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How animal movement defines behaviour: new insights into the ecology of seabirds at sea

Thesis presented by

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for the degree of

Doctor of Philosophy

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&

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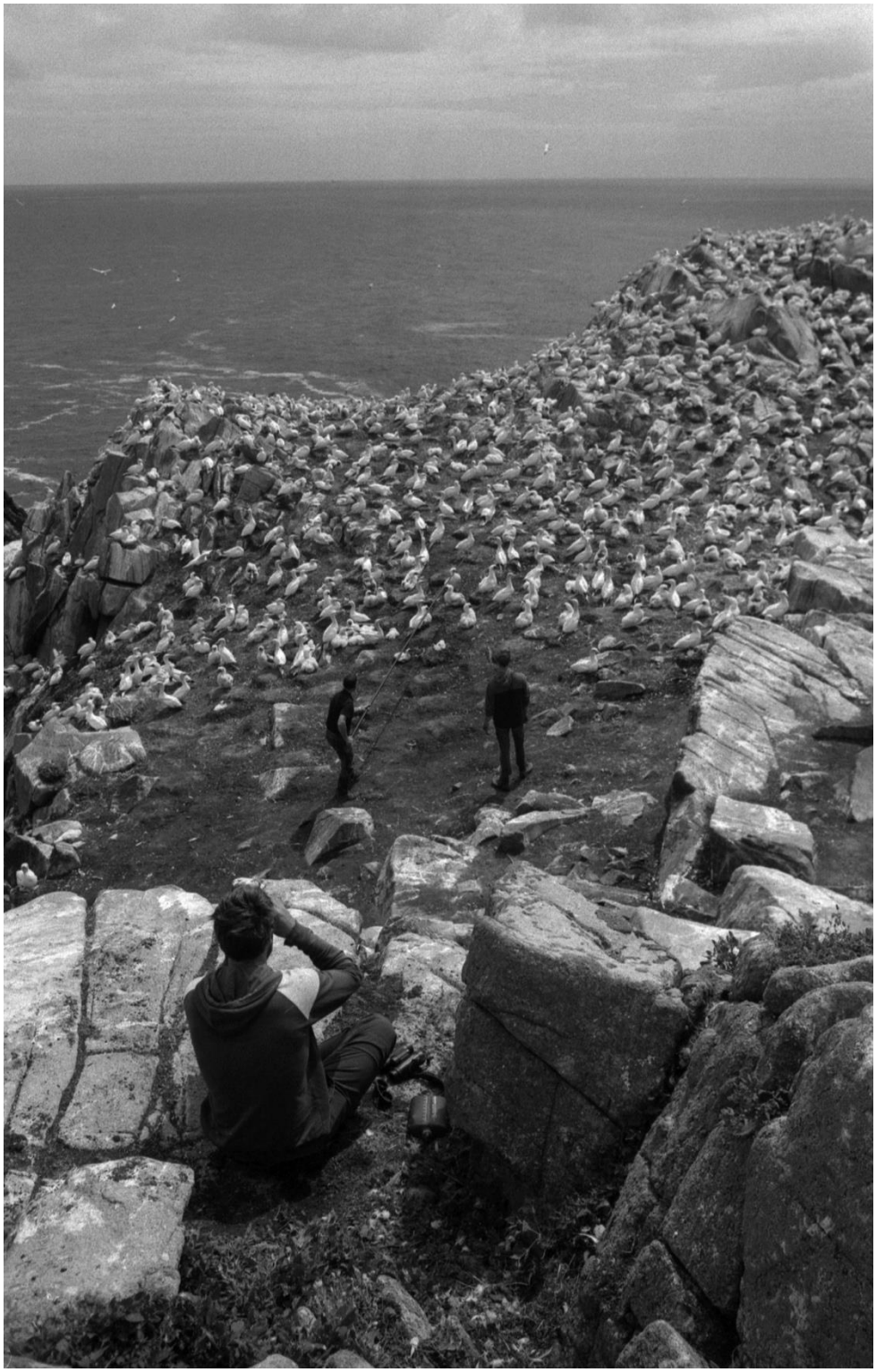
October 2020



“It’s still magic even if you know how it’s done.”
Terry Pratchett

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Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.

Signed:

Ashley Bennison

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Abstract

How animals move through their environment defines their ecology at an individual and population level. All animals must search for food to survive and how they do this can be influenced by the world around them as well as their own internal state. Our understanding of animal ecology has been dramatically expanded thanks to the continued development and miniaturisation of data loggers that can be attached to animals. Data from these biologgers remain challenging to interpret, but shed light on the behavioural ecology of individual animals. In this thesis, I use movement data from seabirds to explore the mechanisms behind foraging and how these are underpinned by the movement of individual animals. In chapter 1, I provide an introductory overview of the literature and introduce my study species. In chapter 2, I examine the methods available to interpreting behaviour from animal relocation data showing that Hidden Markov Models (HMMs) outcompete other behavioural annotation methods – successfully identifying 81% of plunge dives in northern gannets, *Morus bassanus*. I then provide recommendations for best practice when defining periods of search and prey capture behaviour. In chapter 3, I show how environmental features may ultimately disrupt the expected movement of optimal foraging, and show that Atlantic puffins, *Fratercula arctica*, in southeast Ireland have departed from classic Area Restricted Search (ARS). These findings are considered in an energetic perspective and suggest that puffins may be saving between 28-46% of the energy required to fly the same distance. In chapter 4, I utilise acceleration data to document the bioenergetic sex differences of prey capture attempts in northern gannets, examining the links between diet, movement, and energy expenditure. Stable isotope analysis showed dietary differences between the sexes, but energetic content of divergent diets was the same. Prey capture attempts are not energetically expensive for gannets (<4% of energy expenditure in all northern gannets) and females have higher energy demands. However, the differing rate of prey capture attempts highlights that males have a higher minimum prey capture success rate than females to meet energetic demands (29% and 21% respectively). In chapter 5, I further explore acceleration data to determine whether northern gannets display handedness during foraging behaviours. All individuals (n=14) were lateralised in the

direction of their pre-plunge dive roll behaviour, with a 'population' level right-sided bias (64%). While wind has a small effect on the angle of roll, it did not affect the observed lateralisation in individuals. I conclude with a general discussion summarising my main findings and suggesting future research opportunities. This thesis highlights how investigating animal behaviour using movement data can provide new insights into the behavioural ecology of species.

Chapter 1: General Introduction

1.1 The importance of animal movement

The movement of animals is a fundamental process of life and evolution and is a phenomenon common to all living animals. The study of animal movement ecology is a rapidly developing field (Nathan *et al.* 2008) and scientific advances continue to explore the manner and processes by which animals move. From humanity's earliest history, we have considered the way in which animals move; illustrated by cave paintings famously creating the illusion of animal movement (Noxon 1964). In the modern day, the scientific process has helped us to document and understand many of the spectacles of the natural world associated with movement. From studying mass migration of wildebeest, *Connochaetes taurinus*, in the Serengeti (Torney *et al.* 2018), exploring trophic cascades caused by wolf, *Canis lupus*, and elk, *Cervus canadensis*, movements (Fortin *et al.* 2005), to mathematically simulating slime mould movement (Kobayashi, Tero & Nakagaki 2006); movement is a core concept and component within ecology.

Animal movement is often centred around the search for food, mates, shelter, or escape from predators. From a wider perspective, the search for these factors drives animal distribution and habitat preferences (Meadows & Campbell 1972; Swanson *et al.* 1988) but a closer inspection will also find that these preferences drive movement within distributions. Different bird species, living in the same geographic space, have been shown preferentially feeding at different heights and distance from cover (Lee, Kuo & Bollinger 2005) showing that species' habitat preferences drive movement within ecosystems. Species may outcompete each other forcing other species to search for alternate locations (Hoskins *et al.* 2017). Movement may also be driven by differences within a species, such as sexual segregation of foraging grounds (Paiva *et al.* 2017), differing habitat and diet preferences between age groups (Burns *et al.* 1998; Pettex *et al.* 2019), or density dependent foraging – where individuals outcompete conspecifics driving dispersal to new foraging grounds

(Furness & Birkhead 1984). Often the processes acting upon animal movement are driven by both external and internal drivers that act upon both the individual and the population, though determining the cause and effect of this remains difficult.

The search for food often dominates an animal's time and an important avenue of research is that of optimal foraging. MacArthur and Pianka (1966) first discussed the framework of optimal use of patchy environments by an individual animal by balancing energy expenditure with intake. This theory was developed further with the Marginal Value Theorem, in which the movement of a predator whilst foraging in a patchy environment is dictated by the trade-off between diminishing returns from a finite patch and the expense of searching for a new one (Charnov 1976). Recent movement/foraging studies tend to focus on the behaviour of animals between and within patches and often focus on the change point where animals begin search behaviour (van Eeden *et al.* 2016; Trapanese, Meunier & Masi 2019). The concept of Area Restricted Search (ARS) (Kareiva & Shigesada 1983; Kareiva & Odell 1987; Fauchald & Tveraa 2003) suggests that animals are consistently searching for resources, but spatially or temporally change and restrict their search based on the cues individual animals receive. How animals integrate this information and the subsequent effect upon foraging and movement behaviour remains a key challenge within ecological studies.

1.2 Seabird movement ecology

Seabirds are a group of species that lend themselves well to studying foraging and behaviour from movement. They are generally long-lived animals, with high annual survival rates, extended juvenile phases, and have long chick-rearing processes (Hamer, Schreiber & Burger 2001). During the breeding season, seabirds are central place foragers, returning regularly and consistently to the nest to provision chicks, making them good species to work with and study their movements. Seabirds are considered indicators of marine ecosystem health (Furness & Camphuysen 1997), and as top predators they reflect the changes in the oceans around them. Seabirds

are also in large-scale decline (Paleczny *et al.* 2015), meaning that there is a conservation need to understand at-sea behaviour to help identify and protect important habits and high use areas.

Seabirds are mostly found on offshore islands or inaccessible cliffs and are largely colonial nesters. Nests within colonies are either in direct proximity to others or within short distances of one another on the same island. It is thought that colonial living initially may have arisen due to a shortage of suitable habitat (Coulson 2001) but that this then also provided individuals with a social information exchange that aided in foraging on dispersed and unpredictable resources (Weimerskirch *et al.* 2010). Understanding seabird foraging and movement was traditionally undertaken using ship-based surveys. However, the advent of cheaper, smaller biologging technology has enabled a proliferation of studies using tracking technology.

When foraging at sea, seabird movement may be driven by a variety of environmental factors. Weather can play an effect on seabird movement, for example, species are understood to fly with the wind with increasing speeds (Adams & Flora 2010) and can influence how far Cape gannets, *Morus capensis*, forage from their colony (Adams & Navarro 2005). Increased wind speeds affect the behavioural states of individual wandering albatross, *Diomedea exulans*, with increased associated with more travel and less search behaviour (Clay *et al.* 2020). Storm systems have also been shown to influence seabird foraging trips and patterns (Huang, Bass Jr & Pimm 2017).

Seabirds target their foraging towards predictable oceanic features where foraging opportunities are more likely to be successful (Weimerskirch 2007). Seabird movement and distribution has been previously noted to correlate with primary productivity markers such as oceanic chlorophyll from pelagic surveys and during GPS tracking of individuals (Suryan, Santora & Sydeman 2012; Kane *et al.* 2020). Changes in chlorophyll can often be associated with changes in other primary productivity markers such as surface sea temperature the fronts where these changes occur have been documented as important foraging areas for seabirds (Scales *et al.* 2014). For example, northern gannets dive more frequently when foraging on sea fronts (Cox *et al.* 2016). Oceanic fronts can be caused by changes in sea topography (Johannessen

& Foster 1978; Valavanis, Katara & Palialexis 2005) and seabirds often target foraging in areas of changing sea topography including seamounts (Thompson 2007) and reefs (Erwin & Congdon 2007). Changing topography in the ocean may also provide nutrient rich areas of upwelling, which are understood to be foraging areas for a wide variety of seabird species (Brown 1979; Haney 1986; Grecian *et al.* 2016).

Seabirds have also been found to associate with human activities at sea, notably with fishing vessels in the pursuit of fisheries discards (Garthe & Hüppop 1994; Garthe, Camphuysen & Furness 1996; Valeiras 2003; Le Bot *et al.* 2019), with northern gannets found to change their behaviour based upon vessel activity and the potential for discard availability (Bodey *et al.* 2014). Recent research has suggested that black-browed albatross, *Thalassarche melanophris*, remember the locations of predictable fishing boats, even though they prefer foraging elsewhere – suggesting a hierarchical foraging preference strategy (Collet & Weimerskirch 2020).

Seabirds show high repeatability in their foraging patterns, often returning to the same areas (Weimerskirch 2007), particularly where they have had foraging success (Patrick *et al.* 2014; Wakefield *et al.* 2015). Individual foraging site fidelity appears to be a learnt behaviour, juvenile northern gannets display less site fidelity than breeding adults suggesting early life effects on foraging behaviour (Votier *et al.* 2017). Individual level behaviours and specialisations are not only seen in movement data, seabirds often individual specialisations in dietary intake (Furness *et al.* 2006; Bodey *et al.* 2018b; Ramos *et al.* 2020). For example, Australasian gannets, *Morus serrator*, show individual specialisation of dietary intake even when controlling for habitat available between different colonies (Rodríguez-Malagón *et al.* 2020). Seabird foraging strategies have also been tied to animal personality (Patrick & Weimerskirch 2014b). For example, bolder black-legged kittiwakes, *Rissa tridactyla*, have higher levels of foraging site fidelity (Harris *et al.* 2020).

Across all seabirds there are range of sexually dimorphic and monomorphic species (Schreiber & Burger 2001). Sex differences in behaviour are usually pronounced in dimorphic species (Serrano-Meneses & Székely 2006; Weimerskirch *et al.* 2006b; Gianuca *et al.* 2019). These differences may be due to increased aggression between sexes in species which show competitive exclusion (Phillips *et al.* 2004b), or where

different sexes may have access to different foraging areas due to their size (Phillips *et al.* 2004b; Patrick & Weimerskirch 2014a) or foraging preference (Wanless, Harris & Morris 1995). Where sexes differ in size there may also be differences in the associated energetic cost of locomotion; being higher for the larger sex as seen in other taxonomic groupings (Powell & Leonard 1983; Sandell 1989; Browning *et al.* 2006; Lees *et al.* 2011). However, both dimorphic and monomorphic species show sex-specific foraging strategies (Gianuca *et al.* 2019; De Pascalis *et al.* 2020; Lescroël *et al.* 2020), often driven by different nutrient requirements (Maklakov *et al.* 2008; Bond & Diamond 2010), or other less obvious intrinsic differences. Lewis *et al.* (2002) reported that, for northern gannets, females tend to be more selective than males when choosing foraging grounds. Different space use between the sexes has been demonstrated across seabird species (Mancini *et al.* 2013; Camphuysen *et al.* 2015; Miller *et al.* 2018) and this may be due a reduction of intraspecific competition or different nutrient requirements. However, evidence also suggests that one sex may be outcompete the other at busier foraging grounds; as seen in the wedge-tailed shearwater, *Puffinus pacificus*, (Peck & Congdon 2006) and various Southern Ocean petrels and albatross (Phillips *et al.* 2011b).

Not only may species show differences in their direct foraging behaviour, we also find differences in the care of chicks, such as provisioning or guarding from predators. For example, male northern gannets feed chicks less than females (Montevecchi *et al.* 1984) and in contrast to this many auks transition from bi-parental care to paternal care only (Harding *et al.* 2004). Parenting and provisioning differences may present themselves as sexually different diets or foraging areas, as adults search for appropriate prey and/or self-provision (Weimerskirch *et al.* 2003). Sex differences in the foraging behaviour of seabirds are often studied from a perspective of diet or location. This implies differences in the energetics of foraging or nutrient intake, though this is a relatively unstudied area of seabird ecology.

1.3 Using biologging to understand animal behaviour

The development of biologging, the practice of attaching data loggers (tags) to animals, has changed our understanding of how animals, and particularly seabirds, move through their environment. A problem with understanding the movement ecology of a species is often the inability to follow or see an individual animal at all times. This is particularly true from a marine perspective. At-sea survey techniques have provided large-scale distributions of animals (Jahncke, Coyle & Hunt Jr 2005; Serratosa *et al.* 2020; Waggitt *et al.* 2020), but it remains difficult to interpret the origin or behaviour of individuals. Biologging then provides information on the movement of known individuals. When combined with modelling approaches, biologging has had great success in predicting the distribution of marine animals such as seabirds (Grecian *et al.* 2012; Critchley *et al.* 2020). Biologging also provides movement information that can be used to describe the behaviour of animals without directly observing them (Patterson *et al.* 2008; Patterson *et al.* 2009; Dean *et al.* 2012).

From early iterations of VHF radio collars on grizzly bears, *Ursus arctos*, (Craighead 1982) and modified depth loggers on Jackass penguins, *Spheniscus demersus*, (Wilson & Bain 1984), biologging has benefitted from a rapid expansion of technology. Today, ecologists can take advantage of a range of biologging devices to provide movement information of animals at various scales. A summary of the different spatial biologging technologies and their resolutions can be seen in Figure 1.1.

Geolocators are a common platform used to track animals over long distances and time-periods. These tags use changes in the timings of sunrise and sunset to determine two locations a day for up to several years, though at poor spatial resolution (Phillips *et al.* 2004a). Geolocators are often used to identify animal migrations and movements over long temporal and spatial scales (González-Solís *et al.* 2007; Harris *et al.* 2010). For example, geolocators have been used to document and explore the migration of the arctic tern, the longest migration of any known animal (Egevang *et al.* 2010). More recent analysis using geolocators has demonstrated that different populations of terns do not mix during these migrations

allowing researchers to explore the adaptive nature of migration (Alerstam *et al.* 2019).

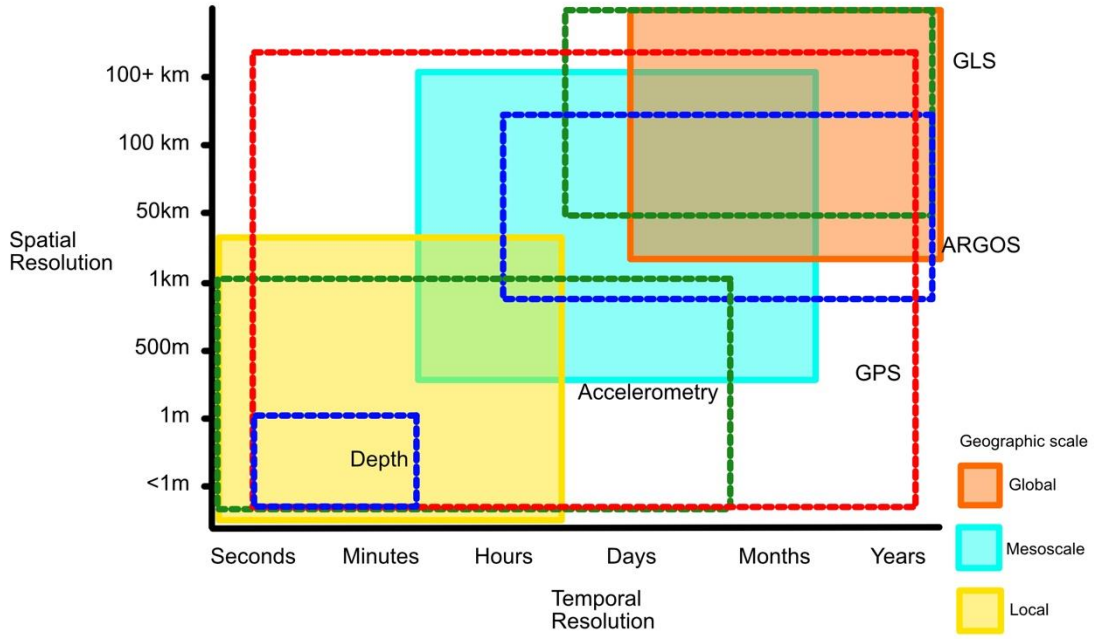

Figure 1.1 A conceptual diagram showing the different kinds of tagging technology available to movement researchers. Different technologies operate at different spatial and temporal resolutions. Boxes reflect resolutions researchers may aim for in experimental design, analysis, or hardware development. It is important to note that all scales of data can be aggregated over time to produce uses wider the boxes shown here. Depth and accelerometry loggers often require combination with another device to gain a spatial component. Solid boxes are provided to show the potential spatial and temporal relationships that can be explored using specific biologging technology. Scales are approximate and are designed to show breadth of technology available. Colours are shown only to differentiate between technologies. References for this figure may be found in Appendix A.

The ARGOS system is another common animal tracking system, commonly used on marine animals (McClintock *et al.* 2015), though also used in terrestrial systems (Schwartz & Arthur 1999). This system uses animal-borne transmitters that

communicate directly with a satellite network to determine locations several times a day (Coyne & Godley 2005). The ARGOS system is generally used on animals capable of bearing a long-term tracking unit and is capable of providing long term behavioural or movement data. For example, monitoring the long-term foraging patterns of loggerhead turtles, *Caretta caretta*, outside of the breeding season (Dujon *et al.* 2018) or the frequency of surfacing events by blue sharks, *Prionace glauca*, (Doyle *et al.* 2015). The ARGOS system has also been used in several influential seabird papers, demonstrating seabirds foraging at predictable locations (Weimerskirch 2007), and following migration across life stages (Péron & Grémillet 2013).

Perhaps the most ubiquitous seabird tagging technology is the Global Positioning System (GPS) tag. Early iterations of commercially available GPS were heavy and suitable for only for larger mammals (Clark *et al.* 2006) but modern tags are now capable of archiving several days worth of GPS coordinates on devices that weigh as little as 1g (Pathtrack 2020). The rise of GPS tagging has resulted in a wide array of studies examining the movement of animals across the Earth (Joo *et al.* 2020b). The first bird tagging studies began appearing in the late 90s and early 2000s with studies on homing pigeons, *Columba livia domestica*, (Hünerbein *et al.* 1997). The first seabird GPS tracking paper to capture wide attention was Weimerskirch *et al.* (2002) who tracked wandering albatross and started the process of understanding foraging behaviour and interactions with environmental covariates. As GPS tags have become smaller and lighter, they have been used to understand the space use of the smallest breeding seabird in the North Atlantic, the European storm petrel, *Hydrobates pelagicus*, (Bolton 2020). GPS tags are now widely used in seabird movement ecology and have provided important insights into the distribution and movement of animals that can directly feed into conservation and management decisions (Lascelles *et al.* 2012; Thaxter *et al.* 2012; Lascelles *et al.* 2016).

Biologging technology focuses not only location data but also on collecting data that may be further used to study a species' ecology. An often-used data logger in seabird ecology is the time depth recorder, a tag that measures the length of time an animal is underwater and the depth it reached during this event. Early versions of this

technology used isotopes of phosphorous (Bain & Wilson 1982) or the adaptation of capillary tubes of from SCUBA dive depth meters (Wilson & Bain 1984) and provided coarse resolution data of maximum depth. Modern time depth recorders use sophisticated pressure sensors to provide high-resolution depth information. These tags can be used to ground-truth foraging events in marine predators (Garthe *et al.* 2014) and to understand underwater search behaviour (Shoji *et al.* 2016). Temperature loggers, attached externally, are devices that may be used to monitor the surrounding environmental conditions (Roquet *et al.* 2017). When placed inside an animal, they may be used to monitor internal temperature, often as an indicator of digestion and successful prey capture (Díez *et al.* 2017). For example, temperature loggers placed in the stomachs of grey-headed albatross, *Thalassarche chryostoma,* can differentiate between solid and liquid prey suggesting many albatross feed on surface jellyfish and salps (Catry *et al.* 2004). Temperature loggers have also been used to explore the interactions between search behaviour and prey ingestion – Weimerskirch *et al.* (2007) demonstrated that increased food intake does not affect the onset of new search behaviours in wandering albatross.

Biologging has also enabled studies of energetics, traditionally using heart-rate loggers coupled with equipment such as respirometry chambers to determine the respiration rate of an animal and correlate this to the volume of oxygen consumed by muscles (Gleim & Nicholas 1989; Butler *et al.* 1995). Double labelled water (DLW) has also been used to study energetics in free-living animals; in DLW studies, water is made using isotopes of hydrogen or oxygen and injected into animals – the blood concentration of the double labelled water over time then provides researchers with an approximation of cellular respiration and the metabolic rate of individual animals (Speakman 1997). DLW and heart rate logger studies are less prevalent in modern research, perhaps due to their more invasive nature, but have the potential to calculate true energetic expenditure in an individual (Brage *et al.* 2015) both at instantaneous events (Green *et al.* 2009) and longer time scales (Green 2011). Results from FMR and DLW are often the basis for widely used estimates of Field Metabolic Rate (FMR); the average energy expended by an individual animal in a given period – often 24 hours (Butler *et al.* 2004; Sparling *et al.* 2008). Whilst several

methods exist for calculating FMR, producing energetic costs for specific behaviours has remained challenging.

In recent years, accelerometry has been used to explore energetic expenditure (Yoda *et al.* 1999; Halsey *et al.* 2009). Dynamic body acceleration measures can be linked with energetic intake and expenditure (Bouten *et al.* 1994; Halsey, Shepard & Wilson 2011; Elliott *et al.* 2013a; Hicks *et al.* 2017), although easy to replicate methodologies remain elusive (Wilson *et al.* 2019). Accelerometers also allow researchers to explore fine-scale behaviour of individual animals, measuring acceleration across three dimensions at temporal scales up to and beyond 50Hz. This information can be used to discern the pitch, roll, and sway of an animal which can then be in turn used to identify/infer behaviours such as wing flapping, walking, or resting (Shepard *et al.* 2008a; Shepard *et al.* 2008b). As new technologies become available, they will surely provide the opportunity to discover the links between animal behaviour, movement, and the surrounding environment.

While biologging studies are able to provide detailed information on location and behaviour, they provide little information on diet. Some studies have attached cameras to marine predators to record foraging behaviour and diet (Hooker *et al.* 2002; Machovsky-Capuska *et al.* 2011; Votier *et al.* 2013); however, these studies are often difficult due weight limitations or poor camera quality.

This thesis will build upon substantial knowledge of seabird ecology by identifying and differentiating behaviours based on movement data, and will then then investigate the role of these behaviours in seabird foraging ecology.

1.3 Study Species and Region

This thesis uses data from three species collected from The Saltee Islands, southeast Ireland: The Northern gannet, *Morus bassanus,* (Chapters 2, 4, and 5), the Atlantic puffin, *Fratercula arctica,* (Chapter 3), and the razorbill, *Alca torda*, (Chapter 3). Chapter 2 also includes data collected from Northern gannets on the Bass Rock, Scotland.

The Northern gannet *Morus bassanus* (Irish: Gainéad, hereafter gannet, Figure 1.2a) is the North Atlantic's largest breeding seabird (Nelson 2002). Juvenile gannets show strikingly different plumage from adults and can be aged up to 5 years before aging becomes impossible, though ringing records report the oldest recorded lifespan of a gannet as 37 years and 4 months (Robinson 2005). Annual adult survivability is high, with 0.91 ± 0.002 survival rate (Nelson 2002). It is thought that gannets do not start breeding until at least 7 years and lay a single egg in late spring each year, both parents undertake incubation and chick-rearing duties, though females undertake a larger role in provisioning (Montevecchi *et al.* 1984). Incubation takes 42-46 days and chicks are fledged within 84-97 days (Robinson 2005). During the breeding season they forage at sea, often travelling in excess of 500 km from colonies (Hamer *et al.* 2000). Gannet foraging ranges and locations are known to be density dependent (Davies *et al.* 2013) and many colonies have separated foraging grounds to facilitate reduced competition (Wakefield *et al.* 2013). Gannets are piscivores, and forage on a wide variety of prey, particularly herring, *Clupea harengus*, and mackerel, *Scomber scombrus*, (Montevecchi & Myers 1997; Lewis *et al.* 2003), but individuals are also understood to specialise on different prey types including fisheries discards which are an important source of food for gannet populations (Votier *et al.* 2013; Bodey *et al.* 2018b). During the non-breeding season, gannets become more pelagic and spend long periods of time offshore, often remaining in the North Atlantic although many also travel south to Western Africa (Kubetzki *et al.* 2009).

Figure 1.2. The northern gannet *Morus bassanus,* shown here as an individual leaves the colony at Great Saltee

The Atlantic puffin, *Fratercula arctica,* (Irish: Puifín, hereafter puffin, Figure 1.3) is the British Isles and Ireland's smallest breeding alcid. Puffins can be aged by counting the notches on their bill, aging individuals up to approximately 5 years, though aging after this becomes impossible (Harris 2014). Ringing records would suggest that puffins live on average 18 years with the maximum recorded reaching 37 years (Robinson 2005). Puffins usually start breeding at around 5 years of age (Harris & Wanless 2011) and lay a single egg in late April to early May each year. Incubation takes 36-43 days and chicks are fledged by 34-44 days, though this is highly variable and dependent on prevailing weather and foraging conditions (Harris & Wanless 2011). During the breeding season, puffins forage relatively closely to colonies, travelling a maximum of 66 km away from the colony (Harris *et al.* 2012). Puffins are bill loaders, carrying prey in the bill, and so their diet is relatively well understood. In the North East Atlantic this is predominantly sandeel, *Ammodytes spp*, but also sprat, *Sprattus sprattus,* and haddock, *Melanogrammus aeglefinus,* (Martin 1989; Harris &

Wanless 2011). During the non-breeding season puffins become entirely pelagic, with birds spreading throughout the North Sea, Atlantic Sea, and even the Mediterranean Sea (Fayet *et al.* 2016; Fayet *et al.* 2017). Puffins tracked overwinter from Skellig Michael, Ireland were found to travel as far as Newfoundland, Canada during winter migrations (Jessopp *et al.* 2013) and it is thought that most Irish populations undertake similar journeys. Atlantic puffins have experienced widespread decline throughout their European range and population trends outside of Europe are unknown, as a result Atlantic puffins are listed as 'Vulnerable' from a global perspective and considered 'Endangered' in a European context (Miles *et al.* 2015; BirdLife International 2017).

