest competition for food supplies during the breeding season. *Nature*, *311*, 655-656.

Furness, R. W., & Tasker, M. L. (2000). Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Marine Ecology Progress Series*, *202*, 253–264.

Furness, R. W., Wade, H. M., & Masden, E. A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, *119*, 56–66.

Gallagher, C. A., Chudzinska, M., Larsen-Gray, A., Pollock, C. J., Sells, S. N., White, P. J. C., & Berger, U. (2021). From theory to practice in pattern-oriented modelling: identifying and using empirical patterns in predictive models. *Biological Reviews of the Cambridge Philosophical Society*, *96*(5), 1868-1888.

Garthe, S., Markones, N., & Corman, A-M. (2017). Possible impacts of offshore wind farms on seabirds: a pilot study in northern gannets in the southern North Sea. *Journal of Ornithology*, *158*, 345-349.

Grecian, W. J., Williams, H. J., Votier, S. C., Bearhop, S., Cleasby, I. R., Grémillet, D., Hamer, K. C., Le Nuz, M., Lescroël, A., Newton, J., Patrick, S. C., Phillips, R. A., Wakefield E. D., & Bodey, T. W. (2019). Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the Northeast Atlantic. *Frontiers in Ecology and Evolution, 7,* 214.

Green, R. E., Langston, H. W., McCuskie, A., Sutherland, R., & Wilson, J. D. (2016). Lack of sound science in assessing wind farm impacts on seabirds. *The Journal of Applied Ecology*, *53*(6), 1635–1641.

Grémillet, D., Ponchon, A., Paleczny, M., Palomares, M.-L. D., Karpouzi, V., & Pauly, D. (2018). Persisting Worldwide Seabird-Fishery Competition Despite Seabird Community Decline. *Current Biology: CB*, *28*(24), 4009-4013.e2.

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1586), 298–310.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., & DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, *310*(5750), 987–991.

GWEC, 2019. *Global Wind Report 2019*. Global Wind Energy Council, Brussels, Belgium

Hamer, K. C., Phillips, R. A., Hill, J. K., Wanless, S., & Wood, A. G. (2001). Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series*, *224*, 283–290.

Harris, M. P., Newell, M., Daunt, F., Speakman, J. R., & Wanless, S. (2008). Snake pipefish *Entelurus aequoreus* are poor food for seabirds. *The Ibis*, *150*(2), 413–415.

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. *The Journal of Animal Ecology*, *80*(1), 4–18.

Heinänen, S., Žydelis, R., Kleinschmidt, B., Dorsch, M., Burger, C., Morkūnas, J., Quillfeldt, P., & Nehls, G. (2020). Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. *Marine Environmental Research*, *160*, 104989.

Howells, R. J., Burthe, S. J., Green, J. A., Harris, M. P., Newell, M. A., Butler, A., Johns, D. G., Carnell, E. J., Wanless, S., & Daunt, F. (2017). From days to decades: short- and long-term variation in environmental conditions affect offspring diet composition of a marine top predator. *Marine Ecology Progress Series*, *583*, 227–242.

Inger, R., Attrill, M. J., Bearhop, S., Broderick, A. C., Grecian, J. W., Hodgson, D. J., Mills, C., Sheehan, E., Votier, S. C., Witt, M. J., & Godley, B. J. (2009). Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *The Journal of Applied Ecology*, *46*(6), 1145–1153.

Kamil, A. C. (1983). Optimal foraging theory and the psychology of learning. *American Zoologist, 23*(2), 291–302.

Keogan, K., Phillimore, A., & Lewis, S. (2018). Global phenological insensitivity to shifting ocean temperatures among seabirds. *Nature Climate Change, 8*, 313-318.

Klomp, N. I., & Furness, R. W. (1992). Non-Breeders as a Buffer Against Environmental Stress: Declines in Numbers of Great Skuas on Foula, Shetland, and Prediction of Future Recruitment. *The Journal of Applied Ecology*, *29*(2), 341–348.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series, 628*, 183–193.

Langton, R., Davies, I. M., & Scott, B. E. (2014). A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes. *Ecological Modelling*, *273*(Supplement C), 31–43.

Lebreton, J. D., & Clobert, J. (1991). Bird population dynamics, management, and conservation: the role of mathematical modelling. Pages 105–125 in C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies. Oxford University Press, New York, New York, USA.

Lefkovitch, L. P. (1965). The Study of Population Growth in Organisms Grouped by Stages. *Biometrics*, *21*(1), 1–18.

Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, *412*(6849), 816–819.

Liukkonen, L., Ayllón, D., Kunnasranta, M., Niemi, M., Nabe-Nielsen, J., Grimm, V., & Nyman, A.-M. (2018). Modelling movements of Saimaa ringed seals using an individual-based approach. *Ecological Modelling*, *368*, 321–335.

Marsden, S. (2018). Protecting wild land from wind farms in a post-EU Scotland. *International Environmental Agreements: Politics, Law and Economics*, *18*(2), 295–314.

Masden, E. A., Cook, A. S. C. P., McCluskie, A., Bouten, W., Burton, N. H. K., & Thaxter, C. B. (2021). When speed matters: The importance of flight speed in an avian collision risk model. *Environmental Impact Assessment Review*, *90*, 106622.

Masden, E. A., Fox, A. D., Furness, R. W., Bullman, R., & Haydon, D. T. (2010). Cumulative impact assessments and bird/wind farm interactions: Developing a conceptual framework. *Environmental Impact Assessment Review*, *30*(1), 1–7.

Masden, E. A., Haydon, D. T., Fox, A. D., & Furness, R. W. (2010). Barriers to movement: Modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. *Marine Pollution Bulletin*, *60*(7), 1085–1091.

Masselink, G., Castelle, B., Scott, T., Dodet, G., Suanez, S., Jackson, D., & Floc'h, F. (2016). Extreme wave activity during 2013/2014 winter and morphological impacts along the Atlantic coast of Europe. *Geophysical Research Letters*, *43*(5), 2135–2143.

McDonald, C., Searle, K., Wanless, S., & Daunt, F. (2012). Effects of Displacement from Marine Renewable Development on Seabirds Breeding at SPAs: A Proof of Concept Model of Common Guillemots Breeding on the Isle of May. *CEH Edinburgh: Final Report to Marine Scotland Science*. http://www.gov.scot/Resource/0040/00404982.pdf

Milner-Gulland, E. J., & Akçakaya, H. R. (2001). Sustainability indices for exploited populations. *Trends in Ecology & Evolution*, *16*(12), 686–692.

Mitchell, I., Daunt, F., Frederiksen, M., & Wade, K. (2020). Impacts of climate change on seabirds, relevant to the coastal and marine environment around the UK. In *MCCIP Science Review 2020* (pp. 382–399). Marine Climate Change Impacts Partnership.

Mitchell, I., French, G., Douse, A., Foster, S., Kershaw, M., Neil McCulloch, N., Murphy, M. and Hawkridge, J. (2018) *Marine Bird Abundance. UK Marine Online Assessment Tool*, https://moat.cefas.co.uk/biodiversity-food-webs-and-marine-protected-areas/birds/abundance/

Morley, T. I., Fayet, A. L., Jessop, H., Veron, P., Veron, M., Clark, J., & Wood, M. J. (2016). The seabird wreck in the Bay of Biscay and South-Western Approaches in 2014: A review of reported mortality. *Seabird*, *29*, 22–38.

Murray, S., Harris, M. P., & Wanless, S. (2015). The status of the Gannet in Scotland in 2013-14. *Scottish Birds*, *35*(1), 13.

Nabe-Nielsen, J., Tougaard, J., Teilmann, J., Lucke, K., & Forchhammer, M. C. (2013). How a simple adaptive foraging strategy can lead to emergent home ranges and increased food intake. *Oikos*, *122*(9), 1307–1316.

Newell, M., Wanless, S., Harris, M. P., & Daunt, F. (2015). Effects of an extreme weather event on seabird breeding success at a North Sea colony. *Marine Ecology Progress Series*, *532*, 257–268.

O’Brien, S. H., Cook, A. S. C. P., & Robinson, R. A. (2017). Implicit assumptions underlying simple harvest models of marine bird populations can mislead environmental management decisions. *Journal of Environmental Management*, *201*, 163–171.

OSPAR (2017) *Marine Bird Breeding Success/Failure.* Intermediate Assessment 2017, https://oap.ospar.org/en/ospar-assessments/intermediate-assessment-2017/biodiversity-status/marine-birds/marine-bird-breeding-success-failure/

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

Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *The Journal of Animal Ecology*, *86*(3), 674–682.

Pettex, E., Lambert, C., Fort, J., Dorémus, G., & Ridoux, V. (2019). Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. *Journal of Avian Biology*.

Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series*, *578*, 117–150.

Pianka, E. R. (1970). On r-and K-selection. *The American Naturalist*, *104*(940), 592–597.

Pickering, H., & Whitmarsh, D. (1997). Artificial reefs and fisheries exploitation: a review of the 'attraction versus production' debate, the influence of design and its significance for policy. *Fisheries Research*, *31*(1), 39–59.

Piper, W. H. (2011). Making habitat selection more "familiar": a review. *Behavioral Ecology and Sociobiology*, *65*(7), 1329–1351.

Pollock, C. J., Lane, J. V., Buckingham, L., Garthe, S., Jeavons, R., Furness, R. W., & Hamer, K. C. (2021). Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea. *Marine Environmental Research*, *171*, 105457.

Ponchon, A., Grémillet, D., Christensen-Dalsgaard, S., Erikstad, K. E., Barrett, R. T., Reiertsen, T. K., McCoy, K. D., Tveraa, T., & Boulinier, T. (2014). When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere* , *5*(1), art4.

Potier, S., Carpentier, A., Grémillet, D., Leroy, B., & Lescroël, A. (2015). Individual repeatability of foraging behaviour in a marine predator, the great cormorant, *Phalacrocorax carbo*. *Animal Behaviour*, *103*, 83–90.

Potts, G. R., Coulson, J. C., & Deans, I. R. (1980). Population Dynamics and Breeding Success of the Shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *The Journal of Animal Ecology*, *49*(2), 465–484.

Railsback, S. F., & Grimm, V. (2019). *Agent-Based and Individual-Based Modeling: A Practical Introduction, Second Edition*. Princeton University Press.

Railsback, S. F., & Johnson, M. D. (2011). Pattern-oriented modeling of bird foraging and pest control in coffee farms. *Ecological Modelling*, *222*(18), 3305–3319.

Regular, P. M., Hedd, A., & Montevecchi, W. A. (2013). Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour*, *86*(3), 545–552.

Reygondeau, G., & Beaugrand, G. (2011). Future climate-driven shifts in distribution of *Calanus finmarchicus*. *Global Change Biology*, *17*(2), 756–766.

Russell, D. J. F., Brasseur, S. M. J. M., Thompson, D., Hastie, G. D., Janik, V. M., Aarts, G., McClintock, B. T., Matthiopoulos, J., Moss, S. E. W., & McConnell, B. (2014). Marine mammals trace anthropogenic structures at sea. *Current Biology*, *24*(14), R638–R639.

Searle, K. R., Butler, A., Mobbs, D., Bogdanova, M., Wanless, S., Bolton, M., & Daunt, F. (2015). At-Sea Turnover of Breeding Seabirds-Final Report to Marine Scotland Science. *Scottish Marine and Freshwater Science*. https://research-scotland.ac.uk/handle/20.500.12594/11192

Searle, K. R., Mobbs, D. C., Butler, A., Furness, R. W., Trinder, M. N., & Daunt, F. (2017). Finding out the fate of displaced birds. *CEH Report to Marine Scotland FCR/2015/19*. https://data.marine.gov.scot/sites/default/files/SMFS%200908%20%282%29.pdf

Skov, H., Heinänen, S., Norman, T., Ward, R., Méndez-Roldán, S., & Ellis, I. (2018). *ORJIP Bird Collision Avoidance Study*. Carbon Trust & Discretionary Project Steering Committee. https://www.carbontrust.com/media/675793/orjip-bird-collision-avoidance-study_april-2018.pdf

Stillman, R. A. (2008). MORPH—An individual-based model to predict the effect of environmental change on foraging animal populations. *Ecological Modelling*, *216*(3), 265–276.

Stillman, R. A., Goss-Custard, J. D., West, A. D., Durell, S. E. A. L. V. D., Caldow, R. W. G., McGrorty, S., & Clarke, R. T. (2000). Predicting mortality in novel environments: tests and sensitivity of a behaviour-based model. *The Journal of Applied Ecology*, *37*(4), 564–588.

Stillman, R. A., Railsback, S. F., Giske, J., Berger, U., & Grimm, V. (2015). Making Predictions in a Changing World: The Benefits of Individual-Based Ecology. *Bioscience*, *65*(2), 140–150.

Stone, C. J., Webb, A., Barton, C., Ratcliffe, N., Reed, T. C., Tasker, M. L., Camphuysen, C. J., Pienkowski, M. W., & Consult, O. (1995). *An atlas of seabird distribution in north-west European waters*. http://www.jncc.gov.uk/PDF/pub95_seabirdatlas5.47.pdf

Thaxter, C. B., Buchanan, G. M., Carr, J., Butchart, S. H. M., Newbold, T., Green, R. E., Tobias, J. A., Foden, W. B., O'Brien, S., & Pearce-Higgins, J. W. (2017). Bird and bat species' global vulnerability to collision mortality at wind farms revealed through a trait-based assessment. *Proceedings. Biological Sciences / The Royal Society*, *284*(1862).

Topping, C. and Petersen, I.K. (2011). *Report on a red-throated diver agent-based model to assess the cumulative impact from offshore wind farms*. Aarhus University. Danish Centre for Environment and Energy https://tethys.pnnl.gov/sites/default/files/publications/Topping-et-al-2011.pdf

Tremblay, Y., Thiebault, A., Mullers, R., & Pistorius, P. (2014). Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PloS One*, *9*(2), e88424.

Urmy, S. S. (2021). Visual trail following in colonial seabirds: theory, simulation, and remote observations. *Ecological Monographs*, *91*(1), e01429.

Van Bemmelen, R.S.A., Soudijn, F.H., Benden, D., Potiek, A., Chen, C., Hintzen, N., Wilkes, T., Van Kooten, T., and Gyimesi, A. (2021). *Individual-based model lesser black-backed gulls in the Netherlands.* No. 21-168 Bureau Waardenburg.

Votier, S. C., Birkhead, T. R., Oro, D., Trinder, M., Grantham, M. J., Clark, J. A., McCleery, R. H., & Hatchwell, B. J. (2008). Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *The Journal of Animal Ecology*, *77*(5), 974–983.

Votier S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E. D., & Patrick, S.C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20171068.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology*, *96*(11), 3058–3074.

Wakefield, E. D., Phillips, R. A., & Matthiopoulos, J. (2009). Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Marine Ecology Progress Series*, *391,* 165-182.

Wanless, S., Harris, M. P., Newell, M. A., Speakman, J. R., & Daunt, F. (2018). Community-wide decline in the occurrence of lesser sandeels *Ammodytes marinus* in seabird chick diets at a North Sea colony. *Marine Ecology Progress Series*, *600*, 193–206.

Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as "information-centres" for food-finding. *The Ibis, 115,* 517-534.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology*, *55,* 503-515.

Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E., Oppel, S., Shearer, L., Soetaert, K. E. R., Weber, N., & Broderick, A. C. (2021). Direct evidence of a prey depletion "halo" surrounding a pelagic predator colony. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(28).

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research. Part II, Topical Studies in Oceanography*, *54*(3), 211–223.

Wittenberger, J. F. (1985). The adaptive significance of coloniality in birds. *Avian Biology*, *8*, 1–78.

Zurell, D., König, C., Malchow, A.-K., Kapitza, S., Bocedi, G., Travis, J., & Fandos, G. (2021). Spatially explicit models for decision-making in animal conservation and restoration. *Ecography*, *44*, 1-16.

Chapter 2: Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea

Abstract

The southern North Sea holds the world's highest concentration of offshore wind farms (OWFs). Northern gannets (*Morus bassanus*), a species considered at high risk from OWF impacts, show a strong seasonal peak there in November, but it is unclear which populations and age classes are most at risk of collision with wind turbines. We tagged adult and juvenile gannets at the world's largest colony (Bass Rock) and reviewed two sources of survey data for different age classes to study their movements through southern North Sea waters. Tracked birds showed peak numbers in the southern North Sea in mid-October, with much smaller numbers there during November. Adults were distributed throughout the area, including waters close to OWFs, whereas juveniles were confined to the coast. Survey data indicated high proportions of immature gannets in southern North Sea waters, suggesting higher collision risk than for adults. Gannets present in November may be predominantly from colonies further north than Bass Rock.

A condensed form of this chapter forms a paper with the same title by Christopher J. Pollock, Jude V. Lane, Lila Buckingham, Stefan Garthe, Ruth Jeavons, Robert W. Furness, Keith C. Hamer published in Marine Environmental Research, Volume 171, October 2021. In addition, Appendix Figure A.2.2 is published in a paper by Jude V. Lane, Christopher J. Pollock and other authors, entitled 'Post fledging movements, mortality and migration of juvenile northern gannets', in *Marine Ecology Progress Series* 671: 207-218 (2021).

2.1 Introduction

Development of renewable energy resources is increasing apace in an attempt to reduce reliance on fossil fuels. Offshore wind farms (OWFs) harvest energy at sea, but their potential impacts on marine environments are a cause for concern. The UK is currently the largest offshore wind market, with 36% of global installed capacity (deCastro et al., 2019), calling particular attention to impacts of OWFs on marine life in UK waters.

Seabirds are declining globally due to multiple stressors including invasive species, bycatch and overfishing of prey (Croxall et al., 2012; Dias et al., 2019). In addition, potential adverse effects of OWFs on seabirds include risks of collision with turbine blades, barrier effects when energy is expended to avoid turbines, and displacement through exclusion from feeding grounds (Furness et al., 2013). The extent of these different effects depends upon birds' behaviour (e.g. home range size, flight height and speed) and varies seasonally (Lane et al., 2020).

Northern gannets (*Morus bassanus*) are long-lived seabirds breeding on coasts and islands of the North Atlantic Ocean. Often characterised by their resilience, recent reported declines in their most southerly breeding colony (Grémillet et al., 2020) indicate they are not impervious to changes in marine environments. Their flight heights, particularly when foraging (Garthe et al., 2014; Cleasby et al., 2015; Lane et al., 2019), place them at high risk of collision with wind turbines (Furness et al., 2013). Research also indicates strong avoidance of OWFs by gannets (Dierschke et al., 2016; Garthe et al., 2017; Peschko et al., 2021) which may result in habitat loss and increased competition for resources. At a relatively small colony on Helgoland, gannets during the breeding season show reduced selection of operational OWF sites, with 89% of tracked birds predominantly avoiding OWF sites, although 11% frequently entered them when foraging or commuting between the colony and foraging sites (Peschko et al., 2021). Most OWF impact studies on gannets, particularly those employing tracking data, have been conducted during the breeding season when most birds are central place foragers. Much less is understood about potential year-round effects, especially those during migration when many birds from European colonies may move through areas like the southern North Sea, which has the highest concentration of OWFs in the world (Figure 2.1).

The coasts of Western Europe to West Africa represent a major flyway for the non-breeding season movements of gannets from colonies in the eastern Atlantic. At a metapopulation level they exhibit chain migration (Fort et al., 2012) wherein populations move approximately equal distances southward from each breeding colony through typical migration corridors, and rarely fly over land. Consequently, birds from more northerly colonies tend to winter further north than birds from more southerly colonies. However, migratory movements of individual gannets within a colony differ considerably, with some overwintering much nearer to the colony than others (Kubetzki et al., 2009; Grecian et al., 2019). In addition, many birds exhibit a clockwise loop migration around Britain and Ireland (Furness et al., 2018), travelling south through the Strait of Dover on their way to wintering grounds but returning via more westerly waters. This pattern is reflected in wind farm baseline survey data and impact assessments, which suggest a strong peak in risk in the southern North Sea during November each year (Furness et al., 2018). Using only aerial and boat-based survey data, however, it is not possible to determine which colonies birds are from, and thus colony-specific risk is hard to assess.

Gannets do not reach sexual maturity until age 4-5 years and in comparison to adults, little is known about the seasonal movements of younger birds. After fledging, gannets do not generally return to land until their third calendar year (Nelson, 2002) and so there is a large gap in our knowledge during this stage of their life cycle. Juveniles tracked during post-fledging migration from two European gannet colonies followed broadly the same path to West African waters as adults from the same colonies (Gremillet et al., 2015; Lane et al. 2021). Hence, it is important to assess the risks to these birds, especially for more northerly populations that are more likely to encounter OWFs during migration.

Neither is there abundant knowledge of the seasonal movements of immature birds aged 2-5 years. During the summer months, many immatures attend breeding colonies from where their foraging trips are much more expansive than those of adults (Votier et al., 2011; Grecian et al., 2018). Investigation of extensive aerial survey data shows strong seasonal segregation of immature and adult gannets in the English Channel and Bay of Biscay (Pettex et al., 2019). During the summer, central-place foraging breeding adults appeared to competitively exclude immature birds to more pelagic waters, whereas in the winter, their distributions overlapped. However, it was not known to what extent adults and immatures were segregated during migration.

Environmental impact assessments (EIA) must be conducted prior to consent of a new OWF development. EIAs tend to assume that all risk falls on adults from the nearest Special Protection Area (SPA) as a precautionary approach and that risk is divided equally across age classes in relation to age structure derived from demographic parameters and population modelling. These assumptions may not hold, however, and better ecologically informed EIAs would increase confidence in conclusions regarding risks to gannet populations. In this study we use both tracking and survey data to obtain insights into which colonies and age classes of gannets are most at risk from OWF developments in the southern North Sea. We tagged adult and juvenile gannets on Bass Rock, the largest gannet colony in the world (Murray et al., 2015), to study their movement through southern North Sea waters during autumn migration. We then compared this with data on age classes of gannets recorded during aerial surveys of proposed OWF sites in UK southern North Sea waters and from selected areas of the North Sea reported in the European Seabirds at Sea (ESAS) database.

2.2 Methods

2.2.1 Tracking data – Study site and sampling

Gannets were tracked from Bass Rock, Scotland (56˚04'N, 2˚38'W, see Figure 2.1) between 2018 and 2020. Adults were caught at the nest site using a 6m telescopic pole during the summers of 2018 and 2019. Each bird was weighed, fitted with a BTO ring or its existing ring number recorded, and fitted with a combined geolocation-immersion logger (MK 3006 British Antarctic Survey, Cambridge UK n=58; Intigeo C65, Migrate Technology Ltd n=4). The maximum combined mass of the ring and logger was ~8.5 g, approximately ~0.3% of the average adult body mass and therefore well within recommended guidelines (Phillips et al., 2003), and a previous study deploying similar geolocator tags on gannets reported no adverse effects on bird welfare (Kubetzki et al., 2009).

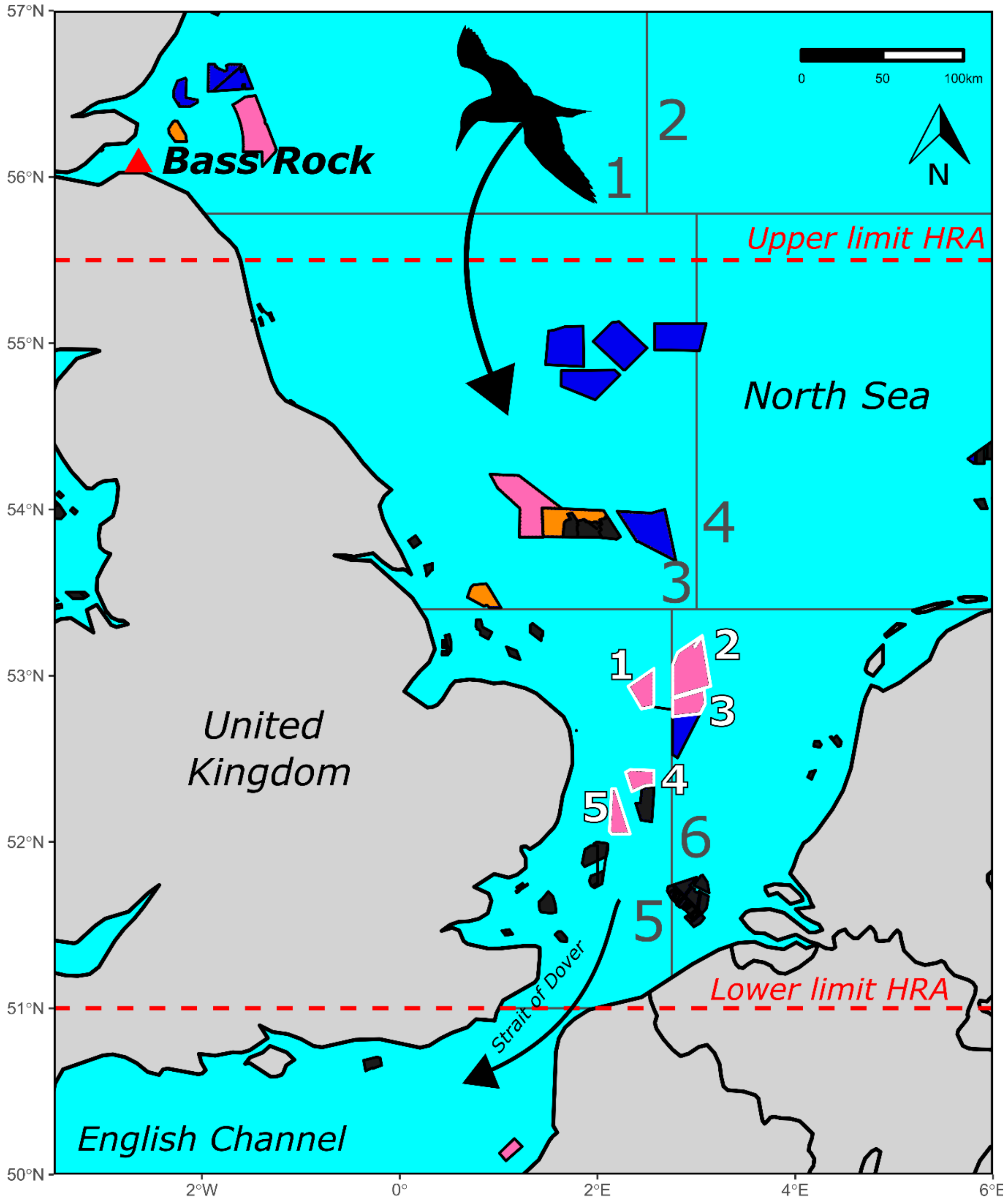


Figure 2.1. OWF sites (polygons) in the southern North Sea with construction stage indicated by fill colour: pink = planned; blue = approved; orange = under construction; dark grey = operational. Polygons with white outlines are OWF sites which have aerial survey data (n=5: 1 = Norfolk Vanguard West, 2 = Norfolk Boreas, 3 = Norfolk Vanguard East, 4 = East Anglia One North, 5 = East Anglia Two). Red dashed lines at 55.5°N and 51.0°N indicate upper and lower limits of the designated high-risk area (HRA; see Methods 4.2.2). Dark grey dividing lines and numbering indicate division of the North Sea into boxes for inspection of ESAS data. Bass Rock is indicated by a red triangle. Black arrows indicate the general direction of migrating gannets in autumn.

We recovered 37 of 62 deployed geolocators in April-August 2019 (22 of 26) and August 2020 (15 of 36), with all recovered devices deployed for one wintering period. We attached a new device to all 21 adults recaptured in 2019 to sample successive wintering periods, with seven individuals (33%) returning data from successive years.

We processed geolocator data following Lisovski et al. (2019). Twilights were annotated from light intensity data using the 'twilightCalc' function in the 'GeoLight' package (Lisovski & Hahn, 2012). The longest period of data from each individual, deduced by visually assessing the quality of light intensity data and cropped accordingly, was used going forwards. Locations were estimated using the 'probGLS' package (Merkel et al., 2016), by running data for each individual through an iterative forward step selection framework in which weight is given to possible locations according to daily median sea surface temperature (SST) recorded by the logger and daily mean NOAA SST data at 0.25^{o} resolution (Reynolds et al. 2007, Physical Sciences Division 2019). Further parameters chosen for this algorithm are provided in Table A.2.1 in the Appendix. The product is a "most probable track", comprising two refined locations per day. The estimated error of all locations reported in the results was 167 ± 724 km. This error is much greater than that associated with the tags used on juveniles (see following paragraph), but the two datasets are nonetheless broadly comparable owing to the large scale movements associated with gannet migration.

Juveniles (n=42) were captured at the colony on 5th October 2018 (n=21) and 20th September 2019 (n=21). Each bird was weighed and fitted with a metal BTO ring. A solar powered Argos GPS-Platform Terminal Transmitter (GPS-PTT; Microwave Telemetry, Columbia, USA), programmed to record a GPS location once an hour between 0600 and 2000 and relayed to the Argos satellite system every 24 hours, was then attached to the upper side of the three central tail feathers using Tesa © tape and cable ties. The total weight of the device plus tape and ties (~49g in 2018, ~34g in 2019) was <2% of body mass. Handling time of birds was no longer than 20 minutes after which birds were released on the colony. Argos locations were filtered by speed and location class (LC) to remove erroneous locations using the R package 'argosfilter' (Freitas, 2010; Langston et al., 2013); speeds >25 ms^{-1} and LC Z were removed. GPS data (precise to < 100m, Argos 2016) and Argos PTT location classes 3, 2, 1, A and B (precision <250m to >1500m) were then combined to reconstruct movements. All locations with duplicated dates and times were screened and only the duplicate with greater precision was retained. Data were received from 38 of the 42 juveniles, from which we selected only the data from birds that travelled south from the colony and passed through the Strait of Dover.

2.2.2 High-risk area

To compare adult and juvenile tracking data, we demarcated a “high-risk area” (HRA, Figure 2.1) in the southern North Sea. The HRA was defined as between 55.5°N and 51.0°N since: (i) many gannets migrate south through the Strait of Dover on autumn migration (Furness et al. 2018); (ii) it encompasses most OWF sites in UK and adjacent North Sea waters; (iii) once birds have passed through the Strait of Dover (51°N) the number and density of OWFs further south is relatively low; (iv) the upper boundary is far enough south of the colony (~100 km) that birds that enter this are likely to have begun migration (i.e. not rafting around the colony), and; (v) the distance between the upper and lower limit (~500 km) is large compared to differences in the precision of the different sets of tracking data. This allowed us to inspect differences between the age classes in passage time (h) through the HRA, their migration phenology, and the distance of location estimates (km) from the shore.

Passage time southwards through the HRA (T_{HRA}) was calculated using the following equation:

$$T_{HRA}\,(\textit{Time in high-risk area, hours}) = T_2 - T_1$$

Where T_1 is the last time a bird crossed the upper boundary while heading southwards (excluding other earlier incursions into the HRA) and T_2 is the first time the same bird crossed the lower boundary. For each track, location estimates on either side of both the upper and lower boundary of the HRA, were directly interpolated in order to obtain T_1 and T_2. This was done for both the adult (GLS) and juvenile (GPS-PTT) data using the ‘adehabitatLT’ package (Calenge & Calenge, 2018). To ascertain migration phenology, allowing comparison with the survey data, the temporal midpoint between T_1 and T_2 was taken for each individual when travelling through the HRA. The shortest distance between each location estimate and the coast were calculated using the ‘sf’ package (Pebesma, 2018).

2.2.3 Proposed OWF site surveys

Data derived from digital aerial surveys were supplied to us by APEM Limited, who carried out the surveys on five prospective OWF sites as part of baseline studies contributing to the required environmental impact assessment. Aerial surveys were undertaken by survey aircraft that obtained high-resolution still images with a reported resolution of 2 cm Ground Sampling Distance (APEM Ltd). For further details on the methods, see “Norfolk Vanguard Offshore Wind Farm Appendix 13.1 Offshore Ornithology Technical Appendix” (https://infrastructure.planninginspectorate.gov.uk/wp-content/ipc/uploads/projects/EN010079/EN010079-001547-Appendix%2013.01%20Ornithology%20Technical%20Appendix.pdf).

Surveys were conducted throughout the year, each lasting a minimum of two years in total, and all were completed within 2012-2018. We were provided data for all gannets observed in each survey, where age was also assigned where possible by APEM. These data were then processed to assess the relative abundance and seasonality of the different age classes across OWF sites in the southern North Sea. The five prospective OWF sites surveyed are all located in the southern North Sea (Figure 2.1). OWF sites range in size from 209 km^2 to 725 km^2, with distance from the shore ranging from 40 to 92 km (Table A.2.2).

2.2.4 European Seabirds at Sea data

The European Seabirds at Sea partnership (ESAS) has conducted extensive surveys of seabirds, predominantly from ships with strip-transect counts, with data going back as far as 1979 (Stone et al., 1995). We extracted data for gannets distributed in the southern North Sea (Figure 2.1) from ESAS database version 5.0 (October 2011), covering the years 1980–2010, to compare seasonal and spatial variation from these surveys with our tracking data and with pre-construction digital aerial surveys of OWF sites.

2.3 Results

2.3.1 Tracking data

In 37 datasets recovered from adults, 26 birds travelled southwards at some point during 2018-2019, six of which did so on consecutive years, and entered the HRA (2018 n=20, 2019 n=13, HRA location estimates=641, Figure 2.2). 18 birds (10 in 2018, 8 in 2019) continued south through the Strait of Dover. Of 38 juveniles tracked, 11 flew south through the Strait of Dover (7 in 2018, 4 in 2019, HRA location estimates=1105, Figure 2.2). Within the HRA adults were apparently located over four times further from the coast than juveniles (mean ± SD; adult=106±61.5 km, juvenile=21.5±22.4 km, Figure A.2.1). Consequently, 11% of adult location estimates inside the HRA (Figure 2.2) appeared to fall inside OWF sites, compared to only 1% for juveniles.

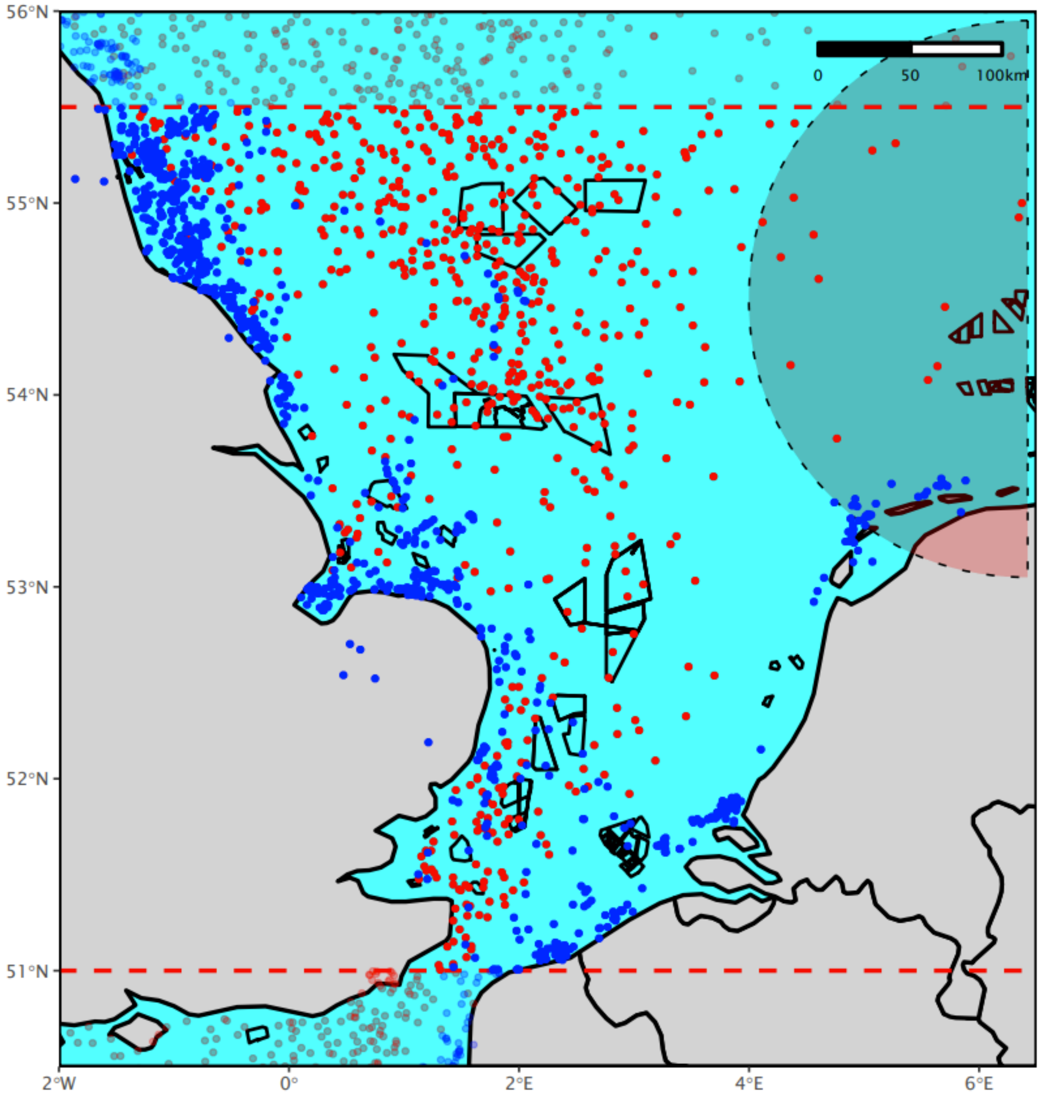


Figure 2.2. Location estimates of adult (red, n individuals = 27), and juvenile (blue, n individuals = 11) during autumn migrations through the southern North Sea in 2018-2019. Red dashed lines indicate upper and lower limits of the designated high-risk area. OWF sites indicated by black polygons. Translucent semicircle with black dashed outline shows the mean estimated error (167km) for adult GLS locations, whereas the error associated with GPS-PTT for juveniles (<1500m) does not exceed the size of the plotted blue points. See Appendix Figure A.2.2 for complete migration tracks of adults and juveniles.

Juveniles had a longer passage time through the HRA than adults appeared to, taking almost twice as long (mean ±SD; juveniles=78.5±27.3 hours; adults=47.5±31.6 hours, data from one juvenile removed as a clear outlier having spent 315 hours in the HRA, Figure 2.3). The midpoint of the HRA was reached by juveniles 3 days earlier than adults (median date, range; juveniles = 16th Oct, 29th Sep – 23rd Oct, adults = 19th Oct, 3rd Oct – 8th Nov, Figure 2.4).

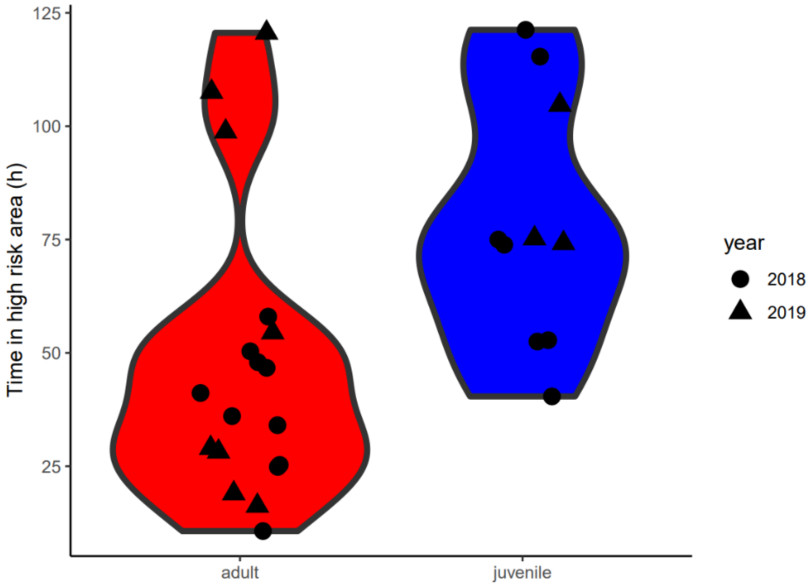


Figure 2.3. Passage time (h) through the high-risk area for adults (n=18, red) and juveniles (n=10, blue) tracked from Bass Rock during autumn migration.

2.3.2 Digital aerial surveys

A total of 3901 gannets were detected during digital aerial surveys of prospective OWF sites in the southern North Sea of which 91% were identified as adults (n=3542), 5.1% as immatures (n=198) and 1.3% as juveniles (n=46). Age could not be reliably determined for 4.5% of birds (n=161).

Seasonal peaks in abundance were evident for both adults and juveniles (Figure 2.4). Peak counts of juveniles occurred in August (n=92) whereas peak counts of adults occurred in November (n=1761). Similar seasonal patterns are seen across surveyed OWF in Figure 4. A much smaller peak of adults was also detected in March (n=166).

When compared with tracking data it is clear that tagged adults from Bass Rock were present in the HRA earlier than the peak seen in digital aerial surveys, whereas tracked juveniles were much later than the peak detected in surveys for immature gannets. The proportion of juveniles in counts in individual OWF sites showed an inverse relationship to increasing distance from the shore (Figure A.2.3), showing spatial consistency with what the tracking data appear to show.

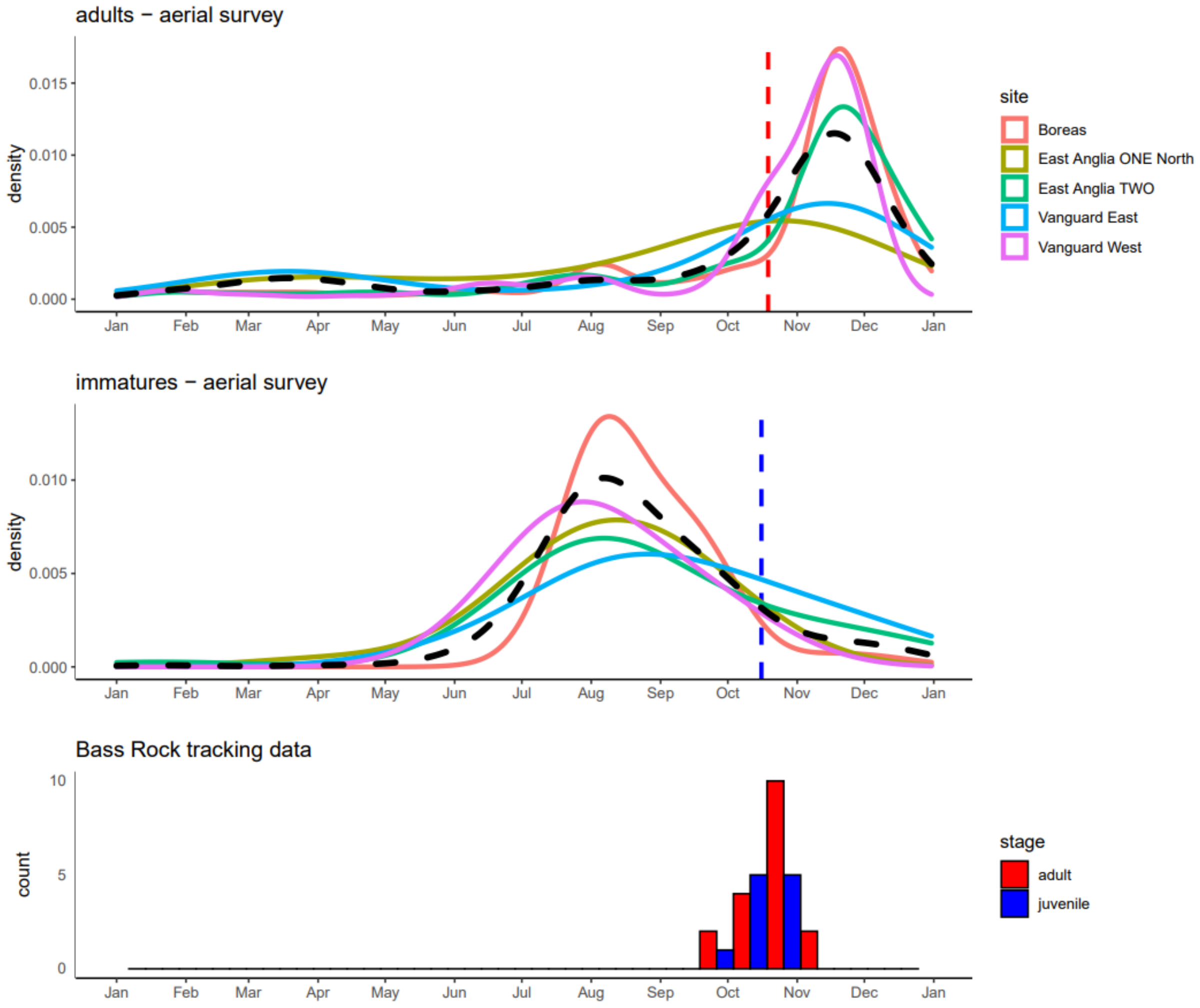


Figure 2.4: Density plots of adults (top) and immatures (middle) from aerial survey data, displaying smoothed counts throughout the year. Individual OWF sites represented by different colours with the dashed black line showing the general trend for all five sites combined. The bottom figure is counts of tracked birds travelling south through the North Sea, at the midpoint in time between entering and leaving the designated high-risk area, with the median date represented on the upper plots for the respective stage (adults; red dashed-line = 19th October, juveniles; blue dashed-line = 16th October). X-axes ticks represent the beginning of the labelled month.

2.3.3 European Seabirds at Sea

The 30 year period (1980-2010) for which ESAS data were examined comprised a total of 168,993 counts of gannets, of which 15% (n=24,790) were classed as immature. These data show differences in seasonal abundance of gannets in different areas of the North Sea. Gannets are generally more numerous on the UK side of the North Sea than on the continental side, and are in higher abundance during the summer in the northern area, whereas in the UK southern North Sea (box 5) peak numbers of gannets are seen in October-November (Figure 2.5 A). In the UK southern North Sea, the majority of gannets present in April to September (the breeding season) were immatures, whereas in October to March, the majority were adults (Figure 2.5 B).

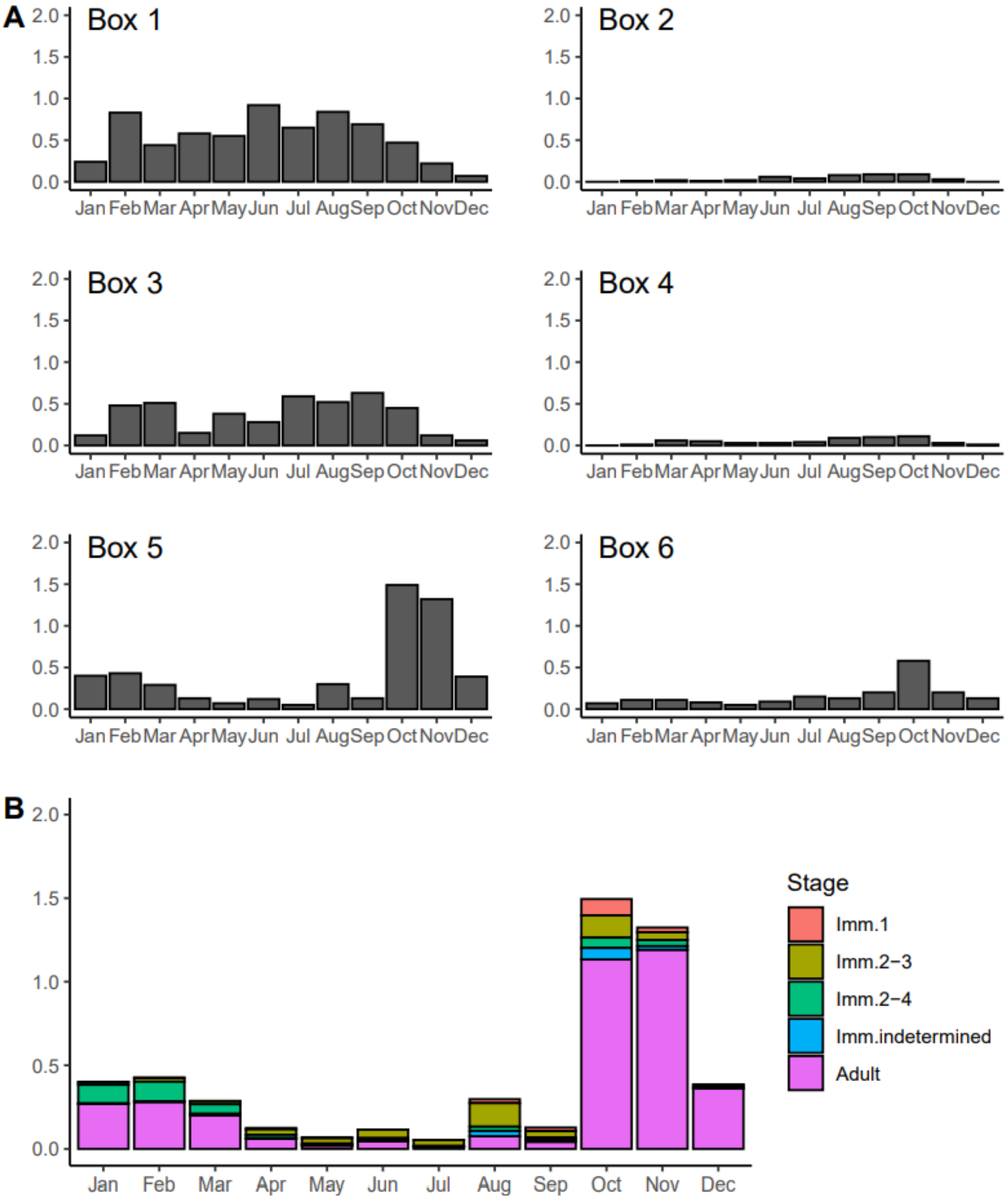


Figure 2.5. A: Seasonal variation in gannet densities in different parts of the North Sea as indicated by ESAS data (see Figure 2.1 for location of each Box). **B**: Densities of each age class of gannets in Box 5 each month.

2.4 Discussion

Tracking and survey data for gannets displayed marked spatiotemporal differences between age classes in the usage of space with a high concentration of OWF sites in the southern North Sea. Adults from Bass Rock were apparently more likely than juveniles to travel on paths that intersected current or planned OWFs, placing them at greater potential collision risk, during their autumn migration. At sea surveys indicate that immature birds travel through the southern North Sea on migration, and potentially foraging trips, but much earlier in the year than adults. As we are confident that our tracking data are representative of the timing of adult gannet migrations from Bass Rock, it is likely that the November peak from survey data consists predominantly of birds from colonies further north than Bass Rock (Fort et al., 2012).

The collision risk to juvenile gannets fledged from Bass Rock was much lower than for adults migrating from this colony, as juveniles tended to migrate much closer to the shore through the southern North Sea. Previous studies at Bass Rock have shown that upon leaving the colony, many adults went northwards to waters around Norway for a short period in early autumn (Kubetzki et al., 2009; Furness et al., 2018), before heading south again. Mackerel (*Scomber scombrus*) stocks in Norwegian waters during autumn may result in their use as a staging ground after the breeding season and before heading to wintering grounds. Similar patterns of movement were seen in our tracked adults. To fly south through the Strait of Dover the adults apparently took the most direct route from Norwegian North Sea waters (see Figure A.2.4 for comparison of adult and juvenile tracks), thus increasing their contact with OWF sites. How this translates to actual risk from OWFs is still not clear, but our data suggest highest risk for immature gannets in summer, highest risk for adult gannets in October-November, and generally low risk for juveniles.

Tracking data suggest that breeding adult gannets may avoid OWFs operating within their foraging ranges (Peschko et al. 2021). If they also avoid OWFs during migration, then potential energetic consequences (barrier effect) might need to be given more consideration. However, it seems likely that any deviations from their default course would have only negligible effects on fitness, given that gannets may migrate over 1,000 km from colony to wintering areas. Moreover, the magnitude of barrier effects will be higher during the breeding season than during migration (Masden et al., 2010; Warwick-Evans et al., 2017) owing to repeated avoidance and higher overall energetic demand when acting as a centrally placed forager.

Tracked juveniles and adults from Bass Rock passed through the southern North Sea at a similar time of year in around mid-late October. The peak of immature counts from aerial surveys of prospective OWF sites was much earlier than this, in keeping with the notion of immatures (excluding juveniles) leaving the colony earlier than adults (Nelson, 2002), after acting as central place foragers over the summer (Votier et al., 2017; Grecian et al., 2018). Lacking experience, juveniles will potentially benefit by learning from adults through local enhancement (Thiebault et al., 2014; Wakefield et al., 2019) and following their direction during the post-breeding migration (Nelson, 2002). It is uncertain, however, whether or not juveniles and immatures react to encountering OWFs in the same way. Juveniles may be more likely to enter OWFs, due to lack of experience, or perhaps less likely, if they are more cautious. Our study provides more support for the latter, given how tracked juveniles apparently hugged the coast on their journey.

A large proportion of gannets in ESAS data for the southern North Sea during the summer months were immature birds, some of which may have been acting as central place foragers from breeding colonies further north and in the English Channel. The southern North Sea around the Strait of Dover is not an area regularly visited by breeding adults on foraging trips (Wakefield et al., 2013), but may be within range of immatures, which range much further than adults from the colony (Votier et al., 2017; Grecian et al., 2018). ESAS data indicating a high proportion of immature gannets in the southern North Sea did not, however, match results from the digital aerial surveys, raising the possibility that the boat-based surveys employed in acquiring ESAS data may have attracted immatures more than adults, hence skewing the data. This seems unlikely, however, because vessels used in ESAS do not include those that catch or discard fish, so should be of little interest to gannets. Rather, the pixel size of our digital aerial survey data (2 cm) probably meant that residual black feathers on the wing and tail of some 3rd year and 4th year birds were not visible, resulting in them being recorded as adults and hence underestimating the proportion of immature birds present, as also found by Pettex et al. (2019).

A recent study in which currently-available GLS data processing methods were tested using birds synchronously double-tagged with GLS and GPS devices (Halpin et al. 2021) has confirmed that we used the optimal available method for open-ocean foraging species (processing data using the ‘ProbGLS’ package with SST refinement). Nonetheless differences in the error estimates for different tracking methods are large. Hence we have been cautious when interpreting results, particularly where we compare GLS with GPS-PTT data, making sure to draw inferences only on large-scale movements and the timing of migration, which we have confidence in. Further confidence is provided by the independent evidence from the ESAS survey data, which match the patterns observed in our tracking data. Nonetheless, we recommend using the same devices across age groups for future studies, ideally at GPS-level precision where funding is not prohibitive.

Adults tracked from Bass Rock passed through the southern North Sea around a month earlier than the peak numbers of adults counted at OWF sites there. This could indicate that the latter was due mainly to birds from colonies further north, such as Shetland, Orkney, Iceland, and Norway, many of which may spend the winter in the North Sea (Fort et al., 2012; Furness et al., 2018). This pulse seen in the digital aerial survey data were also seen for the ESAS data in the southern North Sea, whereas ESAS data from other areas in the North Sea display very different patterns, with the eastern North Sea and German Bight having relatively low numbers throughout the year. The North Sea along the northeast coast of the UK sees higher numbers during the summer months, presumably mainly breeding birds from colonies such as Bass Rock and Bempton Cliffs (Wakefield et al. 2013), emphasising the southern North Sea’s importance as a migratory bottle-neck for gannets and an area of high collision risk during autumn. Looking to the future, it is possible that the number of gannets migrating through or wintering in the North Sea may increase as a result of increasing numbers in the more northern colonies (Murray et al., 2015; Barrett et al., 2017). This trend, together with declining numbers in the southernmost colony (Grémillet et al., 2020), may also indicate a northwards shift in breeding distribution, as predicted from bio-climate modelling (Russell et al., 2015) and proximately linked to northwards movements of the distribution of key prey species such as Atlantic Mackerel due to warming oceans (Berge et al., 2015).

Our results confirm the southern North Sea as being of particular importance in terms of the potential collision risks to gannets from OWFs during the autumn migration period each year. Combining different data sources have allowed for unique insights that would have otherwise gone unnoticed. We ascertain that adults heading south from the large breeding colony at Bass Rock were at higher risk than juveniles of encountering OWFs, as a result of migrating further from the coast. The majority of birds present in the high-risk area from November onwards each year were probably from colonies further north than Bass Rock, and a metapopulation approach to understanding which sites contribute to these numbers would aid considerably in apportioning risk to specific colonies.

2.5 Literature cited

Barrett, R. T., Strøm, H., & Melnikov, M. (2017). On the polar edge: the status of the northern gannet (*Morus bassanus*) in the Barents Sea in 2015-16. *Polar Research*, *36*(1), 1390384.

Berge, J., Heggland, K., Lønne, O. J., Cottier, F., Hop, H., Gabrielsen, G. W., Nøttestad, L., & Misund, O. A. (2015). First Records of Atlantic Mackerel (Scomber scombrus) from the Svalbard Archipelago, Norway, with Possible Explanations for the Extensions of Its Distribution. *Arctic*, *68*(1), 54–61.

Calenge, C., & Calenge, M. C. (2018). *Package 'adehabitatLT'*. https://cran.opencpu.org/web/packages/adehabitatLT/adehabitatLT.pdf

Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C., & Hamer, K. C. (2015). Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. *The Journal of Applied Ecology*, *52*(6), 1474–1482.

Croxall, J. P., Butchart, S. H. M., Lascelles, B., Stattersfield, A. J., Sullivan, B., Symes, A., & Taylor, P. (2012). Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, *22*(1), 1–34.

deCastro, M., Salvador, S., Gómez-Gesteira, M., Costoya, X., Carvalho, D., Sanz-Larruga, F. J., & Gimeno, L. (2019). Europe, China and the United States: Three different approaches to the development of offshore wind energy. *Renewable and Sustainable Energy Reviews*, *109*, 55–70.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537.

Dierschke, V., Furness, R. W., & Garthe, S. (2016). Seabirds and offshore wind farms in European waters: Avoidance and attraction. *Biological Conservation*, *202*(Supplement C), 59–68.

Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J. B., Siorat, F., Furness, R. W., Grecian, W. J., Bearhop, S., Montevecchi, W. A., & Grémillet, D. (2012).

Meta-population evidence of oriented chain migration in northern gannets (Morus bassanus). *Frontiers in Ecology and the Environment*, *10*(5), 237–242.

Freitas, C. (2010). *Package argosfilter: Argos locations filter. R package version 0.62*.

Furness, R. W., Hallgrimsson, G. T., Montevecchi, W. A., Fifield, D., Kubetzki, U., Mendel, B., & Garthe, S. (2018). Adult Gannet migrations frequently loop clockwise around Britain and Ireland. *Ringing & Migration*, *33*(1), 45-53.

Furness, R. W., Wade, H. M., & Masden, E. A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, *119*, 56–66.

Garthe, S., Guse, N., Montevecchi, W. A., Rail, J.-F., & Grégoire, F. (2014). The daily catch: Flight altitude and diving behavior of northern gannets feeding on Atlantic mackerel. *Journal of Sea Research*, *85*(Supplement C), 456–462.

Garthe, S., Markones, N., & Corman, A.-M. (2017). Possible impacts of offshore wind farms on seabirds: a pilot study in Northern Gannets in the southern North Sea. *Journal of Ornithology*, *158*(1), 345–349.

Grecian, W. J., Lane, J., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society, Interface 15*(143), 20180084.

Grecian, W. J., Williams, H. J., Votier, S. C., Bearhop, S., Cleasby, I. R., Grémillet, D., Hamer, K. C., Le Nuz, M., Lescroël, A., Newton, J., & Others. (2019). Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the Northeast Atlantic. *Frontiers in Ecology and Evolution*, *7*, 214.

Grémillet, D., Péron, C., Lescroël, A., Fort, J., Patrick, S. C., Besnard, A., & Provost, P. (2020). No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. *Marine Biology*, *167*(12), 189.

Gremillet, D., Peron, C., Provost, P., & Lescroel, A. (2015). Adult and juvenile European seabirds at risk from marine plundering off West Africa. *Biological Conservation*, *182*, 143–147.

Halpin, L.R., Ross, J.D., Ramos, R., Mott, R., Carlile, N., Golding N., Reyes-González, J.M., Militão, T., De Felipe, F., Zajková, Z., Cruz-Flores, M., Saldanha, S., Morera-Pujol, V., Navarro-Herrero, L., Zango, L., González-Solís, J., Clarke, R.H. (2021). Double-tagging Scores of Seabirds Reveals That Light-level Geolocator Accuracy Is Limited by Species Idiosyncrasies and Equatorial Solar Profiles. *Methods in Ecology and Evolution, 12*(11), 2243-2255.

Kubetzki, U., Garthe, S., Fifield, D., Mendel, B., & Furness, R. W. (2009). Individual migratory schedules and wintering areas of northern gannets. *Marine Ecology Progress Series*, *391*, 257–266.

Lane, J. V., Jeavons, R., Deakin, Z., Sherley, R. B., Pollock, C. J., Wanless, R. J., & Hamer, K. C. (2020). Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research*, *162,* 105196.

Lane, J.V., Pollock, C.J., Jeavons, R., Sheddan, M., Furness, R.W., Hamer, K.C. (2021). Post fledging movements, mortality and migration of juvenile northern gannets. *Marine Ecology Progress Series* 671, 207-218.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series*, *628*, 183–193.

Langston, R. H., Teuten, E., & Butler, A. (2013). Foraging ranges of northern gannets Morus bassanus in relation to proposed offshore wind farms in the UK: 2010--2012. *RSPB Report to DECC*. https://tethys.pnnl.gov/sites/default/files/publications/UK-2010-2012-YR3-Report.pdf

Lisovski, S., Bauer, S., Briedis, M., Davidson, S. C., Dhanjal-Adams, K. L., Hallworth, M. T., Karagicheva, J., Meier, C. M., Merkel, B., Ouwehand, J., Pedersen, L., Rakhimberdiev, E., Roberto-Charron, A., Seavy, N. E., Sumner, M. D., Taylor, C. M., Wotherspoon, S. J., & Bridge, E. S. (2019). Light-level geolocator analyses: A user's guide. *The Journal of Animal Ecology*, *89*(1), 221-236.

Lisovski, S., & Hahn, S. (2012). GeoLight- processing and analysing light-based geolocator data in R. *Methods in Ecology and Evolution*, *3*(6), 1055–1059.

Masden, E. A., Haydon, D. T., Fox, A. D., & Furness, R. W. (2010). Barriers to movement: Modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. *Marine Pollution Bulletin*, *60*(7), 1085–1091.

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B., & Strøm, H. (2016). A probabilistic algorithm to process geolocation data. *Movement Ecology*, *4*, 26.

Murray, S., Harris, M. P., & Wanless, S. (2015). The status of the Gannet in Scotland in 2013-14. *Scottish Birds*, *35*(1), 13.

Nelson, B. (2002). *The atlantic gannet*. Fenix Books.

Pebesma, E. J. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal*, *10*(1), 439.

Peschko, V., Mendel, B., Mercker, M., Dierschke, J., & Garthe, S. (2021). Northern gannets (Morus bassanus) are strongly affected by operating offshore wind farms during the breeding season. *Journal of Environmental Management*, *279*, 111509.

Pettex, E., Lambert, C., Fort, J., Dorémus, G., & Ridoux, V. (2019). Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. *Journal of Avian Biology*, *50*(5).

Phillips, R. A., Xavier, J. C., & Croxall, J. P. (2003). Effects of satellite transmitters on albatrosses and petrels. *The Auk*, *120*(4), 1082-1090.

Physical Sciences Division (2019) NOAA High Resolution SST data https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html Accessed on 09/12/2020

Reynolds, R.W., Smith, T.M., Liu, C., Chelton, D.B., Casey, K.S., Schlax, M.G. (2007). Daily high-resolution-blended analyses for sea surface temperature. *Journal of Climate*, 20:5473–5496.

Russell, D.J.F., Wanless, S., Collingham, Y.C., Huntley, B., Hamer, K.C. (2015). Predicted future European breeding distributions of British seabird species under climate change and unlimited/no dispersal scanearios. *Diversity* 7, 342-359.

Stone, C. J., Webb, A., Barton, C., Ratcliffe, N., Reed, T. C., Tasker, M. L., Camphuysen, C. J., Pienkowski, M. W., & Consult, O. (1995). *An atlas of seabird distribution in north-west*

European waters. Joint Nature Conservation Committee (JNCC): Peterborough. ISBN 1-873701-94-2.

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology*, *25*(6), 1302–1310.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859).

Votier, S. C., James Grecian, W., Patrick, S., & Newton, J. (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology*, *158*(2), 355–362.

Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C., Hamer, K. C. (2013). Space partitioning without territoriality in gannets. *Science*, *341*(6141), 68–70.

Wakefield, E. D., Furness, R. W., Lane, J. V., Jeglinski, J. W. E., & Pinder, S. J. (2019). Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. *Journal of Avian Biology*, *50*(10), 1.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology*, *55*, 503-515.

2.6 Appendix

Table A.2.1. Parameters used for *probGLS* algorithm. (* - flight speed value informed by the following: Mateos-Rodríguez and Bruderer, 2012; Skov et al., 2018)

Model parameter	Description	Value used
Particle.number	Number of particles computed for each point cloud	2000
Iteration.number	Number of track iterations	100
Sunrise.sd & sunset.sd	Shape, scale and delay values describing the assumed uncertainty structure for each twilight event using a log-normal distribution	2.49/0.94/0
Range.solar	Range of solar angles used	-7° to -1°
Boundary.box	The range of longitudes and latitudes likely to be used by tracked individuals	-50, 30, 10, 80
Days.around.spring.equinox & days.around.fall.equinox	Number of days before and after an equinox event in which a random latitude will be assigned	14/21 (spring) & 21/14 (autumn)
Speed.dry	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is not submerged in sea water	14/4/26 $m.s^{-1}$*
Speed.wet	Fastest most likely speed, speed standard deviation and maximum speed allowed when the logger is submerged in sea water	1, 1.3, 5 $m.s^{-1}$
Sst.sd	Logger-derived sea surface temperature (SST) sd	0.5°C
Max.sst.diff	Maximum tolerance in SST variation	5°C
East.west.comp	Compute longitudinal movement compensation for each set of twilight events	Not used

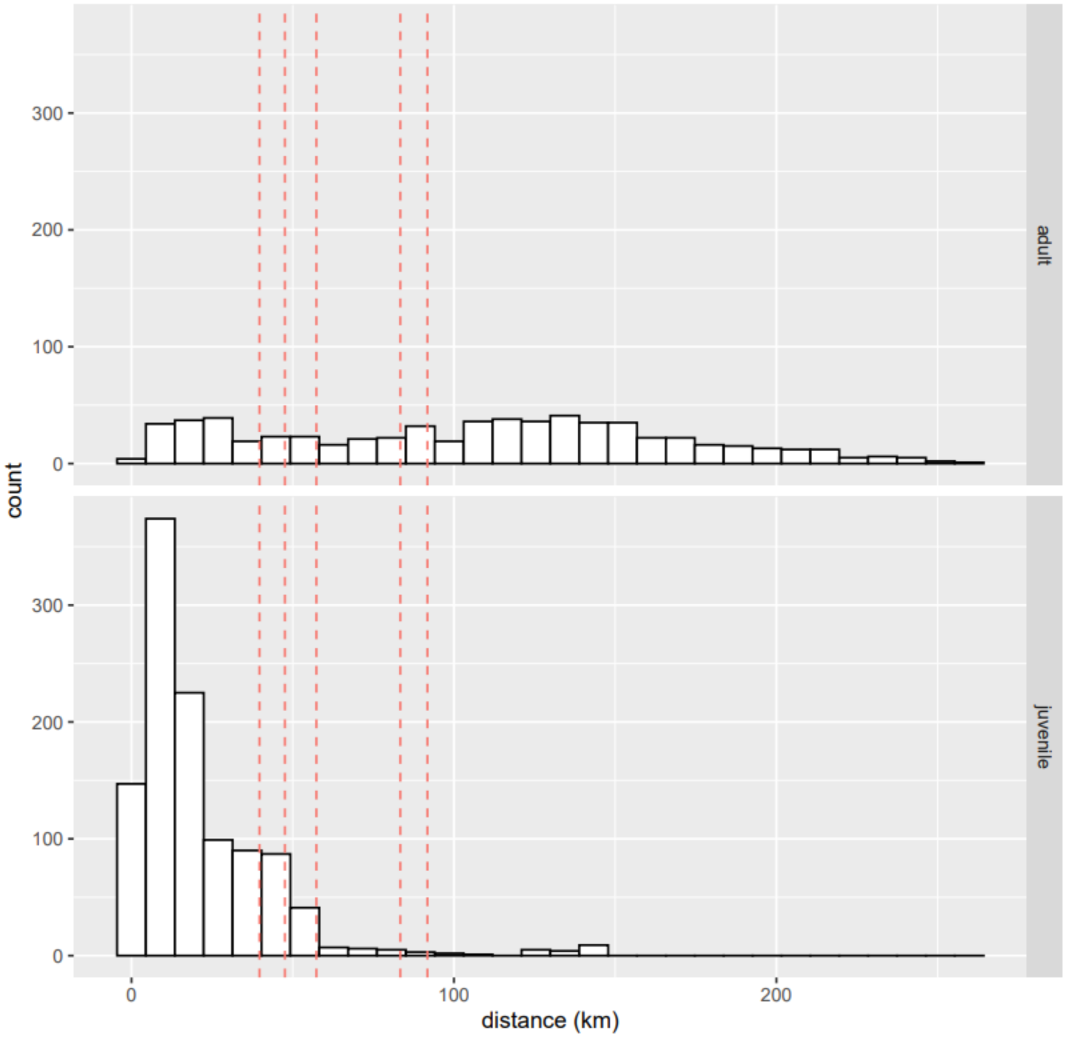


Figure A.2.1. Frequency of the distance from shore (km) of all location estimates recorded for adults (top) and juveniles (bottom) on their journey through the high-risk area (HRA). The five red vertical lines indicate the distance from shore of the offshore wind developments for which we have digital aerial survey data.

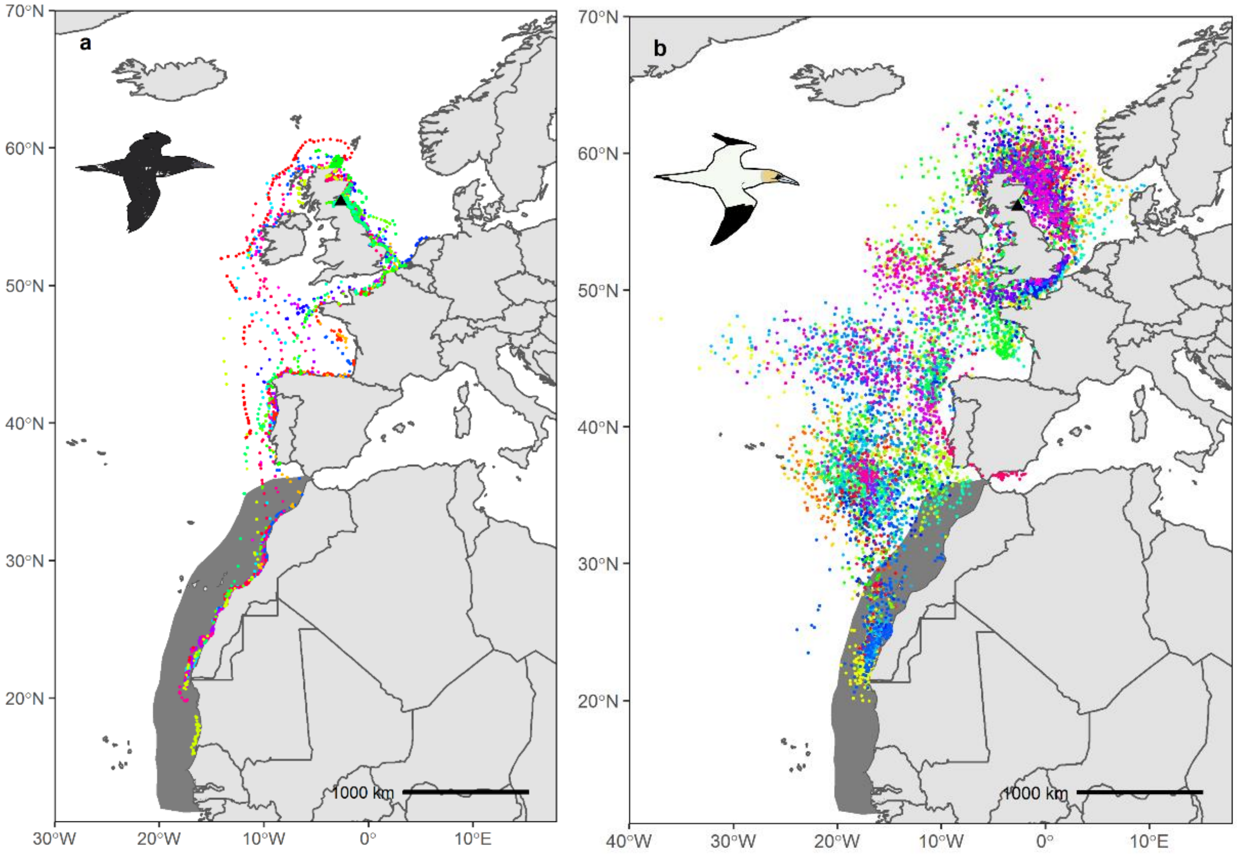


Figure A.2.2. (a) GPS locations of 41 juvenile gannets tracked from Bass Rock (black triangle) between September and November 2018 and 2019; **(b)** GLS locations of 35 adults tracked from Bass Rock between September and January 2018-2019 and 2019-20. Individual birds identified by colour. Shaded area in each case shows the Canary Current Large Marine Ecosystem. Previously published in Lane et al. (2021).