Figure 1.3 The Atlantic puffin, *Fratercula arctica,* in its colony on Little Saltee showing characteristic bill loading.

The razorbill, *Alca torda,* (Irish: Crosán, Figure 1.4) is a small auk that breeds around the coastline of the British Isles and Ireland. It is the closest living relative of the extinct great auk, *Pinguinus impennis*, (Moum, Arnason & Arnason 2002). Records report the oldest recorded lifespan of a razorbill is 41 years and 11 months and, as with most seabirds, annual adult survivability is high, with 0.9 survival rate (Robinson

2005). Incubation takes 32-39 days and chicks are “fledged” within 14-24 days post hatching (Robinson 2005). Razorbill chicks are flightless at fledging and remain waterborne until the development of flight feathers. Razorbill chicks often leave the nest early where males often take up a larger parental role at sea after “fledging” (Insley, Paredes & Jones 2003). During the breeding season razorbills forage at sea, remaining close to the colony often remaining within 26 km though longer trips have been observed (Isaksson *et al.* 2019). Razorbills are piscivores, and mainly forage on small fish prey, particularly sand eel (Family Ammodytidae), butterfish, *Peprilus triacanthus*, and herring (Barrett 2003).

Figure 1.4. The third study species of this thesis, the razorbill *Alca torda,* shown here as a pair of birds stand near their nest.

The Saltee Islands are located in the Celtic Sea approximately 5km offshore from County Wexford, Ireland (located at 52^{o} 7’ 37.92”, -6^{o} 35’ 45.6”, Figure 1.5) and consist of two islands: Great Saltee and Little Saltee. As the name would suggest, Great Saltee is the bigger of the two islands at 2 km long and comprising 0.89 km^{2} whilst Little Saltee, only 500m away, is 1.1 km and makes up 0.37 km^{2}. The islands

both vary from stony shore on the north side to low cliffs on the south. Both islands have been uninhabited since the early 1900s and support a variety of wildlife. The islands are afforded a special protection area status (Site Code 004002) due to the large number of seabird species including: northern fulmar, *Fulmarus glacialis*, northern gannet, great cormorant *Phalacrocorax carbo*, European shag *Phalacrocorax aristotelis*, lesser black-backed gull, *Larus fuscus*, herring gull, *Larus argentatus*, black-legged kittiwake *Rissa tridactyla*, common guillemot *Uria aalge*, razorbill, and Atlantic puffin.

Figure 1.5. The Saltee Islands, highlighted in the red box. Ocean colour throughout the image conveys the strong currents and tides in the area. Image compiled from Landsat-8 satellite imagery.

Great Saltee is home to a relatively small northern gannet colony. The earliest breeding record of gannets at Great Saltee comes from 1929 when Garnett (1929) reported a single pair breeding on the southern cliffs and suspected this represented a new record for the island, by 1943 the colony was still not yet in bloom and it was suspected that only two pairs were attempting to breed (Weaving & Barlee 1943).

The Great Saltee gannet colony remains probably the best documented colony from its origins up to modern records (Nelson 2002), and the last published count of gannets at Great Saltee showed a colony of approximately 4,722 breeding pairs (Newton, Harris & Murray 2015) making it Ireland's third largest colony, behind Little Skellig (35,294 pairs) and The Bull Rock (6,388 pairs) (Cummins *et al.* 2019). The history of puffins on the Saltee Islands is less well known than gannets although some information is available. Garnett (1929) did mention the prevalence of puffins on Great Saltee though provided no information regarding population sizes. Census counts for County Wexford show a total population of 775 pairs in 1969 rising to 1,822 pairs in 2002 (Mitchell *et al.* 2004). However as burrow nesters, population estimates are difficult to obtain, and these are unlikely to be accurate (Arneill *et al.* 2019). Since these surveys, Great Saltee has seen a huge rise in the rat population and tourist activity which has impacted the puffin population. Little Saltee is rat free and recent census suggest approximately 241 ± 101 pairs of puffins (Costello 2016), and counts between the two islands have numbered more than 500 individuals (*personal obs.*).

The Celtic Sea surrounding the Saltees is relatively shallow (<100m) but increases in depth towards the continental shelf edge and predominantly consists of sand and mud substrate (EMODnet 2009). The islands themselves are connected to the coastline by a shallow underwater reef, known locally as Patrick's Bridge. Due to the shallow bathymetry surrounding the saltees, the area is subject to strong tidal currents flowing from west to east when flooding and east to west when ebbing. Figure 1.5, a landsat image of the Saltee Islands and Wexford coastline, shows strong colour contrasting on the ocean's surface representing sediment movement from ocean currents. The area around the Saltees, and more widely The Celtic Sea, is an intensively fished area, with predominant fishing activity comprised mostly of beam trawlers, bottom trawlers, and dredgers (Gerritsen & Lordan 2014). These gear types target the ocean floor, and a large diversity of species (Gerritsen & Lordan 2014), creating opportunities for seabirds to forage on discards (Berrow, O'Neill & Brogan 1998; Rochet, Péronnet & Trenkel 2002).

1.4 Thesis Aims and structure

This thesis aims to explore ways in which behaviour can be inferred from movement data, and then investigate how these behaviours may be driven by both intrinsic and extrinsic factors. Specifically, within each chapter I have examined a particular facet of seabird movement ecology and these are detailed below:

Chapter 2 will test the efficacy of commonly used methods of behavioural annotation on GPS data by validating inferred putative foraging against actual prey capture attempts recorded by co-deployed time depth recorders on northern gannets. This chapter aims to identify behavioural annotation methods with the highest predictive power which is an important step in identifying important foraging areas at sea.

Chapter 3 will explore the foraging behaviour of Atlantic puffins in an area with strong tidal currents. Seabirds show behavioural adaptations to predictable environmental features. Atlantic puffins are a species with high energetic costs of movement. This chapter aims to document and understand the behavioural adaptations of puffins in a tidally active area.

Chapter 4 will investigate sex-based differences in the energetics of northern gannet foraging. Gannets show strong sexually divergent foraging behaviour and this may impact the energy budgets of the sexes. This chapter aims to integrate energetic estimates of prey capture with dietary information to understand sex-based differences in energy budgets of northern gannets.

Chapter 5 will explore lateralised behaviours in northern gannets. Behavioural lateralisation can provide advantages to species in complex foraging systems. This chapter aims to use accelerometry to determine if gannets engage in lateralised roll behaviour during foraging.

Chapter 6 provides a synthesis of the work covered in previous chapters, highlighting important results and suggesting where further studies are likely to arise based on the findings of this research.

Chapter 2: Search and foraging behaviours from movement data: a comparison of methods.

This chapter is also published as:

Bennison, A., Bearhop, S., Bodey, T.W., Votier, S.C., Grecian, W.J., Wakefield, E.D., Hamer, K.C. and Jessopp, M., 2018. Search and foraging behaviours from movement data: a comparison of methods. *Ecology and Evolution*, *8*(1), pp.13-24.

Minor edits have been undertaken to improve clarity and flow, but the text is presented largely unchanged.

This study was conceived between Mark Jessopp, Stuart Bearhop, and I who also designed the initial methodology. James Grecian undertook the analysis for hidden markov modelling, whilst I undertook all other analysis. All authors provided input on the analytical framework and manuscript preparation.

2.1 Abstract

1. Search behaviour is often used as a proxy for foraging effort within studies of animal movement, despite it being only one part of the foraging process, which also includes prey capture. Whilst methods for validating prey capture exist, many studies rely solely on behavioural annotation of animal movement data to identify search, and infer prey capture attempts. However, the degree to which search correlates with prey capture is largely untested.
2. This study applied seven behavioural annotation methods to identify search behaviour from GPS tracks of northern gannets (*Morus bassanus*), and compared outputs to the occurrence of dives recorded by simultaneously deployed time-depth recorders. We tested how behavioural annotation methods vary in their ability to identify search behaviour leading to dive events.
3. There was considerable variation in the number of dives occurring within search areas across methods. Hidden Markov models proved to be the most successful, with 81% of all dives occurring within areas identified as search. K-means clustering and first passage time had the highest rates of dives occurring outside identified search behaviour. First passage time and hidden Markov models had the lowest rates of false positives, identifying fewer search areas with no dives.
4. All behavioural annotation methods had advantages and drawbacks in terms of the complexity of analysis and ability to reflect prey capture events while minimising the number of false positives and false negatives. We used these results, with consideration of analytical difficulty, to provide advice on the most appropriate methods for use where prey capture behaviour is not available. This study highlights a need to critically assess and carefully choose a behavioural annotation method suitable for the research question being addressed, or resulting species management frameworks established.

2.2 Introduction

Movement is major part of a species' ecology. The underlying processes driving the movement of individuals and populations are studied widely, however it is often unfeasible to directly observe animals through constant effort. As a result, movement studies have focussed on remote detection of animals through technologies such as GPS and satellite tracking. The development, miniaturisation, and reduction of cost in remote tracking technologies has enabled its widespread use in ecological studies (Cagnacci *et al.* 2010). Remote tracking enables behaviours to be inferred from an animals' trajectory (Buchin *et al.* 2010), and has led to rapid advances in the understanding of species' ecology (Nathan *et al.* 2008).

While movement patterns are often used to distinguish active phases from rest, or search behaviour from travelling (van Beest & Milner 2013; Dzialak *et al.* 2015), identifying these behavioural states typically relies on more complicated modelling procedures to detect potential underlying mechanisms within behaviour identification (Jonsen, Myers & James 2006; Kerk *et al.* 2015). Considerable progress has been made in developing methods that can categorize behaviours based on simple movement metrics (Edelhoff, Signer & Balkenhol 2016). These methods commonly identify multiple states and ascribe these to predefined behaviours such as search, rest, or travel (King, Glahn & Andrews 1995; Palmer & Woinarski 1999; Hamer *et al.* 2000; Weimerskirch *et al.* 2006a; Guilford *et al.* 2008; Evans *et al.* 2015; Shepard, Ross & Portugal 2016). However, Gurarie *et al.* (2016) argued for closer and more detailed exploratory analysis of movement data to prevent mis-specification of behaviour, suggesting that the strengths of particular methods need to be more carefully considered so they are suitably attuned to the specific questions being asked by researchers.

Within conservation management, there is an increasing reliance on identifying space use by species of conservation concern (Allen & Singh 2016). For example, within the marine environment, foraging areas could be considered for the protection and management of seabird species (Lascelles *et al.* 2016). The use of these approaches may contribute to the establishment of conservation measures

including designation of marine protected areas (Grüss *et al.* 2011). Foraging activity is a key component in an animal's time and energy budget, and it is well established that animals in environments with patchy resources must engage in search behaviour to optimise their foraging effort in terms of maximising prey encounters (MacArthur & Pianka 1966). Therefore, foraging can be considered a two-part system, containing both search and prey capture attempts (Charnov 1976). Understanding the interaction between search and prey capture is a key component in optimal foraging theory (Pyke 1984). For example, while there has been much work identifying area restricted search (Knell & Codling 2012), there is little information on the relationship between search and prey capture. Validation of search behaviour is difficult particularly in animals where direct observation is challenging, such as those in many biotelemetry studies. Many movement studies use path segmentation techniques to detect search behaviour, however many of these are unvalidated estimates of search due to the lack of a second data stream for ground-truthing. Validation of prey capture attempts has been achieved using animal-borne cameras (Moll *et al.* 2007; Bicknell *et al.* 2016), time-depth recorders (Tinker *et al.* 2007; Dean *et al.* 2012; Shoji *et al.* 2015c), stomach loggers (Weimerskirch, Gault & Cherel 2005), and accelerometers (Hansen *et al.* 2007; Sato *et al.* 2007) among others. However, many of these technologies are either expensive resulting in small sample sizes, or are too large to deploy on animals in combination with location loggers without significant adverse impacts (Barron, Brawn & Weatherhead 2010; Hammerschlag, Gallagher & Lazarre 2011; Vandenabeele *et al.* 2012). As a result, many studies still rely on the sole use of location data and path segmentation approaches to identify behaviour. The determination of behaviour from movement data, is an active area of research and the subject of many reviews (Jacoby *et al.* 2012; Edelhoff, Signer & Balkenhol 2016; Hays *et al.* 2016; Allen, Metaxas & Snelgrove 2017). There are several different methods for undertaking behavioural annotation or detecting important areas of high use by animals. Of note, and frequently used, are movement pattern description and process identification. Methods based around movement pattern description are often aimed at trying to split between different behavioural periods or to locate changes in behaviour (Edelhoff, Signer & Balkenhol 2016). Process identification aims to take things a step further and concentrates on methods that are focussed towards

being able to describe the underlying processes, whether extrinsic or intrinsic, and describe how these inform behaviour.

Northern gannets (*Morus bassanus)*, hereafter gannets, are a well-studied species that occur principally in the temperate shelf seas of the North Atlantic during the breeding season. Gannets are visual predators (Cronin 2012) and undertake plunge diving from height, entering the water at speeds of up to 24m/s (Chang *et al.* 2016). Prior to diving, gannets typically slow their flight and increase their path sinuosity (Wakefield *et al.* 2013; Bodey *et al.* 2014; Patrick *et al.* 2014; Warwick-Evans *et al.* 2015). The relationship between slow speed during search, and prey capture attempts has been established both theoretically (Benhamou 2004; Bartoń & Hovestadt 2013) and empirically in a variety of mobile marine and terrestrial species (Anderson Jr & Lindzey 2003; McCarthy *et al.* 2010; Byrne & Chamberlain 2012; Edwards *et al.* 2013; Wakefield *et al.* 2013; Williams *et al.* 2014; Towner *et al.* 2016). Such changes in movement and clearly identifiable prey capture attempts in the form of dives (Garthe, Benvenuti & Montevecchi 2000; Cleasby *et al.* 2015), as well as their ability to carry multiple devices and ease of recapture, make gannets a suitable model species to explore the ability of movement–based analysis to identify search behaviour and prey capture attempts.

In this study, we apply and compare seven methodologies covering movement pattern description and process identification, to predict search behaviour in gannets using GPS location data. If search behaviour is a precursor to prey capture attempts, dives will occur primarily within areas identified as search. With consideration given to opportunistic foraging, we hypothesise that more successful methods of search classification will contain more true positives (dive events occurring within identified search), fewer false positives (search containing no dives), and fewer false negatives (dives occurring outside identified search behaviour). Using this framework, we will also provide recommendations on the appropriate use of methodological approaches.

2.3 Materials and methods

Data Collection

Breeding adults at two island colonies, Great Saltee, Co. Wexford, Ireland (52° 7' 37.92", -6° 35' 45.6") and Bass Rock, Scotland, UK (56° 4' 36.19", -2° 38' 29") were tracked while attending 2-7-week-old chicks over a 38-day period from late June to early August 2011. Nine birds at Great Saltee and eight birds at Bass Rock were caught using a metal crook or wire noose fitted to a 4-6m pole, and fitted with GPS loggers coupled with Time Depth Recorders (TDRs). GPS loggers (i-gotU GT-200, Mobile Action Technology Inc., Taipei, Taiwan, 37g), sealed in heatshrink plastic, recorded locations every 2 minutes. CEFAS G5 TDRs (CEFAS Technology, Lowestoft, UK, 2.5g) were deployed using the fast-log dive sensor at 4Hz and used to identify dive events based on a 1m depth threshold being exceeded, hereafter TDR dives. This was to ensure dives reflected prey capture attempts (median dive depth of 4.6m in plunge diving gannets, and 8m when pursuit diving; (Garthe, Benvenuti and Montevecchi (2000)) rather than other surface related activities such as resting, washing, or preening. Devices were attached following (Grémillet *et al.* 2004b), and involved affixing loggers ventrally to 2-4 central tail feathers using strips of waterproof Tesa tape. Total instrument mass was ≤ 2% of body mass, below the maximum recommended for seabird biologging studies (Phillips, Xavier & Croxall 2003), and tag position was considered to minimally impede gannet aerodynamics and hydrodynamics (Vandenabeele *et al.* 2012). Deployment and retrieval handling times was approximately 10 minutes.

Data processing

GPS tracks were processed using the *AdehabitatLT* package (Calenge 2011) in the R statistical Framework. Location data were transformed into Cartesian coordinates using a Universal Transverse Mercator (UTM) 30N projection before calculating step length and turning angles. Although GPS tags were programmed to take locations every two minutes, if there was no available GPS signal (because a bird was diving

for example), locations may not have been exactly two minutes apart, and so tracks were standardised through linear interpolation to a two-minute interval. Speed, step length, turning angle, and distance from colony were calculated for every point along a bird's track. Points within 5km of the colony were removed to avoid potential locations associated with colony rafting and bathing (Carter *et al.* 2016), as were those occurring at night (between civil sunset and sunrise) because gannets are visual diurnal foragers (Nelson 2002). TDR dives were split into dive events and produced a single timestamp point representing the start of any dive event over 1m for appending to tracks following behavioural classification.

We applied a suite of methods commonly used to identify searching or infer foraging behaviours from movement data, summarised in Table 2.1. The methods are not considered exhaustive, but represent a range of approaches covering movement pattern description, and process identification (Edelhoff, Signer & Balkenhol 2016). Movement pattern description approaches include kernel density, first passage time (FPT), and speed/tortuosity thresholds, while process identification techniques applied covered K-means clustering and two state space models; hidden markov models (HMM) and effective maximisation binary clustering (EMbC). The two forms of state-space models were used to represent diverging classes of state-space model; maximum likelihood methods (EMbC), and Bayesian Monte Carlo methods (HMM) (Patterson *et al.* 2008). While not predicting/identifying search behaviour directly, we also applied machine learning (generalised boosted regression models) to predict dives from track metrics rather than search behaviour. We followed the standard methodology for each technique outlined in the published literature, and provide references for detailed guidance on applying each approach.

Methods of predicting search behaviour routinely identify chains of search in successive locations. Chains can be a single point in length, or may include multiple consecutive points along a movement track (see figure 2.1). Given that in gannets, individual prey capture attempts (dives) occur at discrete locations/times, we extracted metrics of dives occurring within search, dives outside of search, and search containing no dive. Data from the two colonies were processed independently

to account for potential differences in movement metrics associated with differences in local habitat and prey availability.

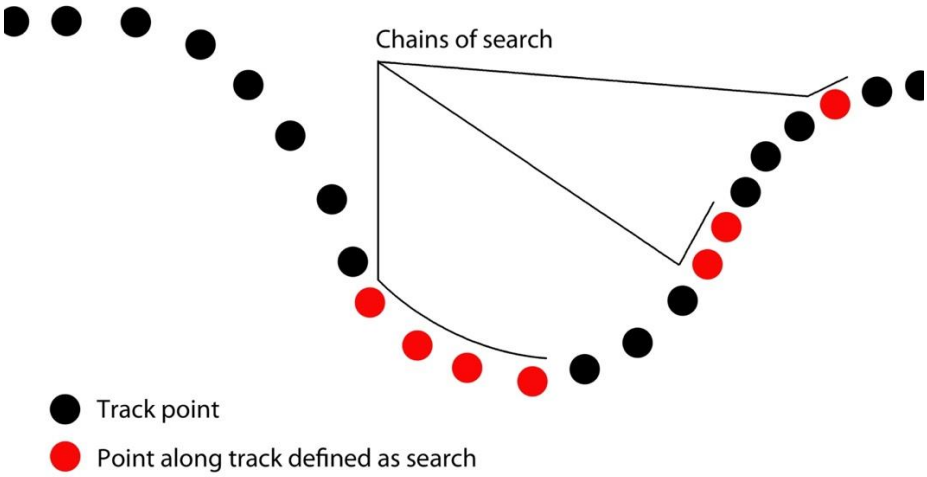

Figure 2.1. Conceptual diagram of locations through time identifying points of search behaviour within the series that reveal search chains of differing lengths

Table 1. Summary of common methodological approaches to identifying search and foraging behaviour in movement data. While all methods require validation data to assess how well the method works, it is not necessarily required to implement the method.

Method	*Analysis complexity*	*Requires validation data*	*Suitable for investigating relationships with environmental variables*	*Immediately applicable to other species/locations*
Machine Learning	High & large data requirement	Yes	Yes	No
k-means	Low	No	Yes	Yes
Thresholds	Medium	Yes	Yes	No
FPT	Medium	No	Yes	Yes
HMM	Medium	No[1]	Yes	Yes
Kernel density	Low	No	Dependent on scale	Yes
EMbC	Low	No	Yes	Yes

[1]HMM do not require validation data in this context, but can employ if desired.

Kernel density

Time-in-space is considered to be a good proxy for foraging effort (Warwick-Evans *et al.* 2015). GPS locations (excluding locations within 5km of the colony and locations at night) were used to estimate kernel densities in ArcMap 10.2, which uses a kernel smoothing function based on the quartic kernel function by Silverman (1986), and had a bandwidth/search distance of 10km. This was used to create a kernel density square grid with sides of 10km. The method produces a $10km^2$ grid with relative intensity of both TDR dives and GPS tracks. Dutilleul's modified spatial *t*-test (Dutilleul *et al.* 1993) was used to determine the spatial correlation between the intensity of dives, and intensity of tracks, accounting for spatial autocorrelation in the data.

First passage time (FPT)

First passage time analysis was undertaken following Fauchald and Tveraa (2003). Though tracks were standardised in time for all other analysis, FPT requires tracks to be redistributed in space to account for changes in bird speed, and so tracks were redistributed using linear interpolation to 500m distances. Analysis was undertaken using the *AdehabitatLT* package in R (Calenge 2011). Based on the behavioural response ranges reported by Bodey *et al.* (2014) for gannets, circles of radii ranging from 50m to 12,000m were used to construct first passage time values. The maximum log-variance of first passage time values were then used to determine appropriate search radii for each individual bird. The slowest sextile of passage times were considered to be relatively higher intensity search behaviour as used by Nordstrom *et al.* (2013), and also indicated in work by Hamer *et al.* (2009) following Fauchald and Tveraa (2003). Search radii were used to create an amalgamated area of search along an individual bird's track, with GPS points along this track treated as "search" points. Though FPT can be used to determine nested levels of area restricted search (Hamer *et al.* 2009), we have considered only the highest levels of search behaviour to maximise the number of dives potentially occurring within search.

K-means clustering

K-means clustering is a method of vector quantization that aims to partition *n* observations into *k* clusters, and has been used to cluster data points consistent with different behaviours (Jain 2010). K-means clustering was undertaken using the MacQueen algorithm (MacQueen 1967) on step-length and turning angle between successive GPS locations. The optimum number of clusters was determined using the 'elbow method' where the percentage of variance explained (the ratio of the between-group variance to the total variance) is plotted as a function of the number of clusters and the point where addition of further clusters results in only marginal increases in explained variance (Ketchen Jr & Shook 1996). This resulted in three clusters, and these were then assigned behavioural states based on logical differences between the means of variables in each group. The cluster with largest step length and smallest tortuosity was defined as travel, short step length and intermediate tortuosity was considered consistent with rest, and intermediate step length and high tortuosity was considered consistent with search behaviour following Zhang *et al.* (2015).

Speed-Tortuosity thresholds

Speed-tortuosity thresholds from Wakefield *et al.* (2013) were applied to the data. These were developed based on prior knowledge of gannet foraging behaviour, and an iterative examination of plausible thresholds of movement indices from those initially suggested by Grémillet *et al.* (2004a). Thresholds suggested by Wakefield *et al.* (2013) were applied since they were based on data from tracked gannets from a range of colonies, including the data analysed in this study. Successive GPS locations were considered to represent search if they met any one of three conditions:

1) Tortuosity <0.9 and speed >1 m/s
2) Speed >1.5 m/s and <9 m/s
3) Tortuosity $\geq$ 0.9 and acceleration <-4 m/s^2

Speed and acceleration were calculated between L_{-1} and L_0 where L_0 is the focal point, while tortuosity is the ratio of the straight line to along the track distance between L_{-4} and L_4. Criteria were defined based on GPS and TDR data from Bass Rock deployments used in this study, and are therefore created from *a priori* information.

Hidden Markov Models (HMM)

Hidden Markov Models are an example of state-space modelling, where models are formed of two parts; an observable series and a non-observable state sequence (Langrock *et al.* 2012). The observable series, in this context, take the form of GPS relocations with consequential step length and turning angle whilst the non-observable are behavioural states. HMM use a time-series to determine what denotes the underlying states and the changes between them. The application of state-switching models to movement data allows behavioural modes to be examined, whilst considering the high degree of autocorrelation present in telemetry data (Patterson *et al.* 2008). When the observational error is low, hidden Markov models offer a more tractable approach to discretize behavioural modes from telemetry data than Bayesian approaches (Langrock *et al.* 2012). Using the R package *moveHMM* (Michelot, Langrock & Patterson 2016), the movement of each individual along a foraging trip was classified into one of three underlying states by characterization of the distributions of step lengths and turning angles between consecutive locations. A three-state model was a better fit to the data than a two-state model, and is consistent with previous work describing gannet movement (Bodey *et al.* 2014) as well as the identification of three states in EMbC and k-means clustering approaches within this study. Model iterations successfully converged to three states suggesting a good fit to the data. A gamma distribution was used to describe the step lengths, a von Mises distribution described the turning angles, and the Viterbi algorithm was used to estimate the most likely sequence of movement states to have generated the observations (Zucchini, MacDonald & Langrock 2016).

Expectation-maximization binary clustering (EMbC)

EMbC protocols are an unsupervised, multivariate example of a state-space modelling framework that can be used for behavioural annotation of movement trajectories, including search behaviour (see Garriga *et al.* (2016)). EMbC has been designed to be a simple method of analysing movement data based on the geometry alone, and can behaviourally annotate movement data with minimal supervision. EMbC is a relatively modern technique that is gaining traction within movement ecology. It has previously been used in a variety of movement studies, including exploring behavioural differences between distinct populations of the red-footed booby (Mendez *et al.* 2017) and coupling energy budgets with behavioural patterns under an optimal foraging framework (Louzao *et al.* 2014). Analysis was undertaken using the *EMbC* package in R (Garriga & Bartumeus 2015), using calculated velocities and turning angles to infer behavioural classifications.

Machine learning

While the methods outlined above all identify search behaviour, machine learning models are trained to specifically identify prey-capture/dive events based on track metrics. Analysis was undertaken using the *Caret* package in R (Kuhn 2008) using generalized boosted regression models to account for zero-inflation (Elith, Leathwick & Hastie 2008). Models were built using step length, speed, turning angle, hour of day, and tortuosity. Models were trained using 75% of the linked GPS/TDR dive data, with the remaining 25% of data kept for validation of predictions, and underwent cross validation 500 times during the training procedure. By combining all individual animal's data in this manner, we ensure that any intra-individual variation is accounted for in the modelling process. Receiver Operator Curves (ROC) were calculated (Fielding & Bell 1997) to determine the model of best fit at each colony.

Comparison of methods using TDR dives

In order to compare the predictive power of the seven methods outlined above in predicting areas in which dives occurred, TDR dive events were linked to GPS co-ordinates by matching the time/date stamps of both datasets for each individually tracked bird. To compare how well the methods, capture dive events within areas of

search, the proportion of dives within identified areas of search (true positive) as well as the number of search chains containing no dives (false positive) were calculated for FPT, k-means, thresholds, HMM, and EMbC. The correlation between kernel densities of GPS tracks and TDR dives was assessed using a Dutilleul's modified spatial T-test (Dutilleul *et al.* 1993). This analysis provides a correlation coefficient across the spatial extent of the tracked data to determine how well the two datasets correlate while accounting for spatial autocorrelation. Model performance for machine learning was assessed using kappa values, a measure of variability explained by the model akin to R^2 values, where 0 is equal to no relationship and 1 is equal to a perfect relationship as per Landis and Koch (1977). Further to this, a confusion matrix was calculated by running models on the remaining 25% test data to assess the number of correctly and incorrectly identified dives.

2.4 Results

Nine GPS & TDR combinations were deployed at Great Saltee, resulting in 31,716 locations after standardisation to a two-minute interval. Eight GPS & TDR combinations were deployed at Bass Rock, resulting in 21,208 relocations when standardised. There were a total of 2,830 TDR dives amongst the tracked birds at Great Saltee and 2,172 at Bass Rock. Examples of maps produced by methods and showing the location of TDR dives can be seen in Appendix B.

FPT, K means, EMbC, thresholds, and HMM all predict search rather than prey capture attempts *per se*. All methods predicted considerable search effort across the tracking period (Table 2.2). FPT identified the longest contiguous chains of search behaviour (mean 24.74 locations/chain), followed by HMM (mean 8.58 locations/chain), speed and tortuosity thresholds (mean 4.57 locations/chain) and EMbC (mean 2.38 locations/chain). K-means method identified the most discrete search areas with the shortest chains (mean 3.08 locations/chain). Using Kendall's tau correlation, there was a weak positive correlation between the length of search chains and the number of dives occurring within them (Table 2.3).

Table 2.2. Comparison of search identification across methods at Great Saltee and Bass Rock with associated TDR dives at each colony. True positives are when a dive occurs within a chain of locations identified as search, false positives are when a chain of locations identified as search does not contain a TDR dive, and false negatives are when a dive occurs outside of areas identified as search, and will include opportunistic foraging events.

	Great Saltee				***Bass Rock***			
	No^{o} relocations: 31716				***No^{o} relocations: 21208***			
	No^{o} dives: 2830				***No^{o} dives: 2172***			
Method	Rate of true positives (% Dives in Search)	Rate of false positives (% Search chains with no dive)	Rate of false negatives (% Dives outside of search)	Time spent in searching[2] (% of relocations searching)	Rate of true positives (% Dives in Search)	Rate of false positives (% Search chains with no dive)	Rate of false negatives (% Dives outside of search)	Time spent in searching[2] (% of relocations searching)
FPT	30.59	57.30	69.41	16.68	29.68	46.42	70.32	16.63
K-means clustering	37.52	74.00	62.48	27.27	21.91	79.92	78.09	19.17
Thresholds	76.81	67.98	23.19	37.15	57.50	63.95	42.50	28.69
HMM	80.81	63.05	19.19	41.53	81.30	56.76	18.70	36.67
EMbC	50.91	73.90	49.09	20.71	46.04	68.61	53.96	27.26
Kernel density	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]
Machine Learning	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]	N/A[1]

[1]Machine learning and kernel density assessed with other metrics due to nature of analysis, see Tables 3,4, and 5.