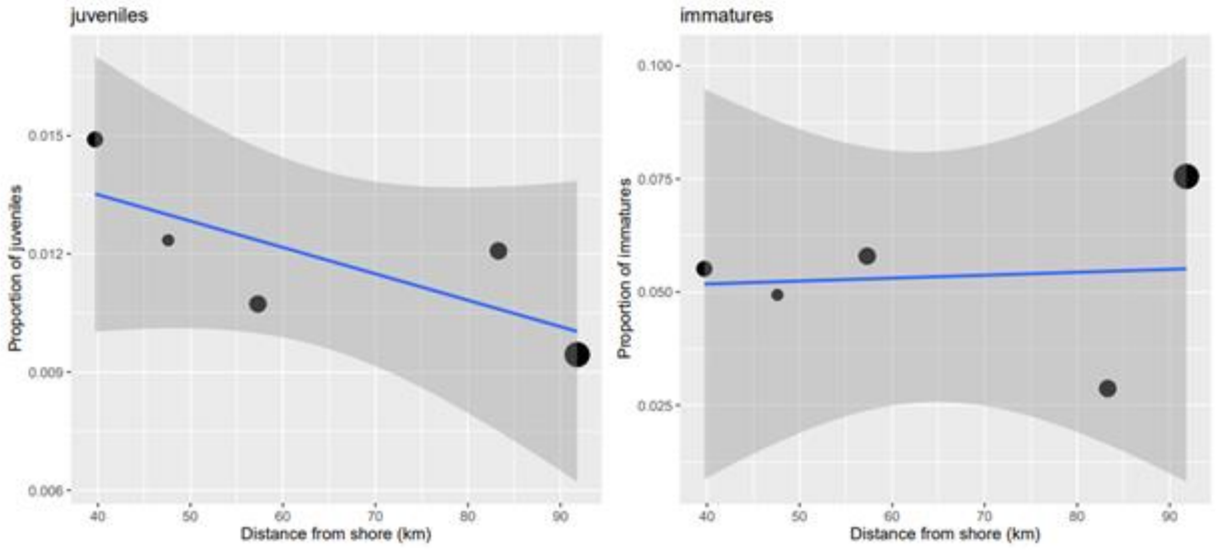
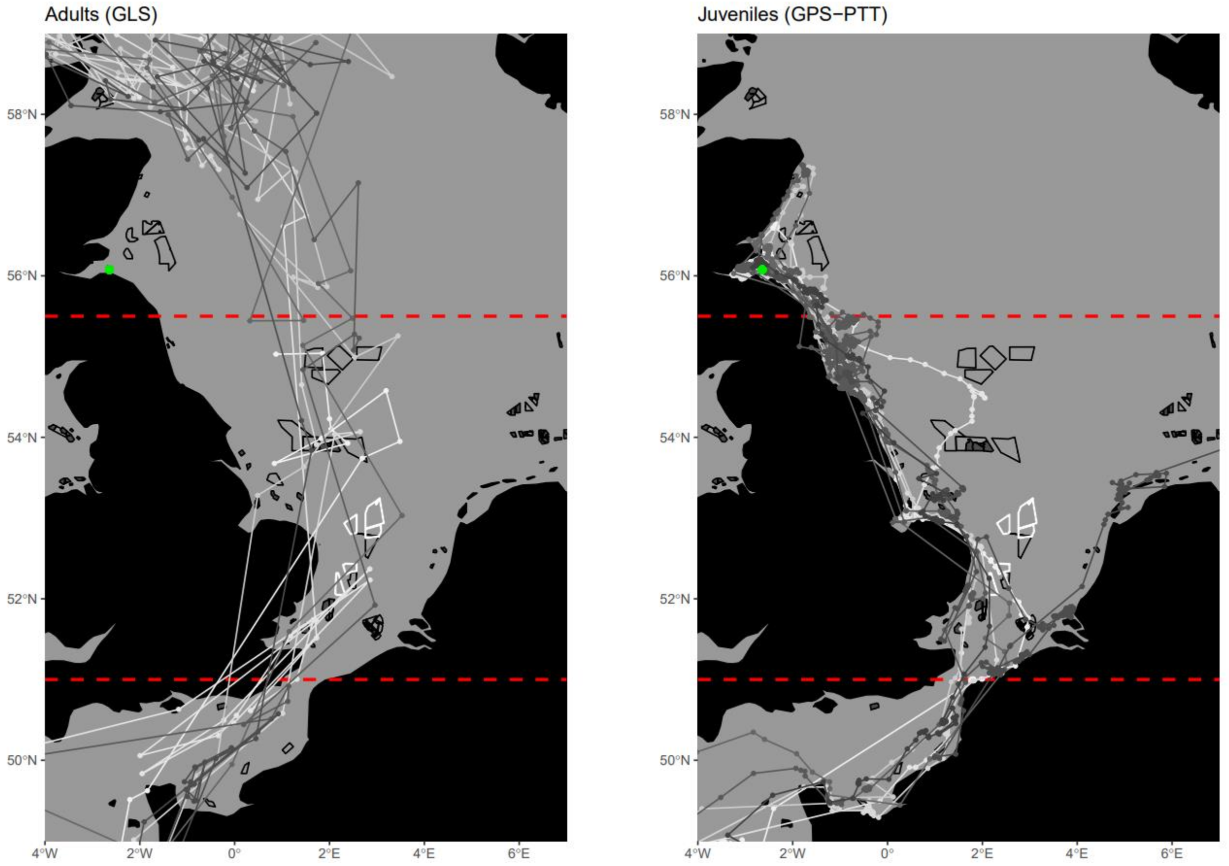


Figure A.2.3. Proportion of juveniles (left) and immatures (right) of total counts at different survey sites against the distance from shore of respective sites. The size of the points is relative to the area of the site.

Table A.2.2. Summary of results from digital aerial survey data

Site	**Area (km^2)**	**Distance from shore (km)**	**Total counts**	**Adults**	**Immatures**	**Juveniles**	**Unknowns**
Boreas	724.8	91.8	953	750	72	9	131
Vanguard East	297.1	83.3	1325	1287	38	16	0
Vanguard West	294.9	57.3	466	435	27	5	4
East Anglia ONE North	208.0	47.6	486	453	24	6	9
East Anglia TWO	255.4	39.7	671	617	37	10	17
Total	*1780*	-	*3901*	*3542*	*198*	*46*	*161*
				90.8%	*5.1%*	*1.3%*	*4.5%*


Adults (GLS)

Juveniles (GPS−PTT)

Figure A.2.4. Tracks from geolocator location estimates of seven individual adults (left) and tracks from GPS-PTT tags for eight individual juveniles. Lines and points with different shades of grey represent different individuals. Red dashed lines indicate the boundaries of the designated "high-risk area". Black polygons represent the different OWFs where those with a grey fill are operational OWFs, and white polygons are OWFs for which we have aerial survey data for proposed OWF sites.

Appendix references:

Mateos-Rodríguez, M., Bruderer, B. (2012). Flight speeds of migrating seabirds in the Strait of Gibraltar and their relation to wind. *Journal of Ornithology.* 153, 881–889.

Skov, H., Heinänen, S., Norman, T., Ward, R., Méndez-Roldán, S., Ellis, I. (2018). ORJIP Bird Collision Avoidance Study. *Carbon Trust & Discretionary Project Steering Committee*.

Chapter 3: Linking foraging decisions to movement patterns in northern gannets using an individual-based model

Abstract

Foraging behaviour and strategies are an essential link between a predator and its ability to obtain resources in an environment with heterogeneous prey distribution. Bottom-up, mechanistic models are tools which can be used to model the potential decisions being made by individuals when on foraging trips, and by evaluating against empirical data we can see how well these programmed behaviours reproduce observed movement patterns. These models have the potential to be applied to predict how a species may respond to changes in its habitat, but for seabird applications there is a paucity of models which represent central place foraging in a realistic manner. We question whether it is possible to parameterise a model which can do so effectively. To this end I present a spatially-explicit individual-based model of chick-rearing gannets at Bass Rock with the purpose of capturing realistic movements of foraging trips that are a consequence of individuals' decisions, based upon their immediate environment and foraging success. The development, calibration and validation was all achieved with the support of an extensive telemetry data set. Through a series of parameterisation procedures and subsequent comparison with real tracking data it appears that the model represents the variation seen in empirical foraging trips. Although there are some strong assumptions, which I discuss further, this initial model seems robust and provides an essential first step before addressing questions which require more behavioural complexity. This progress in simulating realistic movement in seabird IBMs is a step towards incorporating more realistic behaviour in management applications such as understanding the potential impacts of offshore wind farms.

3.1 Introduction:

Attempting to understand how predators respond to non-uniform and ephemeral distributions of their prey has been a perennial question for ecologists (Fauchald, 2009). Under optimal foraging theory, the optimal foraging strategy is defined as the approach which maximises the currency under the constraints of the environment (Sinervo, 1997). This means individuals must make decisions on which patch to exploit and when to leave in search of a more profitable patch (Charnov, 1976). In addition to environmental factors, such as availability of prey, an animal's internal state and physiology should be considered when interpreting the outcomes of movement decisions. These are the key factors that will drive an individual's movement patterns.

In response to such external and internal stimuli, an animal which faces a lot of variability would be predicted to exhibit considerable behavioural plasticity (Halsey, 2016). One example of how this manifests is through modulation of different movement modes (Fryxell et al., 2008) often characterised by different movement parameters such as turning angle and step length when considering movement discretely. Discernible movement modes are likely to serve different purposes such as travelling, resting, or searching for food as a response to the environment an individual occupies in combination with influences from its internal physiological state. Further constraining factors can include offspring, which may be stationary in their early development, and require feeding and other components of parental care, thus creating central place foragers of the parents. Many species of seabird are colonial breeders and may experience acute competition for resources from conspecifics and potentially other species of seabirds and marine predators (Weber et al., 2021).

Global declines in seabird numbers have been attributed to numerous potential drivers (Dias et al., 2019). Climate change is altering previously reliable distributions of prey species, humans compete directly for resources through commercial and industrial fishing operations, and in order to reduce fossil fuel consumption, coastal areas are being developed for offshore renewable energy (Halpern et al., 2012). It is yet to be determined how these factors interact, i.e. whether they are additive, synergistic, or antagonistic (Crain et al., 2008). Traditional population modelling takes a "top down" approach (Lefkovitch, 1965) to understanding population impacts of stressors on seabirds (Major et al., 2013). In the last two decades there has been a steady rise in the use of models of complex adaptive systems (DeAngelis & Grimm, 2014) such as individual-based models (IBMs, also known as agent-based models) to advance our understanding of the impacts of environmental change (Stillman & Goss-Custard, 2010). Through the modelling of stochastic, autonomous individuals, it is possible to link environmental variability to movement patterns through modelling how an individual interacts with its environment.

Recent applications to seabirds include investigating the use of social information to find prey (Boyd et al., 2016) and modelling the impacts of offshore wind farms on a northern gannet (*Morus bassanus*, hereafter gannet) colony in the English Channel (Warwick-Evans et al., 2017). However, there is a paucity of models which represent realistic movements of seabirds. A recent model called “agentSeal” (Chudzinska et al., 2021) has simultaneously captured fine- and broad-scale foraging movements of central place foraging harbour seals (*Phoca vitulina*), driven by behavioural decisions and physiological processes. Such models will prove very useful for advancing realism in applications to management scenarios. For instance, the harbour seal model (Chudzinska et al., 2021) uses pattern orientated modelling (POM, Grimm et al., 2005; Grimm & Railsback, 2012), where equivalent outputs of models are contrasted against the characteristic observed patterns from a real system, to powerfully represent different hierarchies (e.g. individual/population/community) and movement scales.

In this study I addressed the need for a model from which realistic movement patterns emerge from complex behavioural decisions of foraging seabirds resulting from environmental and approximated physiological drivers. I deem this a prerequisite to addressing questions of more complex phenomena, such as IFSF, which emerge from behaviours at fine spatiotemporal scales. This was achieved through the creation of a spatially-explicit IBM of gannets at the world’s largest breeding colony of this species, at Bass Rock, Scotland (Murray et al., 2015). The model was informed by telemetry data, in which the goal was a model capable of producing the typical foraging trips of gannets during the chick rearing period. Gannets are a well-studied species; an important prerequisite for obtaining parameters and inferring behavioural decisions to inform data-hungry IBMs. I used telemetry data from gannets' foraging trips to approximate prey availability in the landscape, and compared the patterns of spatial and behavioural outputs of the model with equivalent patterns derived from empirical data through employing a POM strategy.

At the broad scale gannet foraging trips take the shape of a directional arc in which birds are thought to employ a "trap line" strategy (Wanless et al., 1990) in which individual foraging trips can vary widely both in the shape they take i.e. from linear (straight to maximal distance and back) to elliptical (a more circular trip), and in their distance and duration. Repeated trips from individuals often show consistency in space use which is known as individual foraging site fidelity (IFSF). The characteristic patterns of this phenomenon (i.e. repeatability in departure bearing) strengthen with advancing development, indicating that they learn and refine this consistency over time (Votier et al., 2017). Gannets tend to forage at persistent mesoscale oceanographic fronts (Scales et al., 2014), and this has been linked with IFSF (Grecian et al., 2018). These oceanographic fronts can be areas of enhanced primary productivity, attracting pelagic fish and thus becoming foraging hotspots for seabirds. However, this is not the only environmental driver, and gannets' foraging plasticity has been linked to varying oceanographic features over a range of scales (Patrick et al., 2014; Wakefield et al., 2015). One response to this variability in the prey field is their nested searching efforts, known as area-restricted search (ARS) behaviour, where travel is considerably slower and more sinuous than when commuting (Hamer et al., 2009).

My aim was to build a model of adult gannets during the chick rearing period, wherein fine- and broad-scale movements and the resulting activity budgets from modelled foraging trips are consistent with observed trips from Bass Rock. There are some simplifications of the real system, in that the effect of memory is implicitly assumed in this model, and there is no interaction between individuals. However, I thought it crucial that an initial model of movement be constructed before further complexities are added. The intention is to acquire a robust "tactical" model with enough detail to be able to explain system dynamics and have testable predictions of a highly complex system (Holling, 1966; Evans et al., 2013). I then discuss the shortcomings and assumptions of this model and possible paths to take for further development, including our understanding of seabird ecology or potential applications of this model to understand how specific populations may respond to their rapidly changing environment.

3.2 Materials and methods

This section begins with a background on the aspects of life-history and behaviour of gannets most relevant to the model, including a case study and breakdown of a single empirical trip from Bass Rock. This information was used to develop the model which I subsequently describe using the ODD (Overview, Design concepts, Details) protocol (Grimm et al. 2006; Grimm et al. 2020) which was designed to standardise the communication of complex process-based models.

3.2.1 Biological background

The breeding colony at Bass Rock (56° 4’ N, 2° 38’ W) had 75,259 apparently occupied sites (AOS) in June 2014 (Murray et al., 2015) making it the largest northern gannet colony in the world. As a consequence they experience relatively high levels of intraspecific competition during the breeding season when acting as central place foragers, resulting in the longest foraging trip durations and distances travelled when compared with other colonies in the UK and Ireland (Lewis et al., 2001; Wakefield et al., 2013).

Figure 3.1 depicts a foraging trip that was 16.1 hours long, where a distance of 638 km was travelled, leading to a maximal distance of 267 km from the colony. This particular trip began at dawn with the gannet returning to the colony at 20:56 h. Outbound travel is relatively straight, with occasional ARS zones, before the trip trajectory begins to arc around where ARS zones are most highly concentrated around the outer arc of the trip. Inbound travel is defined as the journey back towards the colony on completion of the arc (~180° turn in orientation), which is characterised by similar linearity as the outbound trip (Pettex et al., 2010), with little to no ARS behaviour taking place. From this I deduce that the individual in question has made the decision to stop foraging and head back to the colony, which is likely due to the required amount of food being acquired for sustenance of themselves and their chick.

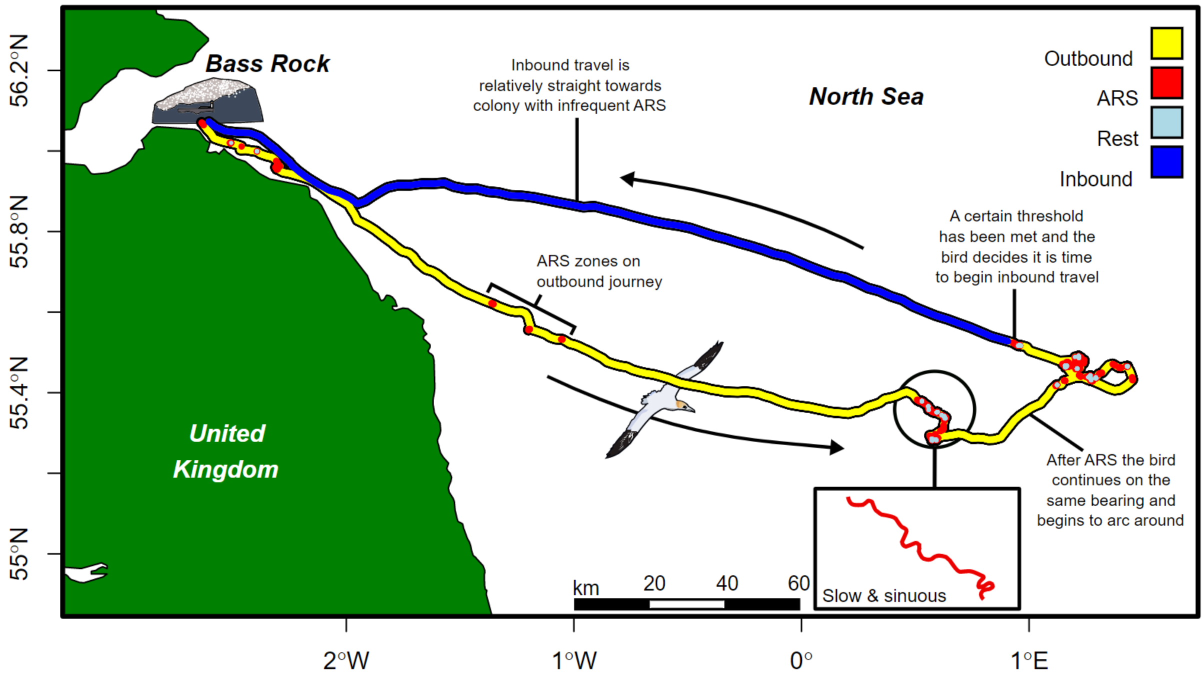


Figure 3.1. Annotated single foraging trip from Bass Rock for a gannet (BTO: 1484924) during the 2015 breeding season.

Commuting to and from the colony is characterised by relatively high speeds and a straight direction of travel. In contrast, when birds enter ARS movement they slow down considerably and the path becomes much more sinuous (Figure 3.1), likely allowing for greater inspection of the sea surface in the local area in order to visually locate and identify prey. Gannets dive to obtain a wide range of prey species, but their success rate and as such their functional response (relationship of prey obtained to prey density) is not well known. However, it has been shown that most dives takes place within ARS movement, and two thirds of dives take place on the outwards phase of the trip, i.e. before reaching the maximal distance from the colony (Hamer et al., 2009).

ARS bouts are punctuated with periods of resting on the sea surface, and a single trip will typically have many short rests of < 20 mins, and one or two longer periods of rest. In this case study trip (Figure 3.1) there were 22 rests that were < 20 mins, with 3 slightly longer periods of rest (26, 32, 34 mins). Inspection of other empirical trips shows that it is not uncommon for these day time rests to last over an hour. Gannets typically have short rests after each dive bout, and some authors have hypothesised that foraging at the beginning of the trip allows birds to feed themselves, followed by a period of resting and digesting prey before commencing foraging for food for the chick (Ropert-Coudert et al., 2004).

In this foraging trip (Figure 3.1) over half (58%, 9.27 hours) of the time was spent travelling, with 72% of this being outbound travel. Just less than a quarter of the trip (21%) was spent in ARS and resting respectively. This trip spans the duration of daylight hours, but often trips can be over 24 hours in length where gannets spend the night at sea. As gannets are visual predators they do not forage at night, and mostly rest on the sea surface (Furness et al., 2018). Consequently, these trips will tend to have a higher proportion of resting time.

One parent remains with the chick while the other is on a foraging trip. On return, it is typical to see a brief overlap where both parents are at the nest before the other parent departs on a foraging trip. Consequently, the time spent by an individual at the colony between trips will be very similar to the duration of the foraging trips at that colony. The diet of gannets at Bass Rock consists of a wide range prey species of different sizes (Hamer et al., 2000) including sandeels (*Ammodytes spp.*), mackerel (*Scomber scombrus*), herring (*Clupea harengus*) and sprat (*Sprattus sprattus*). Information available on the weight of prey items is scarce but Garthe et al. (Garthe et al., 1999) reported a maximum food quantity of 745 g with 101 g being the median.

3.2.2 Telemetry data and usage

Empirical data were used for two main purposes; (i) to assign approximate prey density to cells of the landscape in the model from where birds foraged in reality, and (ii) to extract key patterns of individual foraging trips to guide model development, parameterisation and evaluation of the model. Movement data from chick-rearing adults were obtained in 2011, 2012, 2015 and 2016 using GPS loggers (igotU-GT600, Mobile Action Technology, Taipei, Taiwan) attached to the upper side of the central tail feathers with tape and set to record locations at 2 min intervals (Lane et al., 2019; Wakefield et al., 2015). The whole dataset comprised 504 foraging trips from 118 individuals, which means it is highly likely that this has captured the home range of the Bass Rock gannet colony (Soanes et al., 2013).

To obtain a prey density grid, GPS positions were interpolated to 10 second intervals using the package ‘adehabitatLT’ (Calenge & Calenge, 2018) to account for any irregularities. I then assigned the behaviour of the gannets during each trip into the category commuting, ARS or resting according to thresholds in speed and track tortuosity (Wakefield et al., 2013; Grecian et al., 2018). The ARS category was defined when GPS points had a tortuosity < 0.9 and a speed >1 m/s, indicating areas where gannets foraged. These locations were then used to calculate the time spent in a 2 x 2 km cell of a predefined grid around the colony using the ‘Trip’ package (Sumner, 2016). This grid was exported from R as a raster and imported into NetLogo (Wilensky, 1999) using the ‘GIS’ extension.

Table 3.1 below displays the different patterns that were extracted from empirical data and reported values (if applicable). To calibrate fine scale movement in the model, GPS data were interpolated to 2 min intervals to extract turning angles and step lengths for behaviour assigned to commuting, ARS and rest. For broad scale movements a linearity index was calculated for each foraging trip where a value closer to 1 would indicate a more linear trip:

$$\text{Linearity index for foraging trip } i = \text{Total length of trip } i \,/\, (\text{Maximal distance of trip } i * 2)$$

Another simple metric (difference in bearing) was extracted to approximate the arc of a trip and where:

$$\text{Difference in bearing for trip } i = \text{abs}\,(\text{Bearing at distal point of trip } i - \text{initial bearing of trip } i)$$

where the distal point of the trip is the location furthest from the colony and the initial bearing is at a distance of 10 km from the colony on the outbound portion of the trip (hence excluding initial orientation and activities such as bathing before commencing on directed travel). Other commonly used trip metrics including duration (h), length (km) and activity budgets (proportion of time spent in different behaviours) were extracted from the empirical data to be used in parameterisation and evaluation, as described in Table 3.1 below.

Table 3.1. Summary statistics of key patterns used in the pattern-orientated modelling (POM) process to guide the development and analysis of the model

Pattern	**Classification**	**Where in the modelling process was it used?**	**Empirical values (if applicable)**
Activity budgets	Behaviour	Validation and analysis	Some interannual variation, but typically 37% : 37% : 26 %, travel : forage : rest per trip. Less travel at smaller colonies (Wakefield et al., 2013)
Trip duration	Movement	Parameterisation – functional response	19.2 ± 8.8 hours
Trip length	Movement	Evaluation	386.4 ± 226.6 km
Linearity	Movement	Parameterisation – orientation	1.49 ± 0.36
Bearing difference	Movement	Parameterisation – orientation	14.41 ± 14.64 °
Step lengths	Movement	Calibration	Travel = 1783 ± 371 m/2min ARS = 862 ± 527 m/2min
Turning angles	Movement	Calibration	Travel sd = 0.164 ARS sd = 0.949

3.2.3 The model

I developed a spatially-explicit individual-based model (IBM) to simulate the movements of chick-rearing gannets at Bass Rock. This model was implemented in NetLogo version 6.1.1 (Wilensky, 1999), and processing and analysis of model outputs was conducted in R (R Core Team, 2020). See the attached Supplementary Material which contains annotated NetLogo code for this model. In the following section I describe the model according to the ODD protocol.

3.2.3.1 Purpose

The aim of this model was to capture the movements of chick-rearing gannets during a foraging trip from Bass Rock, both at fine- and broad- temporal and spatial scales, when foraging in a marine landscape with heterogeneously distributed prey with foraging decisions being dependent on their current environment and their previous foraging success on the current trip.

3.2.3.2 Entities, state variables, and scales

The main entity in this model was adult gannets, which are hence forth referred to as *aGannets,* for agent gannet. *aGannets* interact with their landscape, where cells representing the North Sea have a value of prey density assigned to them, and land cells are actively avoided using the avoidance submodel detailed below. One cell is defined as Bass Rock, according to its location in the Firth of Forth, and *aGannets* are aware of where this is located and when they have returned to the colony. They are characterised by their location, speed, turning angle, current movement mode, and how much food intake there has been on the current trip. The focus of this model is individual trips, thus it is assumed that an *aGannet's* chick is alive for the duration of the simulation, and their partner is assumed to share the duties of parental care where alternating foraging trips are made in order to meet the energy needs of the chick (Nelson, 2002). State variables are listed in Table 3.2 below.

Model architecture consists of a grid of 95,472 (272 x 351) square cells which each represent 4 km^2 (2 km x 2 km) thus representing a total area of 381,888 km^2. This area is representative of the extent of the Bass Rock colony's chick-rearing season home range deduced from empirical data, with an extended buffer of ~50 km beyond this so that *aGannets* are not spatially constrained. It has a cell assigned for the colony, which is surrounded by sea (78, 856 sea cells, 83%) representing the North Sea and extending beyond any of the recorded empirical tracks for chick-rearing adult gannets. There are 16,616 land cells (17%). Prey is distributed heterogeneously in the sea cells through each cell having an attributed prey density assigned to it when the model is being initialised. This is determined by the amount of time gannets spent foraging in this area multiplied by a constant to allow for different levels of prey density to be implemented during simulations. Towards the distal fringes of the colony's home range, prey density increases radially with distance (Figure 3.2) so that *aGannets* are very likely to detect prey before reaching the edge of the landscape. On the rare occasion this does occur, it results in a decrease in that trip's abilities to reproduce a visually realistic foraging trip, but does not influence resulting trip metrics. An alternative would have been to specify a maximum range for *aGannets,* at which point they would turn back to the colony, but this would have negated the emergence of trip trajectories as intended.

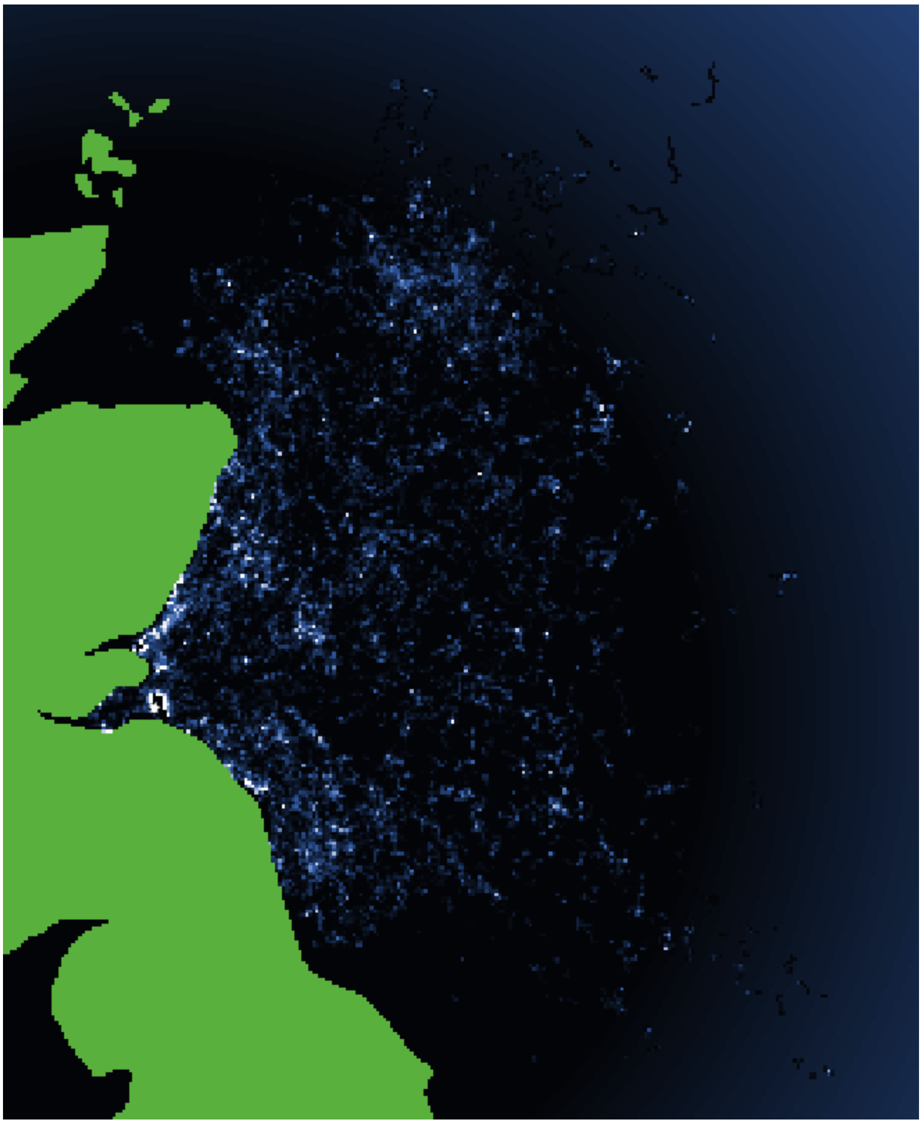


Figure 3.2. The model landscape as seen in NetLogo, where increasing lightness in shade of blue indicates higher prey density as inferred from areas where gannets foraged according to GPS data or at the edges of the model where prey increases radially to reduce the chance of *aGannets* reaching the edge of the landscape.

Table 3.2. State variables used in the IBM

State variable	**Unit (if applicable)**	**Description**
Globals		
minute	min	What minute of the day it is
day-night	day/night	Whether it is day or night in the model currently
day	d	Which day of the simulation it is
Adults		
Food-intake	grams	Food intake on this particular trip
behav	outbound/ ARS/ rest/ inbound/nest	Behaviour the bird is exhibiting
ARS-fish-counter	integer	How many fish has the bird ingested during current ARS bout
clockwise	Boolean	If true the trip will be a clockwise arc, and false means the bird will travel in an anti-clockwise arc.
target	XY coordinates	This is the patch that a bird recalls from assumed previous memory
original-bearing	degrees	At the beginning of travel the bearing towards the target patch is recorded
head-current	degrees	The current direction that an individual is facing in outbound travel, which is derived from the original-bearing and an adjustment based on food-intake on the current trip.
ARS-chance	arbitrary	The chance of beginning ARS when in outbound travel, which is dependent on the unknown parameters “prey-detect”, “ThresholdARS” and the prey density of the current patch.
Home-bearing	degrees	The bearing leading back to the colony when the individual beings inbound travel
Patches		
Prey-density	arbitrary	A proxy of the number of fish currently available to individuals foraging on this patch
use	-	Defines the colony patch as home, used to define whether or not the individual has reached home on its inbound travel
categ	land/water	Defines if the patch is land or water. Land patches are avoided in the avoidance procedure.

The model runs in two minute timesteps for a total of 91 days, representative of the length of the chick-rearing period. This timestep was chosen as this is the temporal resolution at which the empirical data were collected, thus allowing for direct comparison of model outputs with empirical patterns derived from the same data, representing the “virtual ecologist” approach (Zurell et al. 2010).

3.2.3.3 Process overview and scheduling

Processes: At each time step *aGannets* are aware of their current behaviour and assess their foraging success thus far in the trip (*food-intake*) alongside assessing their local environment for prey in order to decide whether to remain in this same behaviour or switch to a different behaviour. Following this, behavioural counters are updated. If activated, individual output files for gannets are updated to their respective .csv files with the minute, day, trip-number, behaviour, and x and y coordinates.

In this model different processes are enacted depending on what current behavioural state the respective *aGannet* is experiencing. As such, what follows is a logical description how a typical foraging trip will proceed in the model, for which a schematic diagram can be seen in Figure 3.3. An *aGannet* at the beginning of the simulation will be on its nest at the colony. For the first trip there is a 0.5% chance of departing the colony at each timestep which translates to departing between 0-8 hours from the beginning of the simulation so that all *aGannets* in the simulation do not depart in synchrony. When beginning their outbound journey from the colony they pick a target patch using the “decide-heading” submodel. Orientation of the trip is decided with an equal chance of being clockwise or anticlockwise. On the outset of the outbound journey the bearing from the colony is recorded (*original-bearing*) to be used in subsequent orientation which is dependent on food intake.

At Bass Rock the average distance of the first dive of each trip is 54 km (Hamer et al., 2009), which was approximated in the model by having threshold of one hour (Average speed of 14 m/s translates to 50 km travelled in an hour) of outbound flying before there is the possibility of switching to ARS movement. Once an *aGannet* has gone past this threshold, it may switch movement modes to ARS through the “Enter-ARS?” submodel wherein depending on the prey density of the patch it is currently on and two unknown parameters (*thresholdARS, prey-detect*) which dictate the parameters of the functional response the modelled birds have to prey density (see Section 3.2.3.7 for more details), which is an approximation of type II response (Holling, 1959).

During ARS, foraging attempts may be made (submodel: "foraging-attempt") which require visual detection of prey first, and this is based on the same type II functional response which has been approximated for the "Enter-ARS?" submodel. This is calculated at each timestep so if an *aGannet* during a particular ARS bout crosses the boundaries of one cell into another then the relevant prey density assigned to the cell currently occupied can influence predator-prey dynamics in a spatially realistic way. The parameters used here are the same as "Enter-ARS?" to avoid unnecessary complexity, and since the movement of an *aGannet* during ARS movement is slower and more sinuous, this is where it increases its chances of capturing prey in a potentially profitable area.

After capturing prey an *aGannet* will rest for either a short period or a longer period if they have reached the food intake requirement (Table 3.3), where rest length is drawn from respective normal or gamma distributions (submodel: "decide-rest-duration") informed by empirical data. During a particular ARS bout, if an *aGannet* has spent over 40 mins in total foraging, excluding any rests, and it hasn't yet acquired the required amount of food it will resume outbound travel. At this point the "calculate-bearing" submodel may bias the direction of travel to begin turning back towards the colony where the relative angle to the colony is dictated by a logistic relationship with how much food has been ingested.

After successive ARS bouts, the *aGannet* will have caught the required amount of food to signal a large rest which is followed by inbound travel. This is a biased random walk towards the general direction of the colony, assuming that individuals can orientate themselves as such (Pettex et al., 2010), which is based on the distance of an *aGannet* to the colony (submodel: "find-distance-home") and an adjustment to the previous bearing according to the current bearing of the colony from an *aGannet* (submodel: "calculate-inbound").

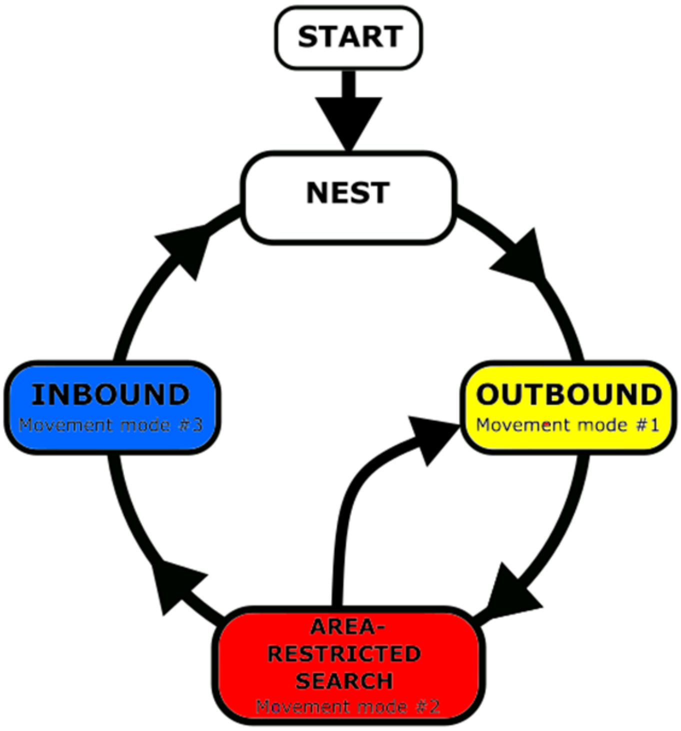


Figure 3.3. Schematic diagram of the different behavioural states which an *aGannet* may be exhibiting at any given timestep. The colours are consistent with how these movement modes are depicted in figures throughout this chapter.

Upon return to the colony behavioural counters for that trip are tallied and then reset to zero for the next trip. The duration of time to spend at the colony before departing for the next trip is drawn from a normal distribution given by the mean and standard deviation of the duration of the last 100 trips completed by any individuals. Thus time spent at the colony will be roughly the length of trips being exhibited at any given point in the simulation. This cycle then repeats until the end of the simulation. Minute 990 during each day indicates the beginning of night, when no matter what the current behaviour or location of the individual, behaviour is set to "rest", as it has been shown that gannets are almost completely inactive during the night (Furness et al., 2018).

Table 3.3. Parameter estimates used in the IBM

Parameter	Value	Source
Step length - travel	1783 ± 371 m / 2min (~15 m/s)	Empirical data
Step length - ARS	862 ± 527 m / 2min (~7 m/s)	Empirical data
Turning angle - ARS	0 ± 0.949 °	Empirical data
Prey size	100 ± 25 g	(Garthe et al., 1999)
Food intake requirement	900 g	Derived from digestion rate and assumption of intake of 1 fish per hour for 10 hours
Longer rest duration	20 – 200 min	Empirical data
Shorter rest duration	0 – 20 min	Empirical data
ARS bout length	Total of 40 min searching per bout	Empirical data
Prey detection	Parameterised value = 0.125	Determined through parameterisation
ThresholdARS	Parameterised value = 20	Determined through parameterisation
First ARS bout after beginning trip	53.9 km from colony	(Hamer et al. 2009)

3.2.3.4 Design concepts

3.2.3.4.1 Basic principles

This model is built on the principles of optimal foraging theory, where *aGannets* are attempting to meet their required food intake per trip to meet the needs of themselves and their chick by efficiently searching an area for heterogeneously distributed prey. *aGannets* employ an arc in an attempt to locate prey, with the ability to switch to more sinuous and slow movements upon perceiving higher densities of prey, while limiting the distance they are flying from the colony to some extent.

3.2.3.4.2 Emergence

The movement patterns of *aGannets* emerge from behavioural decisions made by gannets according to the prey density of their current location in combination with how successful they have been in the respective foraging trip thus far.

3.2.3.4.3 Learning

There is no learning included in this model apart from the knowledge of which departure direction to depart the colony which is assumed to have been gained prior to the simulation.

3.2.3.4.4 Sensing

When beginning a trip it is assumed that *aGannets* have a sense of which general direction to head in order to find profitable areas to forage. *aGannets* have the ability to sense fish through visual detection, and in areas with a higher density of prey gannets are more likely to begin ARS movement to try and forage for fish. They are aware of their how much prey they have captured during the current trip, and what their behaviour was during the previous time step. *aGannets* can also sense where land is within a certain distance so as to avoid flying over it.

3.2.3.4.5 Interaction

The only interaction between *aGannets* is indirect, through intraspecific competition, where prey is depleted for a certain cell when an *aGannet* has successfully foraged here, with prey being reset at the beginning of each new day in the model. However, if there is any effect of this on the system it is very weak, as prey are abundant and simulations do not have over 100 individual *aGannets*. Interference competition (Lewis et al., 2001; Wakefield et al., 2013), wherein there is a reduction of prey availability close to the surface following multispecies feeding associations, as opposed to reduction in actual abundance of prey which is implied in the model, is likely to be an important factor in this system. This is explored further in Chapter 4, along with other forms of interaction.

3.2.3.4.6 Stochasticity

At each timestep in the model the step length for each individual is randomly drawn from a normal distribution for the relative movement mode, where the travel step length (Table 3.3) is used for outbound and inbound movement modes, and ARS step length (Table 3.3) for ARS movement mode. Turning angle for each step an *aGannet* is in ARS movement mode is drawn from a normal distribution (Table 3.3), whereas stochasticity is built into the submodels which calculate turning angles in outbound and inbound movement modes. Other stochastic processes include how long the individual spends at the colony between trips, which patch the *aGannet* picks as a target at the beginning of a trip, the size of the food consumed on a successful foraging attempt, and how long to rest after a fish has been caught.

3.2.3.4.7 Observation

Spatial coordinates of an *aGannet* at each time step during a foraging trip are recorded to a .csv file. These are then imported into R and transformed to be the same coordinate system (UTM) as the empirical data, thus allowing for direct comparison between simulated and observed data. This is key for spatial analysis such as inspection of fine scale movement, bearings, and overall length of foraging trips. Activity budgets are recorded directly from each simulation through tallies which count behaviours being exhibited as each simulation progresses and are recorded in a separate .csv file.

3.2.3.5 Initialisation

The model is initialised by loading raster files containing time spent foraging in grid cells representative of the North Sea which are then used to assign prey density by multiplying by assorted pre-determined constants to assign a level of prey (“high”/ “medium”/ “low”/ “critical”). Another raster is imported to demarcate cells which are land, which *aGannets* actively avoid. One hundred gannets are positioned at the colony and the first time step in the model is the first minute of daylight at the beginning of the chick-rearing period under the assumption that all simulated gannets have a chick that hatches at the same time at the beginning of the run.

3.2.3.6 Input data

There is no input of data for the duration of the model run.

3.2.3.7 Submodels

Below I describe the submodels which are introduced in section 3.2.2.3, and are listed in the order that they are likely to be employed throughout the course of the model.

decide-heading

At the beginning of each trip an *aGannet* picks a random highly visited cell from empirical data which is at least 140km away from the colony. This is an important process in determining the bearing which an *aGannet* leaves the colony from, which is used in a subsequent submodel ("calculate-bearing"), but there is no requirement to reach this patch. This assumes that the agents in the model have a sense of the direction to head from the colony, which will have been gained during earlier life (Votier et al., 2017; Grecian et al., 2018) and fine-tuned for that particular year during the incubation period when they have been acting as central place foragers at the colony but with less constraints allowing them to make more exploratory trips (Lane et al., 2020). At the beginning of each trip a new target cell is picked by each simulated *aGannet*, and hence the often repeatable departure bearing seen in empirical data (Patrick et al., 2014) associated with IFSF is not represented in this model.

enter-ARS?

This submodel performs a stochastic process on the likelihood of switching from outbound to ARS movement mode, depending on the prey density of the cell that the *aGannet* currently occupies. This means that with increasing prey density, it is assumed that it is more likely that a gannet will spot these prey and decide to switch to ARS movement (Hamer et al., 2009).

Empirical evidence of such behaviours is difficult to obtain in the wild and thus understanding of predator-prey interactions of diving seabirds such as gannets is low. Captive experiments with cormorants (*Phalacrocorax auritus*) targeting juvenile rainbow trout (*Oncorhynchus mykiss*) showed varying prey densities had a strong influence on the success of the predator, where success linearly increased to an asymptote at higher densities (Enstipp et al., 2007). I extrapolate this to gannets visually detecting their prey and have characterised the relationship as an approximation of the type II curve (Figure 3.4) based on Holling's functional response model (Holling, 1959).

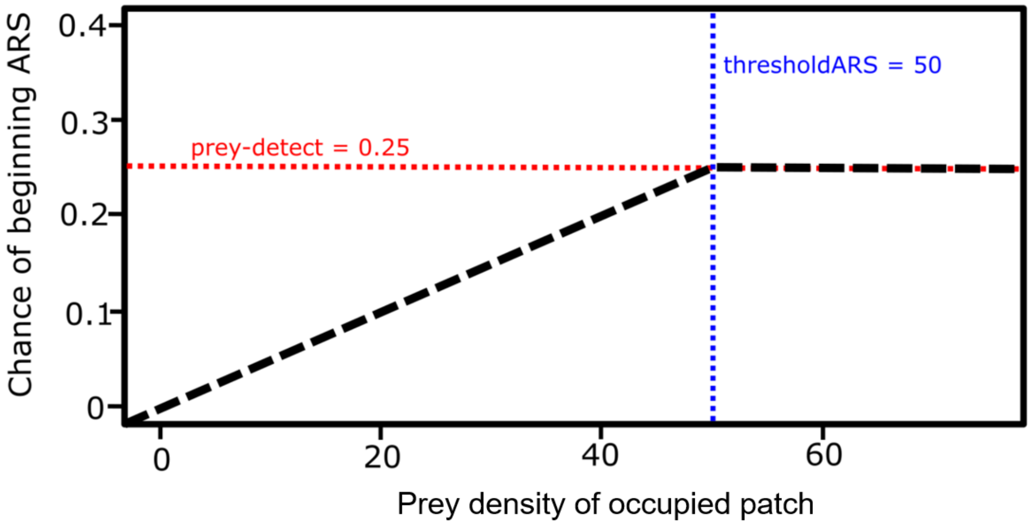
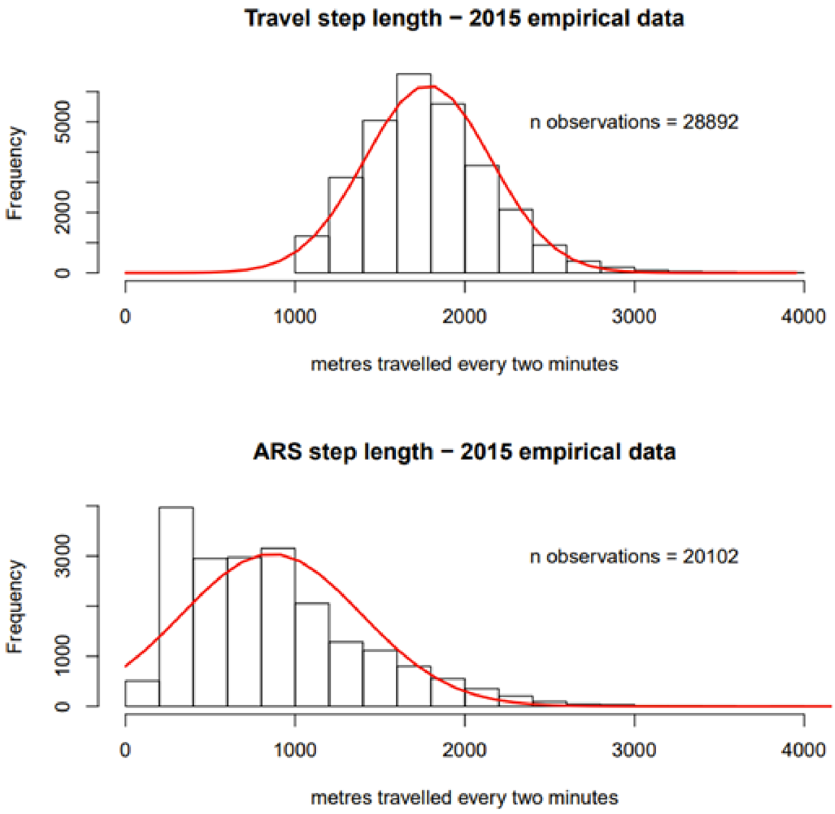


Figure 3.4: Plot showing the relationship between chance of beginning ARS and prey density of the current patch which an *aGannet* may be on at any given moment with the global parameters of "thresholdARS" and "prey-detect" set to 50 and 0.25 respectively.

There are two unknown parameters in this submodel; *prey-detect* and *thresholdARS*. *Prey-detect* determines the chance of switching to ARS movement at any given timestep when an *aGannet* is in outbound travel, and if set to 0.25 will mean that there is never over 25% chance of beginning ARS (Figure 3.4). *thresholdARS* determines what prey density of the occupied patch needs to be exceeded (i.e. prey density of 50 in Figure 3.4) in order to have the maximum chance of detecting prey. The ability to detect prey decreases linearly in correspondence with decreasing prey density of a patch below *thresholdARS* (Figure 3.4).

Adjusting step length and turning angle

These submodels draw randomly from a normal distribution of step length for outbound and inbound movement, and step length and turning angle for ARS movement. For approximations of step length distributions from empirical data see Figure 3.5 below. ARS step length was truncated at zero.


Travel step length – 2015 empirical data

ARS step length – 2015 empirical data

Figure 3.5. Step lengths of travel movement (top) and ARS movement (bottom) extracted from empirical data of adult gannets during chick rearing in 2015 at Bass Rock. Red curves show the corresponding normal distributions used for obtaining step lengths for respective movement modes.

foraging-attempt

At each timestep that an *aGannet* is in ARS movement this submodel is called, so there is the chance of catching a fish which is determined by the same functional response relationship and its associated parameters approximated for the “enter-ARS?” submodel (Figure 3.4). Thus if an *aGannet* moves to another cell where prey density changes there can be an according response in the chance of catching prey at this timestep. If foraging has been successful an *aGannet's* food intake will increase with the prey size being randomly drawn from a normal distribution derived from the literature (Table 3.3), and a Boolean variable will be switched to indicate to the following submodel that a rest is required.

decide-rest-duration

Inspection of empirical data indicates that the majority of rests are for a very short period of time, with the occasional longer rest and that these rests are largely nested within bouts of ARS movement (Figure 3.1). In Cape gannets (*Morus capensis*) it is suggested that rests which are commonly observed at the midpoint of the journey allow time to digest some food before returning home to feed the chick later in the day (Ropert-Coudert et al., 2004). Equivalent explanations have not been suggested in northern gannets, and as such I have decided to include a longer rest, drawn randomly from a normal distribution, towards the end of the trip when the threshold requirement for food intake has been met. Shorter rests after successful foraging attempts during ARS bouts earlier in the trip are randomly drawn from a gamma distribution (shape = 5, scale = 1).

Calculate-bearing

This submodel calculates the direction of outbound travel through an adjustment to the initial bearing which is recorded at the outset of the foraging trip based on the food intake of the gannet throughout the foraging trip. The equation used to calculate this adjustment is as follows:

$$Adjustment_i = \frac{1}{(1 \div (1 + e^{-sqrt\,((food-intake)-mean(food-intake))}) \times 180 + stoch}$$

Where *food-intake* is the total food that an *aGannet* has ingested (g) during that particular foraging trip. Stochasticity is introduced to the adjustment (Figure 3.6) through two coefficients applied so that there is a normal distribution of variation throughout the relationship (curve sd = 0.004, straight sd = 7). The calculated adjustment to the initial bearing, including stochastic variation, is then either added to or subtracted from the initial bearing according to whether the trip has been set as clockwise or anticlockwise, respectively.

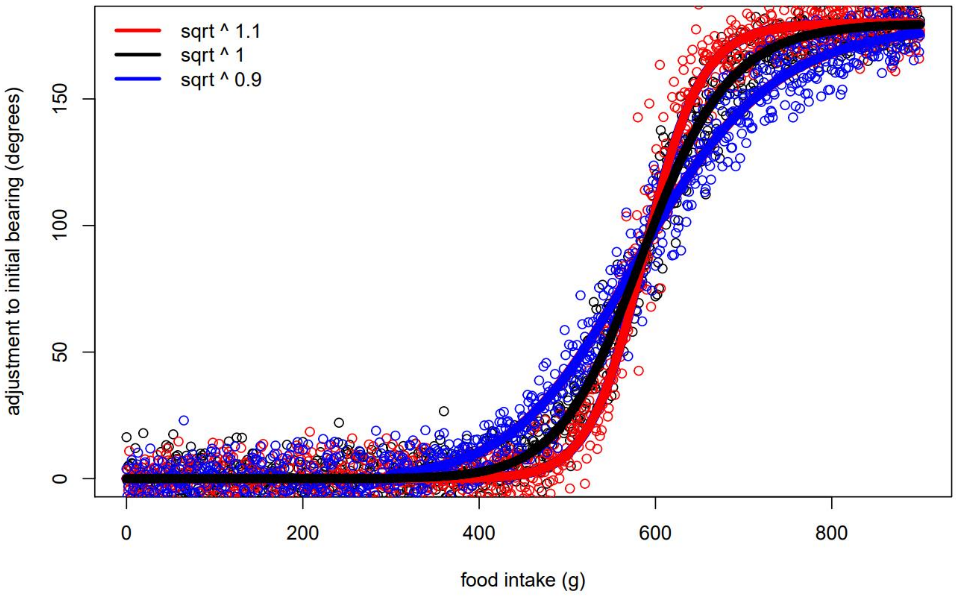


Figure 3.6. Logistic relationship of the adjustment to the original bearing made for food intake during a foraging trip where the different colour lines represent a different steepness implied in parameterisation tests with a visualisation of stochasticity around each line in the relevant colour.

The shallower the curve in this relationship (i.e. the blue curve in Figure 3.6), the more likely it is that the foraging trip will be more elliptical. Whereas when the curve is steeper (red curve in Figure 3.6), it is more likely that an *aGannet* will turn around sharply to face the colony, and the bearing travelling inwards will be very similar to the one which it travelled out on. I obtained the final relationship (Figure 3.6) to use through parameterisation procedures using the POM technique (see section 3.2.4 on parameterisation below).

Calculate inbound

This submodel is called at each step during inbound travel to the colony. It utilises a biased random walk, by including some bias towards facing the colony with a certain amount of stochasticity built into the turning angle. This represents what is seen empirically where it appears gannets know the general direction of the colony and travel towards it with some correction along the way (Figure 3.1). Then when birds are within 10 km of the colony it is assumed that they can see it or obtain directional cues from social information of colony-bound conspecifics, and so travel straight back to the colony.

Land avoidance

This is a series of procedures adapted from code written previously and used to model Saimaa ringed seal (*Phoca hispida saimensis*) movements (Liukkonen et al. 2018). At each timestep during a foraging trip an *aGannet* will check if there is land in front of the direction it is facing (~5 km). If there is land ahead, the amount of land to the left and right of the individual is interpreted, and whichever direction there is more land in the gannet will decide to turn in the opposite direction so as to avoid this land.

Decide length at colony

This submodel decides how long an individual will spend at the colony after completing its foraging trip. It is based on the assumption that chick-rearing gannets have a partner that will be on a foraging trip if they themselves are at the colony. Thus the waiting time at the colony will be approximately the same duration as the foraging trips. As the duration of the foraging trip will differ depending on the initial conditions of the model, this will need to be calculated throughout respective model runs. A list is stored and updated each time an *aGannet's* trip is completed which retains the last 20 trips of any individual returning to the colony. The mean and standard deviation of this list of durations is then used to withdraw a number from a normal distribution on the *aGannet's* return to the colony after its initial and subsequent foraging trips.

Output files

Depending on the output settings an *aGannet's* coordinates at each timestep are written so that movement analysis can be conducted in R, or a summary of times spent in different behaviours in each trip are written to a .csv for all individuals along with how many fish were caught on that trip.

3.2.4 Parameterisation

The majority of the parameter values in this study were given values derived either from literature or empirical data (Table 3.3). However, a few important parameters are unknown so I devised a series of parameter estimation procedures, using POM to obtain unknown parameters which is sometimes referred to as “inverse determination” (Grimm & Railsback, 2012). This was a three step procedure in which one step was completed before beginning the next:

I. Fine scale movements: Before looking at broader scale patterns I ensured that fine scale movements were being modelled well by visual comparison of distribution of step lengths and turning angles of simulated outbound, ARS and inbound movements against those from empirical data (Table 3.1). Here one hundred simulated trips were run with different stochasticity coefficients until they matched what was seen in one hundred randomly selected empirical foraging trips. Simulated outbound and inbound data were compared separately against pooled travel fine scale movement data (i.e. outbound and inbound are not delineated), as they are the result of different submodels thus requiring separate inspection.

II. Functional response parameters: POM was used to identify what combination of three interacting parameters (*prey-density*, *prey-detection*, *thresholdARS*) resulted in emergence of trip durations (h) most similar to what was observed in the empirical data (Table 3.1). The different parameter values used were: (i) four levels of the landscape attribute *prey-density* (critical/low/medium/high) achieved through heuristic determination by using a coefficient to multiply the time spent foraging in particular cells in order to cover the full scope of foraging ranges when all other parameters were kept at a constant intermediate level, (ii) *prey-detection* proved to be very sensitive on pilot experiments, thus it was given high resolution with values in the range 0.05 – 0.3, with 0.025 intervals. (iii) *ThresholdARS* values were in the range of 20 – 100, with intervals of 20. For each of the resultant 220 parameter combinations I ran the model and extracted 100 simulated foraging trips at random. 100 trip durations were extracted from the empirical data for comparison which were used as the observed values for calculation of the root mean square error (RMSE) scores in order to evaluate the agreement between the observed and predicted values:

$$RMSE = \sqrt{\sum_{i=1}^{n} \frac{(\hat{y}\mathrm{i} - \mathrm{yi})^2}{n}}$$

Through grouping the lowest scores and visual inspection of plots I ascertained the best fitting parameter combination and used this going forward.

III. Logistic relationship between food intake and adjustment to initial bearing: The final procedure for parameterisation was designed to capture broad scale movement patterns, i.e. how elliptical or linear the trip was. I varied the steepness coefficient of the curve in the relationship in 3 levels (steep/normal/shallow). With increasing steepness of the curve (Figure 3.6) comes lower possibility to withdraw from the curve on the transition from 0 - 180° as food intake is increasing in any particular foraging trip, and hence the likelihood of having a more directed (less elliptical) foraging trip trajectory. Each of these three parameter levels was run in a simulation and 100 trips were exported for spatial analysis in R where I calculated the linearity index (Section 3.2.2) for each trip, where a value of 1 would indicate a perfectly directed trip to a maximal point and back, with increasing values indicating deviation from this. I then plotted the linearity probability densities for respective simulations against empirical data from 100 trips from two different years (2012, 2016), and it was apparent that different years showed considerable variation in shapes, from which I then visually assessed which parameter level would be best. Another pattern described in section 3.2.2, bearing difference between initial departure angle and maximum point, was considered but did not provide any further insights beyond those obtained from assessment with the linearity index and visual assessment of the shapes trips, so was not included in this process.

3.2.5 Sensitivity analysis

To assess the sensitivity of the model's output to changes in parameter values I performed a local sensitivity analysis. This was achieved by running simulations with singular, successive perturbation of a subset of model parameters. This subset was composed of the majority of important parameters (Table 3.3), including those contributing to stochasticity, with the exclusion of those relating to step lengths and turning angles for different movement modes as this would have resulted in the model's deviation from representative movement patterns. Each parameter was varied by a standard range of

±10% in turn, while all other parameters were maintained at the level discerned through the parameterisation process, and trip durations (h) of 1000 trips from 100 individuals were withdrawn from the simulation. The difference in mean trip duration (h) was then expressed as a percentage difference from that of the baseline trip duration from a model run with no parameter perturbation.

3.2.6 Evaluation

A final evaluation of the model was achieved through side by side visual comparison of 3 random modelled trips with 3 randomly picked empirical trips and inspection to see if the correct activity budgets were being observed. I also observed potential population patterns of this model, although not the focus of this model, by side by side plots of 100 trips from modelled and empirical data on the same plot to see if any population-level patterns were emerging.

3.3 Results

3.3.1 Parameterisation

3.3.1.1 Fine scale movements

After iteratively running different stochasticity levels, step lengths and turning angles and assessing outputs the final parameters were decided for fine scale movement which produced the step lengths and turning angles seen in Figures 3.7 and 3.8, respectively. The modelled step lengths for travel (outbound and inbound movement modes) were 0.91 ± 0.17. Those for ARS were = 0.429 ± 0.23. The final values for stochasticity coefficients which influenced turning angles were as follows: curve stoch sd = 0.004, straight stoch sd = 8, calculate inbound stoch sd = 10, setting for sd of ARS turning angle = 46.

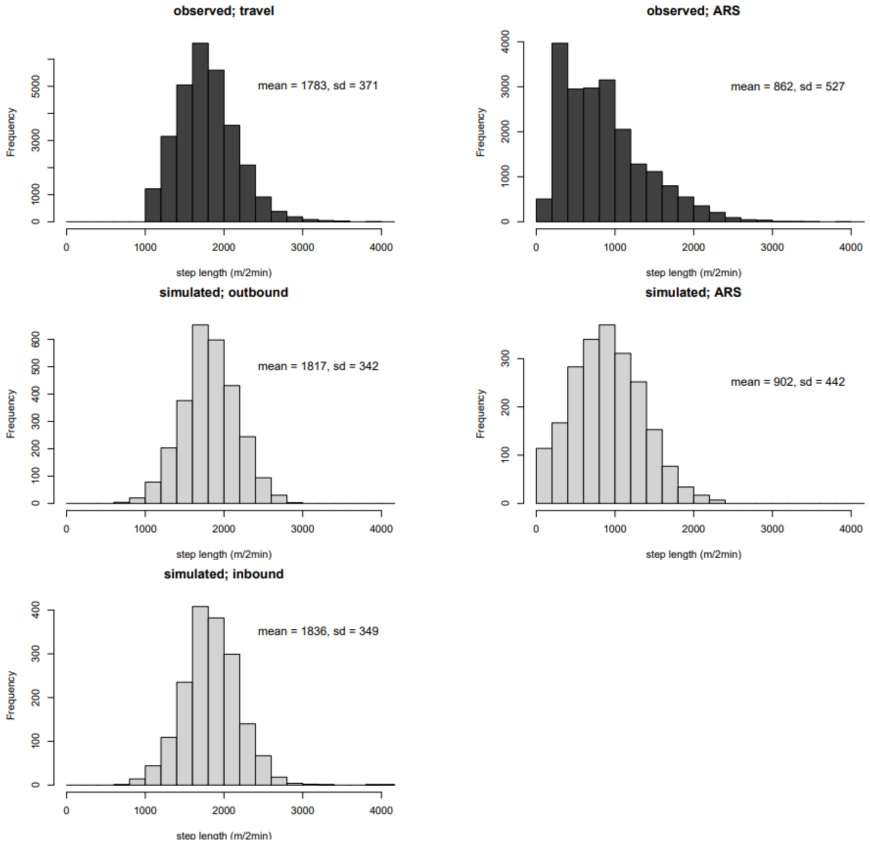


Figure 3.7. Distribution of step lengths for travel are on the left, ARS are on the right. The top row of darker grey plots are the observed distributions from empirical data, with the lighter grey plots below from simulated data.

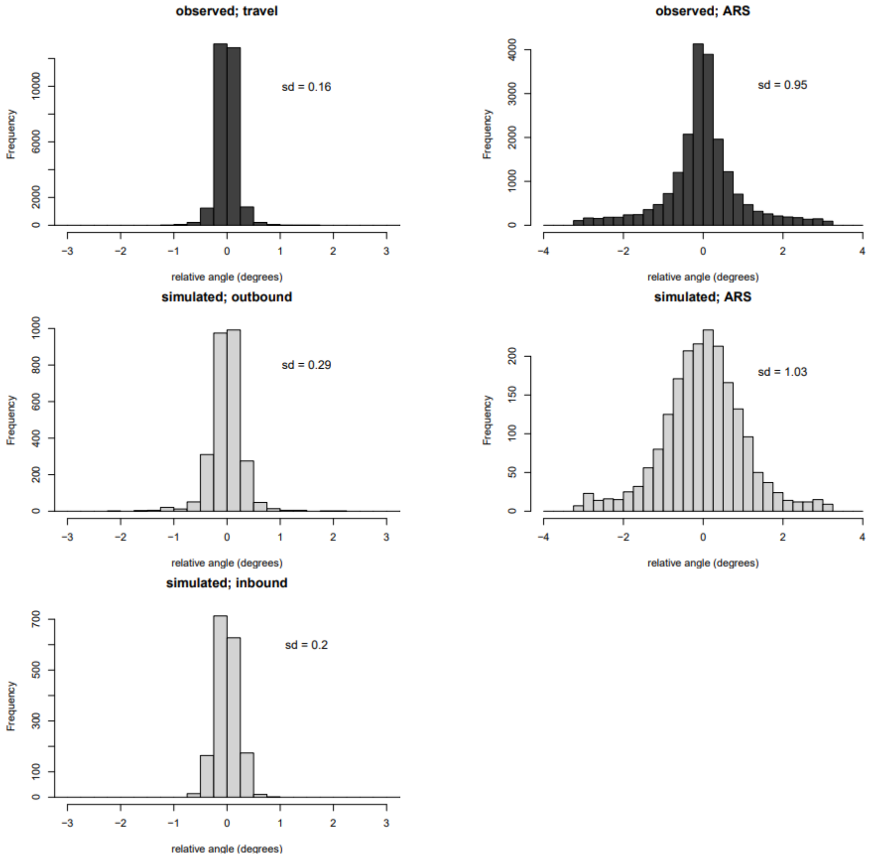


Figure 3.8. Distribution of turning angles for travel are on the left, ARS are on the right. The top row of darker grey plots are the observed distributions from empirical data, with the lighter grey plots below from simulated data.

3.3.1.2 Functional response

There was high variability in the outputs resulting from the 220 different parameter combinations with considerable overlap between their ability to reproduce the chosen empirical pattern (Figure 3.9). This was predictable given the interactive nature in dictating the modelled functional response of the three parameters tested. On further inspection it was clear that beyond the lowest 20 scores (i.e. the top scoring combinations) the pattern being inspected was not well captured. Therefore I selected from the top 20 scores (Table 3.4) by plotting the trip durations against the empirical data (Figure 3.10), and visually deduced the three best fitting parameter combinations according to the mean and variance of the data (represented by yellow and orange highlighted parameter combinations in Table 3.4 and Figure 3.10). I then ran each of these combinations in turn in the model through visualising in the interface and there was not much perceivable difference so settled on the 10th ranked parameter combination, which is indicated by orange in Table 3.4 and Figure 3.10, due to median and interquartile range being well represented (Figure 3.10).

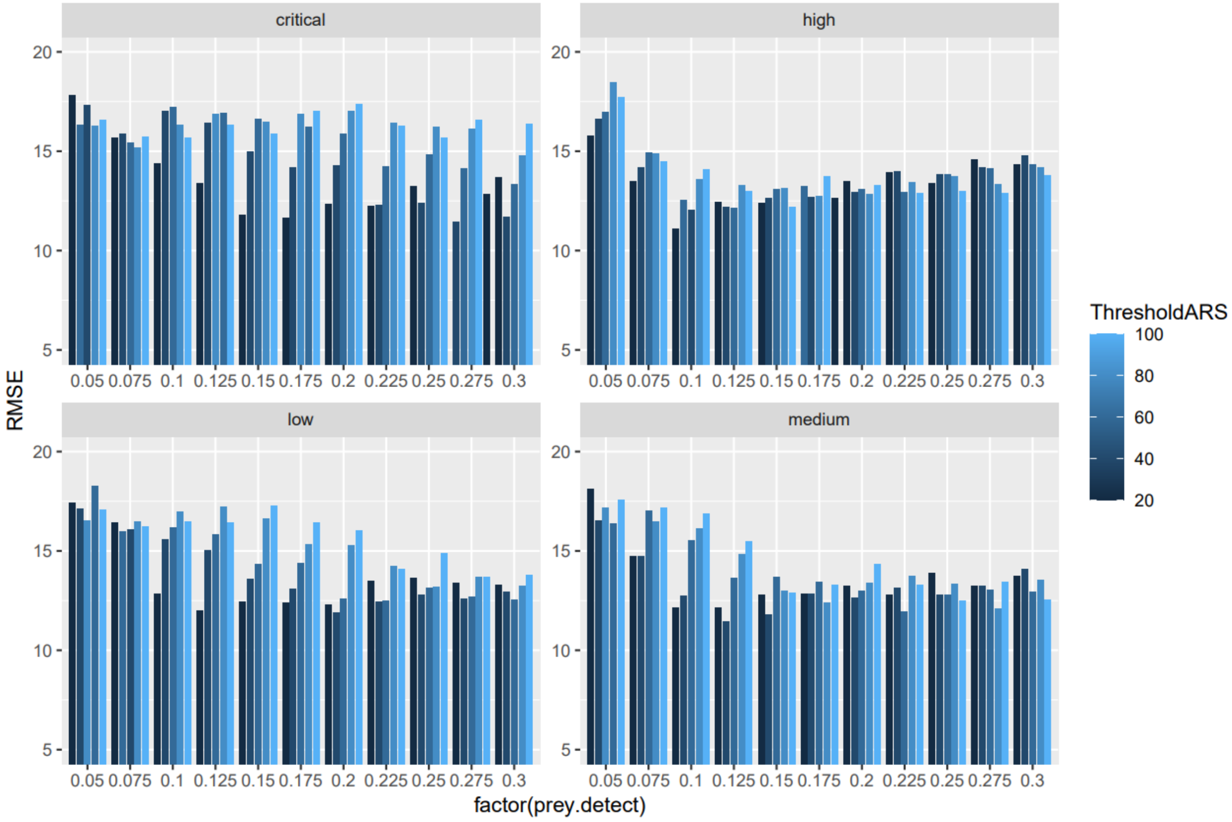


Figure 3.9. Barplots showing root mean square error (RMSE) scores of parameterisation tests for three interacting parameters which dictate foraging behaviour through the functional response approximation process: (i) “Prey density” is related to the overall availability of prey in the landscape and is assigned four levels (high, medium, low, critical) which are shown in the four windows (ii) “ThesholdARS” dictates how the approximated type II functional response asymptotes and was assigned five different values and is displayed by the colour of the bar, and (iii) “prey detect” which dictates the chance of beginning ARS was tested at 11 increments, which are displayed on the x-axes.

Table 3.4. Rankings of top 20 (i.e. lowest) root mean square error (RMSE) scores from our functional response parameterisation. The coloured rows indicate the top 3 combinations picked from visual assessment of trip durations (Figure 3.10).

RMSE	**Rank**	**prey.density**	**prey.detect**	**ThresholdARS**
11.088	1	high	0.1	20
11.42293	2	critical	0.275	40
11.43108	3	medium	0.125	40
11.66516	4	critical	0.175	20
11.70821	5	critical	0.3	40
11.78626	6	medium	0.15	40
11.81091	7	critical	0.15	20
11.87579	8	low	0.2	40
11.93222	9	medium	0.225	60
11.98523	10	low	0.125	20
12.01943	11	high	0.1	40
12.10548	12	medium	0.275	80
12.1196	13	high	0.125	60
12.1619	14	medium	0.125	20
12.16357	15	medium	0.1	20
12.16982	16	high	0.15	100
12.19935	17	high	0.125	40
12.22273	18	critical	0.225	20
12.27497	19	low	0.2	20
12.2784	20	critical	0.225	40

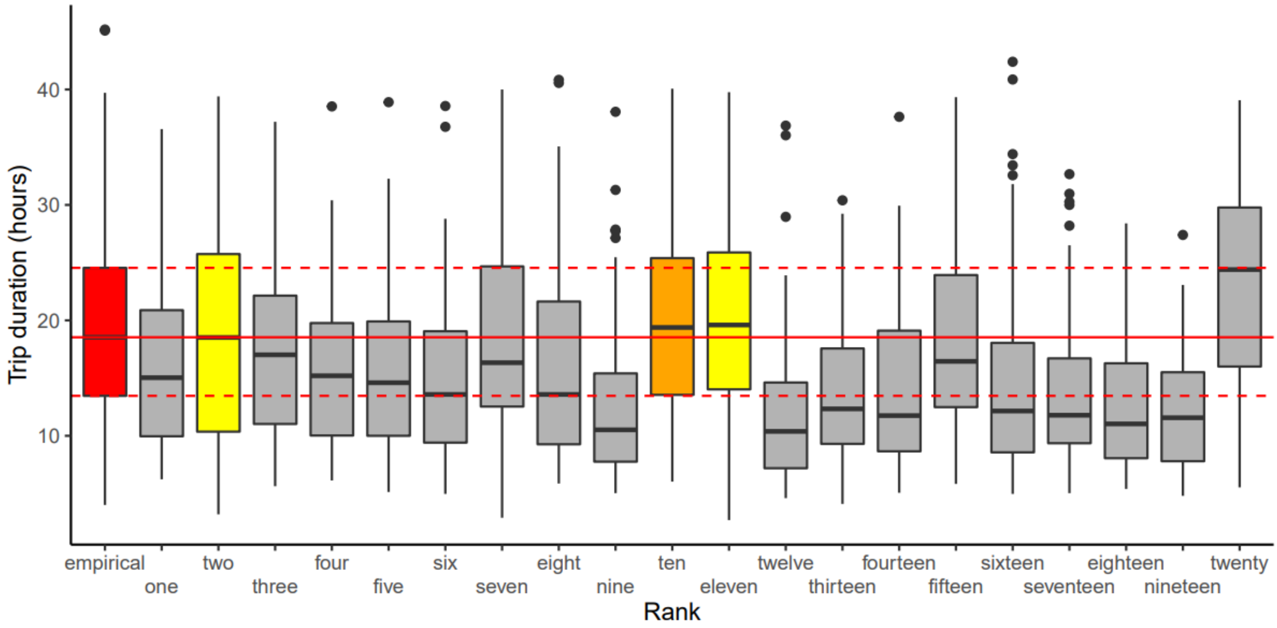
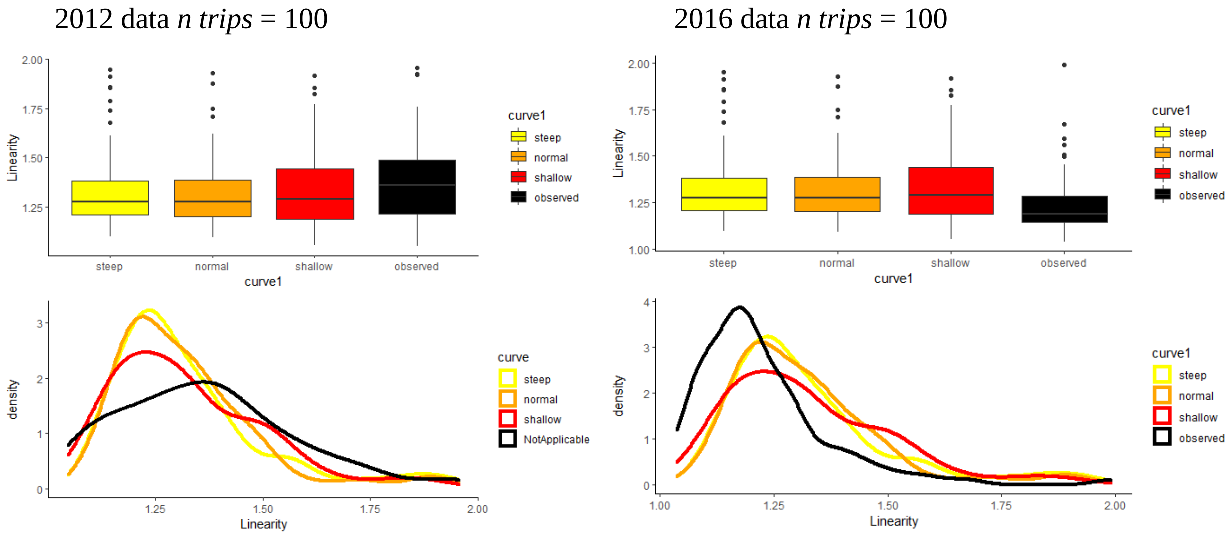


Figure 3.10. Trip durations (hours) of the lowest 20 RMSE scores out of 220 parameter combinations. The red box on the far left is from empirical observations with solid red line indicating the empirical median, and upper and lower red dashed lines indicate the respective quartiles. The other coloured plots indicate the top 3 selected

parameter combinations which were run on the model interface, with orange being the final one selected for the model going forwards.