[2]Night time and locations close to the colony have been omitted. The remaining proportion of relocations are considered to be a combination of rest and travel.

Table 2.3. Kendall's Tau correlation between search chain length and number of dives contained within each chain**.**

Method	***Correlation (tau)***	***P value***	***Z statistic***
FPT	0.43	<0.01	12.67
K-means clustering	0.30	<0.01	21.76
Thresholds	0.45	<0.01	33.72
HMM	0.47	<0.01	23.79
EMbC	0.39	<0.01	31.29

The performance of behavioural classification methods was assessed by comparing the occurrence of TDR dives inside and outside of predicted search behaviour (Table 2). HMM captured the highest proportion of TDR dives (Figure 2.2a) within search areas, and had the second lowest false positive rate (Figure 2.2b). FPT had the longest identified search chains, but these actually captured the lowest number of dives across all methods (Table 2.2, Figure 2.2a). Despite the low true positive rates, FPT had the lowest false positive rate (Figure 2.2b). Thresholds and EMbC were comparatively similar in both the rates of true and false positives, while k-means clustering had the lowest true positive and highest false positive rates of all methods tested.

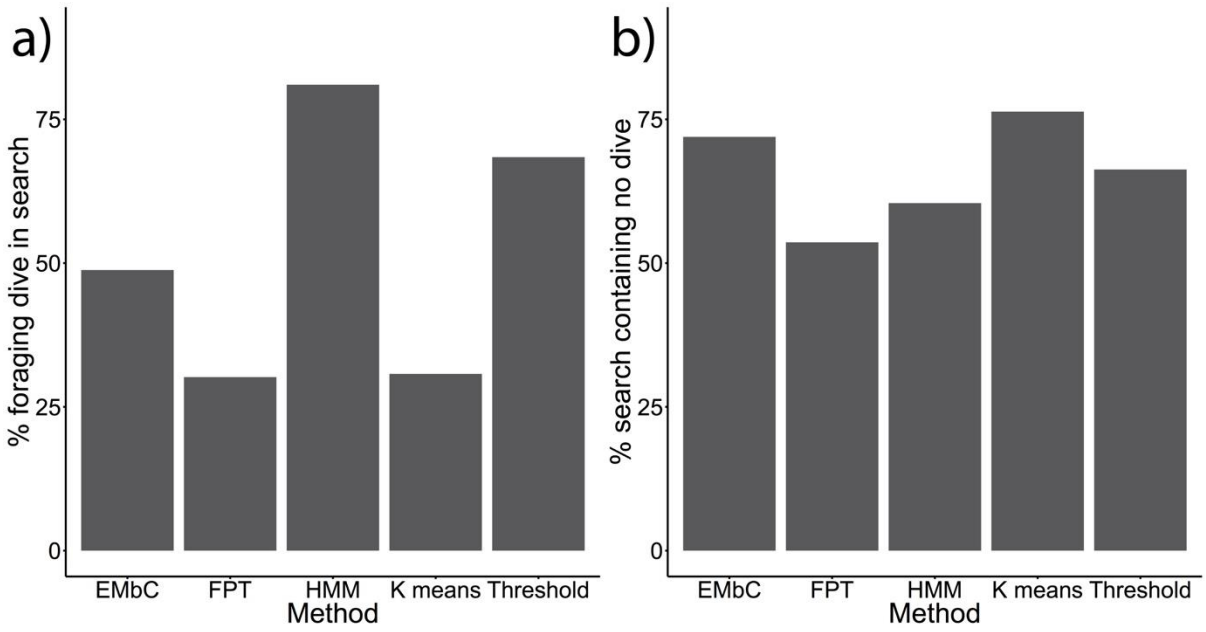

Figure 2.2. Proportion of a) TDR dives occurring within 'search' behaviour (true positives) and b) search chains containing no TDR dives (false positives) using EMbC, FPT, HMM, K means and speed-tortuosity thresholds.

Kernel density of GPS locations did not explicitly identify search behaviour but identified 'hotspots' of foraging corresponding to time spent in each 10x10km grid cell, with a high proportion of time spent in the area surrounding colonies (Figure 2.3). Dutilleul's modified spatial *t*-test demonstrated a good correlation between the spatial distribution of TDR dives and time-in-space (Table 2.4), with the better correlation (0.86) at Bass Rock. Machine learning models directly predicted the location of prey capture events. The models trained and tested on their own colony indicated only a fair or slight agreement within the data (following Landis and Koch (1977), (Table 2.5). Furthermore, the confusion matrix (Table 2.6) showed that the predictive power of the models at both colonies was poor, only successfully predicting 22% of dives in the test dataset. When models built in one colony were applied to others, there was a further loss of predictive power, indicating that model structures and movement patterns between colonies are different (Table 2.4).

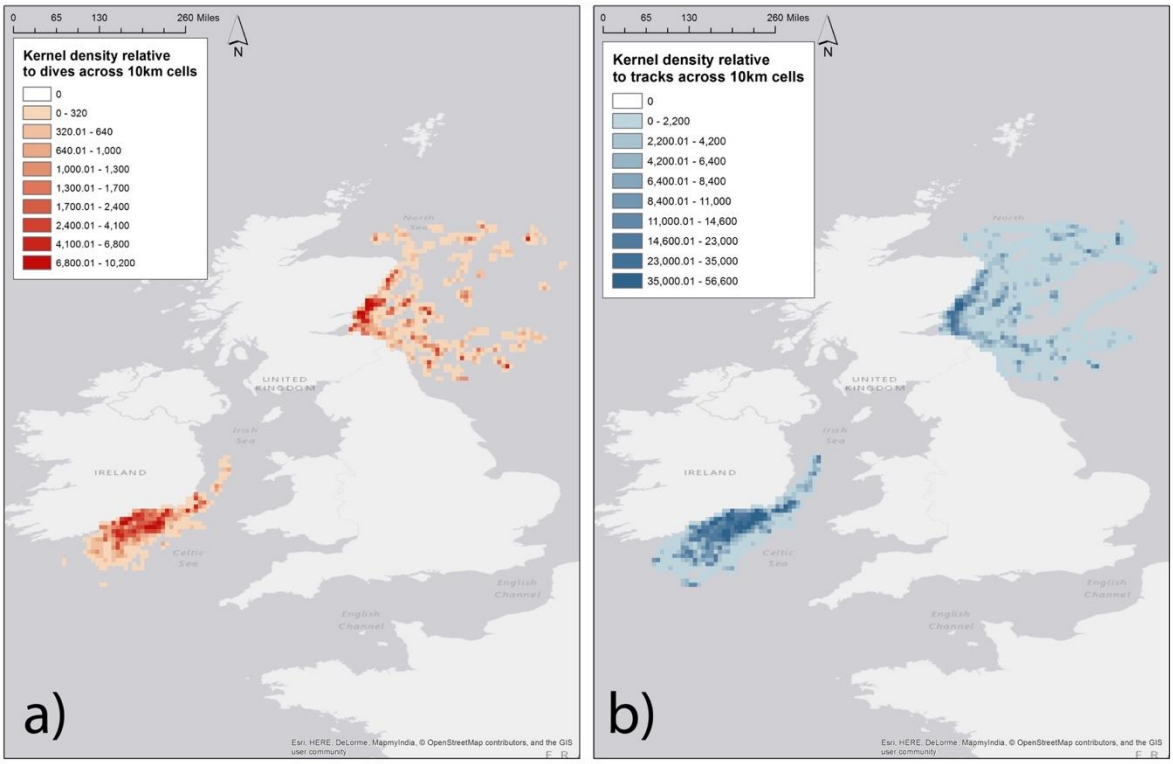

Figure 2.3. Kernel densities of gannet tracks at both Great Saltee and Bass Rock for a) dive locations and b) individual bird tracks. Scale is of relative time in space across the spatial boundary of 10km throughout the tracking area.

Table 2.4. Dutilleul's correlation between kernel densities of all GPS locations and confirmed dive locations.

Colony	***Correlation***	***P value***	***F statistic***	***Degrees of Freedom***
Great Saltee	0.79	<0.01	123.37	69.57
Bass Rock	0.87	<0.01	991.88	329.90

Table 2.5. Kappa values for machine learning models where models developed using colony-specific data are applied at the colony from which training data were taken and at a different colony. Low values for models trained at one colony applied to the other colony suggest very poor model fit.

Model trained at:	***Model applied at:***	
	Great Saltee	**Bass Rock**
Great Saltee	0.2456	-0.0006757
Bass Rock	0.02792	0.1885

Table 2.6. Confusion matrix table totals of predictions made across machine learning models at both Great Saltee and Bass Rock.

	Reference (true value) in test data set:	
Predicted result:	**Dive**	**No Dive**
Dive	222	258
No Dive	779	5332

2.5 Discussion

Seven methods of classifying search behaviour were compared to a validation dataset of TDR dive events in northern gannets to determine their ability to accurately capture the two components of foraging activity - searching and prey encounter/capture. Across methods, the number of prey capture attempts (TDR dives) within search varied considerably, with the highest being captured by hidden Markov models (81%) and the lowest captured by first passage time and k-means clustering (30% and 31% respectively). While HMM had the highest rate of capture of dive events, it also had one of the lowest rates of false positives, identifying fewer search chains where no dive was recorded. While this was still relatively high (60%), all methods produced high numbers of search chains that contained no TDR dives (range 53-76%). There was a weak correlation between chain length and number dives within a chain. While prey capture attempts will increase with trip and search duration (Sommerfeld *et al.* 2013), the weak correlation represents some longer search chains containing relatively few prey capture attempts due to individuals searching over poor quality areas, or simply that search does not always result in prey capture attempts. These findings suggests that significant effort is spent in unsuccessful search behaviour, consistent with low prey encounter rates associated with foraging on spatially and temporally patchy prey resources (Weimerskirch 2007).

While the spatial distribution of tracked gannets will encompass a variety of behaviours including foraging, travel and rest periods, simpler methodologies such as kernel density estimation of track data correlated well with kernel densities of TDR dive events. This supports the assertion that time-in-area is a good proxy for foraging effort (Grémillet *et al.* 2004a; Warwick-Evans *et al.* 2015). However, this approach utilises larger areas of space beyond movement paths and so it is not capable of identifying foraging in association with temporally ephemeral events or features that may directly change an animal's movement trajectory. Within more process-driven approaches, FPT is arguably one of the most ubiquitous methods used to identify foraging areas in both terrestrial and marine systems (Hamer *et al.* 2009; Byrne &

Chamberlain 2012; Le Corre, Dussault & Côté 2014; Battaile *et al.* 2015; Evans *et al.* 2015). FPT captures search behaviour across multiple spatial scales, and is particularly noted for its ability to detect nested scales of area restricted search (Hamer *et al.* 2009). Whilst we did not investigate nested scales of search, FPT, along with k-means clustering had the lowest rate of dives occurring within broad areas of identified search. However, in contrast to k-means, FPT had the lowest rate of false positives (search containing no dives), likely as a result of identifying very large, contiguous areas of search. K-means clustering and FPT had high rates of false negatives, with approximately 70% of all dives occurring outside identified search behaviour. A certain amount of opportunistic foraging is anticipated in any wide-ranging predator (Montevecchi *et al.* 2009), resulting in dive events occurring outside classical patterns of search movement. However, the high rate of dives occurring outside search as defined by FPT and k-means suggests that either the majority of prey capture attempts occur opportunistically, or that the scale of ARS changes spatially, resulting in search behaviour associated with dives being missed.

Speed/tortuosity thresholds 'captured' 68% of TDR dives within areas identified as search. There is evidence to suggest that humans are more capable than machines at pattern recognition when presented with limited data (Samal & Lyengar 1992). It is therefore unsurprising that thresholds performed well considering that they were constructed based on prior knowledge of foraging behaviour and iterative examination of thresholds against a validation dataset in gannets (Wakefield *et al.* 2013). The relatively high rates of false positives (66% of search chains containing no TDR dive) was within the spread of values for other methods, highlighting significant effort spent searching for prey interspersed with relatively few prey encounters.

The state-space modelling framework has been acknowledged as particularly useful in movement ecology (Patterson *et al.* 2008), and is rapidly expanding within path segmentation techniques (Roberts & Rosenthal 2004; Michelot, Langrock & Patterson 2016). Both the EMbC and HMM approaches model the changes in step length and turning angle through time and space to annotate the trajectory of an animal with behavioural states (Garriga *et al.* 2016; Michelot, Langrock & Patterson 2016). EMbC protocols resulted in shorter search chains that encapsulated 49% of all

dive events, while HMM identified longer chains of search that captured the highest number of dives (81%) of any method. While HMM defined the highest number of points as search across all methods, it also had one of the lowest rates of false positives. Less than 20% of dives occurred outside of search. This would be more consistent with opportunistic foraging and provides further empirical evidence of search behaviour leading to prey capture attempts (Weimerskirch *et al.* 2007; Dias, Granadeiro & Palmeirim 2009). The high number of shorter search chains identified by EMbC, coupled with the fact that it is possible to link state transitions to environmental covariates in a HMM framework suggests that both these methods may also be suitable for or investigating behavioural response to ephemeral environmental cues.

Regional differences in habitat and prey, as well as inter-and intra-specific competition are likely to influence the way an animal forages (Zach & Falls 1979; Schultz 1983; Huig, Buijs & Kleyheeg 2016). To account for this the colonies were treated independently during analysis. Machine learning did highlight slight differences between colonies in the movement metrics considered to be of most predictive power, suggesting local differences in movement associated with foraging and search. Machine learning was the only method that directly predicted prey capture events rather than search behaviour. While the explanatory power of the models was deemed to be satisfactory, the predictive ability of models was poor, only correctly identifying 22% of dives in the test data set. The success of this method may have been limited by the available sample size. While a powerful tool, machine learning approaches do require large amounts of data, are computationally complex, and require *a-priori* knowledge of dive events to train the model. However, machine learning protocols are still being developed within ecological research, and such data-mining remains a challenge for accurate classification (Hochachka *et al.* 2007).

An interesting consideration throughout the methods presented here, is the ability to identify multiple behavioural states. HMM, K-means and EMbC are capable of identifying behaviour consistent with rest within the tracking period (typically very low speed and a medium to high tortuosity values). In this context kernel density, FPT, speed-tortuosity thresholds, and machine learning did not identify periods of

rest. The majority of behavioural annotation relies on the principle of animals slowing down and paths becoming more tortuous when searching (Benhamou 2004; Bartoń & Hovestadt 2013). However, slowing down and turning more could also be an indication of rest behaviour, especially when considering potential error from closely positioned GPS relocations (Jerde & Visscher 2005; Hurford 2009). The ability to exclude a period that closely resembles search patterns could have the potential to reduce false positive periods of search, and we accounted for this as much as possible by removing locations in proximity to the colony as well as locations occurring at night before comparing methods. Whilst not directly assigning a rest period, it is important to note that speed-tortuosity thresholds could be adapted to include the annotation of rest and travel, as well as specific search behaviour. In a similar fashion, machine learning protocols could also be applied to predict behaviours other than diving.

Careful choices must be made in the selection and application of behavioural classification methods when inferring foraging. While all methods tested generally supported the hypothesis that search behaviour leads to prey encounter and subsequent prey capture attempts in a wide-ranging pelagic predator, there was considerable variation in the degree to which this was noted. The HMM method produced estimates of foraging behaviour that most effectively encapsulated both search and prey capture components of foraging. As such it would seem a sensible recommendation that HMM be used when identifying foraging (including both search and prey capture) areas is a priority. Across methods, rates of false negatives (dives occurring outside of search behaviour) ranged from 19-70%. While some of this may be attributed to opportunistic feeding outside of search behaviour, methods with high rates of false negatives suggest that care should be taken when using behavioural classification methods. That animals spend considerable time actively searching for prey while prey capture occurs largely outside of this activity seems improbable, and poor classification of behaviours can have implications when considering time-energy budgets and subsequent reproductive success or survival. Methods such as HMM, EMbC, and thresholds had the lowest rates of dives occurring outside of search. These methods may be more attuned to capturing dive events and

therefore represent a more inclusive definition of foraging, while FPT and k-means clustering may be more general in their identification of search. Investigating the differences between methods may lead to increased understanding of the environmental cues used by predators to initiate search and prey capture as well as the scales at which these cues occur. Nevertheless, we reiterate the need for detailed exploratory analysis of movement data to prevent mis-specification of behaviour (Gurarie *et al.* (2016)) and argue for methods to be used based on suitability, and the questions being asked by researchers.

Chapter 3: Tidal drift removes the need for area restricted search in foraging Atlantic puffins

This chapter is also published as:

Bennison, A., Quinn, J.L., Debney, A. and Jessopp, M., 2019. Tidal drift removes the need for area-restricted search in foraging Atlantic puffins. *Biology Letters*, *15*(7), p.20190208.

The publication in Biology Letters is a condensed version due to limited word counts, so this chapter is an expanded version to enable greater reflection of the results and their context within a wider literature.

This study was conceived by myself and Mark Jessopp after being approached to undertake a puffin study by the Zoological Society of London. I was responsible for planning and conducting the two years of fieldwork, data analysis, and leading on development of the manuscript under guidance from Mark Jessopp and John Quinn.

3.1 Abstract

Understanding how animals forage is a central objective in ecology. Theory suggests that where food is uniformly distributed, Brownian movement ensures maximum prey encounter rate, but when prey is patchy, the optimal strategy resembles a Lévy walk where Area Restricted Search (ARS) is interspersed with commuting between prey patches. Such movement appears ubiquitous in high trophic level marine predators.

Here we report foraging and diving behaviour in a seabird with a high cost of flight, the Atlantic puffin (*Fratercula arctica*), and report a clear lack of Brownian or Lévy flight and associated ARS. Instead, puffins foraged using tides to transport them through their feeding grounds. Puffins were tracked at a resolution of one GPS fix per 15 minutes and so to ensure that ARS was not being missed in time poor data, we compared our results to razorbills tracked at a nearby colony at a much higher resolution. Razorbill tracks showed clear ARS movement patterns at three-minute resolution and when subsampled to 15 minute intervals. Razorbills also showed drifting behaviour but no dives were clearly detected during this suggesting that razorbills rest whilst drifting and do not forage like puffins.

Energetic models were adapted from published literature to produce estimates of Trip Energy Expenditure (TEE). TEE was calculated for puffins as they undertook the drifting foraging strategy, and was also costed for birds had they flown the same observed route. Though likely an underestimate, this TEE comparison suggests the cost of foraging trips using the drift strategy is 28-46% less than flying between patches. We suggest such alternative movement strategies are habitat-specific, but likely to be far more widespread than currently thought.

3.2 Introduction

Optimal foraging theory assumes that animals move between patches of prey in order to maximise prey encounter rate and nutritional intake (MacArthur & Pianka 1966; Charnov 1976). Brownian motion or random walks appear to be optimal when prey is uniformly distributed (Bartoń & Hovestadt 2013), and are characterised by movement where turning angles between relocations are effectively random (Jones 1977). In contrast, when resources are patchy, or animals have a preferred direction or orientation, movement is non-random, leading to correlated random walks (CRWs) (Kareiva & Shigesada 1983) or Lévy flights (Viswanathan *et al.* 1996).

CRWs incorporate an element of directional persistence (Bovet & Benhamou 1988), while Lévy flights allow random direction but step lengths between successive locations reflect a power-law distribution (Shlesinger & Klafter 1986). First reported in wandering albatross, *Diomedea exulans*, (Viswanathan *et al.* 1996), Lévy flight has been identified across multiple taxa, however, its universality for explaining foraging ecology has stimulated debate (Viswanathan *et al.* 1996; Benhamou 2007; Edwards *et al.* 2007; Petrovskii, Mashanova & Jansen 2011; Edwards *et al.* 2012; Pyke 2015), and is now considered one element of a number of strategies utilised in foraging for resources (Deshpande, Kumar & Ramakrishnan 2017; Reyna-Hurtado *et al.* 2017; Sakamoto, Sanders & Inazumi 2017).

The foraging component of free-ranging animal movement is generally characterised by Area Restricted Search (ARS): the tendency for animals to concentrate search within relatively small areas before continuing wider range exploration (Kareiva & Odell 1987; Fauchald & Tveraa 2003). ARS is widely accepted as a core component within foraging theory across a wide array of taxa ranging from grazing herbivores (Benedix Jr 1993) to higher trophic level predators (Lode 2000). ARS is scale dependent (Paiva *et al.* 2010; Battaile *et al.* 2015) and because it occurs within CRWs and Lévy flights (Sims *et al.* 2012), has provided a link between movement ecology, optimal foraging theory, and energetics. Seabird research has led much of the development of animal movement theory for Lévy flight and ARS, where individuals travel large distances between prey patches with subsequent fine-scale search

behaviour above water (Bartumeus *et al.* 2005; Weimerskirch 2007). The generality of ARS in seabirds is well established and it therefore can be assumed that ARS is energetically optimal. However, less is known about how interactions with large scale-geographical features may shape or change these movement patterns.

Marine predators must adapt to foraging in a seemingly unpredictable environment. The ocean often appears to be a visually featureless environment with large distances between landmasses, however animals have evolved to take advantage of geographic features and systems found throughout the ocean. Continental shelf edges are areas where upwellings of nutrient rich water produce areas of predictably high primary productivity (Lavoie, Macdonald & Denman 2009; Watanabe *et al.* 2012). Shelf edges have been previously shown to be areas targeted for foraging by seabirds (Fritz, Said & Weimerskirch 2003), pinnipeds (Lewis *et al.* 2006), and cetaceans (Breen *et al.* 2020). The movement of water over shelf edges has also been understood to create frontal zones of oceanic water (Tverberg & Nøst 2009) also often targeted as foraging areas by marine animals (Sims & Quayle 1998; Scales *et al.* 2014; Cox *et al.* 2016). Oceanic fronts are areas of ocean where two different bodies of water mix, often travelling in different directions (D'Asaro *et al.* 2011), and are associated with higher productivity (Lutjeharms, Walters & Allanson 1985). A common feature across many areas targeted for foraging by marine predators is oceanic currents or the mixing of bodies of water. Streaked shearwaters, *Calonectris leucomelas,* have been observed foraging at the edge of oceanic eddies, in ocean currents thought to be associated with higher productivity (Yoda, Shiomi & Sato 2014), whilst bottlenose dolphins, *Tursiops truncatus*, have also been observed concentrating their foraging in areas of high current and tidal flows (Bailey & Thompson 2010). As well as natural environmental features, marine predators may target man-made features; for example, oil rigs often act as artificial reefs and fish aggregating devices (Løkkeborg *et al.* 2002) which are then targeted by predators such as seabirds (Wiese *et al.* 2001) and sharks (Robinson *et al.* 2013). While it is understood that these ocean features can affect the distribution and foraging areas of animals, less is known about how oceanic features may affect the movement patterns and behaviour of individual animals.

Seabird species have been known to focus foraging activity in areas of dynamic currents such as tides (Hunt Jr *et al.* 1998; Johnston *et al.* 2018) and tidal currents are known aggregators of prey (Alldredge & Hamner 1980). Tidal cycles generate the mass movement of water and these movements of water generate regular surface currents that present a predictable environmental feature. Whiskered auklets, *Aethia pygmaea,* have been found to target foraging effort primarily within tidal fronts in the passes between islets on the Aleutians (Day & Byrd 1989) with evidence to suggest that species of auks were segregating in space by tidal fronts (Hunt Jr *et al.* 1998). Tides are a regular oceanic cycle and change how resources are made available, and black-legged kittiwakes, *Rissa tridactyla*, have been found to target specific habitat dependent upon the stage of tidal cycle (Trevail *et al.* 2018). There is clear evidence that tidal cycles can change the local environment or present animals with opportunities for easier access to prey, however, very few studies exist that directly explore movement or search strategies during tidal cycles.

Associations between environmental features and seabird space use is often quantified using the prevalence of ARS within a given geographic range. As a consequence marine protected areas (MPAs) can be designated using inferred ARS (Lascelles *et al.* 2016). Seabirds are experiencing global decline (Paleczny *et al.* 2015) and whilst many efforts are made to undertake effective conservation management, many MPAs do not spatially overlap with projected distributions of many seabird species (Critchley *et al.* 2018); as such there is a priority to understand ecology and behaviour for improved conservation management.

Here we report a lack of ARS in a foraging seabird with high cost of flight, the Atlantic puffin, *Fratercula arctica*, (hereafter puffin). Auks, including puffins, have previously been understood to use ARS between prey patches (Elliott *et al.* 2009; Harris *et al.* 2012; Regular, Hedd & Montevecchi 2013). Unusual track patterns led us to hypothesise that puffins were exploiting tidal movement to transport them over prey patches. The core foraging area of the tracked puffins occured over sand substrate (EMODnet 2009), the habitat of the puffins' main prey species, sandeels (Holland *et al.* 2005) which we also observed chick-provisioning puffins bringing back to the colony. We predicted that this observed strategy must be energetically lower than

engaging in flight/ARS, suggesting a new environmentally mediated, energetically optimal foraging strategy in seabirds.

3.3 Methods

Research was approved by University College Cork Animal Ethics Committee and under licences from the British Trust for Ornithology, National Parks and Wildlife Service, and the Health Products Regulatory Authority of Ireland. Sixteen chick-provisioning puffins were tracked during the breeding season (2017 n=12, 2018 n=4) on Little Saltee, Co. Wexford (52° 8' 13.2", -6° 35' 24" W), Ireland. Birds were caught using purse nets at burrow entrances, and only individuals returning with fish were tagged to ensure they were provisioning chicks. In 2017, birds were equipped with either an Ecotone Uria solar-charging GPS logger (n=10), or a PathTrack NanoFix tag with time depth recorder (CEFAS G5 TDR) (n=2). In 2018, only Ecotone Uria tags were deployed (n=4). Ecotone tags downloaded data remotely, whilst Pathtrack tags required bird recapture.

Both tag types recorded a GPS position every 15 minutes. TDRs were used to log dives deeper than 1m, and longer than 5 seconds duration (Shoji *et al.* 2015b). Ecotone tags deployed in 2018 were programmed to record times of descent and ascent using manufacturer recommended settings. Ecotone tags weighed approximately 9g and pathtrack tags combined with a CEFAS time depth recorder weighed approximately 3g in total. Puffin weight ranged from 320 to 415g. Deployment weight ranged between 2.1% - 2.7% of bird body weight for Ecotone tags and 0.75 -0.78% for PathTrack. Devices were attached ventrally to the lower back using strips of Tesa tape to minimise hydrodynamic and aerodynamic drag following Harris *et al.* (2012) and Elliott *et al.* (2013a). Mean deployment weight was 2.73% of body weight (See Table 3.1 for further details on tag weights).

Tracks were atypical to those previously observed in this species, with no obvious ARS, and characterised by three distinct components: 1) Straight line commuting from the colony out to sea, 2) Slow directed phases in easterly or westerly directions, and 3) Return to the colony in a straight line (Figure 3.1). Tracks of multiple puffins were observed to be synchronised as they moved over the core use area, often starting and ending drifting periods at similar times (Please see accompanying video at: https://doi.org/10.1098/rsbl.2019.0208). GPS tracks were processed in the

AdehabitatLT package (Calenge 2011) using R (RCoreTeam 2015). Tracks were standardised to a 15-minute interval using linear interpolation to account for missed positions and divided into individual foraging trips, using a distance threshold of 350m from the colony to define the start and end of a trip. We used bootstrapping to determine goodness of fit to a power-law distribution for relocation step length using the *poweRlaw* package in R (Gillespie 2014) to determine whether trips were consistent with Lévy flight.

There may be limitations inferring behaviours from low-resolution movement data. Previous tracking studies on puffins and other auks have clearly shown ARS (Elliott *et al.* 2009; Harris *et al.* 2012; Regular, Hedd & Montevecchi 2013) and it could be argued that the 15-minute fixes used to prolong GPS tag battery life may have missed ARS behaviour. To determine whether it was possible for ARS to have been missed at a 15-minute temporal resolution, we investigated tracking data from another auk species that forages at similar ranges, the razorbill (*Alca torda*), collected at finer temporal resolution (3-minute fixes) on the adjacent colony of Great Saltee. Tracks were examined at the natively collected 3-minute period and compared to a version of the same tracks subsampled to 15-minute intervals. GPS coverage, whether GPS position interval is longer than expected, is an indicator of diving in razorbills (Browning *et al.* 2018) and so we also considered whether razorbills may be diving during any observed drifting periods.

Puffin speed was matched to tidal movement by correlating travel speeds with tidal velocity from the Irish Marine Institute's Regional Ocean Modelling System (ROMS) model (http://www.marine.ie/Home/site-area/data-services/marine-forecasts/ocean-forecasts) using linear models. Only puffin speeds below the ROMS maximum tide velocity (2.3 m/s) were correlated to account for potential periods of flight occurring within 15-minute fixes. Speed thresholds produced from movement datasets were used to determine behaviour (Bennison *et al.* 2018), using the midpoint between mean puffin flight speed (13.2m/s) (Pennycuick 1997; Spear & Ainley 1997; Harris & Wanless 2011) and peak current velocity (2.3m/s) to differentiate flight and surface behaviours as both could occur within 15-minute relocations.

Table 3.1. Summary table of deployment details from Little Saltee between 2017 and 2018.