3.3.1.3 Logistic relationship between food-intake and adjustment to initial bearing

The different shapes of logistic curve tested (steep/normal/shallow) showed some variation in their emergent linearity index, where the shallow curve resulted in less linear trips, as intended. “Steep” and “normal” parameter levels produced trips with almost identical linearity, whereas the “shallow” parameter level showed noticeably less linearity (Figure 3.11). However, the variation between parameter levels was small in comparison to that seen in the interannual variation in empirical data (Figure 3.11). All tested parameter levels were on average more linear than empirical trips from 2012, and less linear than trips from 2016, and therefore all tests fell within the range of possibility. After visualising trip trajectories from different parameter levels, it was decided not to use the “shallow” parameter level as it had the tendency to produce unrealistic foraging trip trajectories, and so I opted for the intermediate “normal” logistic curve going forwards.



2012 data *n trips* = 100

2016 data *n trips* = 100

Figure 3.11. Plots of the linearity index of trips from outputs of three tested parameter levels (steep/normal/shallow) for the logistic curve dictating the relationship between food intake and adjustment to intial bearing, compared with the linearity index of empirical trips from 2012 (left) and 2016 (right).

3.3.3 Sensitivity

Eight parameters were varied in the local sensitivity analysis. Out of the 16 simulations (each parameter varied ± 10%) differences in outputs compared to the baseline model were only exceeded on three occasions (Figure 3.12). Changes in model outputs were the most sensitive to the parameter which dictates the chance of detecting prey in the model (*prey detect*) The other two parameters which contribute to the functional response (*ThresholdARS* and *prey level*) did not have as much influence on model outputs. The duration of short rests and fish size (g) had the lowest influence of all tested parameter in influencing model output (Figure 3.12).

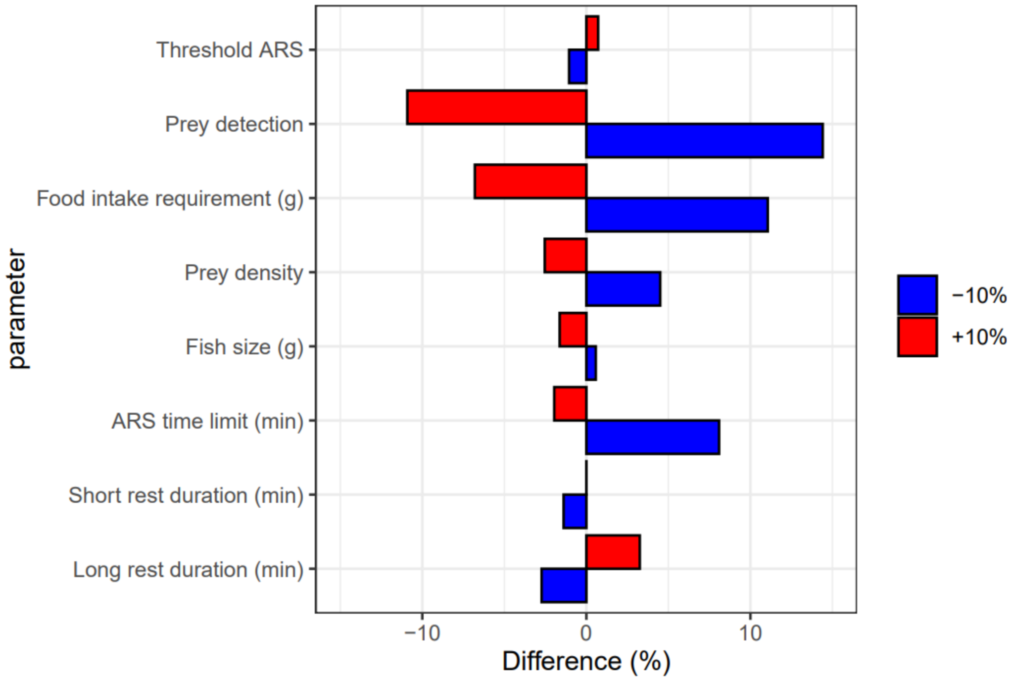


Figure 3.12. Sensitivity analysis of trip duration (h) to single and sequential variation (±10%) of parameters listed on the y-axis where differences are expressed as percentage difference to a baseline where all parameters were kept at their default level.

3.3.4 Evaluation of model performance

When comparing a subset of simulated foraging trips from the fully parameterised model with empirical foraging tracks (Figure 3.13) it is clear that the modelled trips have captured many key attributes of the natural system, in terms of both size and shape. There was considerable variation in the trip metrics which reflected the variation seen in empirical data. The resulting arc from “trap-line” trajectory results in some trips being more elliptical, while others were more direct. The relationship between food intake and adjustment to initial bearing has allowed for trips where foraging can take place once heading back in the general direction of the colony. However, it is still possible to differentiate simulated tracks from empirical due to the relatively straight travel between ARS zones (Figure 3.13), which is an artefact of the bearing adjustment being a product of food intake which can only occur during ARS movement.

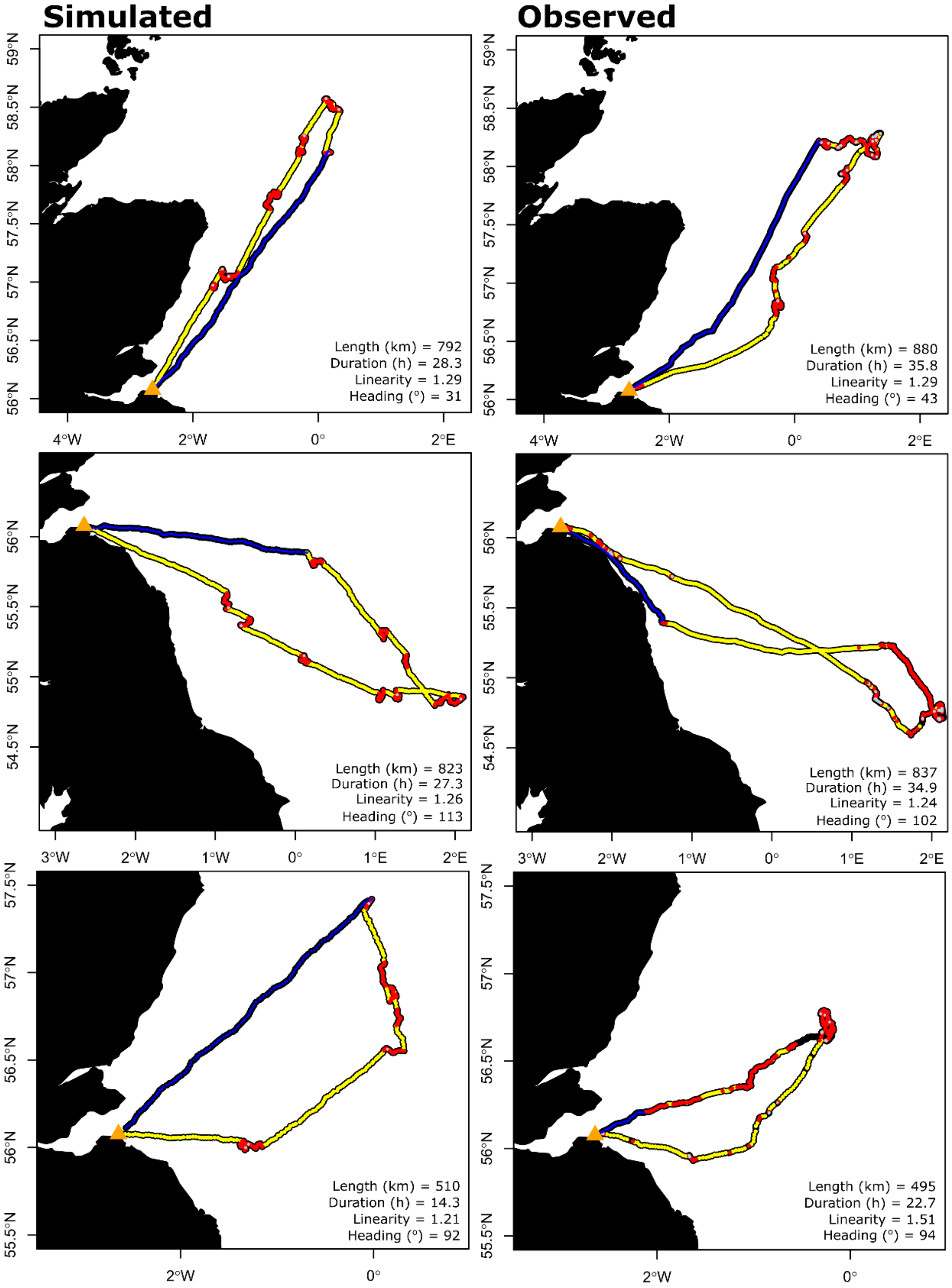


Figure 3.13. Side-by-side comparison of three simulated foraging trips (left) with three similar trips from empirical data (right) with respective trip metrics inset in panels. The orange triangle indicates the location of Bass Rock.

To detect any emergent patterns at the population-level I plotted 100 simulated trips to compare alongside 100 empirical trips (Figure 3.14). Despite not being the model's intended purpose, it is clear that population patterns are being reproduced to some extent, with the accessible space being exploited in a similar fashion. The model shows that most foraging is taking place to the northeast, a consistent pattern in gannets foraging from Bass Rock, and this can be explained by the modelled individuals being informed about which directions have profitable foraging.

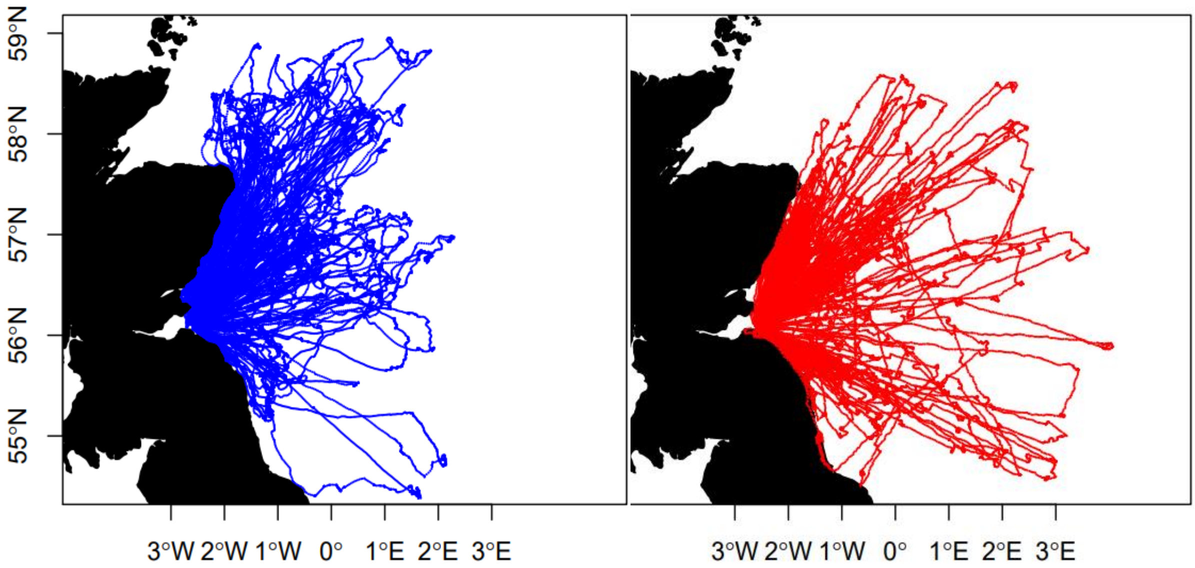


Figure 3.14. Comparison of 100 simulated foraging trips (right) with 100 empirical foraging trips (left).

When the activity budgets of foraging trips from the final model's outputs are compared against empirical data (Figure 3.15) I found the proportion of time spent in ARS movement was representative, but there was a lower proportion of time spent resting, and a higher proportion of time spent in travelling movement modes ("outbound" and "inbound"). It is unlikely that this had much influence on foraging trip trajectory, but this is something that should be addressed in future developments of this model.

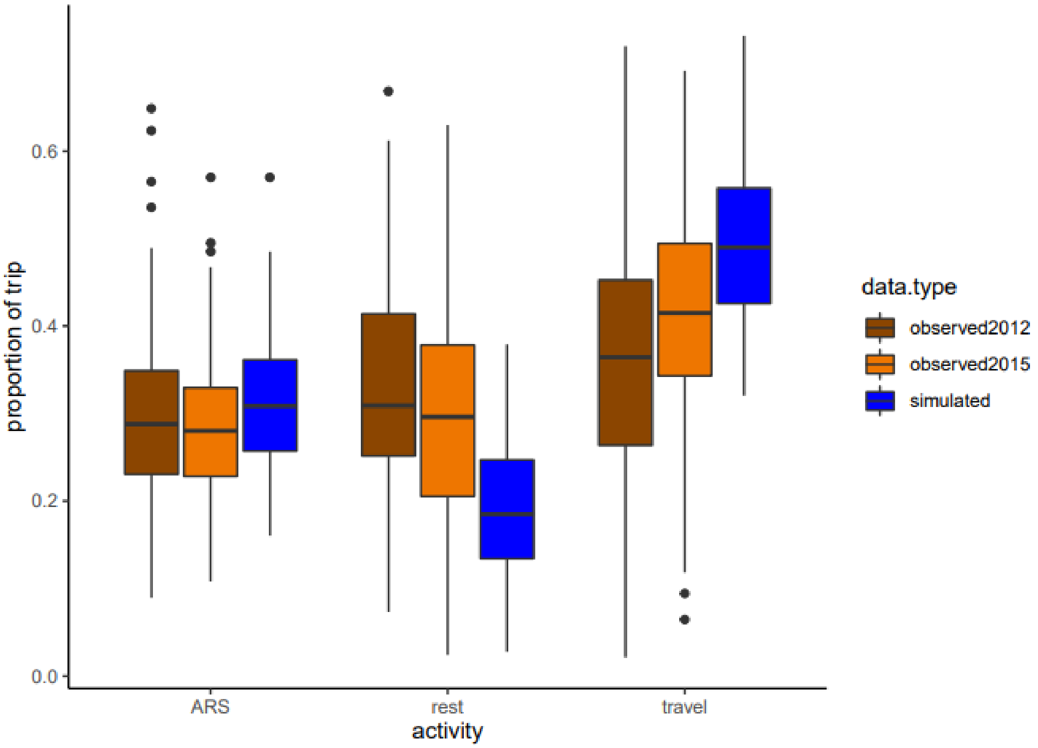


Figure 3.15. Proportion of trip spent in different activities (travel/ARS/rest) for model outputs compared with empirical data.

3.4. Discussion

This study used telemetry data from gannets at Bass Rock to guide the development of a spatially-explicit individual-based model of foraging trip movements of chick-rearing adults. This was based on assumptions regarding behavioural decisions made in response to an individual's current environment and previous foraging success as an approximation of physiological drivers. The majority of parameters were obtained through empirical data, some were derived from literature, and the remaining unknown patterns were determined through POM. The purpose of the model has been fulfilled in respect to capturing both the average trip metrics and their associated variation which is seen within and between individuals on different foraging trips. To my knowledge, this model produces the most realistic approximation of the movements of foraging seabirds to date in an IBM.

Ecological insight is provided through mechanistically linking heterogenous prey to foraging behaviour through modelling of the trap line (Wanless et al., 1990) strategy and its associated behaviours, such as hierarchical movements to aid in location of prey. Through parameterising both broad- and fine-scale movements separately, I have modelled individuals that are “primarily faithful to a directional arc” (Wakefield et al., 2015) with the introduction of stochasticity at the finer scale to represent what is likely to be a degree of navigational error that is seen in reality, as suggested by Pettex et al. (2010). Individuals switched to ARS movement when encountering a patch with higher prey density, where modelled movements where slower and more sinuous than when travelling, giving the opportunity to spend more time in this locale with the potential to make foraging attempts, and thus interaction with a heterogenous distribution of prey emerged from the model. Together, this has captured the general shape of foraging trips, and provides a new technique to model central place foraging.

Other attempts to model how animals search for patchy resources include iterations of the random walk such as Lévy flight motion (Viswanathan et al., 1999, 2011) where step lengths are drawn at random from a Pareto distribution with the result of straight line travel between patches of more intensive searching behaviour. Consequently, this model is better at characterising ARS behaviour than other models of animal movement such as correlated random walks (CRW). Therefore it has been applied to seabirds such as Cory’s shearwater (*Calonectris diomedea diomedea*) and has been able to characterise their movements representing improved searching efficiency in patchy habitats (Focardi & Cecere, 2014). CRW assumes that turning angles are correlated to some degree and therefore is capable of capturing fine scale autocorrelation seen in empirical movements, but its inability to recreate nested searching behaviour limits its application in seabird species. Developments of CRW include adaptive CRW which can incorporate ARS movements based on the habitat (Benhamou, 2007), and incorporating elements of the Lévy distribution (“Lévy mediated CRW”, Bartumeus & Levin, 2008). An IBM of harbour seals has incorporated a memory component to create a “biased CRW” (Chudzinska et al., 2021), where individuals are drawn towards previously visited foraging areas and haul out sites. Future iterations of this model may benefit from incorporation of such movement models, such as introducing error structures in a CRW, which could eliminate the unrealistic straight travel between ARS zones seen in outputs. However, it is unlikely that navigational error was the only thing contributing to deviation from the arc seen in empirical tracking data.

The most flawed assumptions in the model were that there is no interaction with other birds, despite evidence shown from tracking studies (Jones et al. 2020) and bird-borne cameras (Thiebault et al., 2014), and that there are no memory effects, despite strong evidence for such mechanisms displayed by canalisation of space use during development (Votier et al., 2017; Grecian et al., 2018). The influence of sociality on foraging movements caused fallow deer (*Dama dama*) to deviate from the Lévy walk which they exhibit when foraging alone (Focardi et al., 2009), perhaps indicating that such models are not sufficient for describing the movements of animals with multiple behavioural drivers. Mechanistic and bottom-up models such as IBMs provide a potential framework for inferring the influence of interaction (e.g. Boyd et al., 2016) and memory effects (e.g. Chudzinska et al., 2021) on emerging movement patterns. Now that this model is able to reproduce the typical foraging movements of gannets, the next logical step is to try and further understanding of more complex behaviours. For example, by modelling different resource localisation mechanisms it might be possible to decipher how individuals integrate available public and private information, which is likely to be a key driver of IFSF patterns. Differentiating the ability of different simulations to reproduce the strong characteristic patterns of IFSF in seabirds resulting from individual decisions could allow for decryption of the potential drivers of this phenomenon. It appears that this model is capable of producing some population-level patterns in its current iteration, but they have not been adequately quantified. This is something that could be incorporated into models looking at IFSF as it is likely to be, at least partially, a consequence of the intraspecific competition (Araújo et al., 2011).

Abiotic factors may also influence foraging strategy, with wind being shown to have influence on flight heights and activity budgets in gannets (Lane et al., 2019). It would also be possible to investigate the possible impact of anthropogenic disturbance. One example is a model of gannets foraging in the English Channel (Warwick-Evans et al., 2017), that linked movement to body condition and breeding success through an energetics component to understand the potential impacts of offshore wind farms, including collision and avoidance effects. No such energetics component was incorporated into this model, but would be required to investigate the effects of different foraging strategies on body condition and reproductive success. Warwick-Evans et al.s' (2017) model outputs corroborated previous suggestions of higher impact of OWFs when placed nearer to the colony or are larger in size (Masden et al., 2010). OWF developments which are planned for the Firth of Forth are relatively large and situated close to the Bass Rock colony, where individuals experience a pre-existing high level of intraspecific competition (Wakefield et al., 2013). Such conditions are the suggested prerequisite for potential negative impacts on the population from collision, barrier and/or displacement effects, making this particular application a future priority. Model outputs could be compared to those from more conventional population viability analysis (PVA) conducted at this site (Lane et al., 2020).

In addition, the inclusion of energetics in the model would allow for programming of more nuanced decision making from individuals through sensing changes in their condition throughout the breeding season i.e. adults prioritising their own survival above that of their chick in adverse conditions (Ponchon et al., 2014). Another assumption of the model was that on each foraging trip an *aGannet* was required to meet the same threshold in food intake before returning to the nest. This requirement was approximated from metabolic rates from experiments (Jackson, 1992), but as it was fixed it couldn't account for digestion rates etc, and this is something that would need to be included to be able to infer energetic budgets and body condition. Furthermore, it is likely that gannets employ strategy through more complex decisions based on trade-offs weighed against successive trips, such as those seen in Cory's shearwaters (*Calonectris borealis,* Magalhães et al., 2008) in employing a dual-foraging strategy with alternating durations of trips; long-lasting to fuel themselves, and short ones to obtain food for their chick.

Sensitivity analysis indicated the chance of detecting prey is of high importance in this model, which is logical and biologically plausible. However, gannets as a species do not lend themselves well to investigation on the success rate of predation events or what prey species and masses are being consumed. Furthermore, data indicating fish stocks in the North Sea are of a low spatial and temporal resolution, hence other indicators such as primary producers and tidal mixing fronts are used to infer areas of enhanced productivity as a proxy for increased abundance of gannet prey (Wakefield et al., 2015; Grecian et al., 2018). This model required a finer spatial resolution for prey availability than these data could provide, and as such prey availability was approximated from areas where gannets from Bass Rock colony have foraged on over 500 trips from four breeding seasons, and therefore should represent important foraging areas well. Prey availability is thus modelled, not as total abundance of fish in a certain patch, but that prey which is available whether it be more fish near the surface for visual detection, or perhaps representing areas are where high concentrations of multispecies feeding associations (MSFAs) occur (Camphuysen, 2011). Hence the parameterisation procedure to determine the functional response and foraging behaviour could be applied to other colonies or seabird species if there is a reasonable amount of fine scale movement data available and some understanding of their foraging behaviour.

Further analysis, by applying individuals parameterised for Bass Rock to other gannet colonies could provide insights into how robust the model is (Railsback & Grimm, 2019). If this is performed "blind", i.e. empirical data for the birds at the colony which the model is being applied to has not been inspected and used to inform the model, and it performs well when evaluated against fine scale movement data, then there is the possibility for this approach to compliment the widely used technique of species distribution modelling (SDM). This has the potential to ameliorate the transferability issues between populations which is one of the drawbacks of SDM (Sequeira et al., 2018). In this scenario, prey availability could be inferred from other data sources such as surveys of bird distributions or remote sensing of environmental attributes. Further quantification would be required of foraging distributions and other population-level attributes before progressing to this stage.

This chapter describes a model which characterises the movement patterns of chick-rearing gannets at Bass Rock. In doing so it has provided insight into the potential decisions and key processes which link heterogeneously distributed prey to foraging behaviour in a central place foraging seabird. Rigorous parameterisation of realistic movements and interaction with the environment has resulted in a solid foundation for developing more behaviourally complex models. The model did not perfectly capture the activity budgets seen in empirical data, and this was purposely not redressed as the intention was not to overfit the model before more elements are incorporated in future iterations. The analysis highlights the importance of the functional response and visual detection of prey, and as such further fieldwork to discern fine scale foraging behaviours would be useful to refine the model. By incorporating interaction and memory into the model it has the potential to explore the behavioural drivers of IFSF, a phenomenon with a strong display in gannets which may have implications for OWF assessments. Its potential in application to forecasting population dynamics and distributions has also been discussed, where this approach gives the opportunity to incorporate demographic processes through mechanistic means, that is often not feasible with conventional PVA approaches.

3.5 Literature cited

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958.

Bartumeus, F., & Levin, S. A. (2008). Fractal reorientation clocks: Linking animal behavior to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19072–19077.

Benhamou, S. (2007). How many animals really do the Lévy walk? *Ecology*, *88*(8), 1962–1969.

Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. E., Weimerskirch, H., & Bertrand, S. (2016). Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. *Behavioral Ecology, 27*(4), 1223–1234.

Calenge, C., & Calenge, M. C. (2018). *Package 'adehabitatLT'*. https://cran.opencpu.org/web/packages/adehabitatLT/adehabitatLT.pdf

Camphuysen. (2011). Northern Gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. *British Birds, 104*(2), 60.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136.

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., & McConnell, B. (2021). AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, *440*, 109397.

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315.

DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. *F1000prime Reports*, *6*, 39.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537.

Enstipp, M. R., Grémillet, D., & Jones, D. R. (2007). Investigating the functional link between prey abundance and seabird predatory performance. *Marine Ecology Progress Series*, *331*, 267–279.

Evans, M. R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C. M., Merz, M., O'Malley, M. A., Orzack, S. H., Weisberg, M., Wilkinson, D. J., Wolkenhauer, O., & Benton, T. G. (2013). Do simple models lead to generality in ecology? *Trends in Ecology & Evolution*, *28*(10), 578–583.

Fauchald, P. (2009). Spatial interaction between seabirds and prey: review and synthesis. *Marine Ecology Progress Series*, *391*, 139–151.

Focardi, S., & Cecere, J. G. (2014). The Lévy flight foraging hypothesis in a pelagic seabird. *The Journal of Animal Ecology*, *83*(2), 353–364.

Focardi, S., Montanaro, P., & Pecchioli, E. (2009). Adaptive Lévy walks in foraging fallow deer. *PloS One*, *4*(8), e6587.

Fryxell, J. M., Hazell, M., Börger, L., Dalziel, B. D., Haydon, D. T., Morales, J. M., McIntosh, T., & Rosatte, R. C. (2008). Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(49), 19114–19119.

Furness, R. W., Garthe, S., Trinder, M., Matthiopoulos, J., Wanless, S., & Jeglinski, J. (2018). Nocturnal flight activity of northern gannets Morus bassanus and implications for modelling collision risk at offshore wind farms. *Environmental Impact Assessment Review*, *73*, 1–6.

Garthe, S., Grémillet, D., & Furness, R. W. (1999). At-sea-activity and foraging efficiency in chick-rearing northern gannets Sula bassana: a case study in Shetland. *Marine Ecology Progress Series*, *185*, 93–99.

Grecian, W. J., Lane, J., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society, Interface 15*(143), 20180084.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jørgensen, C., Mooij, W. M., Müller, B., Pe'er, G., Piou, C., Railsback, S. F., Robbins, A. M., Robbins, M. M., Rossmanith, E., Ruger, N., Strand, E., Souissi, S., Stillman, R., Vabo, R., Visser, U., & DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling*, *198*(1), 115–126.

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: a 'multi-scope' for predictive systems ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1586), 298–310.

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., Deangelis, D. L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A. S. A., Milles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohwäder, M. S., Stillman, R. A., Thiele, J. C., & Ayllón, D. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Organs: The Official Journal of the Japanese Society for Artificial Organs*, *23*(2).

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W. M., Railsback, S. F., Thulke, H.-H., Weiner, J., Wiegand, T., & DeAngelis, D. L. (2005). Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science*, *310*(5750), 987–991.

Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhouri, J. F., Katona, S. K., Kleisner, K., Lester, S. E., O'Leary, J., Ranelletti, M., Rosenberg, A. A., Scarborough, C., Selig, E. R., Best, B. D., Brumbaugh, D. R., Chapin, F. S., Crowder, L. B., Daly, K. L., Doney, S. C., Zeller, D. (2012). An index to assess the health and benefits of the global ocean. *Nature*, *488*(7413), 615–620.

Halsey, L. G. (2016). Terrestrial movement energetics: current knowledge and its application to the optimising animal. *The Journal of Experimental Biology*, *219*(Pt 10), 1424–1431.

Hamer, K. C., Humphreys, E. M., Magalhães, M. C., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Skov, H., & Wanless, S. (2009). Fine-scale foraging behaviour of a medium-ranging marine predator. *The Journal of Animal Ecology*, *78*(4), 880–889.

Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P., & Wood, A. G. (2000). Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. *Marine Ecology Progress Series*, *200*, 257–264.

Holling, C. S. (1959). Some Characteristics of Simple Types of Predation and Parasitism 1. *The Canadian Entomologist*, *91*(7), 385–398.

Holling, C. S. (1966). The strategy of building models of complex ecological systems. *Systems Analysis in Ecology*, 195–214.

Jackson, S. (1992). Do Seabird Gut Sizes and Mean Retention Times Reflect Adaptation to Diet and Foraging Method? *Physiological Zoology*, *65*(3), 674–697.

Jones, T. B., Green, J. A., Patrick, S. C., Evans, J. C., Wells, M. R., Rodríguez-Malagón, M. A., & Arnould, J. P. Y. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecology Letters*, *23*(7), 1085–1096.

Lane, J. V., Jeavons, R., Deakin, Z., Sherley, R. B., Pollock, C. J., Wanless, R. J., & Hamer, K. C. (2020). Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research*, *162*, 105196.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series*, *628*, 183–193.

Lefkovitch, L. P. (1965). The Study of Population Growth in Organisms Grouped by Stages. *Biometrics*, *21*(1), 1–18.

Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, *412*(6849), 816–819.

Liukkonen, L., Ayllón, D., Kunnasranta, M., Niemi, M., Nabe-Nielsen, J., Grimm, V., & Nyman, A.-M. (2018). Modelling movements of Saimaa ringed seals using an individual-based approach. *Ecological Modelling*, *368*, 321–335.

Magalhães, M. C., Santos, R. S., & Hamer, K. C. (2008). Dual-foraging of Cory’s shearwaters in the Azores: feeding locations, behaviour at sea and implications for food provisioning of chicks. *Marine Ecology Progress Series*, *359*, 283–293.

Major, H. L., Bond, A. L., Jones, I. L., & Eggleston, C. J. (2013). Stability of a Seabird Population in the Presence of an Introduced Predator. *Avian Conservation and Ecology*, *8*(1), 2.

Masden, E. A., Fox, A. D., Furness, R. W., Bullman, R., & Haydon, D. T. (2010). Cumulative impact assessments and bird/wind farm interactions: Developing a conceptual framework. *Environmental Impact Assessment Review*, *30*(1), 1–7.

Murray, S., Harris, M. P., & Wanless, S. (2015). The status of the Gannet in Scotland in 2013-14. *Scottish Birds*, *35*(1), 13.

Nelson, B. (2002). *The atlantic gannet*. Fenix Books.

Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., Hamer, K. C., Wakefield, E., Le Nuz, M., & Votier, S. C. (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* , *123*(1), 33–40.

Pettex, E., Bonadonna, F., Enstipp, M. R., Siorat, F., & Grémillet, D. (2010). Northern gannets anticipate the spatio–temporal occurrence of their prey. *The Journal of Experimental Biology*, *213*(14), 2365–2371.

Ponchon, A., Grémillet, D., Christensen-Dalsgaard, S., Erikstad, K. E., Barrett, R. T., Reiertsen, T. K., McCoy, K. D., Tveraa, T., & Boulinier, T. (2014). When things go wrong: intra-season dynamics of breeding failure in a seabird. *Ecosphere* , *5*(1), art4.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Railsback, S. F., & Grimm, V. (2019). *Agent-Based and Individual-Based Modeling: A Practical Introduction, Second Edition*. Princeton University Press.

Ropert-Coudert, Y., Grémillet, D., Kato, A., Ryan, P. G., Naito, Y., & Le Maho, Y. (2004). A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour*, *67*(5), 985–992.

Scales, K. L., Miller, P. I., Embling, C. B., Ingram, S. N., Pirotta, E., & Votier, S. C. (2014). Mesoscale fronts as foraging habitats: composite front mapping reveals oceanographic drivers of habitat use for a pelagic seabird. *Journal of the Royal Society, Interface / the Royal Society*, *11*(100), 20140679.

Sequeira, A. M. M., Bouchet, P. J., Yates, K. L., Mengersen, K., & Caley, M. J. (2018). Transferring biodiversity models for conservation: Opportunities and challenges. *Methods in Ecology and Evolution / British Ecological Society*, *9*(5), 1250–1264.

Sinervo, B. (1997). Optimal foraging theory: constraints and cognitive processes. In J. R. Krebs & NB Davies (Eds.) *Behavioral Ecology*. Santa Cruz, CA: University of California Press, 105–130.

Soanes, L. M., Arnould, J. P. Y., Dodd, S. G., Sumner, M. D., & Green, J. A. (2013). How many seabirds do we need to track to define home-range area? *The Journal of Applied Ecology*, *50*(3), 671–679.

Stillman, R. A., & Goss-Custard, J. D. (2010). Individual-based ecology of coastal birds. *Biological Reviews of the Cambridge Philosophical Society*, *85*(3), 413–434.

Sumner, M. D. (2016). *Trip: Tools for the Analysis of Animal Track Data* (Version 1.5.0) [R Package]. https://github.com/mdsumner/trip

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology: Official Journal of the International Society for Behavioral Ecology*, *25*(6), 1302–1310.

Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G., Raposo, E. P., & Stanley, H. E. (1999). Optimizing the success of random searches. *Nature*, *401*(6756), 911–914.

Viswanathan, G. M., da Luz, M. G. E., Raposo, E. P., & Eugene Stanley, H. (2011). *The Physics of Foraging: An Introduction to Random Searches and Biological Encounters*. Cambridge University Press.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859).

Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C., & Hamer, K. C. (2013). Space partitioning without territoriality in gannets. *Science, 341*(6141), 68–70.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity—why some gannets don't change their spots. *Ecology*, *96*(11), 3058–3074.

Wanless, S., Harris, M. P., & Morris, J. A. (1990). A Comparison of Feeding Areas Used by Individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the Breeding Season. *Colonial Waterbirds, 13*(1), 16–24.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology*, *55,* 503-515.

Weber, S. B., Richardson, A. J., Brown, J., Bolton, M., Clark, B. L., Godley, B. J., Leat, E., Oppel, S., Shearer, L., Soetaert, K. E. R., Weber, N., & Broderick, A. C. (2021). Direct evidence of a prey depletion "halo" surrounding a pelagic predator colony. *Proceedings of the National Academy of Sciences of the United States of America, 118*(28), e2101325118.

Wilensky, U. (1999). *NetLogo*. Northwestern University. (https://ccl.northwestern.edu/netlogo/)

Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., & Grimm, V. (2010). The virtual ecologist approach: simulating data and observers. *Oikos , 119*(4), 622–635.

Chapter 4: Using pattern-orientated modelling to decipher which foraging mechanisms drive the emergence of individual foraging site fidelity in gannets

Abstract

Central place foragers have been shown to anticipate the broadscale location of profitable foraging areas, which they often return to on successive trips. Known as individual foraging site fidelity (IFSF), this behaviour is thought to be learned during what are often long periods of development, so as to be familiar with a particular site and its foraging opportunities in the face of competition for ephemeral and heterogeneously distributed prey. Additional cues from conspecifics may then be used to fine-tune resource localisation during foraging trips. The way in which these two information sources are used in foraging strategies may strongly affect the emergent movement patterns, but understanding the influence of these drivers through analysis of empirical observations alone is difficult. I therefore adapted an individual-based model of northern gannets foraging in a spatially-explicit environment, to run simulation experiments where I implemented different forms of private and/or public information in resource localisation mechanisms. The outputs of each model were compared with the characteristic patterns associated with IFSF from empirical data to see which mechanisms and information sources best reproduced the observed IFSF patterns. Each hypothesis was also analysed for several population-level patterns, such as how well the simulated foraging distribution matched that observed, in order to assess system functioning on different hierarchical levels. I found support for the most complex hypothesis, suggesting that flexibility to choose between several memorised departure angles, coupled with cues from conspecifics on potential foraging opportunities, may be key drivers of IFSF patterns. However, the most representative hypothesis for IFSF patterns did not correspond with the shortest average duration or length of foraging trips, indicating that IFSF is employed as a form of bet hedging, in compliance with the hypothesis that IFSF is a density dependent phenomenon. I discuss the implications of this result alongside the future

applications of this model in understanding threats to seabird populations, such as offshore wind farms.

4.1 Introduction

Colonially breeding species often experience competition for resources (Ashmole, 1963). When coupled with spatiotemporal variability in prey availability, these animals face a complex environment in which to develop a foraging strategy (Charnov, 1976). This complexity is then heightened during the breeding season, which brings about further constraints on parents' time and other resources. The foraging strategies underlying behavioural decisions used by individuals to exploit the heterogenous distribution of resources in an environment are implicit in the animal's movements (Bell, 2012). Thus by inspecting individual foraging movements within a population context, we can begin to hypothesise the strategies being employed in generating different movement patterns observed at individual- and population-level within their shared environment.