Ring number	*Date*	*Weight (g)*	*Recatch*	*Tag Type*	*Data status*	*Deployment Weight (%)*
EX01301	26/06/2017	415		Ecotone	Recovered	2.1
EX01302	26/06/2017	330		Ecotone	Recovered	2.7
EX01303	26/06/2017	385		Ecotone	Recovered	2.3
EX01304	26/06/2017	375		Ecotone	Recovered	2.4
EX01305	26/06/2017	365		Ecotone	Recovered	2.4
EX01306	26/06/2017	410		Ecotone	No data received	2.2
EX01307	26/06/2017	395	Recaught	Ecotone	Recovered	2.3
EX01308	26/06/2017	380	Recaught	Ecotone	Recovered	2.4
EX01310	27/06/2017	400	Recaught	Pathtrack	Failed tag	0.8
EX01312	28/06/2017	380	Recaught	Pathtrack	Recovered	0.8
EX01324	02/07/2017	400		Ecotone	Recovered	2.2
EX01325	02/07/2017	385		Ecotone	Recovered	2.3
EA15001	07/07/2018	325		Ecotone	Recovered	2.8
EX01316	07/07/2018	320		Ecotone	No data received	2.8
EY53483	01/07/2018	380		Ecotone	Recovered	2.4
EY53484	01/07/2018	400		Ecotone	No data received	2.3

Dive data were retrieved from 2 TDR deployments (due to GPS tag failure, only one TDR deployment had accompanying location data) in 2017 and from three Ecotone tags in 2018. TDR data were reduced to a time-series of dives consisting of dive depth (metres below surface) and dive duration (seconds). Many dives were not recorded accurately by Ecotone tags, resulting in unfeasibly long dives (Mean 29.7 +/-188.7 minutes). Visual inspection of Ecotone tag dive events identified only a single full trip as suitable for energetic analysis. TDR data were used to build a linear model of dive depth based upon dive duration, which was extrapolated onto the Ecotone dive data to produce estimates of dive depth from dive duration.

Trip Energetic Expenditure (TEE)

To explore the energetics of tidal drift versus flight, we modified a daily energetic expenditure equation for auks (DEE, eq 1; Elliott *et al.* (2013b), previously used on puffins (Fayet *et al.* 2016)) to calculate a trip energetic expenditure (TEE) for individual foraging trips. TEE estimates are calculated in Watts, but can be considered as relative energetic costs.

Eq. 1. $$TEE = 148(T_f) + 28(T_{ws}) + 27(T_d) + 28(T_i) + 8.9(T_n)$$

Where T_f denotes time spent flying, T_{ws} indicates time spent sitting on the water's surface (drifting on surface currents), T_d is time spent diving, and T_i is the dive interval (in seabirds oxygen stores are replenished during inter-dive intervals (Houston & Carbone 1992; Butler & Jones 1997)). Whilst Elliott *et al.* (2013b) did not provide a cost for a post dive recovery period, we assumed it was analogous with the cost attributed to sitting on the water's surface. T_i was calculated by modelling the minimum dive interval with general linear models (GLM) and multiplying by the number of dives in a trip. GLMs predicted dive interval using a subset of the dive data (dive interval <200 seconds), dive depth, dive duration, and the interaction between the two. All models were ranked by AIC and the most parsimonious model used to

predict dive interval. Puffins are diurnal predators, not feeding at night (Croll *et al.* 1992; Regular, Hedd & Montevecchi 2011; Shoji *et al.* 2015b), and since no dives were recorded at night, T_n is the overnight period, with a coefficient equal to rest (Elliott *et al.* 2013b).

The energetic cost of the observed 'drift strategy' (TEE_{drift}), was compared with a modelled trip following the same route with the same time spent diving, but with travel costed energetically as flight (TEE_{flight}). This produced an estimate where instead of drifting, puffin behaviour was considered as flight interspersed with dives throughout the trip. We applied a flight speed for puffins of 13.2m/s (Pennycuick 1997; Spear & Ainley 1997; Harris & Wanless 2011), resulting in a faster trip (faster to fly the route than drift) and applied the lowest energetic cost of rest (8.9 (Elliott *et al.* 2013b)) as a conservative estimate to the remaining time to ensure strategies are considered over the same time frame. The resulting TEE_{flight} is likely to be a large under-estimate of actual cost as ARS involves extensive periods of non-linear flight.

3.4 Results

A total of 107 foraging trips were recorded (including 51 overnight trips) from 12 individuals, all of which were atypical of previously published seabird foraging tracks, and did not show ARS. Average distance from the colony was 15km with a maximum of 38km. Mean trip duration was 10 hours 6 minutes (+/- 14 hours 45 minutes). Individuals targeted the same core foraging area (see Figures 3.1 and 3.2) by departing the colony in a more easterly or westerly direction to account for the direction of tidal flow at the beginning of the trip. Puffin movement matched the vectors of local tidal flows (Figure 3.4).

Two adults equipped with Ecotone tags were retrapped and had lost an average of 5.2% of body weight, while two adults with Pathtrack GPS/CEFAS TDR combinations were retrapped and had increased in weight (mean 12.5g), suggesting there was some impact from the heavier tags, although sample size is far too low to state this conclusively. One bird abandoned its breeding attempt in 2017, and one bird failed in its breeding attempt in 2018. Tagged birds were observed returning to the colony with prey items.

Movement did not conform to a power law distribution consistent with Lévy flight (Goodness of fit = 0.0521, $p<0.001$), and did not exhibit ARS (Figure 3.3). Razorbills showed ARS behaviour in tracking data at 3-minute resolution and also when subsampled to 15-minutes (Figure 3.5), suggesting that ARS behaviour is not being missed in puffins due to the temporal resolution of the data. Razorbills were also observed to undertake periods of drifting on tidal currents; GPS fixes remained constant throughout drifting periods suggesting razorbills were not foraging during this period and must therefore be associated with rest (Figure 3.6).

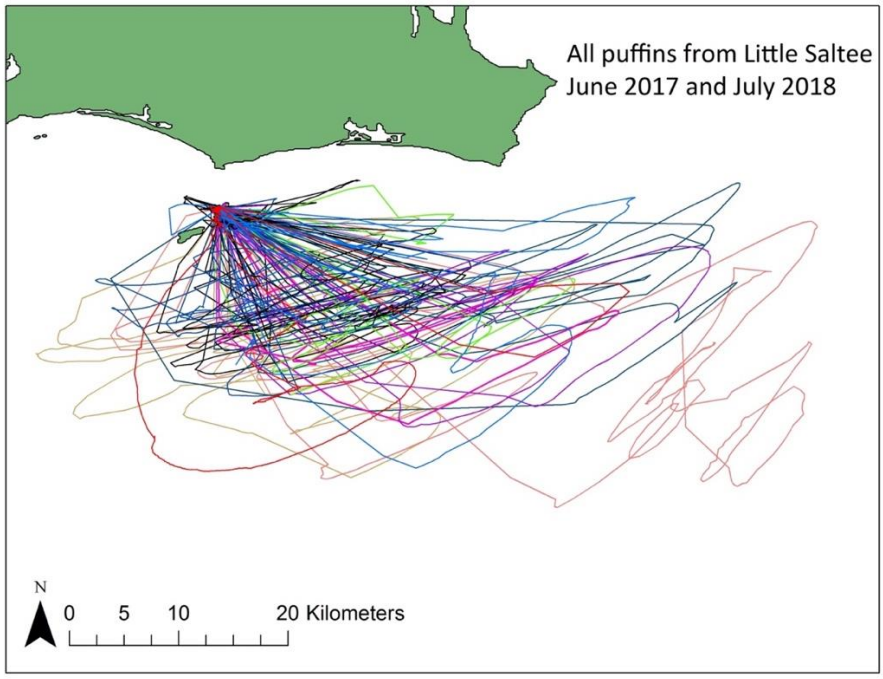

Figure 3.1. A map showing all puffin GPS tracks simultaneously. These tracks all shown together broadly illustrate the quantity of trips seen and the similarity between puffins.

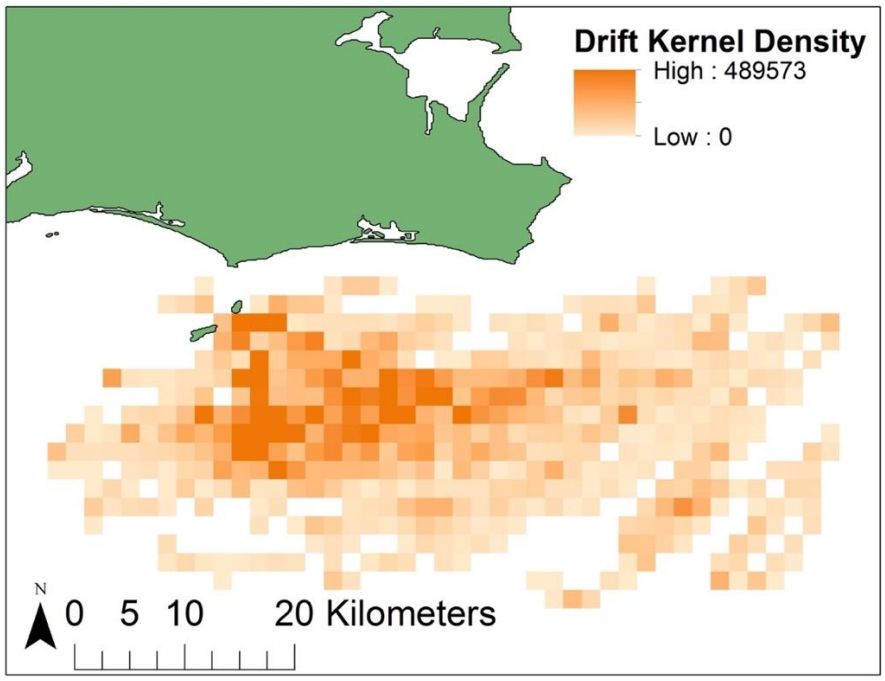

Figure 3.2. Kernel density map of all puffin GPS tracks, showing that individuals are targeting similar areas for drifting. light orange colours represent less overall use whilst dark orange indicates heavier use.

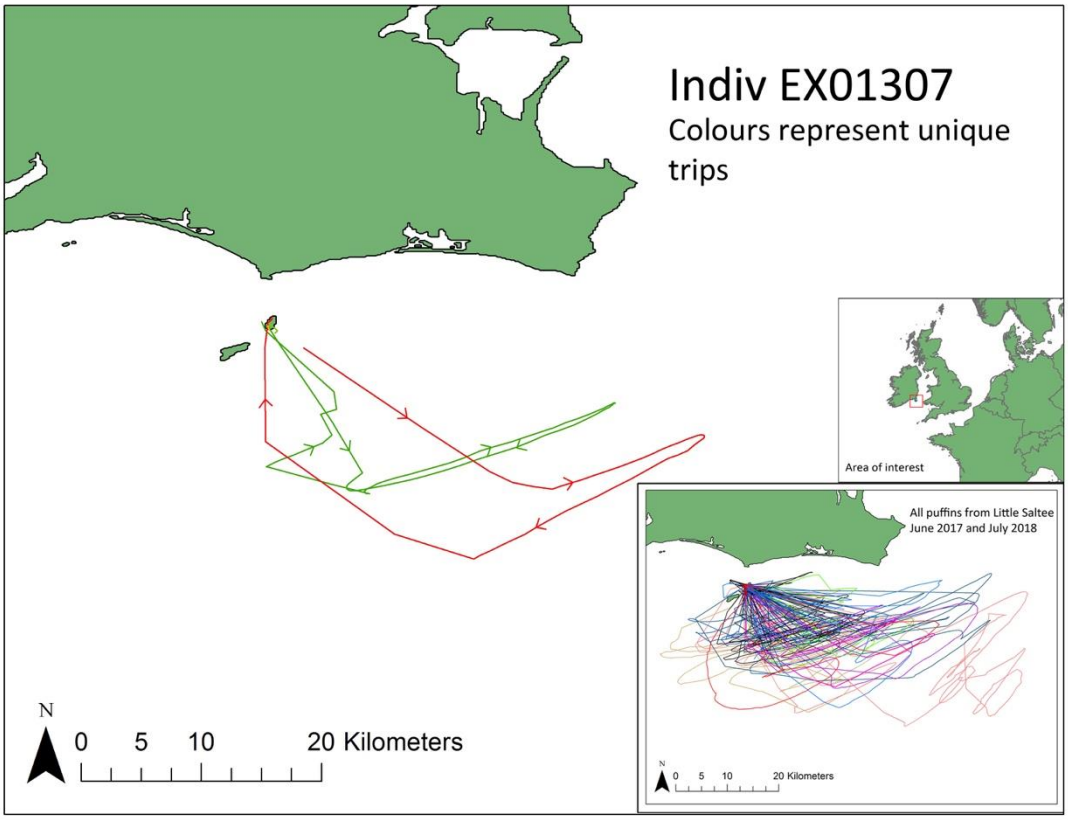

Figure 3.3. An example GPS track from puffin EX01307 tracked from Little Saltee, County Wexford, Ireland in June 2017. Directional arrows have been included on the GPS tracks. The non-typical movement patterns can be seen clearly with a commuting stage before long straight sections in easterly-westerly directions. Different colours represent different foraging trips.

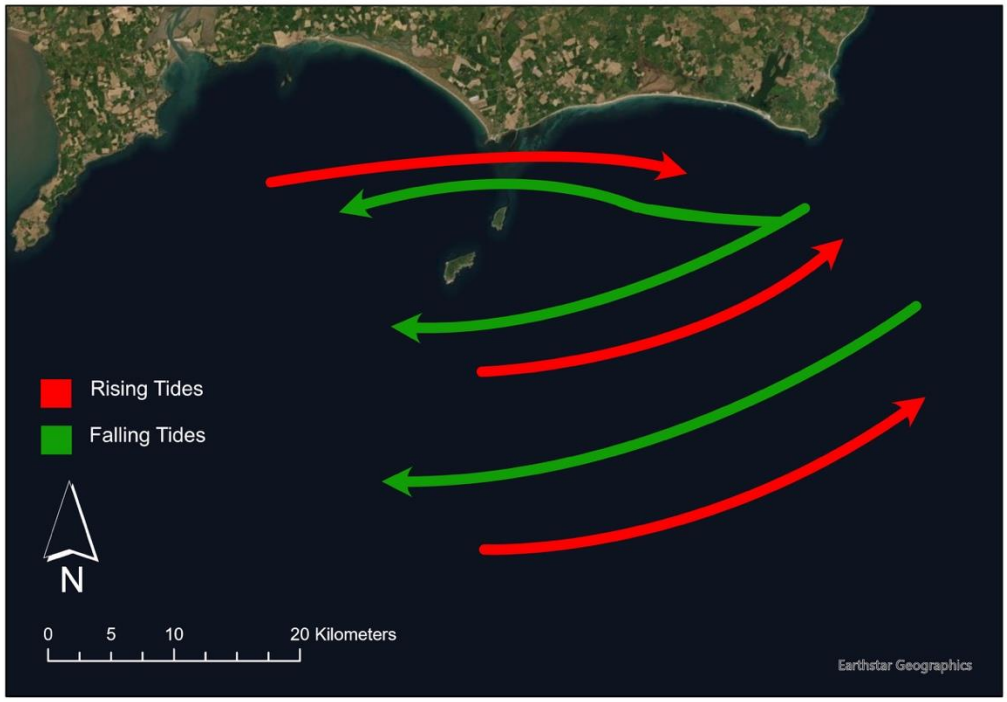

Figure 3.4 A map showing the tidal vectors of ocean movements around the Saltee Islands. On rising tides, water flows from west to east, on falling tides, these flows travel from east to west.

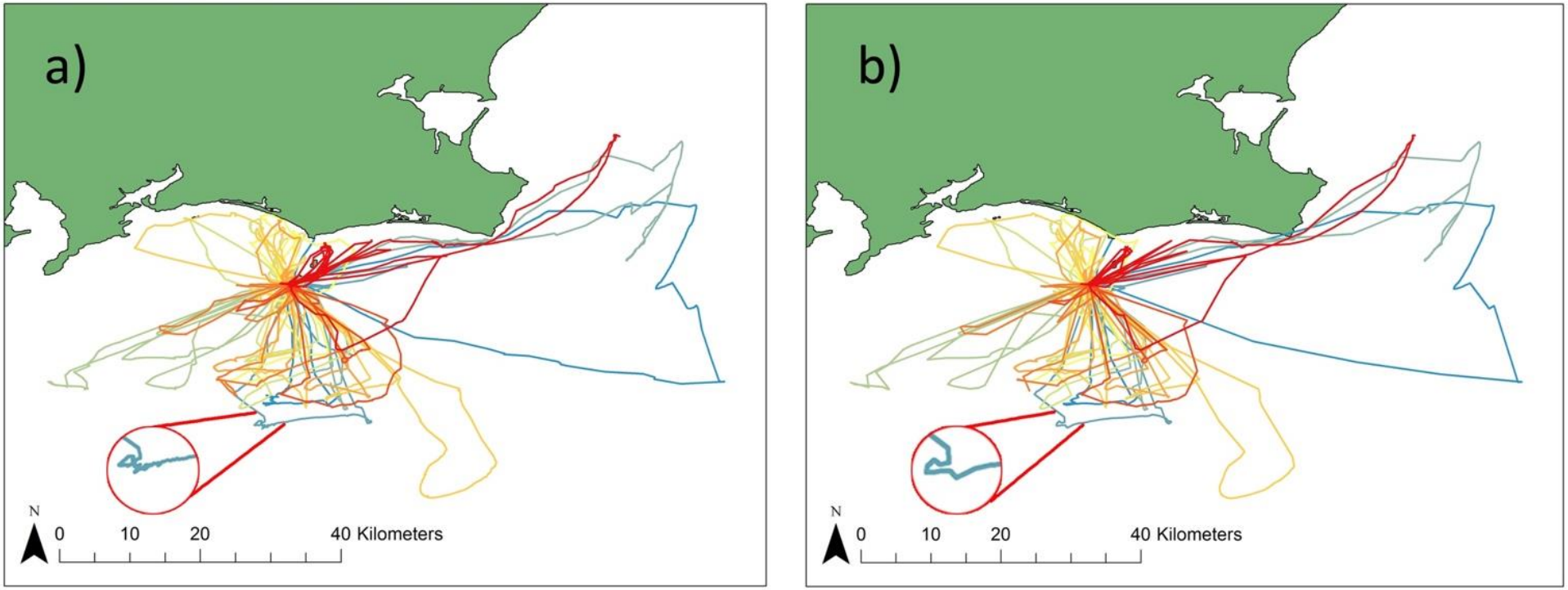

Figure 3.5. Razorbill (*Alca torda*) GPS tracking data from Great Saltee, an island adjacent to Little Saltee. Panel a) shows data recorded at three-minute intervals. Panel b) shows the same data resampled at 15-minute intervals. Clear ARS can be seen in both panels, with zoomed areas showing that if present, ARS is still observed at temporal resolutions similar to our puffin data.

Tidal velocity correlated strongly (coefficient 0.723) with puffin speed during the slow, directed phases of trips (F_{4500}=429.6, p<0.001, Figure 3.7). Dive data showed temporally clustered bouts suggesting an element of underwater search on patchily distributed prey, and no dives occurred during darkness. Mean dive depth from TDRs (n= 2,224 dives) was 9.67m (SD=3.78, range= 2.03-23.43) while mean dive length was 34.4 seconds (SD=19.072, range= 5-82). Linear models to predict dive interval for TEE analysis found the most parsimonious model consisted solely of dive duration predicting dive interval (Coefficient = 0.89, F_{739}=505.27, p<0.001).

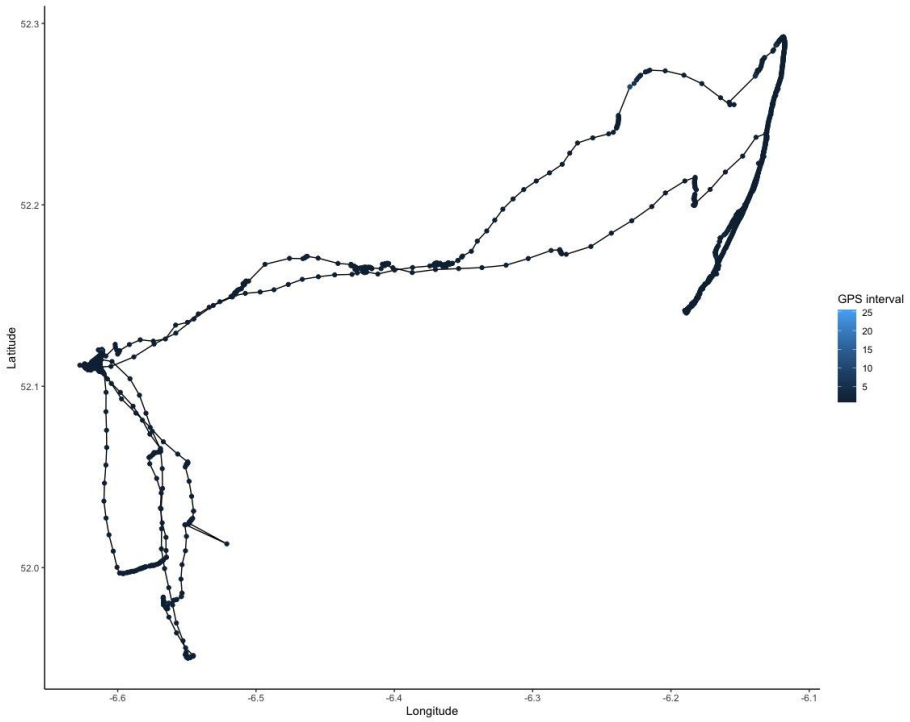

Figure 3.6. An example razorbill track where individual points are coloured by GPS time interval. Whilst razorbills do seem to be experiencing tidal drift, the regular 3-minute interval between drifting points signifies that they are not utilising these for foraging.

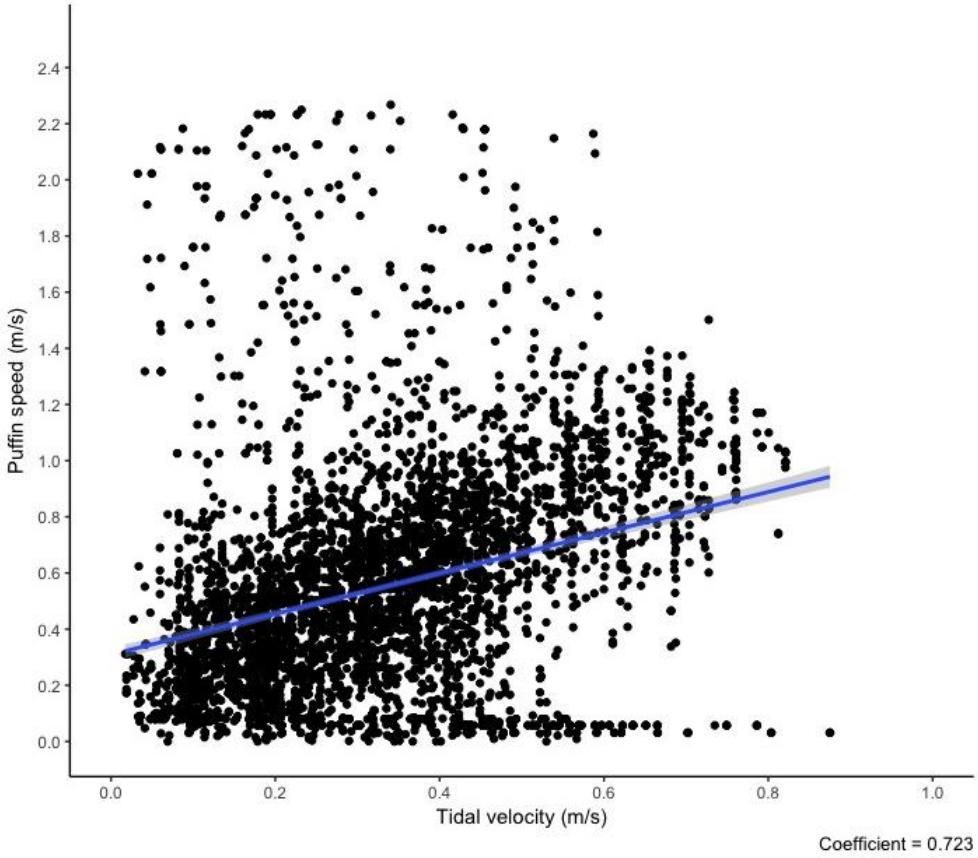

Figure 3.7. The relationship between puffin speed and tidal velocity. The correlation was represented by the linear model coefficient of 0.723.

Trip Energetic Expenditure (TEE) estimates were calculated for three indicative trips (Figure 3.8) to determine whether the drift strategy is energetically optimal for short to long duration trips. TEE for the drift strategy was always lower than for the flight strategy, ranging from 28-45% cheaper (Table 3.2) with the greatest energy saving occurring on overnight trips.

Table 3.2. Trip Energetic Expenditure (TEE) costs during observed drift and simulated flight strategies based on the model by Elliott *et al.* (2013b). Here we see the cost differences between the two strategies for the three trips analysed. Energetic savings from drifting ranged between 28.2 and 45.7% though mean saving was 39%.

Trip ID	***Drift TEE (Kilowatts)***	***Flight only TEE (Kilowatts)***	***Difference***	***Percent saving by drift strategy***
EX01312_1	978	1425	447	46%
EX01312_2	1150	1667	517	45%
EA15001_1	1167	1496	329	28%
MEAN	1098	1529	431	39%

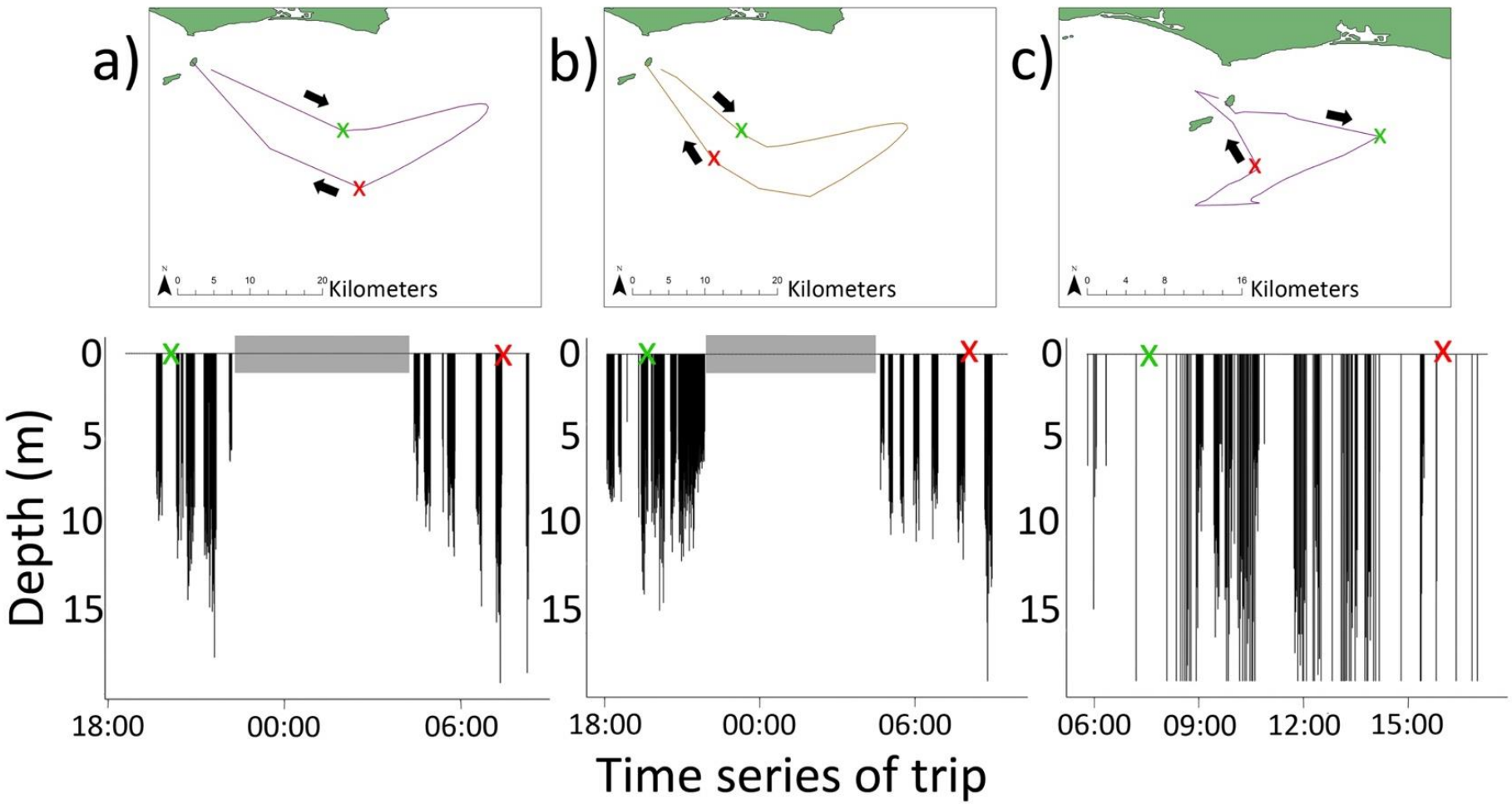

Figure 3.8. Three puffin trips (top) with corresponding TDR dive data (middle) and trip-level energetic expenditure (TEE) (bottom). a) trip EX01312_1. b) trip EX01312_2. c) trip EA15001_1. Green and red x indicate points along the foraging track to illustrate direction of travel (outward and return respectively) and highlight series of clustered dives occurring during drift periods consistent with foraging on patchily distributed prey. Large gaps in dives (grey boxes) observed in a) and b) indicate overnight periods where foraging did not occur.