Animals in a population often show individual specialisation, which may act to reduce intraspecific competition (Bolnick et al., 2003). Many seabird species have been show to revisit foraging areas at a broad geographical scale (Weimerskirch, 2007; Morgan et al., 2018), which is known as individual foraging site fidelity (IFSF). In northern gannets (hereafter 'gannets'), this consistency in space use by individuals has been shown to persist not only for the duration of the breeding season but across years (Wakefield et al., 2015). Grecian et al. (2018) suggested that learning and remembering suitable foraging habitat is why IFSF strengthens with increasing age and constraints that an individual gannet may be experiencing. From inspection of individual foraging trips it has been shown that gannets often take more-or-less linear journeys to and from foraging areas, which indicates that they are anticipating which direction this profitable foraging area will be in (Pettex et al., 2010). That they do this in a repeatable manner (Hamer et al., 2007; Patrick et al., 2014; Wakefield et al., 2015) gives further indication that memory processes are being employed.

Alongside memory, another source of information seabirds may take into account is cues from conspecifics. The forms this information may take are likely to be dictated by the level of competition being experienced, where social foraging may develop when the benefits outweigh the costs, resulting in a higher prey capture rate in the presence of conspecifics (Beauchamp, 2013). Davoren et al. (2003) showed that local enhancement, where an individual alters its path to travel towards a foraging conspecific (Turner, 1964), may act in tandem with memory in common guillemots (*Uria aalge*) by allowing individuals to initially recall an area to orient themselves towards at sea, then follow cues from conspecifics on the fine scale location of prey. The advent of bird-borne camera technology evidenced the importance of social influences at sea, with studies showing that Cape gannet (*Morus capensis*) movement patterns were highly influenced by reaction towards conspecifics and other predators (Tremblay et al., 2014). More recently, social network analysis conducted on tracking data simultaneously collected from 85% of breeding adults from a colony of Australasian gannets (*Morus serrator*) indicated the prevalence of local enhancement in another close relative, which is carried out in an opportunistic and foraging strategy dependent manner (Jones et al., 2020). Hence, the combined use of private and public information and the associated behaviour used to locate resources in a heterogenous environment, coupled with constraints and competition from conspecifics, may be key drivers dictating the emergence of IFSF in seabird populations.

How these different information sources influence an individual's decisions is difficult to ascertain with field observations alone, owing to the different spatiotemporal scales involved. Tracking the majority of a population in order to determine the impact of social interactions is possible only with small populations (e.g. Jones et al., 2018), in which competition is less likely to be driving foraging dynamics. In addition, repeatability studies allow inferences to be made about the effects of memory but provide only limited insight into the varied processes and decisions involved.

Bottom-up approaches such as individual-based models (IBMs) provide a suitable framework to establish a link between individual behavioural decisions and population-level consequences (Railsback & Grimm, 2019), wherein the level of complexity can be ascertained when trying to reproduce the essential dynamics of the system in question. In this context we can create environments in which stochastic foraging and interaction events take place (e.g. Boyd et al., 2016), with the possibility to program in learning and the formation of memory (e.g. Chudzinska et al., 2021). When comparing patterns that models generate with those of empirical data, in a process known as pattern-orientated modelling (POM, Grimm & Railsback, 2012), it is possible to formulate different hypotheses concerning the potential foraging decisions and mechanisms that drive population-level movement patterns.

In this chapter I further develop and use an individual-based model of gannet foraging movements (Chapter 3) to run simulation experiments to examine which behaviour and decisions may be shaping individual foraging consistency of gannets at Bass Rock. By formulating hypotheses on the use of public and/or private information in resource localisation mechanisms and implementing these hypotheses in bottom up models, I aimed to decipher which models reproduced specific patterns observed in empirical data for two specific aims; (1) to determine which mechanisms and information sources best reproduced the characteristic patterns of IFSF, and: (2) to assess whether or not the mechanisms that best reproduced IFSF also corresponded with high foraging efficiency. Below, I first summarise the baseline movement model and how it has been adapted here, followed by a section describing the observed patterns of IFSF present within the study population.

4.1.1 Previous IBM and adaptations

My previous model (Chapter 3) captured the emergence of realistic movement patterns of adult gannets at Bass Rock during the chick-rearing period. Therein, individuals switched between movement modes according to foraging decisions based broadly on two factors. The first was sensing the heterogeneously distributed prey in their environment and the second was sensing a proxy of their physiological state, based on the assumption that gannets are attempting to capture a set mass of prey on each foraging trip in order to feed themselves and their chick. However, this model omitted direct interactions between individuals and didn’t include an active memory to recall profitable locations, and therefore was lacking in elements of behavioural complexity that exist in nature and are likely to play a role in the population-level distribution of birds at sea.

By adapting this basic movement model to incorporate greater behavioural complexity, namely in the use of forms of public and private information, in this chapter I devised a series of simulation experiments where I attempted to decipher which resource localisation mechanisms underpin the emergence of IFSF. This was achieved through POM, where I compared the emergent patterns of different models representing different hypotheses of varying biological plausibility with those observed empirically.

4.1.2 Biological background to fidelity patterns

The gannet colony at Bass Rock (56°6′ N, 2°36′ W, Figure 4.1) is the largest in the world (Murray et al., 2015) and as a consequence its breeding adults exhibit relatively long trip durations compared with smaller gannet colonies elsewhere, indicating intense intraspecific competition (Lewis et al., 2001). Gannets at Bass Rock show foraging site fidelity within and across years (Wakefield et al., 2015) and individuals depart the colony in a consistent direction (e.g. see individual 1446273 in Figure 4.1), which is a pattern also known to exist at other colonies (Soanes et al., 2013; Patrick et al., 2014). From this consistency it’s possible to infer that there may be a degree of reliability in the broad scale distribution of prey over long time periods, or it may be that site familiarity, learned through earlier life, leads to a bet-hedging strategy of visiting the same area on successive trips (Grecian et al., 2018). However, gannets do not show complete fidelity to foraging sites throughout the chick-rearing period, and in Figure 4.1 individual 1484906 has markedly different departure bearings and little overlap between foraging locations during three consecutive trips. This pattern has been observed at this population consistently (Hamer et al., 2001; Wakefield et al., 2015), and could indicate that individuals decide to forage in alternative locations, which may be the result of poor success in that particular area on a previous trip.

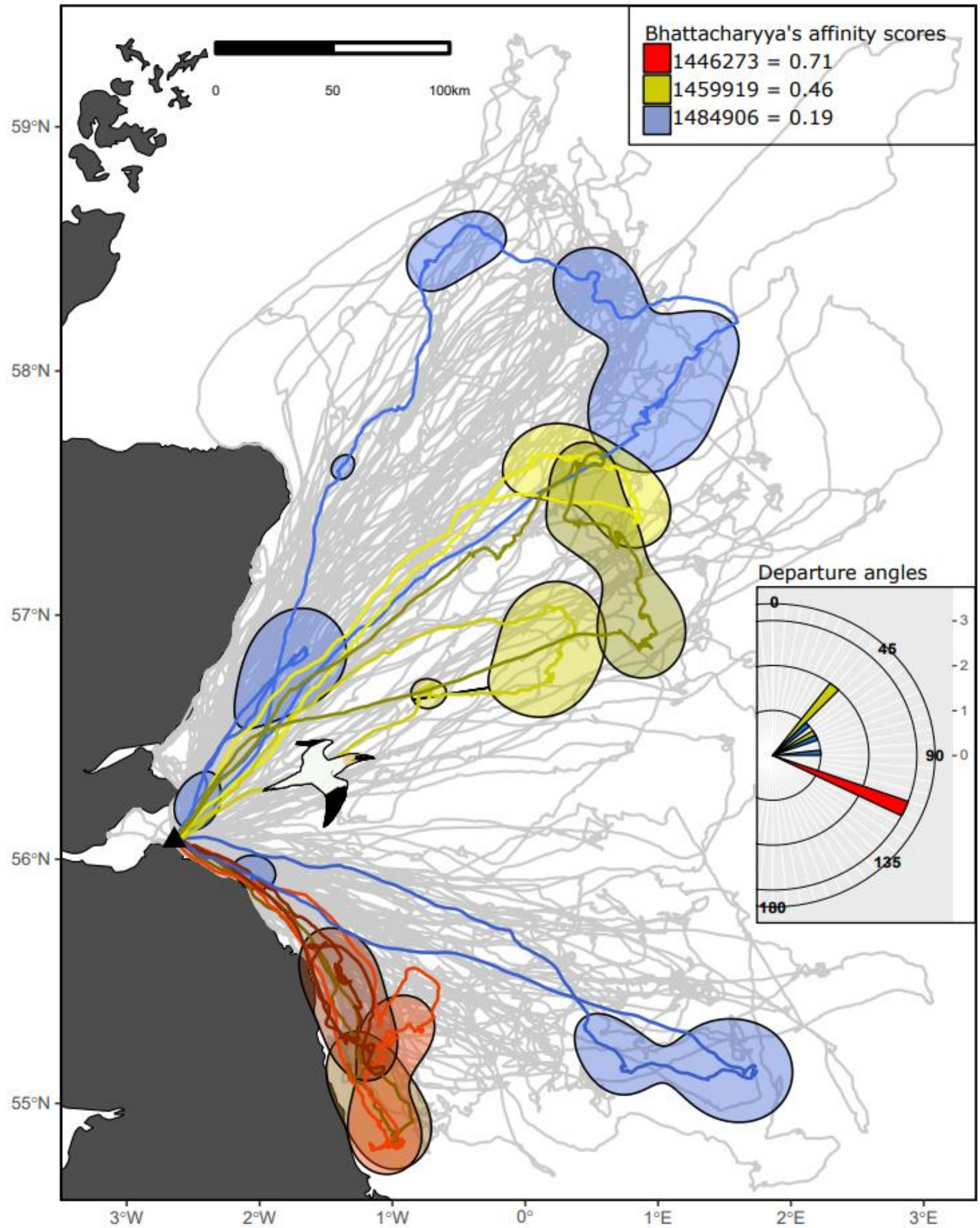


Figure 4.1. Map of empirical gannet tracking data in the North Sea to display the patterns associated with individual foraging site fidelity (IFSF) from the colony at Bass Rock (black triangle). All data are from the chick-rearing period in 2015. Grey lines show 114 trips from 29 individuals. Blue, yellow, and red lines show three foraging trips from three different individuals, with kernels of the same colour displaying the 50% utilisation distributions (UDs) based on foraging locations only. Bhattacharyya's affinity (BA) scores provide quantification of the mean overlap of foraging distributions within each individual by taking a mean of the three pairwise combinations (Note: the UDs are pictured are not those used to quantify BA but instead are included as visual representation). The histogram inset on the right shows the departure bearings (10km from the colony). Pictured gannet in flight is not to scale.

Further to the use of private information, there is also a wealth of public information available to gannets especially at large colonies (Tremblay et al., 2014) which may provide cues on where, and perhaps where not to find prey. The use of public information at the colony to indicate the direction of successful foraging from returning conspecifics, termed the “information-centre” hypothesis (Ward & Zahavi, 1973) has been shown to influence movement patterns and foraging locations in a small population of close relatives (*Morus serrator*), where birds frequently associated with conspecifics while departing from the colony, resulting in co-departing birds having similar initial foraging patches (Jones et al., 2018). However in northern gannets birds often join rafts offshore before departing on foraging trips, probably for purposes such as preening feathers after being at the colony, with no indication that joining such rafts influences foraging trip distance or duration (Carter et al., 2016). Moreover, it is unlikely that individuals would show consistency in departure direction if they were subject to cues from the colony, and gannets have been observed to disperse from Bass Rock individually (Camphuysen, 2011). Therefore it is likely that most social interaction is done after departing the colony.

In Figure 4.1, individual 1459919 (yellow tracks) represents the average level of fidelity observed in the empirical data. There is some overlap in foraging locations, but there are new locations in each trip and there is slight variation in departure angle from the colony. I hypothesise that this is the typical pattern because gannets recall broad scale areas to forage in and depart from the colony at a roughly consistent angle, and will typically travel in a linear fashion towards this area but can deviate from this bearing if they obtain cues from conspecifics to where suitable foraging patches are located, and switch course towards such potential foraging opportunities (Thiebault et al., 2014).

4.2 Material and methods

Below I summarise the baseline model, the conditions imposed on it and the different resource localisation hypotheses, with an explanation of how they were modelled. I then detail how I evaluated the model results against empirical data. Further details such as parameters and state variables are given in Chapter 3 which followed the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2010, 2020).

4.2.1 Model summary

The model includes the following entities: *aGannets*, which is the term I use for simulated gannet individuals, the colony which *aGannets* depart from and return to on foraging trips, and landscape cells. *aGannets* are characterised by their foraging success, which movement mode they are exhibiting (outbound travel, ARS, rest, inbound travel), and their initial departure bearing from the colony. The landscape represents an area of 381,888 km^2 encompassing the part of the North Sea typically comprising the home range of gannets from Bass Rock during the breeding season, and is composed of two different cell types; sea cells and land cells. Sea cells have varying prey density, derived from GPS data for 504 foraging trips by 118 chick-rearing gannets over a period of four years, assuming that the density of foraging gannets at sea is correlated over long time-scales with that of their prey. Land cells are actively avoided by *aGannets* on trips. *aGannets* exhibit a type II functional response (Holling, 1959) wherein the likelihood of entering area-restricted search (ARS) movement and consequently catching fish increases linearly with prey density, up to an asymptote where it remains constant after a defined density is exceeded.

I included 1,000 *aGannet* individuals in the model. Modelling the actual population size for Bass Rock (~150,000 adults, Murray et al., 2015) was unattainable due to time constraints and lack of computational power. Even with the use of high performance computer clusters it is unlikely that I could have modelled over 10,000 gannets given the complexity of the model (Railsback et al., 2017). To abate any resulting misinterpretation occurring from processes in which population size is likely to have a strong influence, such as interaction with conspecifics at sea, I heuristically parameterised the model so that the hypothesis in question was exhibiting a detectable effect on the population (Figure A.4.1).

In those simulations that used private information, *aGannets* stored certain trip metrics in a list, which thus performed as a memory, and embarked on departure angles which previously led to foraging trips with shorter durations, as a proxy for foraging trip efficiency. These simulations required a so-called "burn-in" period in which exploratory trips took place so that any particular *aGannet* could decide on a particular departure angle/angles before the simulation from which outputs were taken began. In these burn-in periods, individuals were subject to all other conditions which were implemented in the model, such as competition or local enhancement. In simulations which used public information *aGannets* could sense conspecifics in their local area when at sea and reacted according to what hypothesis or hypotheses were being explored. More detail on the justification of hypotheses concerning the use of private and public information and how they were modelled is given in section 4.2.2 below.

At the beginning of the simulation all *aGannets* began at the colony and each departed at random over the ensuing 24 hours. Since their partner was not modelled explicitly, upon returning to the colony after the first trip and all subsequent trips, the duration to spend at the colony was drawn from a normal distribution which is characterised from a set of 100 previous trips undertaken during that simulation. Other processes remain largely the same as in the previous movement model, wherein at each timestep gannets check their behaviour and update their behavioural counters. Then, according to their location, current physiology and density of prey, they enact a behaviour or switch to a different movement mode. Each *aGannet's* objective is to obtain the required threshold of prey as efficiently as possible and return to the colony to feed their chick once this is obtained.

The main output of the model was that at each timestep a subset of individuals (n=30) had their behaviour, trip number, and coordinates recorded in a .csv file. This enabled analysis to compare with empirical data and derived patterns from the same landscape. The model stopped when all individuals had completed 20 trips each, excluding exploratory trips during the "burn-in" period for relevant simulations. All simulations stabilised after approximately two or three modelled days and outputs remained similar thereafter. Prey were reset at the beginning of every modelled day, allowing for increasing competition as the day progressed but not across larger timescales, because the main form of competition in gannets appears to be interference rather than prey depletion (Lewis et al. 2001) and there were no other environmental influences that would have affected *aGannet* behaviour.

4.2.2 Hypotheses and justification

Here I describe the different foraging strategies that were modelled, including different combinations of null (no information use), private and public information. As it is likely that gannets use both information types (Davoren et al., 2003) I have combined these different mechanisms (Table 4.1), resulting in 16 different hypotheses; one null model where no private or public information is used, three models using only public information, three using only private information, and nine consequential combinations of private and public information acting concurrently.

Table 4.1. Hypotheses for simulation experiments obtained through different combinations of resource localisation mechanisms using public and private information.

	Public information				
		No social interaction (1); No influence from conspecifics	**Local enhancement (2);** Attraction to local individuals engaged in ARS movement	**Competition (3);** Do not begin foraging in an occupied area	**Enhancement and competition (4);** Exploit enhancement opportunities only when not in an occupied area
Private information	**No memory (A);** Random departure angle from colony for each trip	**Null model** **A1**	**Public** **A2**	**Public** **A3**	**Public** **A4**
	Long-term memory (B); Departure angle determined prior to chick-rearing period, no switching	**Private** **B1**	**Combination** **B2**	**Combination** **B3**	**Combination** **B4**
	Short-term memory/WSLS (C); Consistent, with random departure angle if three previous trips are increasing in duration	**Private** **C1**	**Combination** **C2**	**Combination** **C3**	**Combination** **C4**
	Combination (D); Previously determined departure angles (x3) which can be switched between	**Private** **D1**	**Combination** **D2**	**Combination** **D3**	**Combination** **D4**

The following sections contain the biological background, core assumptions, and logical flow of the different modelled mechanisms. I aimed to represent each in a succinct and tractable way, to give the best chance at deciphering behavioural mechanisms that may underpin individual foraging consistency.

4.2.2.1 Private information

Mechanisms drawing on private information only influenced the departure direction of *aGannets* from the colony. Consequently, individuals had no obligation to reach a particular patch, and thus could engage in foraging opportunities whenever they arose on their outbound path ("trap line" strategy, Wanless et al., 1990).

4.2.2.1.1 Long-term memory

This mechanism was built on the assumption that gannets begin the chick-rearing period having conducted some exploration throughout the home range of the colony and have each settled on one departure bearing which if followed will probably lead to a profitable foraging location. It could be that this was learned earlier in life, in keeping with the "exploration-refinement" hypothesis where IFSF increases with age (Votier et al., 2017; Grecian et al., 2018), or during the immediately prior incubation period where adults experience less constraint and are known to forage further afield (Lane et al., 2020). The model did not differentiate between these two possibilities but simply included a long-term memory as described below.

To simulate this formation of memory, *aGannets* embarked on ten foraging trips, each in a random direction broadly eastwards from the colony (5° to 140°, taken from empirical observations and avoiding travelling overland). Each *aGannet* recorded a daylight trip duration (i.e. total trip duration – any time spent resting on the water during overnight trips) in a list and its accompanying departure bearing. Once ten trips were completed the departure bearing with the lowest daylight trip duration was chosen and used for the subsequent simulation. Daylight trip duration was chosen over the time spent foraging per trip, as the constraints on parents to feed their chicks require them to return to the nest as quickly as possible (Hamer et al., 2007). Therefore, the selection on foraging areas is not driven purely by profitability of a patch, but also by its distance from the colony.

4.2.2.1.2 Short-term memory

Studies have shown that there is a minority of gannets that are inconsistent in departure direction and foraging area in consecutive trips (Hamer et al., 2001; Wakefield et al., 2015). These birds may have been switching to different foraging areas following a previously profitable area no longer proving so, known as “win-stay/lose-shift” (WSLS) foraging (Kamil, 1983). This switch could have stemmed from increased competition or lower prey availability, and most individuals in a population may adhere to similar mechanisms, implying that individuals are continually assessing the efficiency of foraging trips throughout the chick-rearing period. To implement this in the model, individuals kept a list of the daylight durations of the three most recent trips. At the beginning of a new foraging trip, if the three previous trips had all been increasing in duration then the *aGannet* picked a new departure angle at random within the empirically determined confines (5 -140°). If the duration of this trip in a new direction proved to be longer than the previous two trips then it drew another random departure angle (a so-called “sliding-window” mechanism); thus if exploring a new foraging area was not proving profitable it moved on.

4.2.2.1.3 Combined memory

This mechanism assumes that individuals retain a long-term memory of multiple previously profitable departure directions, which can be switched between if a particular site is no longer proving profitable. As in the long-term memory mechanism described above *aGannets* each went through ten foraging trips prior to the simulation beginning. The three departure directions corresponding with the lowest daylight trip durations were stored in the individual’s memory. During the simulation the continued use of a particular direction was subject to the mechanism used in short-term memory detailed above (4.2.2.1.2). As such, if the last three trips had been increasing in daylight trip duration, then the *aGannet* selected another departure direction stored in the long-term memory. Each *aGannet* begins the simulation on the departure direction corresponding with the lowest daylight trip duration and when switching would go in ascending order and cycle back to the earliest departure direction and continue as such.

4.2.2.2 Public information

For the following mechanisms I only considered the use of public information when at sea on a foraging trip (i.e. > 10 km from the colony) with justification provided in Section 4.1.2 above.

4.2.2.2.1 Local enhancement

Observed congregations of feeding gannets are consistent with local enhancement behaviour (Camphuysen, 2011), and bird borne cameras have recorded its prevalence in a closely related species (Tremblay et al., 2014). I modelled this mechanism so that *aGannets* in outbound movement mode could sense other *aGannets* exhibiting ARS movement, in a 270 degree field of vision up to 10 km away (Thiebault et al., 2014). I assumed that with increasing distance of conspecifics the likelihood of any *aGannet* pursuing this opportunity will decrease. I implemented this by having a 10% chance of pursuing a local enhancement opportunity if between 5-10 km away, and this increased to 20% if below 5 km at each timestep if an *aGannet* had any foraging conspecifics in its detectable range.

If the decision was made to pursue a local enhancement opportunity, the *aGannet* could sense the direction and distance of the conspecific and compute roughly how far it needed to travel to get to that patch. Therefore, it did not begin actively following that individual but headed towards the location where it was seen engaging in ARS behaviour. Once it reached the intended area it then resumed standard outbound behaviour and orientation. The functional response approximation was not altered, and hence the only way in which local enhancement could have increased the chance of an *aGannet* beginning ARS was if it had found a patch of higher prey density than those of the path it was previously on.

4.2.2.2.2 Competition

Regardless of whether increased trip duration at larger gannet colonies (Lewis et al., 2001; Wakefield et al., 2013) is driven by depletion of prey around the colony (Ashmole et al., 1971) and/or density-dependent disturbance of prey, it’s evident that some form of competition drives foraging gannets further afield when there are large numbers of conspecifics. Further to this, gannets have been observed to forage in relatively low densities (Camphuysen, 2011), which would indicate that they actively avoid high concentrations of conspecifics. I tested this in my model by programming *aGannets* to react to conspecifics in a contrasting fashion to local enhancement (4.2.2.2.1). When *aGannets* were in outbound travel they could sense the total number of conspecifics in a 270° field of vision up to 5km away. If there were more than two other *aGannets* in their vicinity, birds would not begin ARS movement even if situated on a relatively dense patch of prey. This effectively drove *aGannets* to travel further from the colony to try and find a less busy patch.

4.2.2.2.3 Combination of local enhancement and competition

This mechanism was developed under the assumption that local enhancement and competition may act in concurrence. In this hypothesis, *aGannets* were only able to use local enhancement through sensing foraging conspecifics if they were not experiencing competition as defined above (4.2.2.2.2). Thus, individuals had to find a relatively sparsely populated area before the possibility of beginning ARS movement or pursuing local enhancement opportunities.

4.2.3 Calibration of unknown parameters

I attempted to quantify parameters from the literature where I could for the different resource localisation mechanisms (see Table A.4.1). However, given that such behavioural parameters are hard to determine through empirical studies I first sought expert opinion and discussion on the potential nature of the modelled mechanisms. For mechanisms using public information (local enhancement and competition) I ran simulations while observing the NetLogo interface (Figure A.4.1) and observed outputs while varying parameters (e.g. number of birds to avoid during competition) with the goal of it having a perceivable influence on foraging dynamics without being overbearing.

4.2.4 Evaluation and analysis

To evaluate how well the models predicted the key features associated with IFSF in the real population, I compared patterns extracted from the model outputs with those observed in empirical data (Table 4.2), the latter comprising GPS tracking data of three consecutive trips from 30 individuals (2012 n individuals = 15, 2015 n individuals = 15, total trips = 90) tagged during the chick-rearing period at Bass Rock in July and August 2012 and 2015. See (Wakefield et al., 2015) and (Lane et al., 2019) for further details. Data from the models were "collected" in a similar fashion, i.e. as coordinates observed in two minute timesteps, following the "virtual ecologist" approach (Zurell et al., 2010).

For both model outputs and empirical data, standard trip metrics were extracted (Table A.4.2) including duration (h), length (km), furthest distance from the colony (km) and a linearity measure. To evaluate how well each model reproduced IFSF three patterns were quantified as follows:

(i) *Repeatability of departure angle* – I report the repeatability (R) of the departure angle of three consecutive trips of 30 individuals, computed using circular ANOVAs, for which R values were obtained following (Lessells & Boag, 1987) with associated standard errors from (Becker 1975). Higher values indicate that within-individual variance is lower than between-group variance.

(ii) *Repeatability of trip duration* – The repeatability value for trip duration and its standard error was reported along with a p-value testing the null hypothesis that within-individual variation is equal to between-group variation. This was achieved using the R package 'rptR' and a GLMM structure (Stoffel et al., 2017).

(iii) *Bhattacharyya's affinity (BA)* – This measure of individual consistency in the use of foraging areas was calculated following Wakefield et al. (2015). Kernel densities were estimated on each foraging trip, including only those locations where individuals were exhibiting foraging behaviour, using the package 'adehabitatHR' (Calenge & Calenge, 2018). Then the overlap of the resulting utilisation distributions (UDs) was calculated using Bhattacharyya's affinity (Fieberg & Kochanny, 2005) of all pairwise combinations of the first three trips recorded for each individual in the population in question. A score of zero indicates that there is no overlap between UDs of a certain individual's trips, whereas 1 indicates perfect overlap, indicating that the same foraging areas have been used on consecutive trips. To test if the IFSF of each population (model outputs or empirical data) was greater than expected by chance I created a null distribution of BA scores using a randomisation procedure, where if the null hypothesis was rejected using of a Wilcoxon ranked sum test, then I could infer that the observed IFSF differed significantly from a random assignment of bird ID to trips.

The dataset was also evaluated for four additional patterns with the desired goal of assessing which simulation was the most efficient for individuals, which best exploited the available area of the prey distribution and which best represented population-level patterns seen in the empirical data.

(iv) *Utilisation distribution (UD) overlap with observed distribution* – To assess how informed the population in question was about the putative distribution of available prey in the model I compared the 95% and 50% UDs from the population in question to the equivalent UDs of the GPS data (foraging locations only) used to create the prey landscape. To quantify the space use sharing between the two UDs being compared I used the utilisation distribution overlap index (UDOI) (Fieberg & Kochanny, 2005) within the 'adehabitatHR' package (Calenge & Calenge, 2018). Values are typically between 0 and 1, but can exceed 1 if the two UDs being compared are nonuniformly distributed and have a high degree of overlap.

(v) *Average daylight trip duration (h)* – This metric was selected with the perspective that the lower the daylight trip duration the more efficient that particular trip was in finding enough resources to elicit returning to the colony to feed the chick.

(vi) *Average furthest distance from the colony (km)* – This is another measure of space use, where if gannets were foraging further afield it possibly indicates higher competition, or individuals which are less informed about their environment.

(vii) *Distribution of population departure bearings* – I compared the population-level distribution of departure bearings for each simulation with that of the empirical data using two-sample Kolmogorov-Smirnov tests with the null hypothesis being no difference between the simulated and empirical distribution.

Table 4.2. Patterns used in calibration and evaluation of the model and its outputs using the pattern-orientated modelling (POM) process.

Phase of modelling cycle	**Pattern**	**Category**	**Hierarchical level**
Development/calibration	Visual comparison of tracks	Movement	Individual and population
	Activity budget of foraging trips	Behaviour	Individual and population
Evaluation - IFSF	Repeatability of departure angle (i)	Movement	Individual
	Repeatability of trip duration (ii)	Movement	Individual
	Individual consistency in use of foraging areas using Bhattacharyya's affinity (BA) score (iii)	Spatial	Individual
Evaluation – foraging efficiency and population patterns	Similarity of the simulation's foraging utilisation distribution to the empirical distribution used to inform prey landscape using UDOI (iv)	Spatial	Population
	Average daylight trip duration (v)	Behaviour	Population
	Average furthest distance from the colony (vi)	Movement	Population
	Distribution of departure angles (vii)	Spatial	Population

4.3 Results

4.3.1 Pattern i: Repeatability of departure angles

This pattern was reproduced to varying degrees by all simulations which used private information (Table 4.3), but not by the null model (A1) or those using only public information (A2-A4). All simulations using long-term memory (B1-B4) showed very high repeatability (R>0.95), which is to be expected from the programmed consistent use of one chosen departure angle, but notable in that it was consistently higher than the empirical value (R = 0.755 ± 0.07). Simulations in which there was some plasticity of departure angle (C1-C4, D1-D4) showed repeatability values more similar to the empirical value, with D4 being the closest (0.777), wherein individuals could switch between three chosen departure angles.

Table 4.3. Results of the different patterns used for evaluation of model outputs against empirical data, as detailed in methods section 4.2.4. For the conditions of the hypotheses refer to Table 1. Different colours represent different sources of information use: Grey = null/no information use; yellow = public information only; blue = private information only; green = combination of public and private information use. The simulation value(s) closest to the empirical value for each respective pattern is highlighted with bold type. Significance level of relevant test for repeatability of trip duration and BA against a null distribution: ° p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001.

Hypothesis	**Evaluation pattern**						
	IFSF			Foraging efficiency			
	Repeatability of departure angle	Repeatability of trip duration	Mean BA of successive trips by each individual	Index of % overlap with empirical UD		Daylight trip duration mean & sd (hours)	Maximum distance mean & sd (km)
				95% UD	50% UD		
Empirical	*0.755 ± 0.07*	*0 ± 0.06*	*0.44 (0.08, 0.84) ****	*1.06*	*0.13*	*16.5 ± 7.5*	*215 ± 94*
A1	0.008 ± 0.11	0.14 ± 0.11	0.19 (0, 0.53)	0.79	0.08	13.4 ± 5.9	173 ± 104
A2	-0.03 ± 0.10	0 ± 0.06	0.18 (0, 0.46)	0.81	0.06	13.9 ± 5.4	178 ± 98
A3	-0.22 ± 0.07	0.05 ± 0.08	0.14 (0, 0.46)	0.91	0.07	14.9 ± 6.3	**210 ± 113**
A4	-0.02 ± 0.07	0 ± 0.07	0.15 (0, 0.44)	1.00	0.10	14.6 ± 5.5	202 ± 101
B1	0.96 ± 0.01	0 ± 0.06	0.36 (0, 0.69) ***	0.90	0.10	12.9 ± 5.7	169 ± 98
B2	0.97 ± 0.01	0.08 ± 0.09	0.367 (0, 0.72) ***	0.91	0.09	12.0 ± 4.9	146 ± 84
B3	0.98 ± 0.01	0 ± 0.07	0.31 (0, 0.67) ***	0.93	0.11	14.1 ± 5.9	198 ± 106
B4	0.96 ± 0.01	0 ± 0.05	0.28 (0.03, 0.64) ***	**1.02**	**0.12**	14.9 ± 6.2	206 ± 112
C1	0.81 ± 0.05	0.08 ± 0.09	0.365 (0, 0.68) ***	0.87	0.09	13.2 ± 5.4	172 ± 105
C2	0.85 ± 0.04	0 ± 0.07	0.30 (0, 0.64) ***	0.92	0.09	13.1 ± 5.2	164 ± 94
C3	0.79 ± 0.06	0 ± 0.06	0.26 (0, 0.66) ***	0.83	0.09	**15.2 ± 6.6**	**220 ± 117**
C4	0.96 ± 0.01	0.18 ± 0.11°	**0.371 (0, 0.79) *****	0.94	0.10	14.2 ± 6.2	193 ± 109
D1	0.93 ± 0.02	0.2 ± 0.12°	0.33 (0, 0.76) ***	0.88	0.09	11.4 ± 5.0	147 ± 84
D2	0.87 ± 0.04	0.07 ± 0.09	0.33 (0.07, 0.61) ***	0.92	0.09	12.0 ± 4.9	145 ± 76
D3	0.699 ± 0.077	0 ± 0.07	0.33 (0.08, 0.8) ***	0.94	0.08	14.6 ± 5.1	204 ± 97
D4	**0.777 ± 0.06**	0 ± 0.06	0.35 (0, 0.83) ***	**1.02**	0.11	15.1 ± 6.0	207 ± 104

4.3.2 Pattern ii: Repeatability of trip duration

No simulations displayed significant repeatability of trip duration, which is in keeping with empirical observations.

4.3.3 Pattern iii: Individual consistency in use of foraging areas

Most simulations (B1-B4, C1-C4, D1-D4) reproduced this pattern to a varying degree, with a significantly higher level of individual consistency (BA values) than expected from a null distribution in each case (Table 4.3). However, mean BA scores for all simulations (Table 4.3) were lower than that for empirical observations. The score for the simulation in which the short-term memory, local enhancement and competition hypotheses were implemented (C4, BA = 0.37) was closest to the empirical value (BA = 0.44). All simulations that combined short-term and long-term memory with public information (D1-D4) gave relatively high mean BA values (> 0.33). The lowest score was produced by simulation A3 in which no memory was used and the only public information simulated competition, indicating that such conditions may be unrealistic.

4.3.4 Pattern iv: Similarity of simulated and empirical UDs

Predictably, the 95% UD of the null model (A1: 95% UDOI = 0.79, Figure 4.4) was the least similar to that observed empirically, implying that using no private or public information does not lead to population which is well informed of where to locate available prey. The simulation in which the only source of information was local enhancement (A2) was similar to the null model in this respect (Table 4.3).

Within the three respective memory hypotheses (B, C, D), the 95% and 50% UDOI scores increased alongside the use of public information (Table 4.3). The simulations that included local enhancement and competition together were consistently higher in this respect than those with no information use or with either local enhancement or competition acting alone. The two highest 95% UDOI scores, and consequently the closest overlap with empirical data, were for simulations B4 and D4, where B4 had the highest 50% UDOI score. For a visual comparison of the UDs of these two simulations compared with the null model (A1), please refer to the right-hand panel in Figure 4.4.

4.3.5 Patterns v and vi: Average daylight trip duration and furthest distance from the colony

The simulation that most closely matched the mean daylight trip duration and mean furthest distance from the colony in the empirical data was C3 (Table 4.3), in which short-term memory and competition were modelled in tandem. Individuals in this simulation were among those that travelled the furthest within the modelled landscape (Figure A.4.5). However, the simulation in which only short-term and long-term memory was used with no public information (D1) resulted in the shortest daylight trip duration (11.4 ± 5.0 h, Figure 4.2) and among the shortest mean distance travelled from the colony (Table 4.3, Figure A.4.2). The longest daylight trip durations, and consequently the most consistent with empirical data, were from simulations which had competition acting upon the *aGannets* at sea (A-D 3 & 4; Figure 4.2).

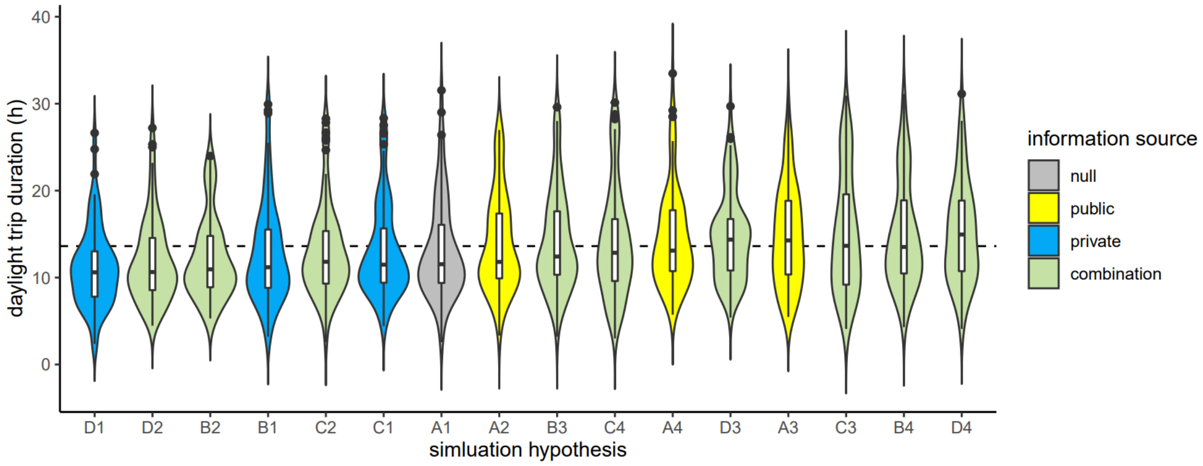


Figure 4.2. Daylight trip duration of different simulations in ascending order of median with the dotted line in the background representing the mean of all simulated daylight trip durations (13.6 hours). Different colours of violin plots represent the different information sources used. Mean observed daylight trip duration was 16.5 hrs (Table 4.3).

4.3.6 Pattern vii: Distribution of departure angles

Most simulations had a distribution of departure angles that was not significantly different from the empirical distribution (Figure 4.3), which itself showed a slight bimodal distribution with peaks indicating more frequent departures in a northeast and southeast direction than elsewhere. Outputs of simulations B2, D1 and D2 were significantly different from the empirical distribution (Figure 4.3), with each displaying exaggerated bimodality of departure angles. The simulation arguably the most representative of other IFSF patterns, D4 (Table 4.3), showed a distribution with slight bimodality in the same fashion as the empirical data, from which it was not significantly different.