3.5 Discussion

Whilst foraging, puffin movement did not conform to a power law distribution, and did not contain ARS. To our knowledge, this is the first time that non-ARS foraging has been reported in a mobile marine predator. Instead, puffins flew directly to foraging areas and used tides to transport them across prey patches. TEE analysis showed that this drifting behaviour ranged between 28-45% energetically cheaper than flying the same route. Drifting behaviour in seabirds is typically associated with periods of rest (Shamoun-Baranes *et al.* 2011; Cooper *et al.* 2018; Sánchez-Román *et al.* 2019), but our dive data show that puffins were diving during drifts. Dives were pelagic, likely due to targeting sandeels which school pelagically (Freeman, Mackinson & Flatt 2004). Our data therefore show that the tracked puffins are employing an alternative foraging strategy by using tidal currents to transport them over sandeel habitat and between patchily distributed sandeel prey. Razorbills tracked from a nearby colony undertook ARS search behaviour and were also documented to show drifting periods in their tracks. The regularity of location fixes in the Razorbill data did not suggest any diving during drifting. Comparison between high resolution razorbill GPS data and low resolution similar to the puffin data still showed ARS movements, supporting our assertion that puffins were not undertaking area restricted search behaviour that was missed between 15-minute GPS fixes. It is interesting to note that puffins may predict the state and direction of the upcoming tide, as their tracking data showed them leaving the colony in a direction consistent with subsequent tidal transport over a relatively small core habitat.

Puffin movement did not show classic patterns of ARS behaviour, instead puffins searched for food during tidal drifts. ARS is considered to be a widely used optimal search strategy for encountering patchily distributed prey (Kareiva & Odell 1987; Bartoń & Hovestadt 2013), observed across a wide variety of marine and terrestrial taxa (Hamer *et al.* 2009; Byrne & Chamberlain 2012; Ross & Winterhalder 2018; López *et al.* 2019), including puffins (Shoji *et al.* 2015b). Many studies exploring the optimality of animal movement and ARS are often only concerned with movement from a 2D perspective. Simulation studies exploring the efficiency of ARS have shown

that we must also consider movement in the third axis; depth (Leising 2002). Whilst some research has investigated ARS from a three dimensional perspective (Bailleul, Lesage & Hammill 2010), there has been limited uptake within the seabird ecology community. Here, puffins are moving throughout their environment before undertaking dives, which could be as part of an ARS-like behaviour. The limited dive data available in this study shows dives clustered in time, suggesting that puffins are restricting their search during drifts. Previous research has found that thick-billed murres, *Uria lomvia*, integrate their foraging behaviour between above and below the water's surface in a manner that does not fit a lévy flight but may still be considered ARS (Elliott *et al.* 2009). However, the behaviour presented here would represent an inverse lévy flight or ARS, puffins during drifts are undertaking small relocations at low speeds (<2.3m/s) before increasing speed and step length to undertake search behaviour by diving to depth. Therefore, we must suggest that puffins are not undertaking ARS behaviour in the 'classic' format but instead are adopting a broader ARS strategy that is energetically optimal and incorporates dives as traditionally seen in foraging alcids (Shoji *et al.* 2015b; Shoji *et al.* 2015c).

This study shows that puffins are foraging using a tidal landscape, in which puffins drift on tidal currents and forage throughout this period, however seabird associations with tides are not unknown. Magellanic penguins, *Spheniscus magellanicus*, change swimming and dive patterns when faced with strong tidal currents (Wilson *et al.* 2001), while Adélie penguins, *Pygoscelis adeliae*, change foraging locations based upon tidal cycles (Oliver *et al.* 2013). Furthermore, black guillemots forage in areas of high tidal activity (Nol & Gaskin 1987; Waggitt *et al.* 2016) where tides are thought to aggregate prey (Alldredge & Hamner 1980). However, these examples still contain ARS. The dive profiles of tracked puffins do suggest search/pursuit occurring underwater. All diving seabirds undertake search/pursuit during dives, in addition to above-surface ARS (that is absent in this study), reflecting finer-scale processes associated with prey capture (Evans *et al.* 2013a; Shoji *et al.* 2015b; Shoji *et al.* 2015c). We suggest that further studies combining diving behaviour and movement patterns are likely to confirm that non-ARS foraging is more widespread, particularly in areas of high tidal activity. Razorbills

tracked during this study showed drifting behaviour, however we could not discern any diving from these periods suggesting that drifting is likely a period of rest for this population, similar to the tracks of lesser black-backed gulls, *Larus fuscus*, reported by Shamoun-Baranes *et al.* (2011). Interestingly, a study on razorbills in Wales, UK, showed extensive periods of drift and little evidence of ARS, and while foraging behaviour was not the focus of that study (Cooper *et al.* 2018), some birds also instrumented with time-depth loggers showed diving during these trips (E. Owen, *pers comm*).

Puffins, and auks in general, are energetically expensive flyers with high wing loading (Pennycuick 1987; Thaxter *et al.* 2010; Vandenabeele *et al.* 2012). Using currents is likely to drastically reduce locomotion costs associated with travelling between prey patches, making it an energetically optimal strategy. The energetic cost of drift trips was on average 39.2% lower than flight, although this is likely a gross underestimate because our flight costings relied on the assumption of straight line flight, while ARS (by definition) consists of more tortuous and looping travel covering a greater total distance. We also did not consider the high cost of take-off following dives between prey patches because these costs are unknown. The drifting strategy, while energetically cheaper, comes at the expense of time. Observed trips were longer than those reported for puffins at other colonies (Harris & Wanless 2011) and likely results in less frequent food deliveries for chicks. How this impacts upon chick development is unknown but it may be that adults coordinate feeding times to ensure healthy chick development (Shoji *et al.* 2015a).

Puffins have adapted their behaviour to take advantage of an environmental feature; tidal flows. Whilst it may appear that puffins are simply departing from their colony and diving for prey is perhaps misleading. The observed behaviour implies that puffins are capable of determining the state of the tide and where they must arrive to ensure a drift over a core use area. This observation of environment and modification behaviour in seabirds is not unknown, black-legged kittiwakes have been observed to change foraging areas based on tidal state (Trevail *et al.* 2018), although how seabirds anticipate future environmental conditions is less understood. Puffins may be relying on environmental cues to determine correct

orientation of departure for foraging; the study colony in this instance has a very exposed wave cut platform at low tide which may provide context for individual puffins. Information foraging (Pirolli & Card 1999) is a theory, originally developed in humans, which suggests that animals may modify behaviour as they collect new information informing behavioural choices. This theory suggests that puffins are simply utilising information around them, such as associating tidal state with foraging patch availability, and consequently developing novel optimal foraging strategies. Puffins may also be taking cues from conspecifics returning from foraging trips to determine best foraging grounds. Multiple seabird species take information from other birds returning from foraging whilst rafting outside the colony (Weimerskirch *et al.* 2010; Thiebault *et al.* 2014) and puffins may be using information in a similar manner.

It is likely that all tag attachments affect bird behaviour in some aspect (Bodey *et al.* 2018a). While we did note weight differences in instrumented birds, sample size was too small to properly assess impact, however we are confident that natural behaviour was not compromised to the extent that birds were unable to perform ARS. Total deployment weight was lower than in previous studies where puffins were observed to undertake typical ARS foraging (Harris *et al.* 2012), all birds undertook similar drifting behaviour over the same core use area, and our tagged birds were observed returning to the colony carrying fish, indicating successful foraging and chick provisioning. Although two puffins were documented to have lost weight, individuals with smaller tags actually increased in weight. All due care should be taken when undertaking tagging studies to ensure ethical standards are upheld (Wilson & McMahon 2006). Whilst previous studies have shown increased tag weight or size may produce unnatural behaviour (Vandenabeele, Wilson & Grogan 2011; Harris *et al.* 2012), we consider that the behaviour documented here is a natural behaviour used to reduce foraging costs.

Optimal foraging theory is driven by the principle that animals will maximise energy gain of foraging whilst minimising energy expenditure during search behaviour. Here, we highlight a previously unreported foraging strategy which departs from the

'optimal' Area Restricted Search for foraging for patchily distributed prey (Charnov 1976; Kareiva & Odell 1987) whilst still remaining optimal.

Effective species conservation management must be informed by a species' ecology and natural history (Caro 1999). Here we show that puffins have adapted their behaviour to take advantage of a natural feature within their environment. Traditional management strategies may not be able to account, or even be aware of, novel behaviours or strategies within a population as seen here. Without effective local monitoring and research, appropriate protection cannot be implemented. Seabirds are experiencing major global declines (Paleczny *et al.* 2015) and without fully understanding their natural history strategies it is difficult to implement effective measures. Puffins in this population have clearly developed a method of foraging that departs from traditional and expected patterns of area restricted search, whilst arguably maintaining the principles of optimal foraging. Whether this strategy is stable over time, how it spreads through a population, and how common it is in other marine foragers or other systems will be an interesting area of further research.

Chapter 4: A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species

Ashley Bennison, Joan Giménez, John L. Quinn, Mark Jessopp

This study was conceived by myself with input from supervisors. I was responsible for planning and conducting the two years of fieldwork, and analysis of movement data. Joan Giménez undertook the stable isotope analysis and we worked together to interpret these results. I was responsible for leading on development of the manuscript under guidance from Mark Jessopp and John Quinn.

Target Journal: Functional Ecology

4.1 Abstract

1. Many animals show sexually divergent foraging behaviours reflecting different physiological constraints or energetic needs. However, the mechanisms behind these observed differences are not always understood.
2. We used a bioenergetics approach to examine sex differences in foraging behaviour of a sexually monomorphic seabird, the northern gannet. We used the relationship between dynamic body acceleration and energy expenditure, and investigated the cost of prey capture attempts and chick rearing in relation to energy gain from prey.
3. Fourteen gannets were tracked from their colony using a combination of GPS, TDR, and accelerometers. Prey capture attempts consisted of a dive and subsequent take-off. The total cost of all prey capture attempts in a foraging trip represented <4% of total energy expenditure, and there were no significant sex differences in the costs of prey capture attempts. Despite females undertaking significantly more dives than males, the low energetic cost of individual prey capture attempts resulted in no sex differences in overall energy expenditure across a foraging trip.
4. Bayesian stable isotope mixing models based on blood samples from the wider gannet population, including tracked individuals, were used to reconstruct diet and highlighted sex differences. However, calorific intake from successful prey capture was estimated to be similar between sexes, though nutritional content may differ.
5. Females experienced 9.6% higher energy demands than males, largely due to females providing more food to chicks than males. After accounting for the number of prey capture attempts and energy content of prey, we estimated that a minimum of 21% of dives would have to be successful for females to meet their daily energy requirements, and 29% for males.
6. Our analyses suggest that northern gannets, a sexually monomorphic species, show sex differences in foraging behaviour primarily related to dive rate and feeding success rather than the energetic cost of foraging or energetic content of prey.

4.2 Introduction

Many animals show sex foraging differences, though it is often difficult to explore the mechanisms behind these differences - particularly in free ranging predators. Sex differences in foraging are often pronounced in sexually dimorphic species (Ginnett & Demment 1997; Beck *et al.* 2003). These differences may be due to increased aggression between sexes in species which show competitive exclusion (Phillips *et al.* 2004b), or where different sexes may have access to different foraging areas due to their size (Phillips *et al.* 2004b; Patrick & Weimerskirch 2014a) or foraging habitat preference (Wanless, Harris & Morris 1995). Divergent sexual behaviours may also represent differences in nutrient requirements or prey preferences (Maklakov *et al.* 2008; Reddiex *et al.* 2013), levels of parental care (Kokko & Jennions 2012), or in the energetic demands of locomotion (Rogowitz & Chappell 2000; Lees *et al.* 2011). Differences can also arise because a more dominant sex will outcompete or displace the other, resulting in sexual segregation (Biggerstaff *et al.* 2017; Galezo, Krzyszczyk & Mann 2017), niche expansion and reduced intraspecific competition (Pincheira-Donoso *et al.* 2018). Giant petrels, *Macronectes giganteus*, where females weigh 80% the mass of males, show spatially segregated foraging areas (González-Solís, Croxall & Wood 2000), a pattern that holds true across a wide variety of taxa (Ruckstuhl & Neuhaus 2000; Tina, Jaroensutasinee & Jaroensutasinee 2015; Ehl *et al.* 2018; Salton *et al.* 2019). Although sex differences in foraging tend to be less obvious in sexually monomorphic species, they still occur (Wearmouth & Sims 2008). For example, female northern gannets, *Morus bassanus*, are more selective than males when choosing foraging areas (Lewis *et al.* 2002). In a similar fashion, female thick billed murres, *Uria lomvia*, foraged in high risk foraging areas during a period of bi-parental care compared to males foraging in more predicable foraging locations – showing spatial and risk partitioning between the sexes (Elliott, Gaston & Crump 2010)

In monomorphic species, sex-specific foraging behaviour can be driven by differing energy requirements between the sexes (Pinet *et al.* 2012). For example, Barau's petrel is a monomorphic seabird where males and females forage in different locations early in the breeding season as females must restore body condition after

egg production (Pinet *et al.* 2012). There is also evidence to suggest that sex-specific foraging strategies in sexually monomorphic species may be driven by intraspecific competition causing one sex to be displaced spatially or to forage in different niches (Elliott, Gaston & Crump 2010). Differing energy budgets and demands between the sexes may also drive the specialisation of prey targeting or foraging range (Smith *et al.* 2015). Foraging theory states that animals attempt to intake food in the most optimal manner possible (MacArthur & Pianka 1966; Tullock 1971; Pulliam 1974) to ensure that net energy gain exceeds gross energy expenditure. However, accurately measuring energy intake and expenditure remains a challenge, especially in free-ranging animals (Brown *et al.* 2013; Wilson *et al.* 2019). Measuring energetic expenditure has previously involved the use of double labelled water (DLW), respirometry chambers, or heart rate loggers (Butler *et al.* 2004). Though heart loggers can be used to investigate behaviour specific energy costs (Green 2011) and respirometers can easily provide resting metabolic rates and calibration for other field techniques (Frappell, Blevin & Baudinette 1989); these techniques can be overtly invasive. In recent years, accelerometry studies on free-ranging individuals have explored energetic expenditure at a much finer scale and over longer time periods (Shepard *et al.* 2008b). These studies can use measures of dynamic body acceleration (DBA) as a proxy for energy expenditure due to a strong correlation with the volume of oxygen consumed by muscles (VO_2) (Halsey *et al.* 2009; Gleiss, Wilson & Shepard 2011; Halsey, Shepard & Wilson 2011). However, developing an understanding of how accelerometry signals relate to energy use and the corresponding energy budgets of an individual animal requires knowledge of diet and energetic intake.

Net energy intake is determined by the energy gained from successful foraging against energy expended in metabolism through activities such as locomotion. Quantifying energy gained through diet in free-ranging animals can be difficult without invasive techniques such as stomach content analysis (Goldsworthy *et al.* 2016) or direct observation of prey capture (Thiebault *et al.* 2016). However, Stable Isotope Analysis (SIA) is a minimally invasive technique that can provide diet information and, in seabird studies, is known to correlate well with other more direct

methods (Hobson 1993; Hobson, Piatt & Pitocchelli 1994; Bond & Jones 2009). Isotopic ratios of $^{12}C/^{13}C$ and $^{14}N/^{15}N$ can also be used to infer specific prey species selected by an individual (Stock & Semmens 2016) and trophic position of prey items in the food chain (Hobson 1987). Using SIA to predict predator diet can therefore provide insight into the energetics of foraging.

The northern gannet (*Morus bassanus*), hereafter gannet, is sexually monomorphic (Stauss *et al.* 2012; Deakin *et al.* 2019), but shows strong sexually divergent foraging strategies. Female gannets are more selective in choosing foraging grounds (Lewis *et al.* 2002) and undertake longer trips, further offshore than males, a pattern that is thought to arise from habitat segregation (Cleasby *et al.* 2015). From a dietary perspective, male gannets consume higher proportions of fisheries discards than females – a distinction only present in breeding adults (Stauss *et al.* 2012). Females which specialise on fisheries discards travel shorter distances than forage fish female specialists, however this distinction is not apparent among males (Bodey *et al.* 2018b). At present, there is no clear evidence for whether sexes target different sized prey in gannets. Female Blue-footed boobies, a closely related sulid, consume larger prey items than males though this is thought to be related to their marked sexual dimorphism (Zavalaga *et al.* 2007). Although female gannets tend to be marginally heavier than males, weight alone cannot be used to sex individuals (Malvat *et al.* 2020). This lack of strong sexual dimorphism suggests that sex differences in foraging strategies and diet may derive from different energetic demands between the sexes. Here we used GPS, accelerometry, and SIA data to gain a better understanding of how northern gannets engage in foraging and how different demands upon the sexes may affect foraging strategies.

In this study, we have explored whether there were any sex differences in foraging in terms of diet, dive types, frequency of prey capture attempts, and the energetic cost of prey capture attempts. We then quantified the energetic requirements of males and females, taking into account energy expended during foraging and, using data from published studies, energetic demands of feeding offspring. Finally, we considered what minimum feeding success rates would have been necessary for males and females to meet their energy demands.

4.3 Methods

All research was approved by the University College Cork Animal Ethics Committee and was conducted under licence from the Health Products Regulatory Authority, the National Parks and Wildlife Service, and the British Trust for Ornithology.

Data Collection

A conceptual diagram of our study is presented in Figure 4.1. Breeding adult gannets (n=8 in 2017, n=6 in 2018) attending 3-4-week-old chicks were tracked from Great Saltee, south-east Ireland (52^{o} 7' 37.92", -6^{o} 35' 45.6"). Birds were caught using an 8-10m pole with a metal crook, weighed, and equipped with a combination of dataloggers. GPS loggers (i-gotU GT-120, Mobile Action Technology Inc., Taipei, Taiwan, 14g) recorded locations every 3 minutes; time depth recorders (TDR, CEFAS G5, 2.5g) recorded depth at 4Hz after exceeding a 0.5 or 1m depth threshold; tri-axial accelerometers (Gulf Coast Data Concepts X16-mini, 17g) recorded *g*-forces (1*g* = 9.807m/sec^{2}) at 50Hz. GPS and TDR loggers were attached ventrally to 2-3 central tail feathers using strips of waterproof Tesa tape. Accelerometers were attached to 10-15 mantle feathers between the wings to ensure proximity to the centre of gravity required for accurate accelerometer readings using strips of waterproof Tesa tape. Three birds in 2017 and six birds in 2018 were equipped with GPS, TDR, and accelerometers, while the remaining birds were equipped with only GPS and accelerometers. Total instrument mass was <2% of body mass, and positioned to minimise impact on gannet movement, both aerodynamic and hydrodynamic (Vandenabeele *et al.* 2012). Two to three breast feathers were also plucked for genetic sexing following the method outlined by Griffiths *et al.* (1998).

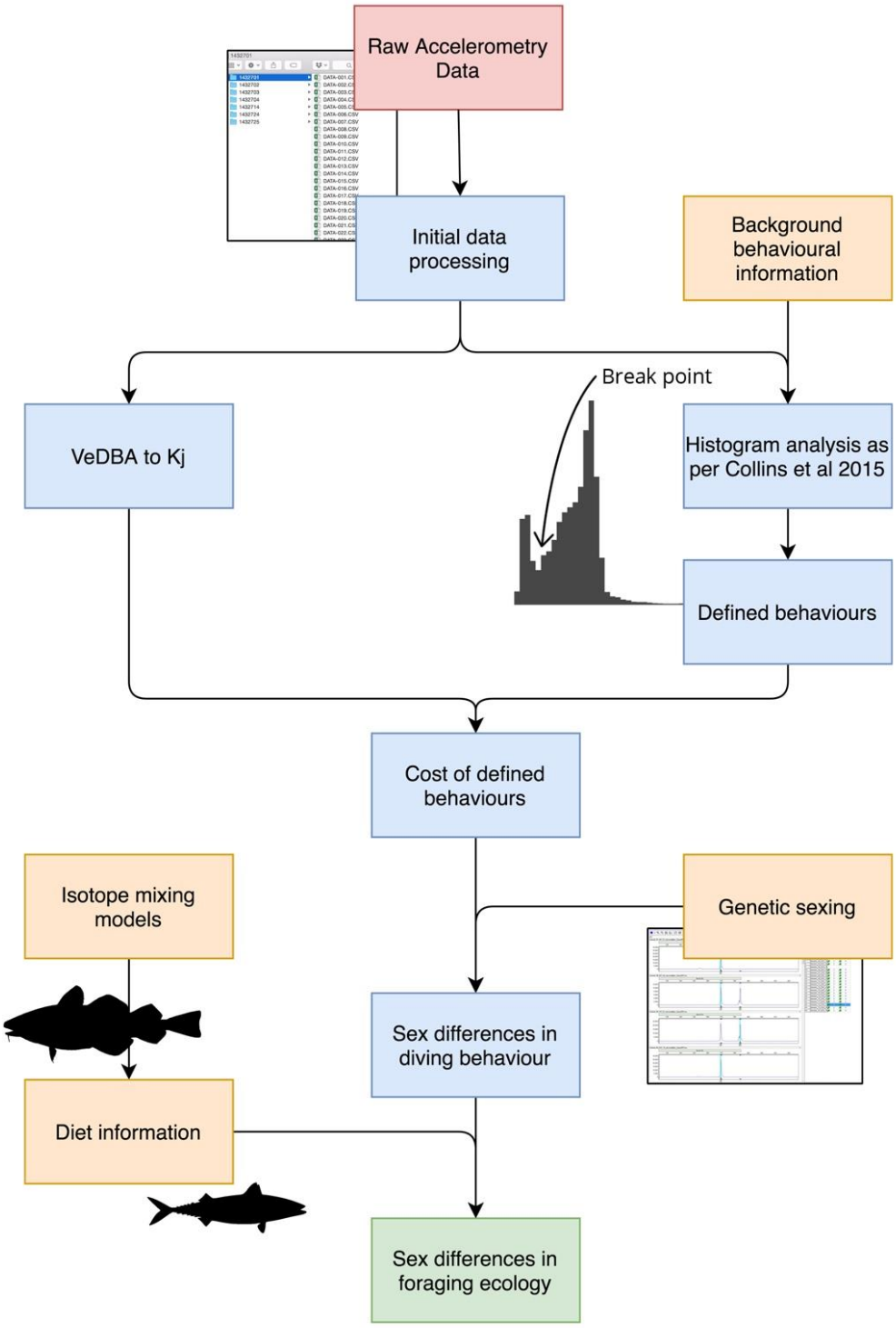

Figure 4.1. Schematic of methodology for data processing and the steps required to explore the sex differences in the foraging of northern gannets. The process starts at top with the red box labelled “raw accelerometry data” and ends with the green box “Sex differences in foraging ecology.” Blue boxes represent the staged methodology for analysing accelerometry data and orange boxes represent further methods that

develop the findings. Histogram analysis to define behaviours is an iterative process using methods defined by Collins *et al.* (2015)

Data processing and dive behaviour definition

Behaviour classification from accelerometry data used a thresholding approach. Thresholds were determined using protocols and guidance set out by Collins *et al.* (2015) and Shepard *et al.* (2008a). Diving events occurred when average acceleration (running average of 2 seconds) in the X-axis was <0*g* and standard deviation (SD) in the mean X-axis was >1.4*g*. The end of a dive was defined by a 1-second lagged maximum of pitch change within a 60 second period from the start of a dive. Take-off events were defined with a threshold where, following a dive, the SD of the Z-axis was >1.8*g* and the SD of the X-axis was >1*g*. Take-off events were considered to have ended and returned to normal flight when the SD of the Z-axis resolved to <1.4*g* and the SD of the X-axis was <1.4*g*. A subset of birds (n=9) tagged with both TDRs and accelerometers were used to validate accelerometer-derived dive events by visually comparing timestamps to TDR confirmed dives. Accelerometer-derived dives had a bimodal distribution and were split into plunge dives and pursuit dives based on a distinct break within the frequency distribution at 5 seconds; plunge dives are dives followed by an almost immediate rise to the surface, whilst a pursuit dive is characterised by sustained chase of prey underwater.

Energetics from Accelerometry

Dynamic body acceleration (DBA) is a relative metric that can be used as a proxy for energetic expenditure from animal movement (Wilson *et al.* 2006b), and can be used to develop highly accurate activity budgets (Patterson *et al.* 2019). We used Vectorial DBA (VeDBA) to account for any variation in tag alignment (Qasem *et al.* 2012). We converted VeDBA into kilojoules (kJ) using published data and allometric equations (Schmidt-Nielsen & Knut 1984). The relationship between energy expenditure (kJ) and VeDBA is linear amongst a variety of animal taxa, including mammals, reptiles, and birds (Halsey *et al.* 2009; Hicks *et al.* 2017; Wilson *et al.* 2019), with slope *k*. Using the process outlined in Figure 4.2, it is possible to produce estimates of kilojoules

expended in movement for given periods or behaviours. The process assumes that energy expended in movement is equal to an animal's Field Metabolic Rate (FMR) minus Resting Metabolic Rate (RMR) for any given period. Totalled 24-hour VeDBA is therefore equivalent to kJ from FMR-RMR, assuming where VeDBA = 0, kJ = 0. Simple algebra can then produce a formula for kJ of any VeDBA score over any time period. Here, we used FMR estimates for Northern gannets provided by the Shiny App by Dunn, White and Green (2018), corrected for individual bird weight and colony latitude (52°N), and RMR estimates provided by allometric equations from Schmidt-Nielsen and Knut (1984) to produce individualised VeDBA to kJ equations. This method aims to produce whole sum approaches to energy expenditure; at present it is not possible to effectively account for periods of rest on water where sea swell may predict energy via acceleration and we assume that all acceleration is from animal movement.

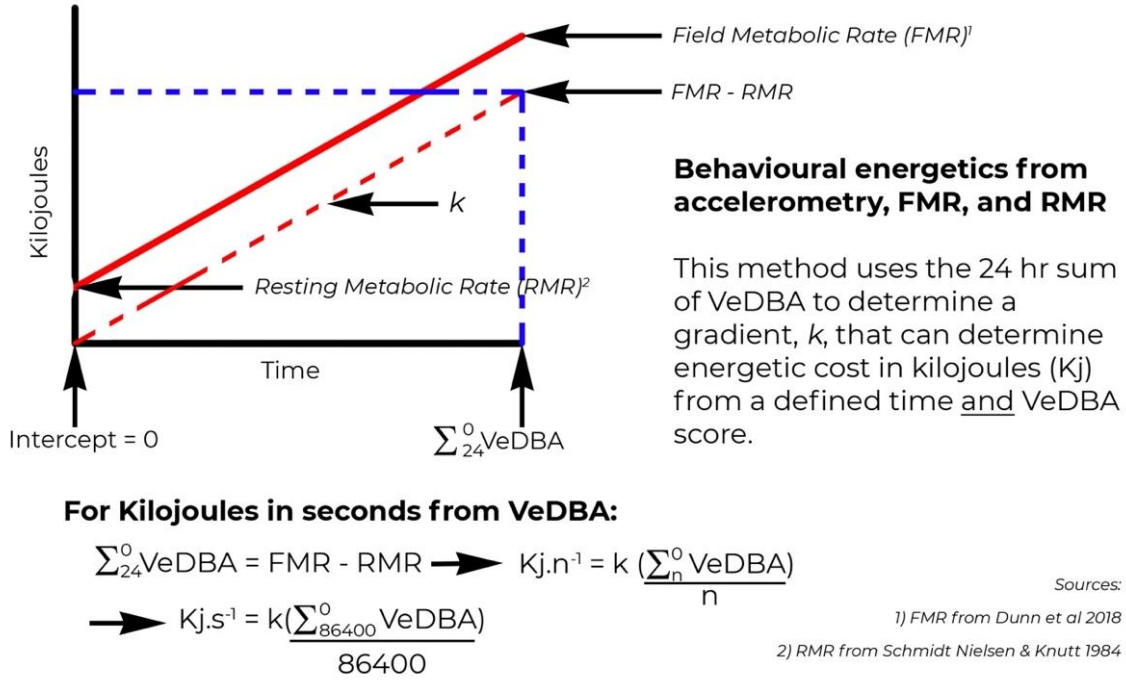

Figure 4.2. Conceptual diagram demonstrating how to extract the kilojoule values of any given specific behaviour or time period within an accelerometry dataset for energy consumed only by movement.

Isotopic Analysis for Diet Composition

Blood samples were taken from 47 birds, including the accelerometer-equipped birds, (n=19 in 2017 and n=28 in 2018) and used to construct a population model of dietary intake from isotope analysis. Blood samples were taken from the tarsus during tag deployment and centrifuged for 10 minutes to separate red blood cells (RBC) from plasma. While RBC therefore represent diet prior to the deployment, preliminary sampling showed that isotopic signatures do not differ significantly between blood samples collected on deployment and recovery of devices approximately 1 week apart (unpublished data) due to the 30-day turnover rate of RBC. RBC were dried for 24 hours at 60° C, homogenised and lipid extracted using repeated addition of a 2:1 mixture of Chloroform:Methanol following (Bligh & Dyer 1959). Stable Isotope Analyses were performed at Elemtex UK (Stable Isotope and & Elemental Analysis Expertise), using a Thermoquest EA1110 Elemental Analyser linked to a Sercon 2020 stable isotope ratio mass spectrometer running in continuous flow mode. Accuracy and precision were monitored through laboratory internal standards and an in-house comparison standard nested within samples.

Prey stable isotope values were obtained from a published dataset of Celtic Sea fish samples (Jennings & Cogan 2015) and our own dataset. Jennings and Cogan (2015) conducted stable isotope analysis of prey samples without lipid extraction. The $\delta^{13}C$ data included in the published data set are not corrected for differences in lipid content, but the % C and N data can be used to make the required corrections, with samples with a ratio higher than 3.5 corrected following Logan *et al.* (2008). As recommended by Phillips *et al.* (2014), a reduced prey dataset was used and included only those species previously recorded in more than 3% of the diet for Great Saltee gannets (Lewis *et al.* 2003). These consist of three pelagic species (Atlantic herring *Clupea harengus*, European sprat *Sprattus sprattus,* and Atlantic mackerel *Scomber scombrus*), one benthopelagic species (Lesser sandeel *Ammodytes marinus*), two species from the Gadidae family (Whiting *Merlangius merlangus* and Norway Pout

Trisopterus esmarkii) and four demersal species (European plaice *Pleuronectes platessa*, European hake *Merluccius merluccius*, Red gurnard *Chelidonichthys cuculus*, and Dragonet *Callionymus lyra*).

Using Bayesian isotopic mixed models, it was possible to compare blood values to reference prey values to reconstruct diet of gannets. The model was run on "long" settings (chains = 3, length = 300000, burn-in = 2000000, thinning = 100), using average diet–to-tissue discrimination factors (2.25 ± 0.61 ‰ for δ15N and 0.24 ± 0.79 ‰ for δ13C) from various studies of piscivorous birds (Hobson & Clark 1992; Bearhop *et al.* 2002; Forero *et al.* 2002; Cherel, Hobson & Hassani 2005). Model convergence was assessed with the Gelman-Rubin diagnostic (Gelman *et al.* 2013). Sex-based diet estimates were obtained through Bayesian mixing models using the R package 'MixSIAR' (Semmens *et al.* 2013). We fit several models of diet with fixed and random effects as covariates, and evaluated the relative support for each model using LOO (leave-one-out cross-validation) weights. LOO is a method to estimate pointwise out-of-sample prediction accuracy from a fitted Bayesian model using the log-likelihood evaluated at the posterior simulations of the parameter values (Vehtari, Gelman & Gabry 2017). Model outputs were then used to construct prey proportions in the diet of males and females in 2017 and 2018.

Statistical analysis

To explore sex differences in the overall cost of prey capture attempts (dive and subsequent take-off), a linear mixed effect regression (LMER) was used to test for sex differences in dive and take-off characteristics. Factors included year, sex, weight, dive type, and the interaction between sex and dive type to predict kilojoules expended. Individual was included as a random effect to account for repeated measures of the same individual. To select the most parsimonious model, the dredge function from the 'MuMin' package was used (Barton 2011). Any models within 6 AIC values were kept and model averaging undertaken (Harrison *et al.* 2018).

We used the relationship between VeDBA and kJ shown in Fig. 4.2 to estimate total energetic *expenditure* for an individual bird from the time it left the colony, to the point of recapture. Gannet trips may range from one to several days and so this

whole sum approach allowed our predictions to account for a full range of behaviours, from in colony, transiting, and foraging. As gannet foraging trips may last several days, they incur increasing energetic costs during a foraging trip such as feeding chicks upon return, we have included this in the analysis by considering energetic differences from a whole sum approach and use gannet trips as the energetic unit. We also consider individual energy expenditure per 24 hour period. We then calculated energetic *demands* by adding to this value the energetic demand of raising a four week old chick of 1397.14 kJ/day (Montevecchi *et al.* (1984), with females contributing 60% of this cost due to unequal chick feeding in gannets (Montevecchi *et al.* 1980; Montevecchi *et al.* 1984). Though it would be most appropriate to have information on feeding rates of chicks in this study, we do not have this information and instead consider the overall energy requirements of chicks which act as a proxy to feeding rates. This produced a value of Total Energetic Demand (TED) for each gannet for the time it was tracked. Using sex-based SIA model outputs, we predicted the proportion of prey species in the diet of male and female gannets.

We assumed the sizes of individual prey species were similar to those in Lewis *et al.* (2003), a study from the same colony that did not identify any difference in the size of fish caught between the sexes. The size and mass of the fish were then used to calculate the kJ value of each fish species (using allometric equations referenced by Lewis *et al.* (2003) and assuming a 76.1% assimilation efficiency following Cooper (1978), See Table 4.1). For each sex-specific diet, the energy content (kJ) of each fish was multiplied by the proportions of species in the diet and these proportional values were summed to provide an average kJ intake value (KIV) for a successful dive (a dive resulting in prey capture) for each individual gannet, assuming that successful prey capture results in capture of one prey item. A Mann-Whitney-Wilcoxon test was used to test for differences in KIV between sexes. For each gannet, TED was divided by KIV to determine how many successful dives were required to maintain body condition, forage, and provision for a chick. This number was then used as a proportion of dives recorded to derive realistic individual minimum prey capture rates.

Table 4.1. Energy values for fish species in gannet diet, values use 76% assimilation efficiency. Energetic values are presented as kJ/g wet weight multiplied by average biomass of fish as per Lewis *et al.* (2003).

Species	***kJ (with 76% digestion efficiency)***
Lesser Sandeel 0 group	4.6
Lesser Sandeel 1+ group	54.3
Greater sandeel 0 group	38.7
Greater sandeel 1+ group	209.1
Mackerel	1928.2
Herring	187.3
Garfish	1198.6
Plaice	227.1
Whiting	820.3
Norway pout	195.0
Hake	387.1
Red gurnard	1119.3
Dragonet	2824.5
Shortfin Sculpin	76.3
Salmon	616.5
Scad	625.7
Sprat	47.3

4.4 Results

Of the 14 gannets tracked, five were female, eight were male, and one was of unknown sex. The individual of unknown sex was not included in analysis of sex differences. Male gannets were on average lighter than females; male weight was 2.70kg ±0.19 with females weighing 2.99kg ±0.15 (Wilcoxon test: W=35.5, r=0.88, p=0.025).

Sex differences in dive behaviour

1046 visually validated dives and subsequent take-off events were detected. 24% of these were pursuit dives with females having a slight tendency towards increased pursuit dives compared to males. Combined cost of a single prey capture attempt (dive + take-off) in females was 2.17 ±0.73kJ while for males it was 1.97 ±0.92kJ. An averaged LMER indicated a significant effect of dive type and year on energy expenditure associated with dives while sex was retained as a non-significant factor (Table 4.2). The estimates for cost of all prey capture attempts represent < 4% of the daily total energy expenditure for each individual. Accounting for unequal provisioning of the chick, and the cost of foraging, daily energetic demands were 9.6% higher for females than males (female TED = 4601kJ ±121.60; male TED = 4207kJ ±278.37, Wilcoxon test: W=34, $p<0.05$, total number of female days: 14.84, total number of male days: 31.88).

Table 4.2. Conditional model summary from the averaged mixed effect linear regression used to predict kilojoules (kJ) expended during a prey capture attempt. Input variables were year (2017 and 2018), sex (male and female), dive type (pursuit or plunge), and weight. The interaction between sex and dive type was also included. Dive type (plunge) and sex (Female) were absorbed into the intercept.

Dive energetics model	***Coefficient***	***Std. Error***	***Adjusted SE***	***Z value***	***P value***
Intercept	-1976.374	794.301	795.059	2.486	0.01293
Type(Pursuit)	0.6008	0.0480	0.0481	12.480	**<0.001**
Year	1.0327	0.330	0.331	3.117	**<0.01**
Weight	0.1837	0.856	0.857	0.214	0.8302
Sex(Male)	-0.0895	0.411	0.411	0.217	0.8278

Females undertook significantly more dives per day than males (25.9 and 17.3 respectively, GLM F_{13}=8.63, p<0.01). However, because the cost of individual prey capture attempts is so low, a linear mixed effect regression predicting the energy expenditure (kJ) per day for each individual from sex and year, with ID as a random effect, found no significant effect of sex on daily energy expenditure (LMER Chi^2_{38} = 0.0004, p = 0.98)

Isotopic analysis

The isotope mixing model predicted that the most consumed prey species were Atlantic mackerel (*Scomber scombrus*) (27.83 % ±4.34) and European sprat (*Sprattus sprattus*) (19.16% ±2.06) followed by Lesser sandeel (*Ammodytes marinus*) (11.47 % ±0.99) and Atlantic herring (*Clupea harengus*) (11.26 % ±1.46). The remaining species included in the models were each predicted to contribute less than 8% to the overall

diet. Seven different models were tested (Table 4.3) and the best model included *Year* as a covariate (Model weight: 76.8 %, Model 4). The second-best model included *Sex* and *Year* as variables with a relative weight of 23.1%, and was used to predict sex-specific diets in each study year. There was no support for a model using individual ID only. Diet between the sexes was similar in both years (Table 4.4), though mackerel made a higher contribution to male diet (3.4% in 2017 and 4.3% in 2018). Between years, 2017 had a wider range of species consumed, in 2018 the predominant species consumed was mackerel (68.7% 64.4% of diet for males and females respectively)

Table 4.3. Bayesian mixed effect model outputs to determine predictors of diet. The best model lent support for a Year only model, however the second-best model was Sex +Year with a model weight of 23.1%. This model was used to predict diet of the sexes. Leave One Out cross validation Information Criteria (LOOic) were used to assessed model suitability.

Model	***Variables***	***LOOic***	***Standard error LOOic***	***Delta LOOic***	***Standard error delta LOOic***	***weight***
4	Year	87.5	11.8	0	NA	0.768
6	Sex + Year	89.9	11.6	2.4	3	0.231
5	Year (by ID)	106.8	8.6	19.3	6.4	0
2	Sex	109.7	10.9	22.2	6	0
1	Null	110.7	11	23.2	5.5	0
7	ID	139.2	10	51.7	9.5	0
3	Sex (by ID)	140.4	9.9	52.9	9.9	0

Table 4.4. The diet composition (%) of males and females in 2017 and 2018 as predicted by Bayesian mixed effects modelling as reported in Table 4.3.

		2017		***2018***	
Species Name	**Common Name**	**Female (%)**	**Male (%)**	**Female (%)**	**Male (%)**
Ammodytes spp.	Sandeels	13.3	13	4.5	4.5
Callionymus spp.	Dragonet	4.4	5.5	5.8	7.7
Chelidonichthys cuculus	Red Gurnard	3.8	4.9	2.2	3
Clupea harengus	Atlantic Herring	6	6.9	2.8	3.4
Merlangius merlangus	Whiting	6.4	8.3	1.6	2.2
Merluccius merluccius	Hake	6	6.9	4.2	4.6
Pleuronectes platessa	Plaice	2.5	3	2.4	3.3
Scomber scombrus	Mackerel	37.3	33.9	68.7	64.4
Sprattus sprattus	Sprat	15	12.1	5.8	4.8
Trisopterus esmarkii	Norway Pout	5.1	5.6	2	2.2

Applying average energy content of prey in proportion to its occurrence in the diet, a successful dive was estimated to have an average energy intake (KIV) of 1006 kJ for females, and 1005 kJ for males in 2017. In 2018, this figure rose with changing diet to 1563 kJ for females and 1553 kJ for males.

Based on the number of dives performed and average energy content of prey in proportion to their occurrence in sex-specific diets, female minimum feeding success rate was calculated as 21.21% ±8.42, whilst the male rate was 29.22% ±15.10 (Fig. 4.3). A summary of all results including dives, energy expenditure and success rates can be seen in Table 4.5.

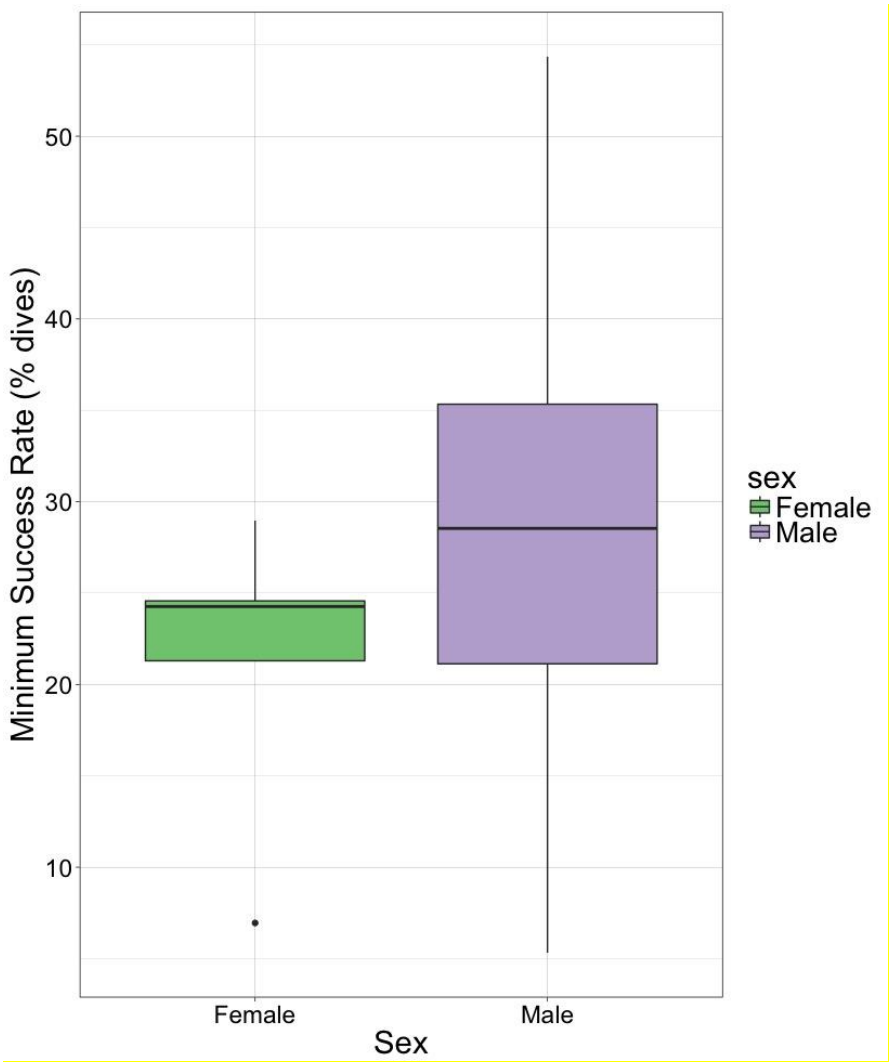

Figure 4.3. Minimum feeding success rates between the sexes to maintain body condition and feed a chick. Males were predicted to require a higher feeding success rate due to the lower numbers of dives undertaken.

Bird ID	*Sex*	*Year of study*	*Tracking duration (Days)*	*Number of dives*	*Dives per day*	*Total energy expenditure during tracking (kJ)*	*Total energy expenditure during tracking plus chick demands (kJ)*	*Energy expenditure per day with chick demands (kJ)*	*Modelled average kJ per successful dive*	*Number of successful dives to meet energy demands*	*Percent of recorded dives needed to be successful*
D01	Male	2017	4.90	113	23.06	19017.89	21756.33	4440	1005.04	21.65	19.16
D02	Male	2017	2.86	36	12.56	9977.19	11577.81	4042	1005.04	11.52	31.99
D03	Unknown	2017	5.08	189	37.15	17676.91	21941.57	4313	NA	NA	NA
D04	Female	2017	0.97	65	66.89	3728.53	4543.13	4675	1005.96	4.52	6.94
D05	Female	2017	1.83	39	21.31	6820.18	8354.34	4565	1005.96	8.30	21.29
D12	Female	2017	4.68	90	19.19	18037.97	21968.74	4685	1005.96	21.84	24.27
D13	Male	2017	4.72	87	18.44	16414.58	19050.09	4040	1005.04	18.95	21.79
D16	Male	2017	1.99	18	9.06	6742.38	7852.85	3952	1005.04	7.81	43.41

D25	Female	2018	3.04	37	12.17	11665.59	14212.90	4677	1563.34	9.09	24.57
D26	Male	2018	2.92	36	12.31	12383.63	14017.50	4794	1552.61	9.02	25.08
D28	Male	2018	4.61	230	49.84	16418.62	18997.12	4117	1552.61	12.24	5.32
D41	Male	2018	4.83	39	8.07	17065.3	19766.91	4089	1552.61	12.73	32.64
D52	Female	2018	4.32	42	9.72	15395.66	19016.77	4402	1563.34	12.16	28.96
D53	Male	2018	5.05	25	4.95	18274.86	21095.85	4179	1552.61	13.59	54.35

Table 4.5. Summary of results from tracked birds between 2017 and 2018. Energy expenditure is calculated from the formulae in figure 2 and chick demands are included by the amount of energy required by a four-week-old chick. Modelled average kJ per successful dive includes results from a Bayesian mixed model from isotope analysis and is produced as a figure for each sex per year.

4.5 Discussion

Here we show that, for gannets, sex differences in foraging behaviour are not the result of divergent energetic costs of foraging or different energetic content of consumed prey. We suggest that sex differences in foraging behaviour are likely to have arisen from unequal energetic demands between the sexes coupled with resource partitioning to avoid intraspecific competition. SIA indicated sex-specific diets, but there was no difference in energy intake between the sexes. Cost of individual prey capture attempts associated with differing diets was low compared to total energetic expenditure, and despite females diving more than males, there was no difference in energetic expenditure per day between the sexes.

To the best of our knowledge, this is the first time that the energetic cost of individual prey capture attempts has been estimated in seabirds. Dynamic body acceleration is an established proxy measure of energy expenditure (Elliott *et al.* 2013a), though difficulties remain in converting DBA to a true measure of energy expenditure (Wilson *et al.* 2019). Studies comparing DBA with energy expenditure must ensure that summed values of energy expenditure must not be regressed against sum values of DBA through time, a problem known as the time trap (Halsey 2017; Ladds *et al.* 2017). In this study we accounted for time, allowing for meaningful estimates of energy expenditure per unit time from DBA. The resulting energetic cost of prey capture events was low, even after including the cost of take-off from the sea surface following a dive, with all prey capture attempts across a foraging trip accounting for <4% of total energy expenditure. This suggests that the cost of diving probably does not limit the number of prey capture attempts in gannets, though we acknowledge this may not be true for birds struggling to meet daily energy demands. Sex differences in the energetic cost of individual prey capture attempts were minor and non-significant, albeit based on a small sample size. Despite females undertaking an average of eight more dives per day, the low cost of prey capture attempts resulted in no differences in daily energetic expenditure between males and females. Females diving more may expend relatively more energy as they spend more time underwater moving through a thicker medium, however this is likely not the case as it has been

found that metabolic energy expenditure is not affected by the medium an animal moves through (Laich *et al.* 2011). Year and dive type (plunge versus pursuit dive) had the largest effect on energetic cost of diving, reflecting yearly differences in diet noted in SIA analysis, that are likely related to the proportion of different dive types. 76% of dives were plunge dives with an almost immediate rise to the surface, though 2017 contained 12.9% more pursuit dives than 2018. The increased cost of underwater pursuit following a 'failed' plunge dive suggests a cost-benefit trade-off, and Machovsky-Capuska *et al.* (2011) noted higher feeding success in pursuit dives in Australasian gannets, *Morus serrator*, that would support this hypothesis.

Gannets forage on a wide variety of prey (Hamer *et al.* 2007), and SIA models indicated divergent diets between males and females, consistent with previous studies in gannets (Stauss *et al.* 2012). Prey proportions from our SIA models were similar to those previously reported by Lewis *et al.* (2003) at the same site, and we found females took proportionately more mackerel and less whiting, Norway pout, and herring compared to males. Applying the average calorific content of prey species to sex-specific diets, energetic gain per dive did not differ between sexes. However, females make a greater contribution to chick provisioning (Montevecchi *et al.* 1984), which may require a proportionate increase in targeting of smaller sized prey for chick consumption. While this has been observed in other seabird species (Davoren & Burger 1999), there is little evidence to suggest such specific prey targeting in provisioning gannets whose chicks are capable of consuming quite large prey items. Our results suggest that divergent diet is not the result of differing energetic cost of prey capture, or energy content of prey, but may be a result of niche partitioning to reduce intraspecific competition, as seen in albatross (Phillips *et al.* 2011a), or as a means of meeting differing nutritional needs (Maklakov *et al.* 2008).

Intraspecific competition is expected to be higher with increasing proximity to a breeding colony (Ashmole 1971; Wakefield *et al.* 2013) and this competition may drive differing sexually divergent foraging behaviour in gannets. Several studies report that male gannets forage closer to breeding colonies whilst females travel further (Lewis *et al.* 2002; Stauss *et al.* 2012). This may be due to male gannets outcompeting females forcing them to travel further and undertaking different dive

behaviour as they are forced to forage in different habitat than males (Cleasby *et al.* 2015). However, these studies concede that there is no strong compelling evidence that sexual separation is entirely due to males outcompeting females and that foraging in different habitat may increase chances of finding different prey of different nutritional value. Different nutritional requirements between the sexes may also drive divergent foraging behaviour. As the sexes search for different prey, they may engage in alternative prey capture and foraging behaviour. One component of birds' life history strategy that may induce specific nutrition demands is moulting. Moulting is a particularly energetically expensive component of birds' life history (Cyr, Wikelski & Romero 2008) and some seabird species have been noted to undertake sexually different moult staging (Weimerskirch 1991; Ramos *et al.* 2009). It is currently unknown if gannets show sex differences in moult staging, though they do undertake a semi-continuous moult which is not thought to affect their energetic demands during the breeding season (Nelson 2002). A further consideration is that egg production by females may cause a nutrient deficit (Scanes, Campbell & Griminger 1987; Perrins 1996), specifically of calcium (Keshavarz 1986), which may drive different foraging behaviour as birds seek to recover this loss (Reynolds & Perrins 2010). Gannets are known to lay small eggs in comparison to their body size (Nelson 2002) so it is currently unknown how this may affect foraging requirements.

Female gannets dived significantly more frequently than males which may reflect differing provisioning roles (Grieco 2001; Limmer & Becker 2009), with female gannets estimated to have a 9.6% higher daily energetic demand, largely because of their greater contribution to chick feeding (Montevecchi et al., 1984). After accounting for the increased energetic demands in females, the energetic cost of foraging, the mean calorific content of prey in sex-specific diets, and the number of dives performed, males were predicted to have a higher minimum feeding success rate than females (21% of dives in females and 29% of dives in males). These estimates of feeding success are lower than more direct estimates of approximately 50-66% for Australasian gannets based on identifying prey captures from bird-borne cameras (Wells, Angel & Arnould 2016; Cansse *et al.* 2020). Our estimates reflect *minimum* success rates required to meet energy demands, and the discrepancy

suggests that gannets may routinely catch more food than required to meet minimum energy demands that may be invested in chick provisioning, or that they engage in energetically demanding activities around and within the colony such as preening and aggression (Nelson 2002) that are not accounted for in our analysis.

Energy acquisition and allocation provide a useful framework to study ecological problems, including management and evolution (Karasov 1986). This study highlights how DBA can be used to estimate energetic cost of discrete behaviours as well as overall energetic expenditure across defined time periods, providing insights into the foraging ecology of free-ranging animals. While gannets are sexually monomorphic, they show divergent foraging behaviour and diet, which our results suggest are not the result of differing cost of foraging or energy content of prey. Such sexually divergent foraging strategies in monomorphic species are thought to be driven by intersexual competition or differing energy demands (Pinet *et al.* 2012), and our study supports the hypothesis that in gannets, sex differences in foraging are driven by the higher energetic demands in females due to unequal chick provisioning. Female gannets meet this additional need through increased dive rate, a strategy that has no appreciable additional cost given the small overall cost of individual dives. Over the course of a breeding season, this extra energetic expenditure equates to approximately 1567 kJ, less than the energy provided by one mackerel. However, after accounting for the cost of dives, the energetic content of prey, and the number of dives performed, females appear to have lower overall success rates to meet energetic requirements, suggesting some subtle difference in foraging behaviour that remains unknown.

Our methodology and results have highlighted that in northern gannets, a sexually monomorphic species, the sexes show differences in foraging behaviour primarily related to dive rate and feeding success rather than the energetic cost of foraging. Evaluating sex differences in foraging behaviour from an energetic perspective may provide a clearer picture for understanding sexually divergent foraging strategies in both sexually monomorphic and dimorphic species. Future research should consider an energetics approach in exploring the fine scale behavioural differences between sexes.

Chapter 5: Handedness in northern gannets: Lateralised dive behaviour during foraging

Ashley Bennison, John Quinn, Mark Jessopp

This study was conceived by myself and Mark Jessopp. I was responsible for planning and conducting the two years of fieldwork, as well as collation and analysis of data. I was responsible for leading on development of the manuscript with input from Mark Jessopp and John Quinn.

Target Journal: The Auk

5.1 Abstract

Many vertebrates show lateralised behaviour, or handedness, where an individual preferentially engages in behaviour on one side of the body more than the other. This behaviour is caused by brain lateralisation and functional specialisation of, for example, sight, locomotion, and decision-making. In this study, we employ accelerometers on northern gannets, *Morus bassanus*, to explore the potential for behavioural lateralisation during foraging. When plunge diving, gannets 'roll' to one side, and we found individuals all passed criteria to be considered lateralised, that is, they consistently rolled to one direction more than the other. Furthermore, lateralisation highly repeatable at the population level ($R = 0.605$, $p<0.001$). There was a small right-sided population-level bias, with 36% of individuals being left-sided and 64% right-sided, though sample size was small ($n = 14$). We found a small effect of wind speed and direction relative to the bird on the magnitude of the roll angle, presumably to aid stability in high wind conditions. Lateralisation studies on wild animals are still relatively rare and this is the first study to confirm lateralised behaviour during the prey capture attempts of a seabird. Whether lateralisation affects foraging efficiency and fitness remain unknown, but it is likely this emerging topic will influence future seabird research.

5.2 Introduction

Behavioural lateralisation, or handedness, the process of preferentially using one side of the body over the other, is the result of functional brain asymmetry and may be the result of both genetics and environment (Schaafsma *et al.* 2009). Different hemispheres of the brain are thought to control different activities among vertebrate species, and differences in brain structure are thought to influence behavioural specialisation (Vallortigara & Rogers 2005). Traditionally, behavioural lateralisation is thought to have evolved as a mechanism to avoid costly duplication of neural circuitry for the same or similar functions (Levy 1977). Behavioural lateralisation is considered widespread amongst vertebrates and is known to occur amongst fish (Sovrano & Andrew 2006), amphibians (Rogers 2002), reptiles (Bonati & Csermely 2011), birds (Moorman & Nicol 2015), and mammals (Perelle & Ehrman 1994). From a quantitative perspective, lateralisation can be considered as individuals engaging in behaviours on one side of the body statistically more often than the other.

Whilst lateralisation in considered widespread, there are still species that do not show any lateralisation (Rodgers & Cain 2019). Furthermore, species that are known to exhibit lateralisation behaviours may also engage in un-lateralised behaviours. For example, chimpanzees, *Pan troglodytes*, are understood to show a handedness preference during normal foraging behaviour such as handling food and eating (Fletcher & Weghorst 2005) but show a lack of lateralisation whilst engaging in ant fishing (Marchant & McGrew 2007). Lateralisation is often found associated with one behaviour though this does not signify a lateralisation in all behaviours; for example killer whales, *Orcinus orca*, exhibit lateralisation during foraging but not during social-based breaching events; individuals lunged towards prey on the right side but did not show a preferential side during breaching behaviour (Karenina *et al.* 2016). This mismatch in lateralisation can shed light on the evolution of lateralisation, as it has been theorised that the mismatch shows a hemispheric specialisation for visualising and processing prey, and that there is a fitness advantage to the evolution of sensory lateralisation (Rogers, Vallortigara & Andrew 2013).

It is important to consider natural variation of lateralisation within a given population. At a population level, animals may be lateralised to one direction or another but also the strength of laterality expressed by an individual can vary greatly (Rogers 2017). Many animal populations that show laterality also show a population bias (Rodgers & Cain 2019) and this is thought to evolve where individuals are in the presence of other lateralised conspecifics (Ghirlanda & Vallortigara 2004). Within any given lateralised population, it is also expected that there will be a portion of individuals that lateralise in opposite fashion to the majority of a population or will be variable in the strength of their lateralisation. Individuals that do not follow the population bias are then exploiting a frequency-dependent advantage in their population; with many individuals exploiting one niche there is opportunity to adapt to an alternative behaviour, however, if there is no specific advantage for different strengths or direction of lateralisation within a population then we do not expect to any population level bias and individuals will be normally distributed in direction and strength (Ghirlanda & Vallortigara 2004).

Many lateralised behaviours are tied to predator vigilance and escape response, with studies tying these directly to fitness advantages (Lippolis *et al.* 2002). Indeed, lateralised behaviours in Australian magpies, *Cracticus tibicen,* were associated with anti-predator response and fear behaviour, which the authors posit were having a direct effect on fitness; such as individuals using the left eye more than right gave more anti-predator alarm calls (Hoffman *et al.* 2006). Another direct marker of fitness potential is the ability to process food. Rogers, Zucca and Vallortigara (2004) found that domestic chickens, *Gallus gallus domesticus*, that were more lateralised in their behaviour were better at discerning food pellets on mixed substrate whilst remaining vigilant for predators. A similar finding was found for dark-eyed juncos, *Junco hyemalis*, and American tree sparrows, *Spizella arborea*, which both used one eye more than the other for spotting predators (Franklin III & Lima 2001). Since lateralisation helps individuals forage and remain wary of predators, its presence likely improves lifespan and breeding potential. There has also been limited evidence to suggest that amongst humans, the strength of lateralisation (handedness) can be directly linked to fitness potential (van der Feen *et al.* 2020).

Whilst animals may engage in lateralised behaviours, the strength of these could be influenced by environmental factors. Lateralised individuals will preferentially use one side of their body compared to the other, however, location or other environmental factors may change the strength of lateralisation. For example, blue whales, *Balaenoptera musculus*, feeding at depth were less lateralised in feeding lunges than at the surface, a pattern thought to be associated with visual assessment of prey, suggesting that lateralisation of feeding blue whales may help individuals' foraging efficiency in heterogeneous environments (Friedlaender *et al.* 2017). Not only can location influence lateralisation, evidence suggests that the presence of conspecifics may also be an influence. Both chimpanzees and lowland gorillas, *Gorilla gorilla gorilla*, have been observed to ensure that other individuals are kept on their left side and these actions are associated with maintaining dominance structures (Quaresmini *et al.* 2014). In a similar manner, an increase in the perceived risk of predation increases the tendency for lateralised predator escape behaviour (preferred turning and travel direction) in coral reef fish (Ferrari *et al.* 2015; Chivers *et al.* 2016). Environmental changes and uncertainty are also known to affect how lateralisation is expressed, for example when sheep, *Ovis aries*, were placed onto unpredictable moving floors the prevalence of right foot stabilisation increased beyond the left (Robins *et al.* 2019). Very few studies however have explicitly looked at environmental conditions and how this may affect the lateralisation of species which use environmental cues for movement. Seabirds use wind to facilitate movement and foraging (Weimerskirch *et al.* 2002). Though there is limited knowledge of seabird lateralisation it is also currently unknown how environmental features such as wind may interact with individual lateralisation.