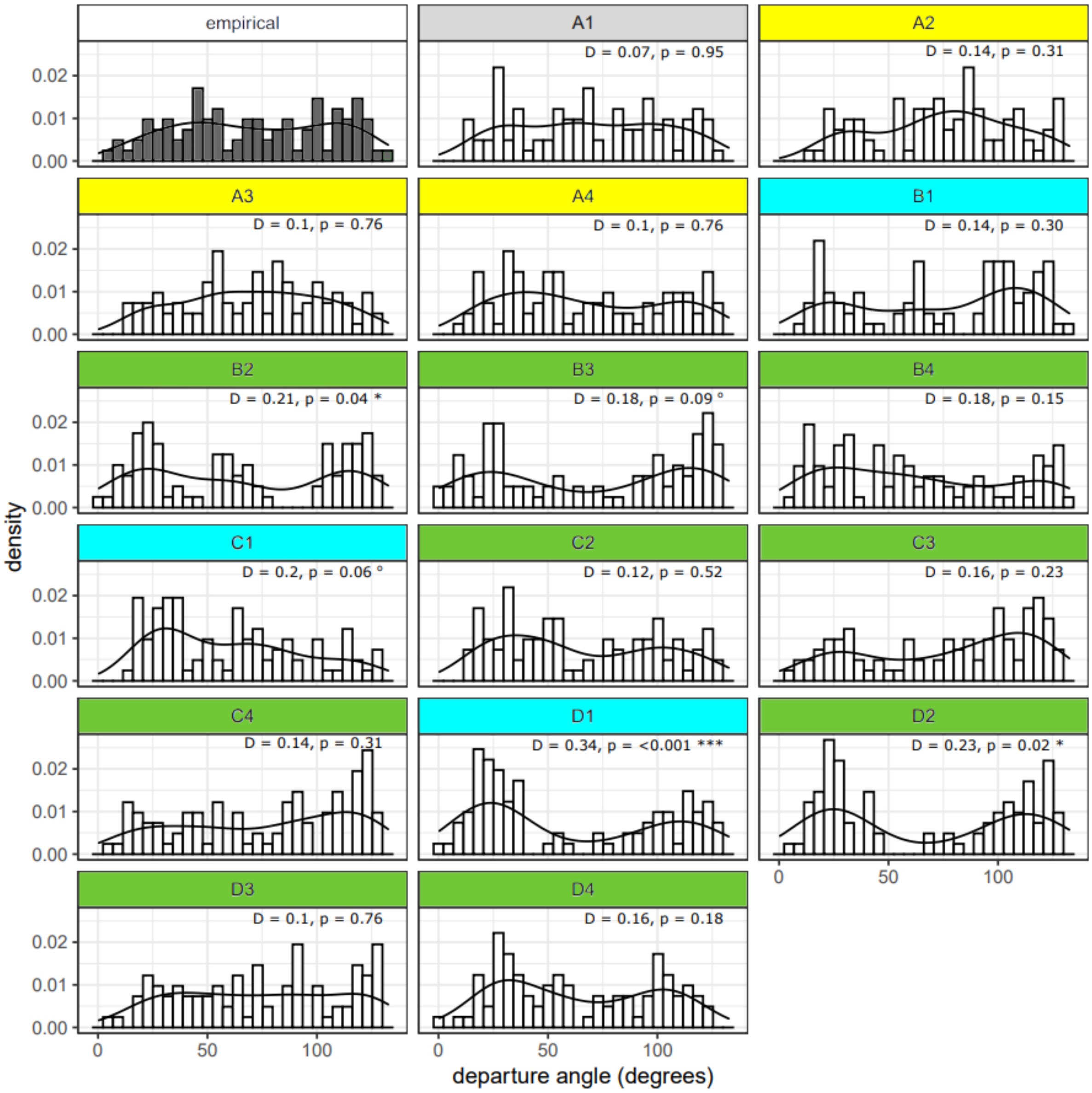


Figure 4.3. Histograms displaying the distribution of departure angles for empirical data (top left) and the different simulations, with colour representing the different sources of information used in different hypotheses; grey = no information, yellow = public information, blue = private information, green = combination of public and private information. Test statistics in the top right of each panel are from two-sample Kolmogorov-Smirnov tests with the null hypothesis being no difference between the respective simulated distribution and the distribution from empirical data.

4.3.7 Visual comparison of simulated trips with empirical tracking data

The outputs of three simulations (A1, B4, D4) in Figure 4.4 were chosen for the variation in ability to display certain patterns. A1 did not represent any patterns well. B4 showed high repeatability in departure angle, which incorporated the long-term memory hypotheses, but resulted in unrealistic movement patterns when compared with empirical visualisations (Figure 4.1). In comparison, simulation D4 which allowed flexibility in choosing from several departure angles showed trips that aligned closely with empirical visualisations, with one highlighted individual showing high repeatability and overlap in foraging areas, whereas others switched bearings on successive trips. Trips under the null model (A1) show some superficial similarities to those of D4 (Figure 4.4.) but lack repeatability of departure angles and have no overlap in foraging locations of successive trips.

The UD from the null model (A1) had the least overlap with empirical data (Figure 4.4). B4 and D4 had higher overlap (Table 4.3), and it is clear from Figure 4.4 that both overlapped well with 95% and 50% UDs of the empirical data, although the 95% UD for D4 seems to be more contained within the boundaries of the empirical UD. The separate patch of the empirical 50% UD roughly 260km north east of the colony (Figure 4.4) was not covered by any of the simulated hypotheses, implying that modelled individuals were not making effective use of a dense patch of available prey.

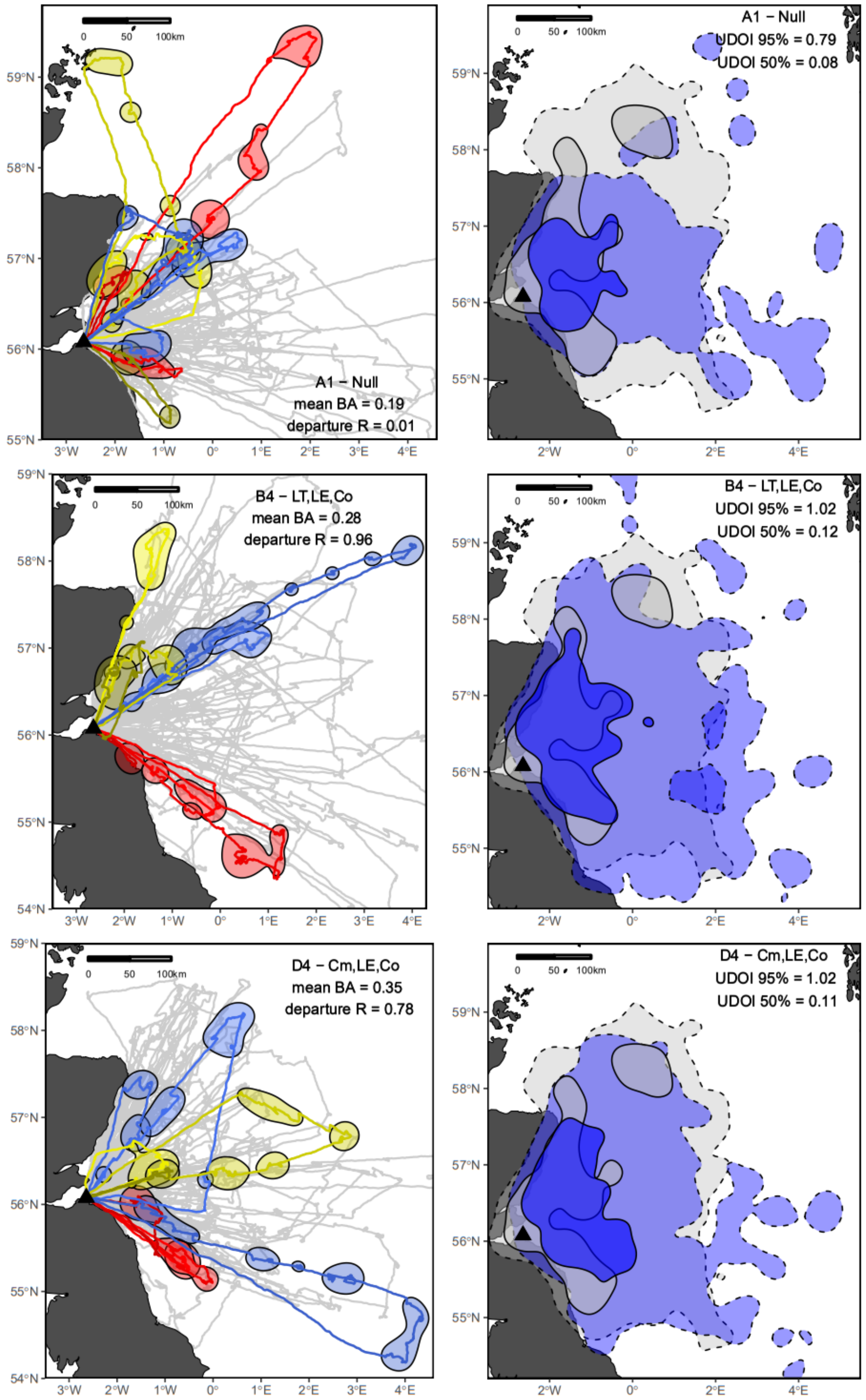


Figure 4.4. Maps of simulated gannet tracking data (left) and utilisation distributions (UDs) of foraging locations from respective simulations (right). Each row represents a different simulation: Top – A1, middle – B4, bottom – D4. Short hand for different hypotheses implemented in those simulations: Null = no information available; LT = long-term memory; LE = local enhancement; Co = competition from conspecifics; Cm = combined memory. In tracking data plots (left), grey paths show all 90 trips from 30 individuals, where blue, yellow, and red paths show three foraging trips from three different individuals, with kernels of the same colour displaying the 50% utilisation distributions (UDs) of each trip based on foraging locations only. Blue contours on the UD plots (right) are based on locations where aGannets were in ARS movement displaying 95% (lighter

blue and dashed border) and 50% (darker blue and solid border) UDs overlaid on grey contours showing the same respective dimensions which represent the distribution of prey in the model landscape.

4.4 Discussion

In this chapter I ran simulation experiments to decipher which resource localisation mechanisms may be driving emergent IFSF patterns through adapting an IBM which reproduces the foraging trips of gannets during the chick-rearing period at Bass Rock. Through individuals' decisions to use different sources of public and private information, represented by different simulated hypotheses, the majority of patterns observed in empirical tracking data were reproduced closely. With the use of 16 different hypotheses it was possible to falsify candidate resource localisation mechanisms and provide context for those that were useful in reproducing the observed patterns. The resource localisation mechanisms that did reproduce IFSF patterns indicate the importance of private and public information for both individual- and population-level processes. Models with memory and social information, both as an indicator of competition and cues for resource localisation, performed better at capturing empirical patterns. These findings support the suggestion that memory serves in locating broad-scale foraging areas, where social information is then used to fine-tune resource localisation (Davoren et al., 2003).

The simulation that best reproduced IFSF patterns was apparently the least efficient owing to its relatively long average trip durations and furthest distances from the colony. Foraging strategies developed in the face of environmental variation may lead to the evolution of behaviours that benefit long-lived species over long time scales (Lewontin, 1979). Site familiarity is likely to be developed in response to a dependable prey patch, even if energy gains are not consistent every year (Bradshaw et al., 2004). This strategy is possibly being reproduced by certain mechanisms in this model, where individuals are driven to sites that are not necessarily the closest to the colony or with the highest density of available prey, but do provide consistent foraging opportunities (Piper, 2011).

Individuals may use short-term memory as part of a win-stay/lose-shift (WSLS) foraging strategy, although (Wakefield et al., 2015) found that IFSF in gannets was persistent over both short and longer (interannual) time scales, which did not support WSLS as under this strategy IFSF would have been expected to decay over time. In this study, the simulation that best reproduced empirical data was having a memory of several departure angles that could be switched between. This finding suggests that individuals may show fidelity to several sites, with the option to switch between them. However, this conclusion is based on a small numbers of trips with relatively few individuals and to provide more reliable inference here I would suggest longer term tracking to capture 10 or more successive trips from several individuals and compliment this with empirical investigation to ascertain the potential cause/causes of this perceived "switching" behaviour.

This model represents the previously postulated strategy of being faithful to a directional arc, which often results in foraging in similar areas but also allows for further exploration if required (Hamer et al., 2001; Wakefield et al., 2015). From quantification of overlapping foraging areas, all simulations fell short of reproducing the amount of foraging area overlap which is observed in the real system, even those which were highly repeatable in use of departure angles. Hence, this might indicate a hybrid approach where a directional arc is pursued in combination with memory recall of particularly productive sites. Of course, it could be the case that the modelled landscape might not have represented the spatial and temporal dynamics of prey availability suitably to allow for such dynamics to emerge from the model.

The simulations most useful for reproducing IFSF patterns were also those which showed most similarity to the putative distribution of prey in the model from our comparison of UDs. This illustrates the usefulness of IBMs in this approach, through showing the potential variation in population-level patterns as a consequence of individuals' decisions, and highlights how in this instance both private and public information may be contributing to this population's spatial distribution. The simulation which had no memory effects but both local enhancement and competition had a high overlap with the prey distribution leading to the conclusion that when competition and local enhancement acting concurrently are key drivers in the emergence of a realistic spatial distribution. Furthermore, the simulations which best matched IFSF patterns had longer trip durations which consequently aligned much closer with empirical patterns (Table A.4.2), which was an improvement on the outputs of the model in Chapter 3.

A study which used bird borne cameras to investigate local enhancement suggested that it constitutes a crucial aspect of seabirds’ foraging behaviour, and gave caution to interpretation of seabirds as negatively impacting each other through competition (Thiebault et al., 2014). There are several factors which may contribute to the trade-off between the benefits of local enhancement and costs of competition from conspecifics, including prey availability and persistence coupled with its reaction to predation events, and the numbers of conspecifics/other predators competing for that resource. The aforementioned study was conducted on Cape gannets (*Morus capensis*), which forage for shoaling pelagic fish which are known to be ephemeral and appear in higher abundance (O’Donoghue et al., 2010), compared to the higher predictability of prey species which northern gannets exploit in more temperate latitudes (Hamer et al., 2007). Such a scenario would result in short-lived but high abundance feeding opportunities, so that intraspecific competition is temporarily reduced, thus creating the conditions for social foraging to arise i.e. the benefits outweigh the costs (Beauchamp, 2013). Observations of northern gannets at sea around Bass Rock indicated that the majority of gannets foraging in relatively low density of conspecifics, and that if aggregations did form, they dissipated quickly (Camphuysen, 2011). This suggests that feeding conditions are considerably different for northern gannets, and that they are acting on some level to avoid patches with high densities of conspecifics. Model results support this as simulations which included competition generally increased the models’ abilities to reproduce empirical patterns.

If competition is driving movements in similar ways in the real system, this density-dependent mechanism (Araújo et al., 2011) may partially account for the positive relationship between colony size and trip duration (Lewis et al., 2001). Foreseeably, a similar mechanism is also behind the emergence of colony segregation (Wakefield et al., 2013), where the interface of two colonies would be a more crowded area, and as such would lead to individuals favouring other areas not within this overlap. Wakefield et al. (2013) developed a theoretical IBM to inspect how memory, local enhancement, and the information centre hypothesis interacted in producing colony segregation. Only one of their models (using all three information sources) resulted in any significant segregation between the two colonies. It is perhaps the case that gannets actively seek to avoid competition, which was not included in their model. Emergence of colony segregation is something that could be addressed in a future development of this model, offering the advantage of parameterisation and evaluation against real data. I would suggest modelling two colonies which have a high level of interface in their distributions, such as Grassholm and Great Saltee (permitting there is sufficient tracking data), as there does not seem to be much interface between birds from Bass Rock and its closest colony at Bempton Cliffs (Wakefield et al., 2013).

Alongside developing understanding of the ecology of seabirds, the obvious application of this model is to address the potential impacts of OWFs which are an imminent threat to the birds of Bass Rock. With the incorporation of an energetics component (Warwick-Evans et al., 2017) it would be possible to forecast population dynamics within a model with individuals exhibiting emerging IFSF behaviour. Previous IBMs investigating the impact of OWFs on seabirds have overestimated mortality from collision (Van Bemmelen et al., 2021) and displacement (Searle et al., 2017), which may be attributable to there being no adaptation i.e. individuals consistently forage behind an OWF and have to fly around it, instead of deciding to forage in another area entirely, thus mitigating the energetic costs. Incorporating memory and interaction in the models would allow for adaptive populations, which is of interest not only for population dynamics, but also to forecast potential changes in distribution. It is foreseeable that an adaptive population could see impacts from cumulative OWFs, as more of their foraging area is taken it will drive them further out to sea resulting in longer trip durations which could have implications for populations such as the Bass Rock that already seem to be approaching an energetic ceiling (Hamer et al., 2007).

Such forecasting is dependent on a good understanding of how seabirds react to OWFs. Current evidence indicates that gannets largely avoid OWFs but a fraction show attraction towards them (Peschko et al., 2021) when they are situated in their breeding colony’s home range. Previous studies show exclusive avoidance (Skov et al., 2018), but it is likely most of these gannets were migrating and not under the constraints imposed during the chick-rearing period. Therefore exclusive avoidance cannot be reliably applied to modelling scenarios as it would render any resulting findings dubious. IBMs are not a silver bullet to understanding species’ responses, but when fieldwork is informed by modelling, and vice versa, it can open up new lines of enquiry and provide the tools to achieve answers in a robust fashion (e.g. Urmy 2021). Currently, the priority for fieldwork should be to continue tracking the birds of Bass Rock during offshore wind farm construction (which is ongoing) and operation of the Neart na Gaoithe OWF in order to determine how individuals habituate to such structures over time, not ruling out the possibility of attraction due to increased productivity (Inger et al., 2009).

The foraging movements of seabirds are driven by the spatiotemporal variation in resource availability. When constrained to rearing a chick and being faced with competition from thousands of conspecifics, further information to guarantee foraging opportunities are sought out (Boyd et al., 2016; Urmy, 2021). I show that through modelling individuals that remember the direction of profitable foraging areas and complimenting this with additional cues from conspecifics it is possible to reproduce the strong, characteristic patterns of IFSF in gannets. This highlights the importance of both public and private information in influencing movement patterns at the individual and population-level. Using this approach has allowed inspection of mechanisms acting at different time scales, and is novel in its investigation of the use of memory and social information in the same model. Future investigations could help develop theory, such as colony segregation, and help forecast the size and distribution of populations under different management scenarios (Warwick-Evans et al., 2017; Lane et al., 2020).

4.5 Literature cited

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958.

Ashmole, N. P. (1963). The Regulation of the Numbers of Tropical Oceanic Birds. *The Ibis*, *103b*(3), 458–473.

Ashmole, N. P., Farner, D. S., & King, J. R. (1971). Seabird ecology and the marine environment. *Avian Biology*, *1*, 223–286.

Beauchamp, G. (2013). *Social Predation: How Group Living Benefits Predators and Prey*. Elsevier.

Becker, W. A. (1975). Manual of quantitative genetics. *Manual of Quantitative Genetics., Ed. 3*.

Bell, W. J. (2012). *Searching Behaviour: The behavioural ecology of finding resources*. Springer Science & Business Media.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28.

Boyd, C., Grünbaum, D., Hunt, G. L., Punt, A. E., Weimerskirch, H., & Bertrand, S. (2016). Effectiveness of social information used by seabirds searching for unpredictable and ephemeral prey. *Behavioral Ecology*, *27*(4), 1223–1234.

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, *68*(6), 1349–1360.

Calenge, C., & Calenge, M. C. (2018). *Package 'adehabitatLT'*.

Camphuysen. (2011). Northern Gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. *British Birds*, *104*(2), 60.

Carter, M. I. D., Cox, S. L., Scales, K. L., Bicknell, A. W. J., Nicholson, M. D., Atkins, K. M., Morgan, G., Morgan, L., Grecian, W. J., Patrick, S. C., & Votier, S. C. (2016). GPS tracking reveals rafting behaviour of Northern Gannets (*Morus bassanus*): implications for foraging ecology and conservation. *Bird Study*, *63*(1), 83–95.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136.

Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., & McConnell, B. (2021). AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, *440*, 109397.

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs*, *73*(3), 463–481.

Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *The Journal of Wildlife Management*, *69*(4), 1346–1359.

Grecian, W. J., Lane, J., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society, Interface*, *15*(143) , 20180084.

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J., & Railsback, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling*, *221*(23), 2760–2768.

Grimm, V., & Railsback, S. F. (2012). Pattern-oriented modelling: a ‘multi-scope’ for predictive systems ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *367*(1586), 298–310.

Grimm, V., Railsback, S. F., Vincenot, C. E., Berger, U., Gallagher, C., Deangelis, D. L., Edmonds, B., Ge, J., Giske, J., Groeneveld, J., Johnston, A. S. A., Milles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohwäder, M. S., Stillman, R. A., Thiele, J. C., & Ayllón, D. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Organs: The Official Journal of the Japanese Society for Artificial Organs*, *23*(2).

Hamer, K. C., Humphreys, E. M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R. A., Harris, M. P., & Wanless, S. (2007). Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series*, *338*, 295–305.

Hamer, K. C., Phillips, R. A., Hill, J. K., Wanless, S., & Wood, A. G. (2001). Contrasting foraging strategies of gannets *Morus bassanus* at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series*, *224*, 283–290.

Holling, C. S. (1959). Some Characteristics of Simple Types of Predation and Parasitism 1. *The Canadian Entomologist*, *91*(7), 385–398.

Inger, R., Attrill, M. J., Bearhop, S., Broderick, A. C., James Grecian, W., Hodgson, D. J., Mills, C., Sheehan, E., Votier, S. C., Witt, M. J., & Godley, B. J. (2009). Marine renewable energy: potential benefits to biodiversity? An urgent call for research. *The Journal of Applied Ecology*, *46*(6), 1145–1153.

Jones, T. B., Green, J. A., Patrick, S. C., Evans, J. C., Wells, M. R., Rodríguez-Malagón, M. A., & Arnould, J. P. Y. (2020). Consistent sociality but flexible social associations across temporal and spatial foraging contexts in a colonial breeder. *Ecology Letters*, *23*(7), 1085–1096.

Jones, T. B., Patrick, S. C., Arnould, J. P. Y., Rodríguez-Malagón, M. A., Wells, M. R., & Green, J. A. (2018). Evidence of sociality in the timing and location of foraging in a colonial seabird. *Biology Letters*, *14*(7), 20180214.

Kamil, A. C. (1983). Optimal foraging theory and the psychology of learning. *American Zoologist*, *23*(2), 291–302.

Lane, J. V., Jeavons, R., Deakin, Z., Sherley, R. B., Pollock, C. J., Wanless, R. J., & Hamer, K. C. (2020). Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research*, *162*, 105196.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series*, *628*, 183–193.

Lessells, C. M., & Boag, P. T. (1987). Unrepeatable Repeatabilities: A Common Mistake. *The Auk*, *104*(1), 116–121.

Lewis, S., Sherratt, T. N., Hamer, K. C., & Wanless, S. (2001). Evidence of intra-specific competition for food in a pelagic seabird. *Nature*, *412*(6849), 816–819.

Lewontin, R. C. (1979). Fitness, survival, and optimality. *Analysis of Ecological Systems*, *3*, 3.

Morgan, E. A., Hassall, C., Redfern, C. P. F., Bevan, R. M., & Hamer, K. C. (2018). Individuality of foraging behaviour in a short-ranging benthic marine predator: incidence and implications. *Marine Ecology Progress Series, 609,* 209-219.

Murray, S., Harris, M. P., & Wanless, S. (2015). The status of the Gannet in Scotland in 2013-14. *Scottish Birds*, *35*(1), 13.

O’Donoghue, S. H., Whittington, P. A., Dyer, B. M., & Peddemors, V. M. (2010). Abundance and distribution of avian and marine mammal predators of sardine observed during the 2005 KwaZulu-Natal sardine run survey. *African Journal of Marine Science, 32*(2), 361–374.

Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., Hamer, K. C., Wakefield, E., Le Nuz, M., & Votier, S. C. (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* , *123*(1), 33–40.

Peschko, V., Mendel, B., Mercker, M., Dierschke, J., & Garthe, S. (2021). Northern gannets (*Morus bassanus*) are strongly affected by operating offshore wind farms during the breeding season. *Journal of Environmental Management, 279,* 111509.

Pettex, E., Bonadonna, F., Enstipp, M. R., Siorat, F., & Grémillet, D. (2010). Northern gannets anticipate the spatio–temporal occurrence of their prey. *The Journal of Experimental Biology*, *213*(14), 2365–2371.

Piper, W. H. (2011). Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology, 65*(7), 1329–1351.

Railsback, S. F., Ayllón, D., Berger, U., Grimm, V., Lytinen, S., Sheppard, C., & Thiele, J. (2017). Improving Execution Speed of Models Implemented in NetLogo. *Journal of Artificial Societies and Social Simulation, 20*(1), art. 3.

Railsback, S. F., & Grimm, V. (2019). *Agent-Based and Individual-Based Modeling: A Practical Introduction, Second Edition*. Princeton University Press.

Searle, K. R., Mobbs, D. C., Butler, A., Furness, R. W., Trinder, M. N., & Daunt, F. (2017). Finding out the fate of displaced birds. *CEH Report to Marine Scotland FCR/2015/19.*

Skov, H., Heinänen, S., Norman, T., Ward, R., Méndez-Roldán, S., & Ellis, I. (2018). *ORJIP Bird Collision Avoidance Study*. Carbon Trust & Discretionary Project Steering Committee.

Soanes, L. M., Atkinson, P. W., Gauvain, R. D., & Green, J. A. (2013). Individual consistency in the foraging behaviour of Northern Gannets: implications for interactions with offshore renewable energy developments. *Marine Policy, 38*, 507-514.

Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution / British Ecological Society*, *8*(11), 1639–1644.

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, *25*(6), 1302–1310.

Tremblay, Y., Thiebault, A., Mullers, R., & Pistorius, P. (2014). Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. *PloS One*, *9*(2), e88424.

Turner, R. A. (1964). Social Feeding in Birds. *Behaviour, 24*(1/2), 1–46.

Urmy, S. S. (2021). Visual trail following in colonial seabirds: theory, simulation, and remote observations. *Ecological Monographs*, *91*(1), e01429.

Van Bemmelen, R. S. A., Soudijn, F. H., Benden, D., Potiek, A., Chen, C., Hintzen, N., Wilkes, T., Van Kooten, T., & Gyimesi, A. (2021). *Individual-based model lesser black-backed gulls in the Netherlands*. No. 21-168 Bureau Waardenburg.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences, 284*(1859).

Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C., Hamer, K. C. (2013). Space partitioning without territoriality in gannets. *Science, 341*(6141), 68–70.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity—why some gannets don’t change their spots. *Ecology*, *96*(11), 3058–3074.

Wanless, S., Harris, M. P., & Morris, J. A. (1990). A Comparison of Feeding Areas Used by Individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the Breeding Season. *Colonial Waterbirds*, *13*(1), 16–24.

Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as “information-centres” for food-finding. *The Ibis, 115,* 517-534.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology*, *55,* 503-515.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research. Part II, Topical Studies in Oceanography*, *54*(3), 211–223.

Zurell, D., Berger, U., Cabral, J. S., Jeltsch, F., Meynard, C. N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., & Grimm, V. (2010). The virtual ecologist approach: simulating data and observers. *Oikos* , *119*(4), 622–635.

4.6 Appendix

Table A.4.1. Parameters implemented for the relevant hypotheses in different simulation experiments.

Information source	**Parameter**	**Relevant hypotheses**	**Value**	**Source**
Public	Reaction distance	Local enhancement	Up to 10 km	(Thiebault et al., 2014)
	Likelihood of venturing towards foraging conspecific	Local enhancement	20% if < 5 km away; 10% if >= 5 km away	Derived heuristically
	Field of vision	Local enhancement and competition	270 degrees	Derived heuristically
	Competition conspecific threshold	Competition	2 conspecifics (equivalent to >100 gannets when scaled up to actual population size)	Derived heuristically
	Distance conspecifics are considered competitors	Competition	Up to 5 km	Derived heuristically
Private	Number of trips used to ascertain my departure bearing (long-term)/bearings (combined)	Long-term and combined memory	10 foraging trips	Derived heuristically
	Number of departure bearings stored in memory following selection based on duration	Long-term and combined	Long-term = 1; Combined = 3	Derived heuristically
	Number of immediately prior foraging trips assessed to decide whether to change direction	Short-term and combined memory	3 foraging trips	Derived heuristically

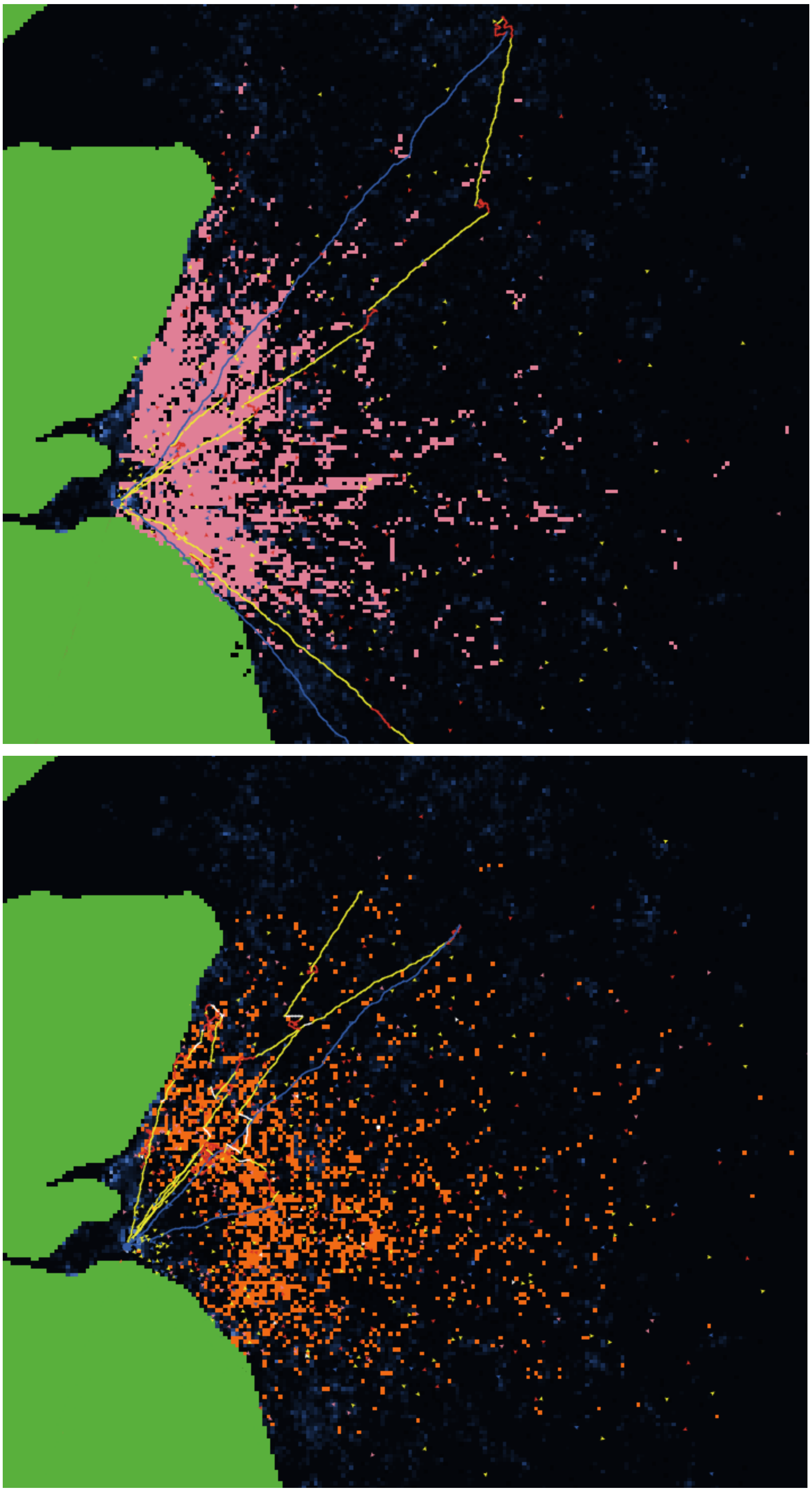


Figure A.4.1. Screenshots of the interface of our NetLogo model when calibrating for competition levels (top) and local enhancement (bottom). The green area is land, and cells with various colours of blue/black indicate prey density (lighter blue = higher density). Small coloured arrows represent other *aGannets* at sea on foraging trips with colours representing their current movement mode (yellow = outbound, red = ARS, blue = inbound, white = local enhancement, bottom only), with a subset of individuals displaying their tracks. Pink cells (top) indicate areas in which *aGannets* have experienced competition, the majority of which are close to the colony as is perceivably the case in reality. Orange cells (bottom) indicate areas which *aGannets* have moved to when pursuing local enhancement opportunities.

Table A.4.2. Metrics for simulations and empirical data.

simulation	**conditions**	**duration.mean**	**dur.sd**	**length.mean**	**length.sd**	**displ.mean**	**displ.sd**	**linearity.mean**	**linearity.sd**	**daydur.mean**	**daydur.sd**
Empirical	*NA*	*23.29*	*10.38*	*551.90*	*244.28*	*214.63*	*93.51*	*1.30*	*0.18*	*16.47*	*7.47*
A1_1	null	18.95	9.41	477.95	266.18	173.41	103.73	1.41	0.22	13.39	5.86
A2_1	LE	18.98	8.48	499.27	242.71	177.71	97.68	1.46	0.24	13.92	5.38
A3_1	Co	21.39	9.62	558.68	288.92	209.97	112.97	1.35	0.17	14.89	6.30
A4_1	LECo	21.04	8.46	547.45	255.73	202.43	101.35	1.38	0.19	14.60	5.50
B1	LT	17.42	8.72	462.17	250.70	169.02	97.91	1.41	0.21	12.85	5.69
B2	LTLE	15.50	8.01	414.48	218.87	146.01	84.04	1.47	0.25	12.00	4.94
B3	LTCo	20.47	8.66	535.12	268.40	198.06	106.18	1.38	0.25	14.10	5.90
B4	LTLECo	21.49	9.23	562.56	280.56	205.72	111.89	1.41	0.26	14.92	6.24
C1	ST	18.26	8.31	469.76	254.80	172.21	105.34	1.41	0.23	13.20	5.43
C2	STLE	17.28	8.30	464.04	234.81	163.86	93.65	1.47	0.27	13.09	5.25
C3	STCo	22.01	9.69	575.05	293.44	219.86	117.35	1.33	0.18	15.20	6.56
C4	STLECo	20.90	9.04	526.27	280.16	192.63	109.22	1.41	0.21	14.15	6.22
D1	Cm	15.11	7.89	400.42	215.47	146.87	83.76	1.39	0.25	11.42	4.99
D2	CmLE	15.26	7.71	409.06	202.18	144.93	76.00	1.44	0.19	12.01	4.89
D3	CmCE	21.29	7.46	540.95	230.51	204.16	96.94	1.36	0.18	14.60	5.06
D4	CmLECo	22.21	8.95	566.56	265.94	207.14	103.86	1.42	0.33	15.14	6.00

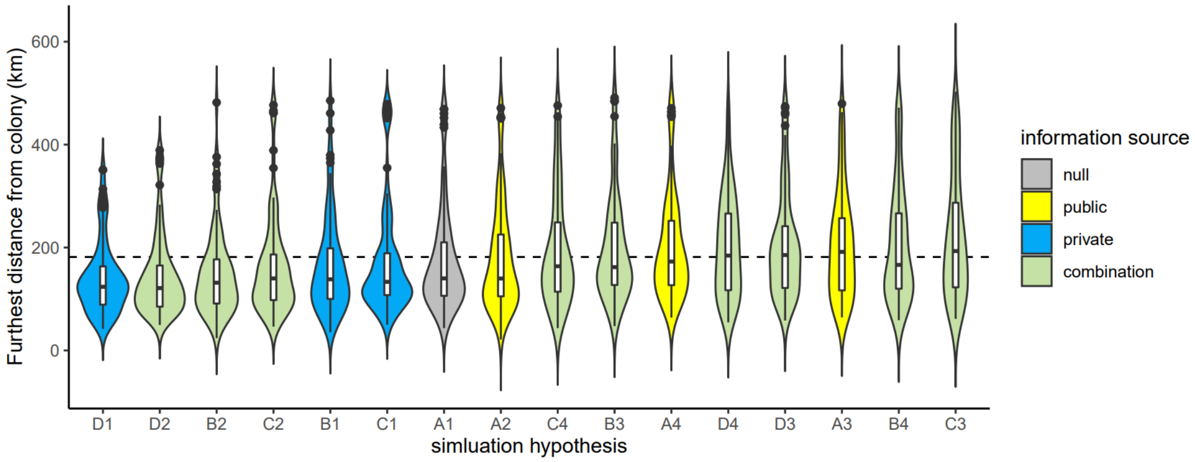


Figure A.4.2. Furthest distance from colony of different simulations in ascending order of median with the dotted line in the background representing the mean furthest trip of all simulation (183 km). Different colours of violin plots represent the different information sources used.