Lateralisation can be theoretically expressed in any species, though there is a propensity for this to be more likely in species that encounter difficult or challenging tasks (Levy 1977; Hirnstein, Hausmann & Güntürkün 2008). Animals that forage over vast distances may benefit from the advantages of lateralisation by being able to navigate and search for prey simultaneously. Seabirds routinely forage over large

distances in seemingly featureless environments, requiring both specialised foraging techniques (Phillips *et al.* 2017) and navigation (Wynn *et al.* 2020). Lateralisation has previously been documented in seabirds, with both king penguins, *Aptenodytes patagonicus*, and magellanic penguins, *Spheniscus magellanicus*, showing lateralised behaviour in aggressive fighting behaviours when in colonies (Lemaire, Viblanc & Jozet-Alves 2019; Stor *et al.* 2019), however, there was only marginal evidence for lateralised foraging behaviours in magellanic penguins. The northern gannet, *Morus bassanus*, hereafter gannet, is a long-lived seabird with a complex foraging behaviour. Individuals undertake long foraging trips at sea where they search for food (Hamer *et al.* 2009) and engage in plunge diving. Plunge diving is a behaviour undertaking by a variety of seabirds, whereby flying individuals will fold their wings behind them, forming a straight arrow-like shape. For gannets, individuals then hit the water at speeds up to 86km/h (Chang *et al.* 2016). At the start of this process, when gannets begin to fold their wings and start plummeting, they roll to one side, presumably to orientate themselves in a steeper declination angle or to maintain visual contact with sighted prey. Gannets are visual predators and it is thought that they sight their prey before diving (Nelson 2002). Lateralisation of rolling behaviour during plunge dives could therefore allow gannets to engage in a specialist behaviour that requires multiple actions (such as diving and prey visualisation) to occur at the same time (Howard *et al.* 2014).

Here we identify dive events using accelerometry and investigate lateralisation in gannet foraging. We use a lateralisation index to determine if birds show lateralised behaviour before using a repeatability analysis to determine if gannet dive roll angles are repeatable within the individual and if this is driven by individual lateralised state. Within this process, we also determine whether dive roll direction is influenced by wind conditions and assess population bias in lateralisation.

5.3 Methods

All research was approved by the University College Cork Animal Ethics Committee and was conducted under licence from the Health Products Regulatory Authority, National Parks and Wildlife Service, and the British Trust for Ornithology.

Data Collection

Breeding adult gannets (n=8 in 2017, n=6 in 2018) attending 3-4-week-old chicks were tracked from Great Saltee, south-east Ireland (52° 7' 37.92", -6° 35' 45.6"). Birds were caught using an 8-10m pole with a metal crook, weighed, and equipped with a combination of dataloggers. GPS loggers (i-gotU GT-120, Mobile Action Technology Inc., Taipei, Taiwan, 14g) recorded locations every 3 minutes; time depth recorders (TDR, CEFAS G5, 2.5g) recorded depth at 4Hz after exceeding a 0.5 or 1m depth threshold; tri-axial accelerometers (Gulf Coast Data Concepts X16-mini, 17g) recorded G-forces (1*g* = 9.807m/sec^2) at 50Hz. GPS and TDR loggers were attached ventrally to 2-3 central tail feathers using strips of waterproof Tesa tape. Accelerometers were attached to 10-15 mantle feathers between the wings to ensure proximity to the centre of gravity required for accurate accelerometer readings (Wilson *et al.* 2006a) using strips of waterproof Tesa tape. Three birds in 2017 and six birds in 2018 were equipped with GPS, TDR, and accelerometers, while the remaining birds were equipped with only GPS and accelerometers. Total instrument mass was <2% of body mass, and positioned to minimise impact on gannet movement, both aerodynamically and hydrodynamically (Vandenabeele *et al.* 2012). 2-3 breast feathers were plucked for genetic sexing following the method outlined by Griffiths *et al.* (1998).

Data processing and behaviour definition

Identification of dives from accelerometry data used a thresholding approach. Thresholds were determined using protocols set out by Collins *et al.* (2015) and Shepard *et al.* (2008a). Diving events occurred when average acceleration (running average of 2 seconds) in the X-axis was <0*g* and standard deviation (SD) in the mean

X-axis was >1.4*g*. A subset of birds (n=9) tagged with both TDRs and accelerometers were used to validate accelerometer-derived dive events by visually comparing timestamps to TDR confirmed dives. Roll was calculated as the rotation of the individual in the X-axis and is calculated using the following formula:

$$Roll = \left(\frac{y}{\sqrt{x^2 + z^2}}\right) \times \left(\frac{180}{\pi}\right)$$

In this formula, roll is determined by the manipulation of the three acceleration channels, where *x* is equal to acceleration in the forward-facing surge channel, *y* is the acceleration in the lateral sway channel, and *z* represents the acceleration in the vertical heave channel. Roll is calculated from -180^{o} to +180^{o}, where negative values infer a left sided roll and positive values a right sided roll. Roll was calculated every second and for the purpose of determining pre-dive roll, we used the mean roll in the five second period preceding a dive. When plunge diving, gannets have been observed to: 1) roll to one side, 2) fold back their wings, and 3) plunge directly at the ocean surface (Figure 5.1) (Nelson 2002). From field observation of foraging gannets, it was determined that the preceding 5 seconds to a gannet entering the water would capture the entire roll-dive behavioural sequence. Although a pre-dive roll may take less than five seconds, this figure was calculated to ensure that all dive rolls were captured sufficiently. See figure 5.1 for a diagram explaining dive roll. Figure 5.2 Shows an example accelerometry trace from the preceding ten seconds before a dive and a dive event to show how this is interpreted in the data.

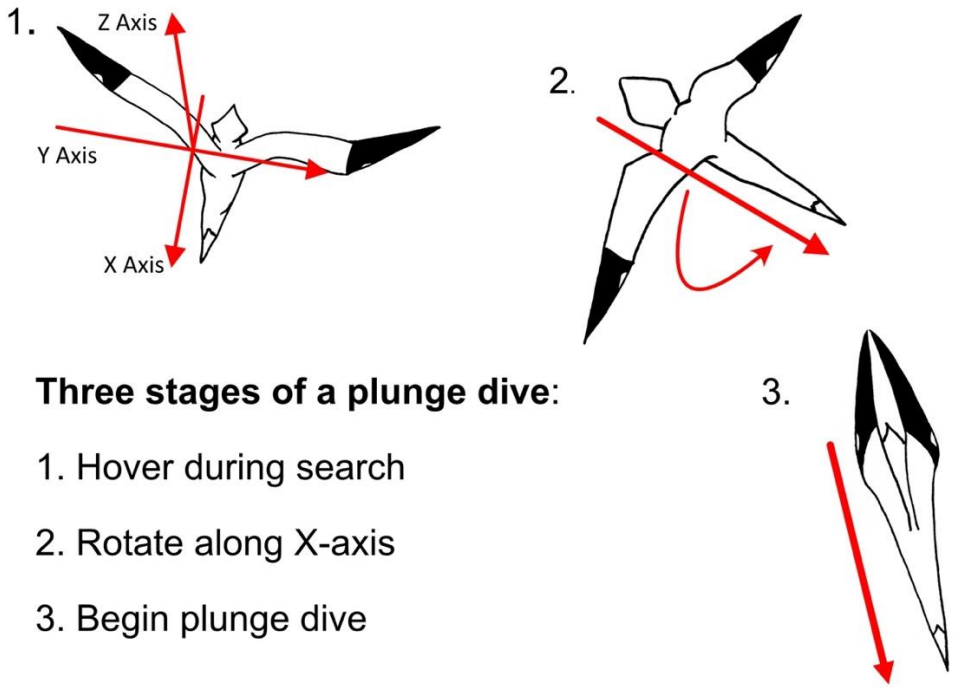

Figure 5.1. A diagram showing the process of determining the roll of a dive. Raw acceleration values at 1. are converted to binary roll (left/right) at 2. before the gannet plunge dives at 3.

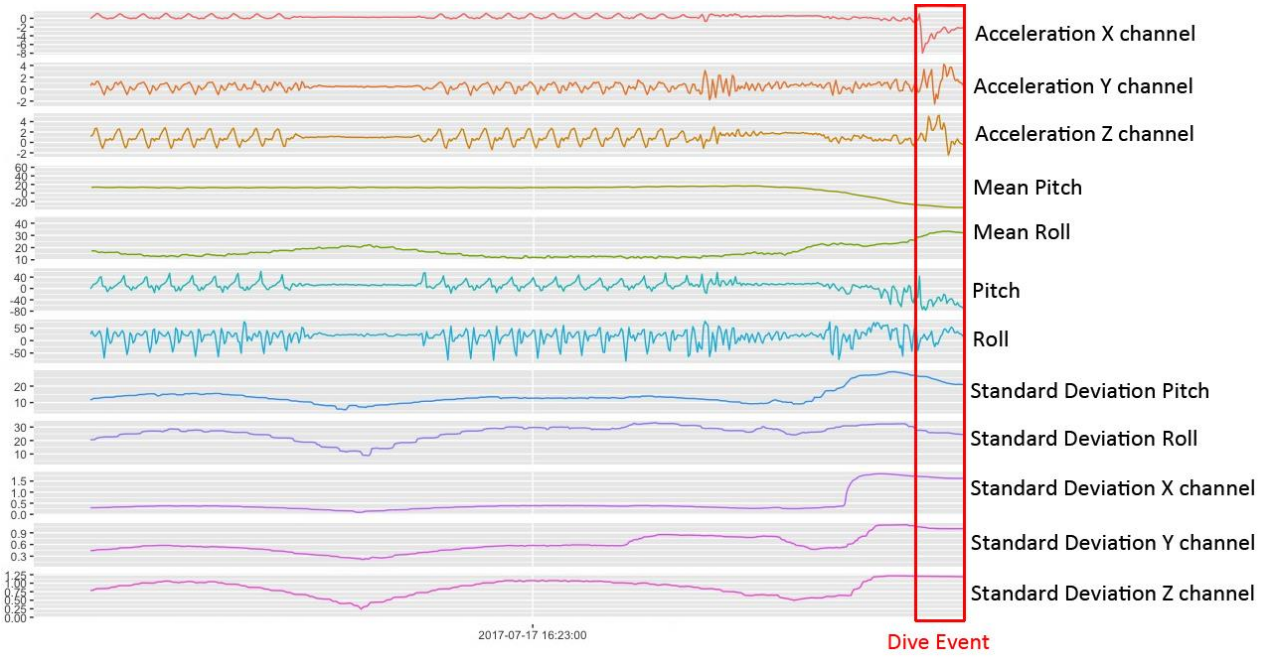

Figure 5.2 An accelerometer trace of a dive event and the preceding ten seconds of flight. Note the increase in mean roll prior to and during the dive event showing the individual roll to the right.

Pre-dive lateralisation

Pre-dive roll was extracted from accelerometry data and the mean roll in degrees calculated. To determine lateralisation of behaviour in individuals, we used a lateralisation index (*LI*) from (Richardson 1976). *LI* is computed with the following formula:

$$LI = \frac{Rd - Ld}{Rd + Ld}$$

In this equation, *Rd* is equal to the number of right roll dives and *Ld* is equal to left roll dives. *LI* ranges from -1 to 1; where -1 shows 100% of dive rolls to be left sided, whilst 1 is 100% of dive rolls to be right sided. Following from previous studies, the *LI* proportions can be used to mark if individuals have a right-side bias (*LI* = 1.0 to 0.25), a left side bias (*LI* = -1 to -0.25), or are ambidextrous (*LI* = -0.25 to 0.25) (Friedmann & Davis 1938; Weir *et al.* 2004; Rodgers & Cain 2019). A Wilcoxon rank sum test was used to test for sex-specific lateralisation.

Population repeatability of dive roll angle and the influence of wind

Though lateralisation index scores provide information on whether individuals engage in lateralised behaviour, it is important to account for any potential environmental drivers of this behaviour. Any bias in roll direction may be an artefact of wind, for example gannets may turn into or out of the wind to gain speed, avoid plumage disturbance, or to gain lift prior to a dive for example. To determine if the observed lateralisation was caused by wind, we investigated the effect of wind direction and speed on dive rolls. We used European Centre for Medium-Range Weather Forecasts' Global Atmospheric Surface Forecast data to annotate GPS tracks using the MoveBank track annotation service (Dodge *et al.* 2013). ECMWF wind data is supplied at 0.75 degree spatial and three-hourly temporal resolutions. Wind data is supplied as velocity in V and U components (north-south and east-west directions respectively) at 10m above sea level, and these were converted to bearing direction and velocity using the 'rWind' package (Fernández-López & Schliep 2018). Wind *offset* relative to a gannet was defined as a binary variable as either headwind or tailwind compared to a gannets' bearing. Wind direction and wind *speed* (m/s) were

appended to the nearest dive event. It is important to acknowledge that the wind data is at a much coarser resolution than the acceleration and GPS data. Whilst it is possible that this may reduce the signal available to describe the relationship between roll angle and wind, we consider the movement of the individual gannets would be still be affected should there be a strong relationship.

When comparing wind direction and dive events we also considered when gannets were rolling into the wind or out of the wind i.e. if the wind was incoming from the gannet's left side does the bird roll left or right. *Windroll* was appended to the dive events as either "with" or "against" dependent on if a bird rolled with the wind or against the wind.

The effect of wind on dive roll angle was investigated using linear mixed effects models in the rptR package in R (Stoffel, Nakagawa & Schielzeth 2017). The rptR package builds a linear mixed effects model using the lme4 package (Bates 2013) to explore the population level repeatability of behavioural events, and the effect that other variables may have upon them.

Models produced in the rptR framework produce two main components: 1) Estimates of repeatability (R) for grouping factors (random effects) ranging from 0 to 1 where 0 is no repeatability whilst 1 is perfect repeatability for all groups, and 2) Linear mixed effect regressions predicting, in this case, dive roll angle. Date was used as a random effect to account for autocorrelation on foraging trips, and individual ID was also used as a random effect. Three models were constructed to investigate the individual repeatability of dive roll angle:

1) Random effects only

This model predicted dive roll angle from only the random effects of individual and date. This model produced an R value for individual that would act as a baseline level of repeatability.

2) Wind effects only

This model predicted dive roll angle from the wind variables of *speed*, *offset*, and *windroll* (and the interactions between these variables), and ID and Date were used

as random effects. Comparing the R value of ID in this model to model 1 would explore how wind may affect the repeatability of dive rolls.

3) Wind and lateralised side of individual

This model predicted dive roll angle from the wind variables of *speed*, *offset*, and *windroll* (and the interactions between these variables) but also included a "left"/"right" term based upon whether a bird was left or right lateralised as determined by the LI index. ID and date were again included as random effects. Comparing this model's R value would show if lateralised side drives the roll angle (and as a result the dive side). It is important to note that the rptR framework produces a population level of repeatability grouped by the levels of a random effect, here we use gannet ID. This produces an overall value of R, showing how repeatable the population of gannets is in roll angle (Higher R implying individuals have a more repeatable angle of roll).

All models used a Gaussian data structure. Models were run using a bootstrapping approach and were run 1000 times in comparison to 1000 permutations of the same data set where variable values were randomised to simulate a null data set. Mean R value models were then compared using a likelihood ratio test.

5.4 Results

Pre-dive lateralisation

A total of 1046 dives from 14 gannets were used to test for lateralisation among individuals. All birds LI scores were consistent with lateralised behaviour (LI scores <-0.25 or >0.25 for all individuals) with no ambidextrous birds (Table 5.1); there were 9 right-sided birds and 5 left-sided birds (Figure 5.3). There was no discernible sex-specific lateralisation (Wilcoxon rank sum test: W = 11 p = 0.19). There was no discernible difference in the tracked location of left or right sided birds during this study (Figure 5.4), though this may be limited to due to sample size and inter-year effects.

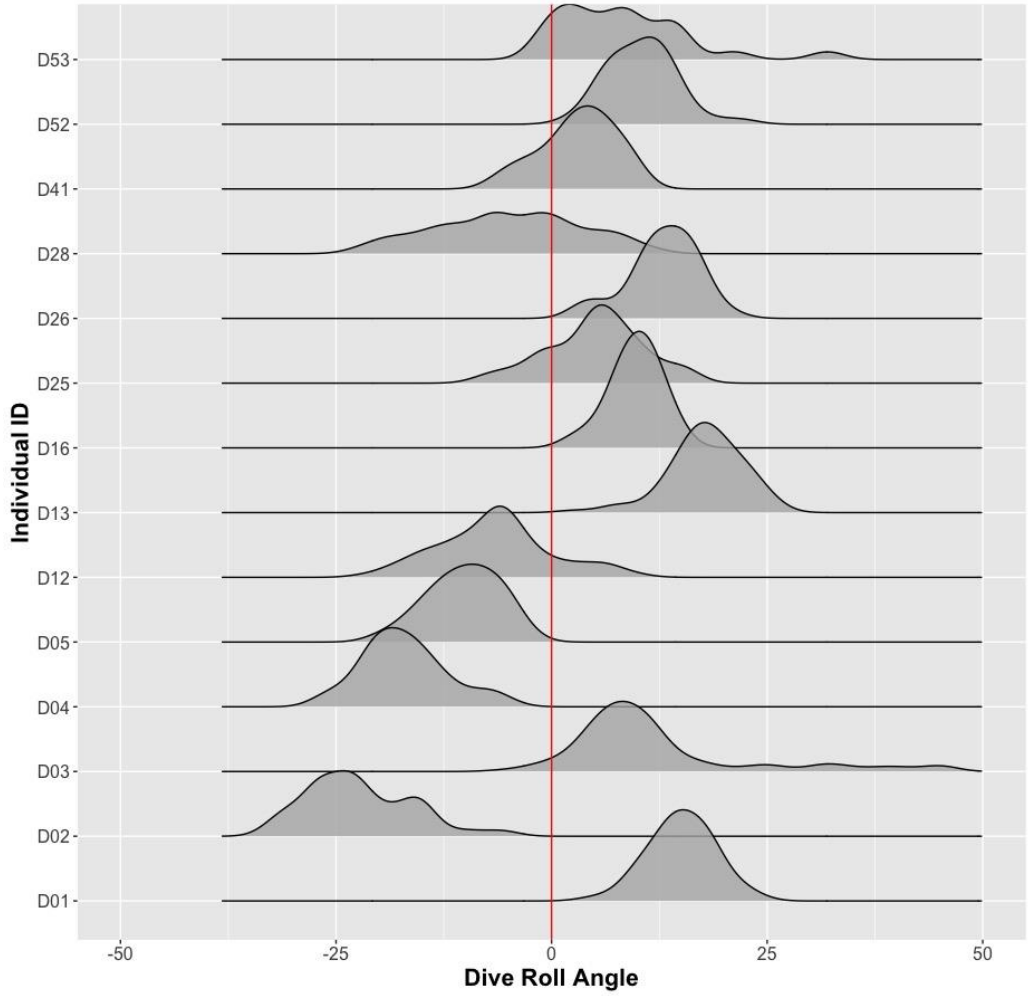

Figure 5.3. Distribution of roll in pre-dive behaviour, the red line crosses through 0 where non-lateralised individuals would be expected to be distributed.

Table 5.1. Wilcoxon one sample signed ranks test results comparing all dive roll distributions to 0 (non-lateralised), dive roll distribution data is also supplied, and the lateralisation index scores for all gannets.

	Dive details				*Pre-dive Roll Direction (Degrees)*			*Lateralisation Index*			
Bird ID	**Sex**	**Number of dives**	**Tracking duration (Days)**	**Dives per day**	**Median Roll angle (degrees)**	**Upper 95% Confidence interval**	**Lower 95% Confidence Interval**	**Left Roll Dives**	**Right Roll Dive**	**LI**	**Side bias**
D01	Male	113	4.9	23.06	15.1	15.8	14.3	0	113	1	Right
D02	Male	36	2.86	12.56	-22.8	-20.4	-24.7	36	0	-1	Left
D03	Unknown	189	5.08	37.15	10.7	12.6	9.4	6	183	0.93	Right
D04	Female	65	0.97	66.89	-17.3	-16.0	-18.	65	0	-1	Left
D05	Female	39	1.83	21.31	-10.0	-8.6	-11.5	39	0	-1	Left
D12	Female	90	4.68	19.19	-6.6	-5.4	-8.0	77	13	-0.71	Left
D13	Male	87	4.72	18.44	18.0	18.8	17.2	0	87	1	Right
D16	Male	18	1.99	9.06	9.7	11.1	8.2	0	18	1	Right
D25	Female	37	3.04	12.17	5.2	7.0	3.3	8	29	0.56	Right
D26	Male	36	2.92	12.31	13.2	14.4	11.7	0	36	1	Right
D28	Male	230	4.61	49.84	-4.9	-3.8	-6.1	164	66	-0.42	Left
D41	Male	39	4.83	8.07	3.3	4.7	1.8	9	30	0.53	Right
D52	Female	42	4.32	9.72	10.3	11.6	9.1	0	42	1	Right
D53	Male	25	5.05	4.95	7.4	10.6	4.6	2	23	0.84	Right

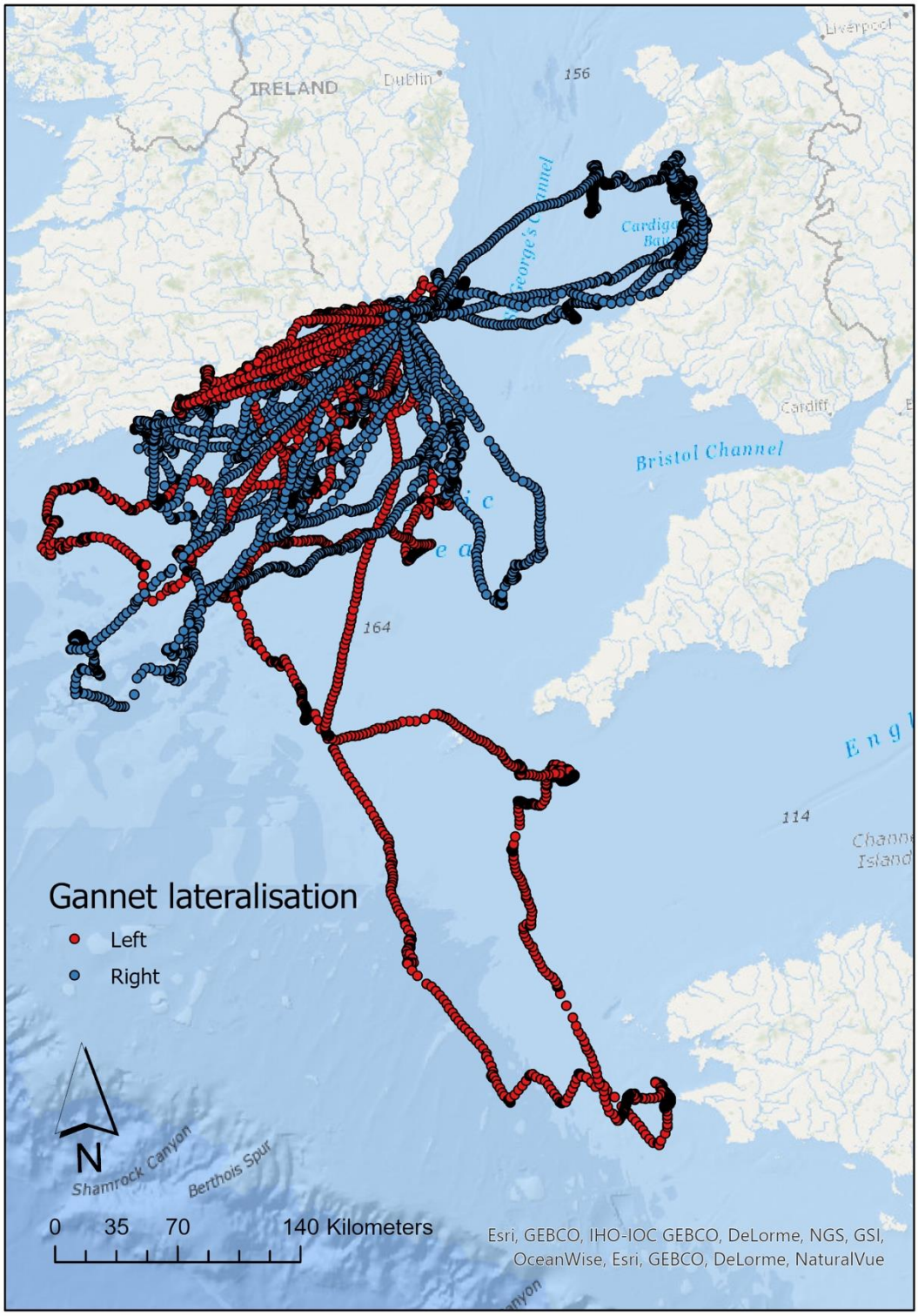

Figure 5.4 A map showing the GPS locations for left and right sided birds during the tracking period. Left-sided birds are shown in red and right-sided birds shown in blue. Though limited by sample size, there is no overt difference in the spatial extent to which left or right lateralised travel during foraging trips.

Population repeatability of dive roll angle and the influence of wind

Wind speed experienced by gannets ranged from 0.8 m/s to 13.2 m/s (mean: 6.07 m/s $\pm$ 2.43).

Repeatability models showed high levels of individual repeatability in dive roll angle (Table 5.2). The model using only random effects showed the highest repeatability of dive roll angle (R = 0.605, Table 5.2), and repeatability only drops marginally when considering wind effects (R =0.601, Table 5.2) on the repeatability of dive roll. When adding the fixed effect of lateralised side of the individual there was large drop in repeatability (R = 0.294, Table 5.2) showing that this is driving the direction of the roll angle. However, the repeatability of individual still remains at R = 0.294 which suggests there are further individual effects of dive roll angle yet to be accounted for.

Table 5.2 Repeatability estimates of dive roll angle across the study population. Estimates are calculated from 1000 bootstrapped iterations and p values are calculated via likelihood ratio tests from randomly permutated models.

Model	*Repeatability of ID*	*Standard Error*	*Lower Confidence Interval*	*Upper Confidence Interval*	*p value*
No fixed effects	0.605	0.114	0.355	0.755	<0.001
Wind Only	0.601	0.116	0.325	0.765	<0.001
Wind and lateralised side	0.294	0.103	0.113	0.496	<0.001

Within the linear mixed effect regressions, only offset (headwind or tailwind), lateralised side of individual, and the interaction between offset and windroll (rolling with or against the wind) were significant effects. The relationship between dive roll angle predicted by offset, and windroll is shown in Figure 5.5. When birds are rolling with the wind and in a headwind, the roll angle is slightly reduced compared to a tailwind. This relationship is then mirrored when birds are rolling against the wind direction.

Table 5.3 Summary of fixed effects from the complete wind and lateral side model (model 3). Offset (Headwind), Windroll (With the wind), and Lateralised side (left) were absorbed into the intercept of this model.

Fixed effects	Estimate	Standard Error	t value	p value
(Intercept)	-6.1861	4.6761	-1.323	0.19991
Offset (Tailwind)	-4.2397	1.7746	-2.389	**0.01708**
Windroll (Against the wind)	0.3373	1.8728	0.18	0.85711
Wind speed	-0.2264	0.2917	-0.776	0.43786
Lateralised side (Right)	17.4898	4.9678	3.521	**0.00474**
Offset (Tailwind) : Windroll (Against the wind)	5.5778	2.4368	2.289	**0.0223**
Offset (Tailwind) : Wind speed	0.421	0.2831	1.487	0.13723
Windroll (into the wind): Wind speed	-0.1271	0.2965	-0.429	0.66823
Offset(Tailwind) : Windroll (Against the wind) : Wind speed	-0.5882	0.3782	-1.555	0.12019

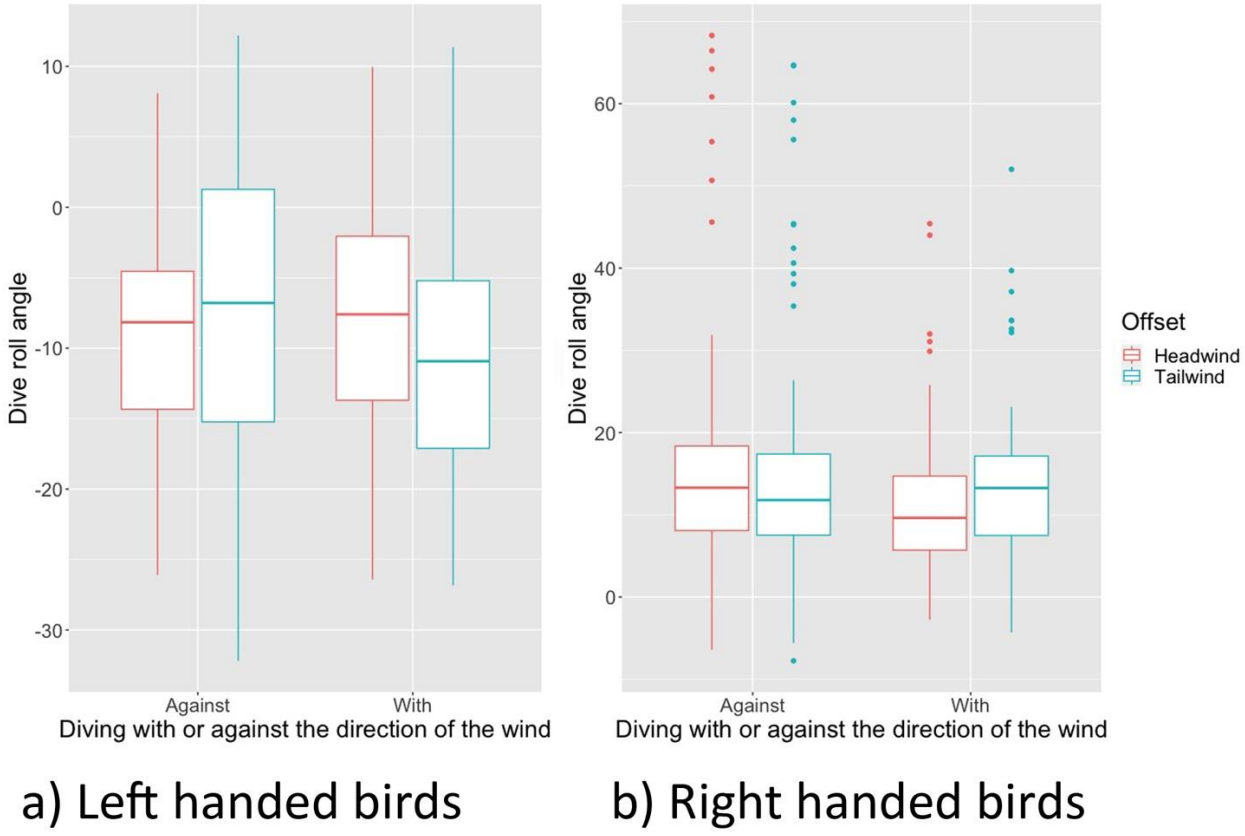

Figure 5.5. The interaction between wind offset and if birds are diving with or against the direction of wind on dive roll angle shown for a) left-sided birds and b) right-sided birds.