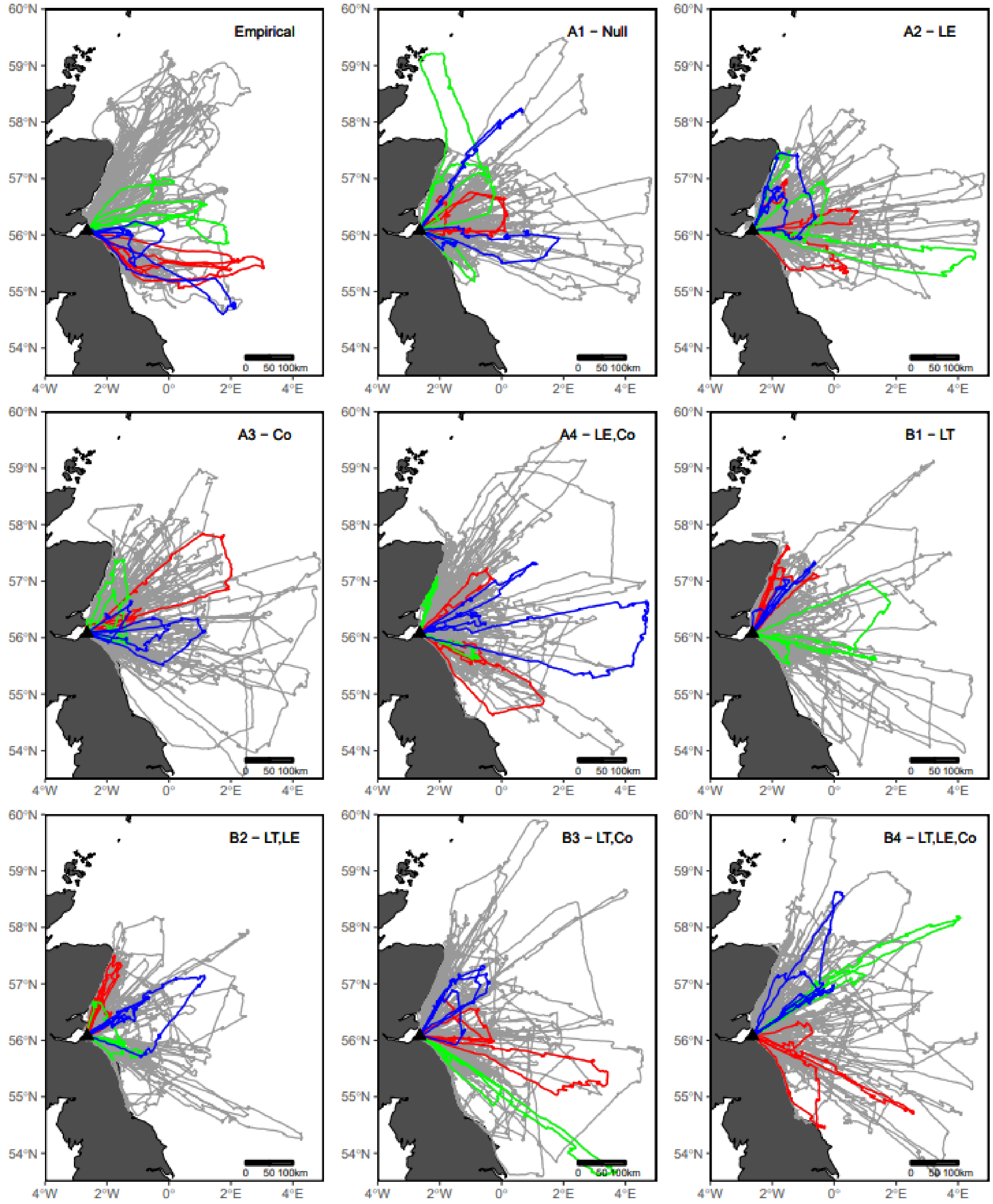


Figure A.4.4. Maps displaying tracking data of 90 trips from 30 individuals (grey) with blue, green, and red paths highlighting three random individuals with three tracks each. The top left is from our empirical data subset, and from top middle, going left to right and top to bottom displays different simulations (A1 – B4) with the hypothesis code and its conditions in the top right. Short hand for different hypotheses implemented in these simulations in the order they appear: Null = no information available; LE = local enhancement; Co = competition from conspecifics; LT = long-term memory.

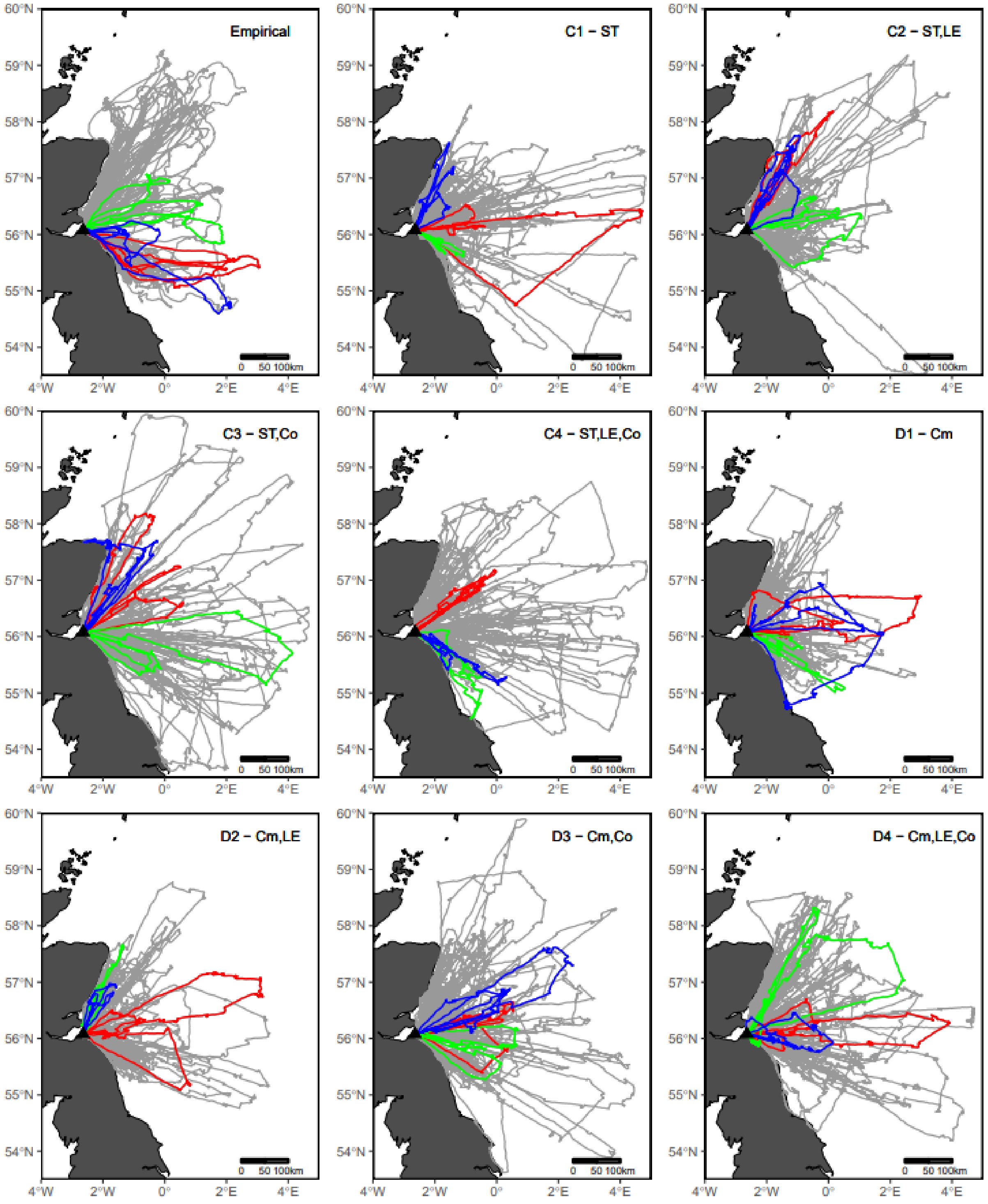


Figure A.4.5. Maps displaying tracking data of 90 trips from 30 individuals (grey) with blue, green, and red paths highlighting three random individuals with three tracks each. The top left is from our empirical data subset, and from top middle, going left to right and top to bottom displays different simulations (C1 – D4) with the hypothesis code and its conditions in the top right. Short hand for different hypotheses implemented in these simulations in the order they appear: ST = short-term memory; LE = local enhancement; Co = competition from conspecifics; Cm = combined memory.

Chapter 5: General Discussion

5.1 Introduction

In an attempt to slow the rate of climate change many countries are trying to reduce their reliance on fossil fuels by developing renewable energy sources. Climate change is a major threat to seabirds (Dias et al., 2019), and so these efforts may ameliorate potential impacts. However, offshore renewable developments pose their own threats to seabird populations which may interact with the footprint of these developments, whether it be during the breeding season, migration or wintering period (Fox et al., 2006). The waters surrounding the UK are an area of global importance for several seabird species (Mitchell et al., 2004). This area has seen largescale development of offshore wind farms (OWFs) in the past decade with plans for continued expansion in the coming decade to quadruple installed capacity (BEIS, 2020). Consequently, marine areas including the North Sea, which already has relatively high concentrations of offshore wind farms, are set to see further proliferation. With rising attention being given to cumulative impacts in environmental impact assessments (Stelzenmüller et al., 2018), developers in the North Sea are facing difficulties as the concentration of offshore wind farms there means that environmental impact assessments (EIAs) are predicting impacts exceeding acceptable levels (e.g. Hornsea Three; Ørsted 2020).

Without detailed knowledge on the spatiotemporal patterns of seabird populations that may interact with proposed OWF developments, confidence in the results of population viability analysis (PVA) used for EIAs drops considerably. As a result, the upper estimates of mortality are taken as a precautionary figure, which is beginning to impede the progress in the development of OWFs. Hence, there is a drive to better understand how seabirds may interact with OWFs and use empirical data to inform and develop modelling efforts to predict population impacts. Tracking data is essential for understanding space use, and can help inform management efforts, but can also give great insight into life history, behaviour and the strategies being employed by individuals. Survey data can provide a snapshot of the distribution of many birds of various species over large areas. Together tracking and survey data are the two main data sources used to inform such assessments.

EIAs typically focus on apportioning of collision risk to seabird populations which have home ranges that overlap with the prospective footprint of the planned OWF when acting as central place foragers during the breeding season. However, other important periods such as migration have not been thoroughly assessed despite the potential risks (e.g. Fijn et al., 2022). Through comparing survey and tracking data, it is possible to gain new insights into which colonies and age classes might be passing through key bottlenecks on migration, such as the southern North Sea which has a relatively high concentration of OWFs. Assessment of impacts such as those from displacement and barrier effects are often inconclusive owing to their impacts being indirect which may require more sophisticated modelling techniques.

Models attempting to predict the impacts of displacement effects have advanced greatly in the past decade (McDonald et al., 2012; Langton et al., 2014; Searle et al., 2015; Searle et al., 2017), explained in part by the adoption of IBMs which simulate individuals in mechanistic and process-based models that represent the key processes in the system being studied. Previous applications include assessing the impact of OWFs on body condition and breeding success in a gannet colony in the English Channel (Warwick-Evans et al., 2017), predicting the impacts of displacement in seabird species in the Forth and Tay (Searle et al., 2017), and most recently, estimating collision mortality of lesser black backed gulls (*Larus fuscus*) in the Netherlands (Van Bemmelen et al., 2021). These models have advanced understanding by linking the potential effects of OWFs to population-level consequences through simulated interaction. However, they are more complex and data-hungry than other forms of PVA, and further developments are required to capture complex behaviours and density-dependent processes, which such models have the capability to provide, to use this approach to its full potential.

The aim of this thesis was to address gaps concerning the risks to gannets from OWFs. First, by investigating migratory movements of different age classes and populations using tracking and survey data (Chapter 2). Second, by investigating variability in foraging behaviour between individuals throughout the breeding season with the aim of developing an IBM capable of accurately representing foraging behaviour of gannets at Bass Rock (Chapters 3 & 4) as a module intended to be incorporated into future marine spatial management tools. What follows is a summary of the key findings before proceeding to discuss the broader implications of this work and potential future directions.

5.2 Key findings

Chapter 2 – Through comparing two types of survey data, including digital aerial surveys conducted as part of a baseline study at five prospective OWF sites, with tracking data from adults and juveniles at Bass Rock it was possible to gain new insights into the potential risk that different age classes and populations face during migratory movements through the southern North Sea. It is likely that adults are more at risk from collision due to flying offshore in comparison to juveniles that hugged the coast. This was reflected in the survey data which also indicated immatures may be more at risk during summer possibly due to their more exploratory foraging trips. Additionally, the peak of survey numbers in November are likely from colonies further North than Bass Rock, as our tracking data indicated that Bass Rock gannets pass through this area around a month earlier.

Chapter 3 – This chapter documents the parameterisation and evaluation of a spatially-explicit IBM of chick-rearing gannets at Bass Rock with the purpose of reproducing the fine- and broad-scale movements of foraging trips. The model was guided and developed using several empirical patterns with individuals making decisions based on the previous foraging success of the current trip, and the environment they are situated in. Individuals employ the trap line strategy where they engage in a directional arc and only return once they have obtained the threshold requirement of resources through interacting with the available prey in a realistic way via an approximated functional response. This was a prerequisite step in looking towards more behaviourally complex questions.

Chapter 4 – By adapting the movement model (Chapter 3) to incorporate memory and interaction processes it was possible to run different simulation models investigating which resource localisation mechanisms might be driving the strong characteristic patterns of IFSF. The most complex hypotheses, in which individuals could recall several departure angles determined through previous exploration, and interacted with conspecifics both to avoid crowded areas and for local enhancement, was the best at reproducing the empirical patterns of IFSF at Bass Rock. Simulations in which there were two types of interaction, even in the absence of recalling departure angles from memory, led to a population which matched the putative distribution of prey well, indicating a well-informed population. This model could now be applied to understanding OWF impacts on gannet colonies from which realistic IFSF emerges from adaptive individuals, as opposed to programming it deterministically.

5.3 Broader implications and future research

5.3.1 Risks to gannets outside the breeding season

Data on the distribution and movements of seabirds are collected for a wide range of purposes including academic research, conservation monitoring and surveys for commercial purposes such as renewable energy developments. The potential benefits of combining such data sets is beginning to receive more attention, with the possibility for greater explanatory power and predictive ability from informing species distribution models (SDMs) with integrated data (Fletcher et al., 2016). Methods have been developed to integrate survey data in seabird applications and presented in an accessible manner with an accompanying R package (Matthiopoulos et al., 2022). However, there are difficulties recognised in integrating tracking and survey data due to inherent differences in data structures, so this is yet to be established (although see Michelot et al., 2020). This may lead to a comparative approach being taken (e.g. Carroll et al., 2019), as we have done in Chapter 2.

Gannets are a species of high concern for vulnerability to OWFs (Furness et al., 2013) due to their relatively long foraging ranges putting them at a higher likelihood of encountering OWFs, and their flight heights then putting them at risk of colliding with rotating turbines (Cleasby et al., 2015; Lane et al., 2019). There is little knowledge on how flight heights may vary during migration, with some indication from the ORJIP Bird Collision Avoidance study of bimodal flight heights (Skov et al., 2018), also found for breeding birds by Cleasby et al. (2015) and Lane et al. (2019), where birds flew higher while foraging than when commuting to and from the colony. Gannets show high levels of both macro-avoidance of wind farm areas and micro-avoidance of individual turbines when within a wind farm area (Garthe et al., 2017; Cook et al., 2018) but as OWFs increase in number and gannets potentially become more habituated it would nonetheless be worthwhile to try to gain further insights into flight heights through biologging techniques during migration. Further to this, multi-colony tracking studies (e.g. Buckingham et al., 2021) could provide better insight into apportioning risk to different colonies. The results in Chapter 2 compliment the findings from a previous study of two colonies from (Furness et al., 2018), which also used geolocators. By tracking adults from several colonies with more precise devices, such as GPS-PTTs, confidence in predicting the potential interactions with OWFs in the southern North Sea would be greatly improved.

Knowledge of gannets' movement and behaviour outside of the breeding season is not as developed as within it. Therefore, potential threats like competition with illegal fisheries in the coastal waters of West Africa (Agnew et al., 2009; Gremillet et al., 2015) where many gannets overwinter (Kubetzki et al., 2009; Grecian et al., 2019), are not well understood. Further efforts should be invested into uncovering the entire yearly cycle of gannets, with particular regard given to identifying carry-over effects, whereby events in one season can influence subsequent seasons (Metcalfe & Monaghan, 2001; Harrison et al., 2011). The consequences of carry-over effects on fitness and population dynamics are potentially profound, and with a year-round perspective it is possible to link breeding success between breeding seasons as has been recently done with Kittiwakes (Bogdanova et al., 2017). A greater empirical understanding would allow more robust population projection modelling (Lane et al., 2020), that could encompass the non-breeding season, and OWF impact scenarios could then be applied.

Tracking juveniles and immatures is more challenging than tracking adults which remain at a territory throughout the breeding season. However, as advanced tracking technology becomes more cost effective (i.e. remote transmission of fine scale movement), studies of juvenile (Gremillet et al., 2015; Lane et al., 2021) and immature gannets (Votier et al., 2011, 2017; Grecian et al., 2018; Wakefield et al., 2019) are furthering our understanding of their ecology. Gaps are still present, and the movements and behaviours of birds between the ages of 0.5-3 years are relatively poorly known. After this, immature birds gradually integrate into a colony before breeding (Pettex et al., 2019). As European Seabirds at Sea (ESAS) survey data indicate (Chapter 2), immature birds are more likely than adults to be in the southern North Sea during the summer months. This age class exhibits much more exploratory movements, and when coupled with relative inexperience this may put them at higher risk of collision with OWFs. This potentially warrants further study through more tracking of immatures beginning to associate with different colonies. However, given their lower contribution to population viability when compared to breeding adults, this is probably not a priority over further understanding how breeding adults interact with OWFs.

5.3.2 Individual-based models of movement and IFSF patterns

It was possible to reproduce the foraging movements of gannets during the breeding season successfully by parameterising the apparent essential processes. This provided some inference on modelled behaviours, such as the trap line strategy. However, the models' inference could be strengthened in several ways. For example, running simulations with altered prey distributions, such as having prey change distribution daily, to test how this impacts on the model and if the modelled gannets were able to withstand such variation. Further testing could be to apply this model to other colonies, using the blind approach I discussed in chapter 3. Thus, this model might be able to address some of the issues of transferability seen in SDM (Sequeira et al., 2018).

Chapter 3 provided the foundations to address more complex questions regarding the emergence of IFSF. The strong characteristic patterns of IFSF in gannets provided a means for quantifying outputs from models looking into resource localisation mechanisms deriving different combinations of public and/or private information. IFSF is a form of individual specialisation where individuals return to the same patch to forage. Such specialisations vary widely between species, and can have profound ecological and evolutionary consequences, such as population stability and regulating intraspecific competition (Bolnick et al., 2003). IFSF has been displayed in many long lived marine species (e.g. Bradshaw et al., 2004; Weimerskirch, 2007; Morgan et al., 2018) and may infer fitness advantages through increased foraging efficiency (Patrick & Weimerskirch, 2017). The processes which drive

IFSF are not well known, such as whether residual variation among individuals is a result of individual niche specialisation (Bonnet-Lebrun et al., 2018), or a process of site familiarity learned during development (Grecian et al., 2018). Site familiarity is suggested as the main driver in gannets (Wakefield et al., 2015), with the use of memory to recall broad-scale foraging areas, and fine-tuning thought to be derived from social information such as local enhancement (Wittenberger, 1985; Davoren et al., 2003). IFSF is implied in space use such that individuals within a population could overlap with anthropogenic threats such as OWFs to varying degree. If it is possible to get an insight into the mechanisms underpinning such behaviours it could aid greatly in predictive abilities by being able to reproduce individual specialisation in future applications investigating OWF impacts.

The model indicated that mechanisms drawing on both public and private information are important in reproducing the patterns of IFSF, and with varying simulations it was clear that these mechanisms can have a large influence on the movements of individuals and the wider population. A drawback to the simulation experiments of Chapter 4 was that I was only able to include 1,000 individuals in the model, which is a fraction of the actual population size. Consequently, confidence in the accuracy of how interactions were represented in the model is reduced. By applying this model to a smaller colony for which all individuals could be represented, then interaction with conspecifics would not need to be approximated through upscaling. Parameterisation procedures could be used to identify the true number of conspecifics which might induce local enhancement and competition effects, under the assumption that this holds in smaller populations. This could help in validation of my findings on which resource localisation mechanisms are driving IFSF.

It would be of interest to run more simulation experiments with two or more colonies to enquire as to whether the conditions which we found for IFSF also reproduced colony segregation (Wakefield et al., 2013). A recent model has shown that memory alone was sufficient to create spatial segregation among central place foragers (Aarts et al., 2021). However, this model was motivated by patterns observed in harbour seals (*Phoca vitulina*), for which public information transfer will be much less likely owing to visibility. Therefore, unlike the seal system it is likely that avoidance of areas with high concentrations of conspecifics could have developed as a key driver for colony segregation in seabirds owing to their ability to sense conspecifics >10km away (Thiebault et al., 2014). This would help develop theory relating to the IFSF phenomenon, and increase confidence in the model's predictive abilities.

If the developments suggested above confirm the model is robust and that it can be applied to different colonies with minimal further parameterisation, then this holds two implications for future investigation into OWF impacts. The first is concerning the intention of developing the behavioural complexity of seabird IBMs, for integration with previous applications which look at the effects of collision, displacement and barrier effects on body condition and reproductive success of seabird populations (Searle et al., 2017; Van Bemmelen et al., 2021; Warwick-Evans et al., 2017). The purpose being to have a model in which IFSF emerges naturally, so that more realistic inferences can be drawn to understand population dynamics in the context of EIA. The second, is the potential to use these models to predict species distributions, both at other colonies which have limited tracking data thus overcoming the transferability difficulties with SDM (Sequeira et al., 2018), and to predict how populations might respond to anthropogenic developments like OWFs. By modelling individuals which have the ability to adapt to changing conditions, with selection based on efficient resource localisation when competing with individuals in a dynamic distribution, this could be the most promising method for predicting the effects of displacement, mediated through a density dependent response. As OWFs proliferate, this could be particularly useful in forecasting changing distributions in light of cumulative effects from multiple OWF developments within one colony's foraging range.

The inclusion of how individuals respond to threats in such models is entirely reliant on a good empirical understanding of how birds interact with OWFs. The best empirical indication of how gannets interact with OWFs during the breeding season is at the Helgoland colony (Peschko et al., 2021), where the majority of tracked individuals avoided the OWF, with a small proportion showing attraction to these sites. Further tracking of individuals' interactions with OWFs is key in determining how individuals initially react and then habituate to OWFs as a prerequisite to more powerful predictive modelling. The colony at Bass Rock is a suitable study site as there are many years of GPS data already collected prior to OWF construction. Therefore, the typical levels of interannual variation are well understood, and now that OWFs are beginning to be built we can begin to understand how individuals in a colony experiencing high levels of intraspecific competition may react. This information could then be used to parameterise a model to predict the cumulative impacts of additional OWFs. Both modelling chapters (3 & 4) have identified knowledge gaps for future empirical work. This highlights the ability of a mutually beneficial approach where modelling and empirical work form an iterative process (Urmy, 2021). I would urge the continuation of this approach when investigating the potential impacts of OWFS on the gannet colony at Bass Rock

5.4 Final conclusion

Construction of OWFs in the North Sea is due to increase dramatically (BEIS, 2020). Current EIAs and studies have pointed to limited detrimental effects on gannets so far (Lane et al., 2020; Warwick-Evans et al., 2017), but this may change as cumulative impacts of OWFs intensify. When combined with impacts of climate change and commercial and industrial fisheries (Crain et al., 2008), it is possible that seabird declines in the UK (Mitchell 2018) could accelerate. It is necessary to have the appropriate predictive tools to confidently estimate the potential population-level impacts of the rapid changes which the UK’s waters will experience. In this study I have deciphered some resource localisation mechanisms which may be driving IFSF, and shown that this can have serious implications for how an adaptive population occupies a given space. I recommend that future models of gannets and other seabirds used for marine spatial planning should try and incorporate individual specialisation by using the IBM approach to its full potential through incorporating individual memory and local interactions. This could help in the robust modelling of gannet movements to examine the impacts of additional OWFs as they are proposed in future.

5.6 Literature cited

Aarts, G., Mul, E., Fieberg, J., Brasseur, S., van Gils, J. A., Matthiopoulos, J., & Riotte-Lambert, L. (2021). Individual-Level Memory Is Sufficient to Create Spatial Segregation among Neighboring Colonies of Central Place Foragers. *The American Naturalist*, *198*(2), E37–E52.

Agnew, D. J., Pearce, J., Pramod, G., Peatman, T., Watson, R., Beddington, J. R., & Pitcher, T. J. (2009). Estimating the worldwide extent of illegal fishing. *PloS One*, *4*(2), e4570.

BEIS. 2020. Energy White Paper: Powering our Net Zero Future.Page Prime Minister's Office Brunei Darussalam. HM Govern-ment, London UK. http://www.ret.gov.au/energy/facts/white_paper/Pages/energy_white_paper.aspx.

Bogdanova, M. I., Butler, A., Wanless, S., Moe, B., Anker-Nilssen, T., Frederiksen, M., Boulinier, T., Chivers, L. S., Christensen-Dalsgaard, S., Descamps, S., Harris, M. P., Newell, M., Olsen, B., Phillips, R. A., Shaw, D., Steen, H., Strøm, H., Thórarinsson, T. L., & Daunt, F. (2017). Multi-colony tracking reveals spatio-temporal variation in carry-over effects between breeding success and winter movements in a pelagic seabird. *Marine Ecology Progress Series*, *578*, 167–181.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, *161*(1), 1–28.

Bonnet-Lebrun, A.-S., Phillips, R. A., Manica, A., & Rodrigues, A. S. L. (2018). Quantifying individual specialization using tracking data: a case study on two species of albatrosses. *Marine Biology*, *165*(10), 152.

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D., & Michael, K. J. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour*, *68*(6), 1349–1360.

Buckingham, L., Bogdanova, M. I., Green, J. A., Dunn, R. E., Wanless, S., Bennett, S., Bevan, R. M., Call, A., Canham, M., Corse, C. J., Harris, M. P., Heward, C. J., Jardine, D. C., Lennon, J., Parnaby, D., Redfern, C. P. F., Scott, L., Swann, R. L., Ward, R. M., Weston, E. D., Furness,

R. W., & Daunt, F. (2021). Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. *Marine Ecology Progress Series, 684,* 181-197.

Carroll, M. J., Wakefield, E. D., Scragg, E. S., Owen, E., Pinder, S., Bolton, M., Waggitt, J. J., & Evans, P. G. H. (2019). Matches and Mismatches Between Seabird Distributions Estimated From At-Sea Surveys and Concurrent Individual-Level Tracking. *Frontiers in Ecology and Evolution*, *7*. https://doi.org/10.3389/fevo.2019.00333

Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C., & Hamer, K. C. (2015). Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. *The Journal of Applied Ecology*, *52*(6), 1474–1482.

Cook, A. S. C. P., Humphreys, E. M., Bennet, F., Masden, E. A., & Burton, N. H. K. (2018). Quantifying avian avoidance of offshore wind turbines: Current evidence and key knowledge gaps. *Marine Environmental Research*, *140,* 278-288.

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315.

Davoren, G. K., Montevecchi, W. A., & Anderson, J. T. (2003). Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs*, *73*(3), 463–481.

Dias, M. P., Martin, R., Pearmain, E. J., Burfield, I. J., Small, C., Phillips, R. A., Yates, O., Lascelles, B., Borboroglu, P. G., & Croxall, J. P. (2019). Threats to seabirds: A global assessment. *Biological Conservation*, *237*, 525–537.

Fijn, R. C., Govers, L. L., Lutterop, D., Middelveld, R. P., & van Bemmelen, R. S. A. (2022). Evidence of Nocturnal Migration over Sea and Sex-Specific Migration Distance of Dutch Black-Headed Gulls. *Ardea*, *110*(1), 15–29.

Fletcher, R. J., McCleery, R. A., Greene, D. U., & Tye, C. A. (2016). Integrated models that unite local and regional data reveal larger-scale environmental relationships and improve predictions of species distributions. *Landscape Ecology*, *31*(6), 1369–1382.

Fox, A. D., Desholm, M., Kahlert, J., Christensen, T. K., & Krag Petersen, I. B. (2006). Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. *The Ibis*, *148*, 129–144.

Furness, R. W., Hallgrimsson, G. T., Montevecchi, W. A., Fifield, D., Kubetzki, U., Mendel, B., & Garthe, S. (2018). Adult Gannet migrations frequently loop clockwise around Britain and Ireland. *Ringing & Migration*, *33*(1), 45-53.

Furness, R. W., Wade, H. M., & Masden, E. A. (2013). Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management*, *119*, 56–66.

Garthe, S., Markones, N., & Corman, A.-M. (2017). Possible impacts of offshore wind farms on seabirds: a pilot study in Northern Gannets in the southern North Sea. *Journal of Ornithology*, *158*(1), 345–349.

Grecian, W. J., Williams, H. J., Votier, S. C., Bearhop, S., Cleasby, I. R., Grémillet, D., Hamer, K. C., Le Nuz, M., Lescroël, A., Newton, J., Patrick, S. C., Phillips, R. A., Wakefield E. D., Bodey, T. W. (2019). Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the Northeast Atlantic. *Frontiers in Ecology and Evolution*, *7*, 214.

Grecian, W. J., Lane, J., Michelot, T., Wade, H. M., & Hamer, K. C. (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society, Interface 15*(143), 20180084.

Gremillet, D., Peron, C., Provost, P., & Lescroel, A. (2015). Adult and juvenile European seabirds at risk from marine plundering off West Africa. *Biological Conservation*, *182*, 143–147.

Harrison, X. A., Blount, J. D., Inger, R., Norris, D. R., & Bearhop, S. (2011). Carry-over effects as drivers of fitness differences in animals: Carry-over effects in animal populations. *The Journal of Animal Ecology*, *80*(1), 4–18.

Kubetzki, U., Garthe, S., Fifield, D., Mendel, B., & Furness, R. W. (2009). Individual migratory schedules and wintering areas of northern gannets. *Marine Ecology Progress Series*, *391*, 257–266.

Lane, J. V., Jeavons, R., Deakin, Z., Sherley, R. B., Pollock, C. J., Wanless, R. J., & Hamer, K. C. (2020). Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research, 162*, 105196.

Lane, J. V., Pollock, C. J., Jeavons, R., & Sheddan, M., Furness, R. W., & Hamer, K. C. (2021). Post-fledging movements, mortality and migration of juvenile northern gannets. *Marine Ecology Progress Series, 671*, 207-218.

Lane, J. V., Spracklen, D. V., & Hamer, K. C. (2019). Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series, 628*, 183–193.

Langton, R., Davies, I. M., & Scott, B. E. (2014). A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes. *Ecological Modelling*, *273*(Supplement C), 31–43.

Matthiopoulos, J., Wakefield, E., Jeglinski, J. W. E., Furness, R. W., Trinder, M., Tyler, G., Mccluskie, A., Allen, S., Braithwaite, J., & Evans, T. (2022). Integrated modelling of seabird-habitat associations from multi-platform data: A review. *The Journal of Applied Ecology*, 59(4), 909-920.

McDonald, C., Searle, K., Wanless, S., & Daunt, F. (2012). Effects of Displacement from Marine Renewable Development on Seabirds Breeding at SPAs: A Proof of Concept Model of Common Guillemots Breeding on the Isle of May. *CEH Edinburgh: Final Report to Marine Scotland Science*. http://www.gov.scot/Resource/0040/00404982.pdf

Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, *16*(5), 254–260.

Michelot, T., Blackwell, P. G., Chamaillé-Jammes, S., & Matthiopoulos, J. (2020). Inference in MCMC step selection models. *Biometrics*, *76*(2), 438–447.

Mitchell, P. I., Newton, S. F., Ratcliffe, N., & Dunn, T. E. (2004). Seabird populations of Britain and Ireland. *T. & AD Poyser, London*.

Mitchell, I., French, G., Douse, A., Foster, S., Kershaw, M., Neil McCulloch, N., Murphy, M. and Hawkridge, J. (2018) Marine Bird Abundance. UK Marine Online Assessment Tool, https://moat.cefas.co.uk/biodiversity-food-webs-and-marine-protected-areas/birds/abundance/

Morgan, E. A., Hassall, C., Redfern, C. P. F., Bevan, R. M., & Hamer, K. C. (2018). Individuality of foraging behaviour in a short-ranging benthic marine predator: incidence and implications. *Marine Ecology Progress Series*, *609*, 209-219.

Ørsted (2020). *Hornsea Project Three Offshore Wind Farm Response to the Secretary of State's Minded to Approve Letter Appendix 2: Kittiwake compensation plan*. Ørsted Power Ltd., London.

Patrick, S. C., & Weimerskirch, H. (2017). Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *The Journal of Animal Ecology*, *86*(3), 674–682.

Peschko, V., Mendel, B., Mercker, M., Dierschke, J., & Garthe, S. (2021). Northern gannets (Morus bassanus) are strongly affected by operating offshore wind farms during the breeding season. *Journal of Environmental Management*, *279*, 111509.

Pettex, E., Lambert, C., Fort, J., Dorémus, G., & Ridoux, V. (2019). Spatial segregation between immatures and adults in a pelagic seabird suggests age-related competition. *Journal of Avian Biology*.

Pollock, C. J., Lane, J. V., Buckingham, L., Garthe, S., Jeavons, R., Furness, R. W., & Hamer, K. C. (2021). Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea. *Marine Environmental Research*, *171*, 105457.

Searle, K. R., Butler, A., Mobbs, D., Bogdanova, M., Wanless, S., Bolton, M., & Daunt, F. (2015). At-Sea Turnover of Breeding Seabirds-Final Report to Marine Scotland Science. *Scottish Marine and Freshwater Science*. https://research-scotland.ac.uk/handle/20.500.12594/11192

Searle, K. R., Mobbs, D. C., Butler, A., Furness, R. W., Trinder, M. N., & Daunt, F. (2017). Finding out the fate of displaced birds. *CEH Report to Marine Scotland FCR/2015/19*. https://data.marine.gov.scot/sites/default/files/SMFS%200908%20%282%29.pdf

Sequeira, A. M. M., Bouchet, P. J., Yates, K. L., Mengersen, K., & Caley, M. J. (2018). Transferring biodiversity models for conservation: Opportunities and challenges. *Methods in Ecology and Evolution*, *9*(5), 1250–1264.

Skov, H., Heinänen, S., Norman, T., Ward, R., Méndez-Roldán, S., & Ellis, I. (2018). *ORJIP Bird Collision Avoidance Study*. Carbon Trust & Discretionary Project Steering Committee. https://www.carbontrust.com/media/675793/orjip-bird-collision-avoidance-study_april-2018.pdf

Stelzenmüller, V., Coll, M., Mazaris, A. D., Giakoumi, S., Katsanevakis, S., Portman, M. E., Degen, R., Mackelworth, P., Gimpel, A., Albano, P. G., Almpanidou, V., Claudet, J., Essl, F., Evagelopoulos, T., Heymans, J. J., Genov, T., Kark, S., Micheli, F., Pennino, M. G., … Ojaveer, H. (2018). A risk-based approach to cumulative effect assessments for marine management. *The Science of the Total Environment*, *612*, 1132–1140.

Thiebault, A., Mullers, R. H. E., Pistorius, P. A., & Tremblay, Y. (2014). Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. *Behavioral Ecology*, *25*(6), 1302–1310.

Urmy, S. S. (2021). Visual trail following in colonial seabirds: theory, simulation, and remote observations. *Ecological Monographs*, *91*(1), e01429.

Van Bemmelen, R. S. A., Soudijn, F. H., Benden, D., Potiek, A., Chen, C., Hintzen, N., Wilkes, T., Van Kooten, T., & Gyimesi, A. (2021). *Individual-based model lesser black-backed gulls in the Netherlands*. No. 21-168 Bureau Waardenburg.

Votier, S. C., Fayet, A. L., Bearhop, S., Bodey, T. W., Clark, B. L., Grecian, J., Guilford, T., Hamer, K. C., Jeglinski, J. W. E., Morgan, G., Wakefield, E., & Patrick, S. C. (2017). Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1859), 20171068.

Votier, S. C., Grecian, J., W., Patrick, S., & Newton, J. (2011). Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology*, *158*(2), 355–362.

Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C., & Hamer, K. C. (2013). Space partitioning without territoriality in gannets. *Science, 341*(6141), 68–70.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., Newton, J., Votier, S. C., & Hamer, K. C. (2015). Long-term individual foraging site fidelity—why some gannets don’t change their spots. *Ecology, 96*(11), 3058–3074.

Wakefield, E. D., Furness, R. W., Lane, J. V., Jeglinski, J. W. E., & Pinder, S. J. (2019). Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. *Journal of Avian Biology, 50*(10), 1.

Warwick-Evans, V., Atkinson, P. W., Walkington, I., & Green, J. A. (2017). Predicting the impacts of wind farms on seabirds: An individual-based model. *Journal of Applied Ecology, 55,* 503-515.

Wittenberger, J. F. (1985). The adaptive significance of coloniality in birds. *Avian Biology, 8*, 1–78.

Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep-Sea Research. Part II, Topical Studies in Oceanography, 54*(3), 211–223.