5.5 Discussion

The use of acceleration data has allowed us to determine that northern gannets show behavioural lateralisation during foraging events. Individual birds were highly consistent in their preference to rolling either to the left or the right side during plunge dives. This individual-based consistency occurs across all individuals in our study population. The lateralisation index showed that individual birds were lateralised in their behaviour whilst the repeatability analysis provided statistical rigour in this conclusion. Repeatability across the study population was significantly high for individual effects but also dropped when considering the lateralised side of the individual bird, suggesting this was the driver of dive roll angles. There was no sex bias in the lateralisation direction and cognizant of the small sample size, we suggest a population bias towards right-sided individuals. Wind offset (headwind or tailwind) and whether birds were rolling with or against the wind both showed a significant interaction on roll angle, however, the repeatability of roll angle was not effected greatly by wind effects and so whilst wind can affect plunge dive roll, it is not the driver of gannet dive lateralisation.

To our knowledge this is the first study that shows behavioural lateralisation of a seabird species during prey capture. Both king and magellanic penguins have been found to show behavioural lateralisation in colony behaviours (Lemaire, Viblanc & Jozet-Alves 2019; Stor *et al.* 2019). Magellanic penguins were thought to show morphological adaptations to lateralisation during foraging, but this remained unproven. Caspian terns, *Hydroprogne caspia*, have also been documented repeatedly delivering prey to chicks in a lateralised manner to help chick handling of food items (Grace & Craig 2008). Here, we show that gannets engage in lateralised behaviour during prey capture.

Lateralised prey capture implies a link to sensory lateralisation; the hemispheric processing of prey information (Karenina *et al.* 2016), in this case potentially through visual cues. Behavioural lateralisation is thought to enable the development of complex behaviours (Vidal *et al.* 2018) and allows animals to engage in multiple activities at once (Levy 1977). As gannets are visual predators, locating prey before a

dive (Cronin 2012), the evolution of lateralisation during prey capture likely enables more successful foraging, though the explicit mechanism behind this remains unknown. Previous research has found that many bird species display visual lateralisation (Rogers 1980) which can affect vigilance (Franklin III & Lima 2001), navigation (Prior *et al.* 2004), and prey discrimination (Templeton & Christensen-Dykema 2008). It is likely that gannets gain some cognitive benefit from lateralised dives, with evidence suggesting that right-biased birds have better prey discrimination and prey handling (Ventolini *et al.* 2005), whilst left-biased birds may benefit from heightened predator detection and aggression (Hoffman *et al.* 2006; Anderson, Williams & Bono 2010).

Gannet dive roll angle was found to be affected by wind offset and whether a bird was diving into the wind or not, however this effect was small. Models suggest that as gannets are rolling with the wind and in a headwind, the roll angle is slightly reduced compared to a tailwind. However, we see the opposite relationship when birds are rolling against the wind direction, where a headwind reduces roll angle. This relationship could be related to keeping gannets aerodynamically stable in turbulent conditions or for minimising plumage disturbance. Seabirds are well understood to interact and utilise wind for movement and foraging (Weimerskirch *et al.* 2002). Northern gannets benefit from increased speeds whilst flying on tail winds (Garthe, Montevecchi & Davoren 2007) and wind direction has also been shown to influence the foraging locations of the closely related cape gannet (Adams & Navarro 2005). The lack of strong relationship between dive roll and wind may also be due to mismatches in the temporal resolution of the accelerometry, GPS and wind data. GPS resolution, and therefore data on the bearing of birds, was at three-minute intervals, and within this time a gannet may re-orientate into or out of the wind. None the less, if gannets do change orientation with wind for diving, we are confident that wind is not the primary driver for lateralised dives. Evidence suggests that gannet movement may benefit from interaction with prevailing winds, but we report no evidence that this affects lateralised behaviour of plunge dives.

Whilst the repeatability of dive angle was found to be driven by the individual lateralised state, it is interesting to note that individual level effects still remain. A

bird's lateralised state drives the direction of a dive roll, but there remains an internal effect that also seems to drive the strength of the angle (i.e. little rolling or steep banking roll) and this may represent some form of currently unknown behavioural specialisation in plunge diving. Consistent differences in individuals within a population and behavioural diversification can often be the cause of animals exploiting small niches in an ecosystem (Bergmüller & Taborsky 2010) and this may explain why gannets show differences in dive roll angle. However, further work is required to fully understand the individual level effects of prey capture and roll effects in gannets.

Many species show population biases in lateralisation (Andrew & Brennan 1984; Vallortigara, Rogers & Bisazza 1999), and bearing in mind the relatively small sample size, we report a right-sided bias within our study population. Similarly, other bird species also show right-side population biases including pigeons (Prior *et al.* 2004), corvids (Clayton & Krebs 1994), and finches (Alonso 1998). A lateralised population bias is thought to show that animals evolved to have a lateralisation whilst coordinating behaviour with other asymmetrical conspecifics (Ghirlanda & Vallortigara 2004). This can best be observed when considering the lateralisation of animals that live in high densities such as shoaling fish (Bisazza & Dadda 2005) – and may be the root cause of a lateralised population bias in gannets, a species that live and forage in high densities (Nelson 2002). A right-sided population bias may also present foraging advantages in gannets. Previous research suggests that birds with a right-side lateralisation may be better at prey discrimination and object specific navigation (Vallortigara & Rogers 2005). These capabilities would clearly be an advantage for gannets foraging at sea. However, not all gannets are right-side lateralised, 36% of our study population are left-side biased. For an unequal lateralisation bias to maintain, there must be a frequency-dependency cost-benefit; where the minority lateralised direction (e.g. left-handers in humans) retain a survival advantage when at low frequency (Raymond *et al.* 1996). Left-side lateralisation has previously been associated with a reliance on spatial memory and cues during foraging (Templeton & Gonzalez 2004) and aggression (Hews, Castellano & Hara 2004). Gannets are an aggressive species (Nelson 1965) that show a spatial

memory through foraging site fidelity (Wakefield *et al.* 2015). A small left-side lateralised portion of the population that perform better in the left-lateralised associated traits may help sustain a foraging and fitness advantage that maintains any population bias.

However, we must acknowledge that our sample size is small (n = 14). A simple post-hoc power analysis using the "pwr" package in R (Champely *et al.* 2018) reveals that we lack statistical power to detect a population structure (α >0.95) and with 14 individuals we only have a 27% probability of detecting one. A sample size of 77 individuals would be required to detect a population structure at the observed ratios. Where no specific advantage is given at different frequencies of lateralisation, then different population structures do not need to be maintained (Ghirlanda & Vallortigara 2004). Whilst we do observe a population bias in our sample we must concede that this may not be the case in gannets. New Caledonian crows show lateralisation in tool use but do not show any population structure in lateralisation bias (Weir *et al.* 2004), showing that not all species that engage in lateralisation show a population bias.

Behavioural lateralisation shows the development of a cognitive ability that allows animals to develop complex behaviour and the ability to process multiple forms of information readily (Levy 1977; Magat & Brown 2009). Lateralisation is widely prevalent amongst animal species and understanding how it ties with wider animal behaviour may reveal how hidden behavioural processes can inform a species' ecology (Vallortigara & Rogers 2005). The observed lateralisation suggests a cerebral specialisation, and likely confers some form of foraging advantage, though how so remains unknown. It is not yet known how behavioural lateralisation may affect larger patterns of behaviour in northern gannets and this may be reflected in broader patterns at the population level. Further research should prioritise how these adaptations affect gannet ecology but should also consider the prevalence and influence on the wider seabird community. The impacts of lateralisation are poorly understood in seabird foraging and this emerging field of understanding may yet provide an important consideration in ecological studies and conservation management.

Chapter 6: General Discussion

Movement is a universal concept across life, and by understanding animal movement, observing the patterns by which an animal experiences its own environment, ecologists can answer key questions related to concepts in evolutionary and ecological theory (Nathan *et al.* 2008). Movement studies can answer questions relating to life history strategies, ecosystem structure, and foraging amongst many others. This thesis aimed to explore the movement ecology of seabirds during the breeding season, and to understand how movement patterns relate to the foraging behaviour of individuals. This work also provided an integrated understanding of the intrinsic and extrinsic drivers of animal behaviour. The chapters presented here considered how environment may interact with foraging behaviour; changing how animals may be expected to move (Chapters 2,3, and 5). Energetic demands placed upon individual animals, and energy expenditure itself, was also shown to determine foraging strategies both at a population level and as a manifestation of sex differences (Chapters 3 and 4).

Seabirds are excellent study species for understanding the relationships between movement patterns, behaviour, and wider ecology (Fauchald 2009; Wakefield, Phillips & Matthiopoulos 2009). Seabirds are well known for having long and predictable life history strategies; after fledging and immaturity, many seabird species breed annually and show philopatric tendencies – often returning to the very same nest as previous years (Schreiber & Burger 2001). During the breeding season, seabirds are central place foragers and will undertake foraging trips at regular intervals to provision chicks.

Three species of seabird are studied in this thesis; the northern gannet, *Morus bassanus,* (hereafter gannet), the Atlantic puffin, *Fratercula arctica*, (hereafter puffin), and the razorbill, *Alca torda*. Gannets are the largest seabird in the North Atlantic undertaking foraging trips that may last several days (Hamer *et al.* 2009) and show dietary specialisation – feeding on both fisheries discards and naturally caught pelagic prey (Bodey *et al.* 2018b). In contrast, puffins are the smallest breeding auk

in the British Isles and Ireland and together with the razorbills, rank amongst the smaller seabirds. Both puffins and razorbills undertake short foraging trips (Harris *et al.* 2012), feeding primarily on sand eel and other small fish prey (Shoji *et al.* 2015b) and do not overtly interact with fisheries. The foraging differences between the species also make for interesting comparison. Gannets undertake dramatic foraging plunge dives, searching above air before diving onto prey items during prey capture attempts (Nelson 2002). Alternatively, auks undertake prolonged dives from the surface undertaking both search and prey capture attempts underwater (Evans *et al.* 2013a; Shoji *et al.* 2014). Despite these differences, foraging behaviour seems to be a minor energetic expense to both species, both Chapters 3 and 4 showed that the foraging costs for both species are low. Gannet foraging totalled less than 4% of total energy expenditure (Chapter 4) and puffin diving was approximately equal to the same energetic cost as sitting on the water's surface (Elliott *et al.* (2013a) and Chapter 3) – with behavioural adaptations reducing energy expenditure during foraging further. Gannets and auks show differences in diet and foraging strategy but also have remarkably similar ecology when considered from energetic and movement perspective. As higher predators, seabird movement can be considered a good proxy for understanding the processes of the environment around them (Cairns 1987; Piatt *et al.* 2007; Brisson-Curadeau *et al.* 2017).

6.1 Main Findings and relation to movement ecology

This thesis has undertaken a broad range of movement-based studies on seabirds and these chapters can be viewed within the larger theoretical framework of movement ecology as proposed by Nathan *et al.* (2008). This paper states that movement ecology is made up of five key areas in a conceptual framework. These components are: external factors, internal state, navigation capacity, movement capacity, and the animal's movement path. The main findings of this thesis will now be presented under the central themes of the movement ecology paradigm presented by Nathan *et al.* (2008).

External factors affecting an animal's movement ecology are environmental features that may dictate the patterns in which animals move. These may include landscape scale features such as mountain ranges, or smaller features such as urban developments. From a marine perspective, these may represent wind patterns, oceanic currents, or bathymetry. Throughout a species' range, animals will encounter different environmental conditions and this will manifest as different movement behaviours. Chapter 2 differentiated the behaviour of two gannet colonies at opposite ends of the British Isles and Ireland and found variation between the methodologies used to differentiate behaviour between sites, suggesting that local environment may affect the efficacy of methods and this should be considered in large-scale studies.

Whilst large–scale environmental factors may influence animal movement, such as where to forage or direction of navigation (Goto, Yoda & Sato 2017), there are also smaller as yet unknown effects on movement. Chapter 5 showed a small effect of wind on the dive roll angle of plunging gannets; whilst this did not determine which side they dived on, it did affect the angle of roll prior to a dive. Previous research has highlighted that wind conditions can impact the rate at which gannets forage but that it does not affect foraging trip length (Lane, Spracklen & Hamer 2019). This then suggests that environmental impacts on foraging and movement decisions may not be overt yet may still affect smaller processes within overall foraging behaviour.

Whilst foraging it is expected that many animals will undertake area restricted search behaviour (Kareiva & Odell 1987; Fauchald & Tveraa 2003). Chapter 3 documented the departure from expected area restricted search in puffins whilst foraging in a tidally active area. This chapter showed that puffins utilising tidal currents to transport them across/between prey patches saved between 28-46% of energy compared to conspecifics that may fly the same distance. Sympatrically breeding razorbills, were then shown to drift on tidal currents but did not engage in foraging during these periods and is likely associated with rest. This chapter shows that novel adaptations to environmental features are likely to be more prominent that previously thought.

Though external influences affect the movement patterns and behaviours of animals, Nathan *et al.* (2008) also considered how the internal state of an individual animal may affect movement. Internal factors can be considered as intrinsic qualities that may affect a species' ecology. In this thesis, the two predominant internal factors are behavioural sex differences and lateralised foraging in gannets.

Sex differences in foraging are well established in seabird ecology and differences in monomorphic species represent an opportunity to explore the mechanisms of such differences (Pinet *et al.* 2012). Chapter 4 undertook a bioenergetics study using accelerometers deployed on gannets to show how foraging differences in monomorphic species may be driven by energy expenditure and demand. This chapter drew together acceleration data and published energetic values with isotopic dietary analysis to provide an insight to the energetic costs of foraging in gannets. Female gannets experienced a 9.6% higher energy demand during the breeding season and this is likely due to the demand of unequal chick provisioning. The different rates of diving between males and females indicate different minimum foraging success rates, with females required to be successful at prey capture on 21% of dives compared to 29% for males. Finally, the cost of prey capture attempts is small compared to overall energy expenditure, with dives costing <4% of total energy expenditure. This highlights that, at least for gannets, sex differences in foraging may be based on foraging rate and success rate rather than the cost of foraging itself. Foraging theory can be considered as a balance between energy gain and expenditure (Karasov 1986) and as a result investigating the responses of movement during energy expenditure informs us of wider behavioural patterns.

Lateralisation of brain function suggests the capabilities to undertake complex actions (Levy 1977) though this phenomenon remains largely unstudied in seabirds. Previous research suggests that lateralised individuals may approach situations differently to either un-lateralised individuals or those lateralised in opposite directions, currently it is not known how this affects wider seabird ecology. Chapter 5 showed that gannets are lateralised in their behaviour and that key differences were driven by the internal state of being left or right aligned. An interesting finding in this chapter is that even after accounting for the side to which an animal is likely

to roll – there are still individual level effects that drive the angle to which the birds are diving, and this has not yet been accounted for. There are likely many new avenues of research to explore investigating the drivers of animal movement.

Animal movement strategies are shaped by the external and internal factors of a species' ecology, however these strategies may be further changed or developed based upon the physical abilities of animals. Nathan *et al.* (2008) considered this to be a species' or individual's motion capacity. Chapter 3 showed the use of predictable tidal currents by puffins across an area of sand banks for foraging during the breeding season, a behavioural response to high flight costs. Puffins have evolved to be able to undertake long and effective pursuit dives whilst searching for prey, their morphology having changed to have short stubby wings more suited for swimming than flying (Elliott *et al.* 2013b) and this new behaviour has allowed them to maximise net energy gain whilst using a predictable environmental feature. Animals have previously been documented using environmental features to reduce locomotion costs; such as cane toads using more direct dispersal routes along roads (Brown *et al.* 2006) or gulls using orthogonal lift to facilitate less energetically expensive movement (Shepard, Williamson & Windsor 2016). Animal movement, and even distributions, can be linked to energy available to individuals within a habitat and the associated energetic expenditure of moving through it (Shepard *et al.* 2013). As energetic costs define the motion capacity of movement; different animals have evolved different solutions to searching for food.

The final component within the movement ecology paradigm is to consider an animal's movement path. Movement behaviour and patterns are influenced by internal and external factors, and an animal's motion capacity. It is then important to consider how scientists interpret movement. When understanding animal behaviour from movement it is important to follow best practice when assessing behaviour from GPS relocation data (Edelhoff, Signer & Balkenhol 2016). Chapter 2 began by exploring 7 different methods of predicting foraging behaviour from GPS movement data. This chapter showed that ARS identified using Hidden Markov Models correlated best with actual prey capture attempts (associating 81% of dives

with search behaviour), though the chapter also lent support for expectation-maximisation binary clustering. While this may provide a basis for best-practice in identifying foraging behaviour from movement data, each method may still be suitable for specific research questions. This chapter aids establishment of best practice in biotelemetry behavioural studies, enabling direct comparison between studies. Chapter 2 also highlights differences in successful behavioural state determination between two gannet colonies, suggesting that when comparing behaviour between colonies only suitable methods should be used.

6.2 Limitations

The field of the movement ecology has been advanced considerably by the development of biologging technology and statistical analysis (Nathan *et al.* 2008; Williams *et al.* 2019; Joo *et al.* 2020a) and this thesis has developed these to produce meaningful contributions to the wider scientific field. However, before discussing the full implications of this thesis it is necessary to address any limitations within the studies and datasets themselves.

A core concept within animal biotelemetry studies is that the animal must not be impeded by the device so as to best capture natural behaviour. Methodologies to capture any deleterious effects often remain lacking and underreported (Bodey *et al.* 2018a). From an ethical standpoint, all studies were monitored for negative tagging impacts as best as possible, and all methods were approved by the UCC Ethics Committee and the British Trust for Ornithology. Current best practice in avian biotelemetry is to ensure that tags do not exceed 3% of body weight, and are placed to reduce aerodynamic and hydrodynamic drag (Vandenabeele, Wilson & Grogan 2011; Vandenabeele *et al.* 2012; Bodey *et al.* 2018a). Impacts on animals are measured by monitoring individual weight change during tagging, though this may not be the most appropriate as effects can be small (Bodey *et al.* 2018a). Instead it is perhaps best to report the tagging impacts from a holistic approach; as well as reporting weight, it is important to consider similarity in behaviour, fledging success, and tag loss. GPS loggers were deployed on puffins, razorbills, and gannets. There were also several co-deployments of tags; puffins were equipped with GPS and TDR

(though only when using a low weight 1g tag) and gannets were given GPS, TDR, and accelerometers. Most bird deployment weights were kept below the 3% threshold (Maximums: 2.8% on puffins, 3.2% on razorbills, and 1.2% on gannets) and were placed as best as possible to minimise drag. Despite meeting all the required thresholds, it is possible that there was still an effect of tag attachment.

Puffins are a particular species of concern for tagging studies; Harris *et al.* (2012) found puffins to be sensitive to tag attachment, though many birds were tagged with heavier tags than used in this study. Chapter 3 did report effect of tag attachment however; two birds failed their breeding attempts, and of the four individuals recaught, two had lost weight. Whilst tagging razorbills, it was noted that individuals preened their tags off readily and retrieval rates were low. Of 12 razorbill retrievals, 8 had lost an average of 6% body weight. In comparison to the auks, gannets are a much larger and sturdier bird and there was much less of an effect on these birds as all birds returned at a similar weight. Gannets do seem to be aware of the deployment devices – sometimes returning with lost tags that may suggest preening, although this could also have been due to hydrodynamic drag. Unfortunately, the nature of the fieldwork and the ecology of the species meant that chick fledging success could not be monitored reliably without causing significant further disturbance to individuals or colonies. In all study species though, tagged individuals were observed to have foraged successfully, through observations of puffins and razorbills bringing back fish in their beaks, or by observing feeding in gannets. While effects of device attachment cannot be eliminated, it is likely that the behaviour observed in all species was representative of true foraging behaviour; similarities in location and behaviour between individuals as seen in all chapters implies that behaviour is unimpeded.

A large component of animal movement studies using datalogging devices involves incorporating multiple data sources to provide a clear picture of the mechanisms behind movement. From a temporal perspective, this thesis used data that spans from 50Hz (accelerometry – Chapters 4 and 5) to remotely sensed modelled wind data at three hourly intervals (Chapter 5). Different scales of spatial data from GPS data (resolution of approximately 3-10m, Chapters 2,3, and 5) and remotely sensed

weather predictions (0.75-degree spatial scale, Chapter 5) were also used. Effective merging of datasets ensures ecologically relevant analyses/conclusions are obtained; many of these datasets are appropriate scales for use and often can be joined using a nearest neighbour interpolation – either directly or through a second variable. For example; Chapter 5 saw accelerometry data (50Hz with no spatial dimension) joined to GPS data (three-minute interval with small spatial scale) which then in turn joined with medium range weather forecasts (three hourly intervals with wide spatial scales) to provide a clear picture of wind effects upon gannet dives. Data integration will always remain a challenge with developing research, and is a field of research within its own right (Jing-Chun 2004). By its very nature, ecology is multi-disciplinary, and so long as researchers maintain a view or collaboration with other developing fields then these issues should remain manageable.

Scientific studies require an appropriate sample size to reach appropriate conclusions. Therefore, it is difficult to extend the interpretation of some findings beyond the study system used given the small sample sizes involved. Chapter 3 initially undertook one year of GPS tracking of puffins, however after examining findings from the first year, it became apparent second year of data was required. Data collected was only capable of recreating three entire tracks from the puffin GPS with accompanying dive data for energetic analysis, but the conclusions were appropriately backed up by the larger amount of GPS only data collected as part of the study. Chapters 4 and 5 relied heavily upon accelerometry tags, the expensive nature of these tags meant that only had five were deployed which then had to be deployed and recovered repeatedly. Fourteen deployments were undertaken before losing all the accelerometers in the 2019 season. Whilst the data collected was enough to undertake the analysis presented, larger sample sizes could have made conclusions clearer. For example, chapter 5 presented the lateralisation of gannets and a population bias was documented in favour of right-sided birds. However, a power analysis showed there was only a 27% chance of having found a true population bias.

From a more theoretical perspective, this thesis addresses research areas and questions that may span an entire individual seabird's life. However this thesis

focuses on chick rearing during the breeding season. In many ways, this is the easiest time to work with seabirds; chick rearing ensures the birds are central place foragers – returning to the same place to feed their chick. This allows for the easy attachment of devices and quick return of data. Chick-rearing also allows for easy comparison to ensure that birds are not impeded by devices; allowing for the monitoring of untagged conspecifics to monitor trip lengths and individual's weight. Nonetheless, the question remains of how findings in this study will apply over the course of a year, or in non-breeders and juveniles.

Chapter 2 explored differences in the effectiveness of methods for inferring foraging behaviour across two gannet colonies, suggesting that HMMs were the 'best' at capturing actual prey capture attempts. Some methods showed high variability between colonies compared to other methods. While this may be due to intrinsic behavioural differences between colonies, it also suggests that care should be taken when selecting and interpreting the outputs of behavioural annotation methods. Chapter 3 may be able to shed some light on the behaviour of non-breeders in comparison to breeding adults – one puffin failed in its breeding attempt but returned to the colony allowing data retrieval. Similar to juvenile gannets, this puffin undertook a longer more tortuous path before returning to the colony. Recent evidence in non-breeding grey-headed albatross suggests that non-breeders segregate from breeding populations but target similar foraging features (Clay *et al.* 2016). This suggests that findings from Chapters 2 and 3 may be applicable to non-breeders as well as breeding birds. However Clay *et al.* (2016) did note that non-breeders rarely showed sexual segregation, potentially warranting further investigation into the findings of Chapter 4 from a non-breeding perspective.

6.3 Future directions

This thesis integrated multiple data sources to develop the knowledge and understanding of individual level behaviour from movement patterns. The findings presented here naturally allow for the development of further topics of research.

Chapter 5 saw the documentation of lateralised foraging behaviour in gannets. It would be interesting to see further research done into the effects of lateralised behaviour on seabird foraging success and subsequent fitness. Whilst the fields of lateralisation and movement are both strong areas of research, there has been little research joining the two fields. Of particular interest that may encourage further debate and research is to compare the results of Chapters 4 and 5. It would be interesting to see if there is a link between lateralised behaviour and larger movement and foraging patterns. Evidence suggests that individuals lateralised in different directions may have propensities for different individual specialisations (Vallortigara & Rogers 2005) and this may result in unique movement behaviours. Seabirds may be of particular interest as they navigate large distances and undertake specialist foraging behaviour. A potential extension of this study would be to utilise the large backlog of biotelemetry data held by researchers worldwide to look for patterns of lateralisation and adopt a phylogenetic approach to explore the evolution of lateralisation with respect to animal movement.

Many ecological processes can be viewed from an energetic perspective. Chapter 4 showed that considering foraging from an energetic perspective can provide insights into foraging ecology and sexual differences in foraging behaviour. For monomorphic species such as gannets, this is particularly interesting, as it has allowed the consideration of energetics as a driver in the evolution of divergent foraging strategies. Within this study was a key question of how monomorphic species may differ from that of dimorphic species. This study would yield very interesting results if replicated across a range of monomorphic and dimorphic species. This then might explain the different foraging pressures between the sexes along a dimorphism gradient, shedding light on both the evolution of sexual dimorphism but also the advantages to either system. Accelerometry is a data-rich form of movement analysis, and has the potential to describe many small and large-scale behaviours and link them to energetic expenditure. Accelerometry is a tool which can be feasibly used in any system provided it is employed and analysed correctly.

Puffins represent a research priority considering their ‘vulnerable’ status, and any research that might shed light on their ecology and the risks to their populations

should be considered important. Chapter 3 found that puffins are undertaking foraging patterns that do not fit the classic definition of area restricted search. A natural extension of this work would be to undertake comparative studies in areas also known to be tidally active (such as the Skellig Islands in Southwest Ireland) or non-tidally active areas simply to understand more of their ecology. To date, very few puffin tracking papers have been published, the most notable of which found puffins were sensitive to tag attachment (tags approximately 4% of body mass) that made interpretation of results difficult (Harris *et al.* 2012). An interesting observation from the tidal foraging observed in Chapter 3 is that puffins arrive at a drift site, drift, and then return to the colony. Their return to the colony was at the angle of return which minimises travel distance even after drifting. This finding raises several questions regarding the puffins' ability to navigate and implies that puffins must be aware of their location in relation to the colony during a drift. A particularly interesting future avenue of research may be to undertake further studies (or to reanalyse the current dataset) to look at mechanisms of navigation in puffins. The Saltee Islands are already part of a marine protected area and a small extension to this would protect the foraging grounds of the puffins from this colony. Puffins are considered a species sensitive to disturbance (Harris & Wanless 2011) and this small piece of protection may afford one population some respite during foraging.

How animals move through their environment; the manner in which they move, the behavioural choices they make when presented with stimuli, and how these choices affect wider ecological processes are paramount to integrated ecological studies. The studies presented in this thesis explored the fundamentals of movement theory and seabird ecology to further our knowledge of both of these fields. Future research should look to remain integrated with other fields; common processes across specialities may yield surprising results and new insights.

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Appendices

Appendix A – References for Figure 1.1

Below is a series of supporting references that influenced the creation of figure 1.1.

This figure is meant to be only representative of the various tagging methodologies available and, though it was informed by from personal experience, information for this figure can be drawn from a variety of sources, these are detailed below but information can also be garnered from generic references (Nathan *et al.* 2008; Edelhoff, Signer & Balkenhol 2016; Joo *et al.* 2020a; Joo *et al.* 2020b).

Tagging Methodology	***Scale references***
Accelerometry	(Shepard *et al.* 2008b; Collins *et al.* 2015; Leos-Barajas *et al.* 2017; Williams *et al.* 2017)
Depth Recorders	(Bain & Wilson 1982; Evans *et al.* 2013b; Garthe *et al.* 2014; Linnebjerg *et al.* 2014)
GPS	(Hulbert & French 2001; Witt *et al.* 2010; Dujon, Lindstrom & Hays 2014; Forin-Wiart *et al.* 2015)
VHF	(Lewis *et al.* 2002; Coulombe, Massé & Côté 2006; Pellerin, Saïd & Gaillard 2008; Muller *et al.* 2019)
ARGOS	(Vincent *et al.* 2002; Nicholls, Robertson & Murray 2007; Patterson *et al.* 2010; Witt *et al.* 2010)
GLS	(Fudickar, Wikelski & Partecke 2012; Lisovski *et al.* 2012; Lisovski *et al.* 2020)

Appendix B – Supplementary figures for Chapter 2

Below is a series maps to demonstrate the output of each method. Two random individuals were chosen to demonstrate the methods from each colony.

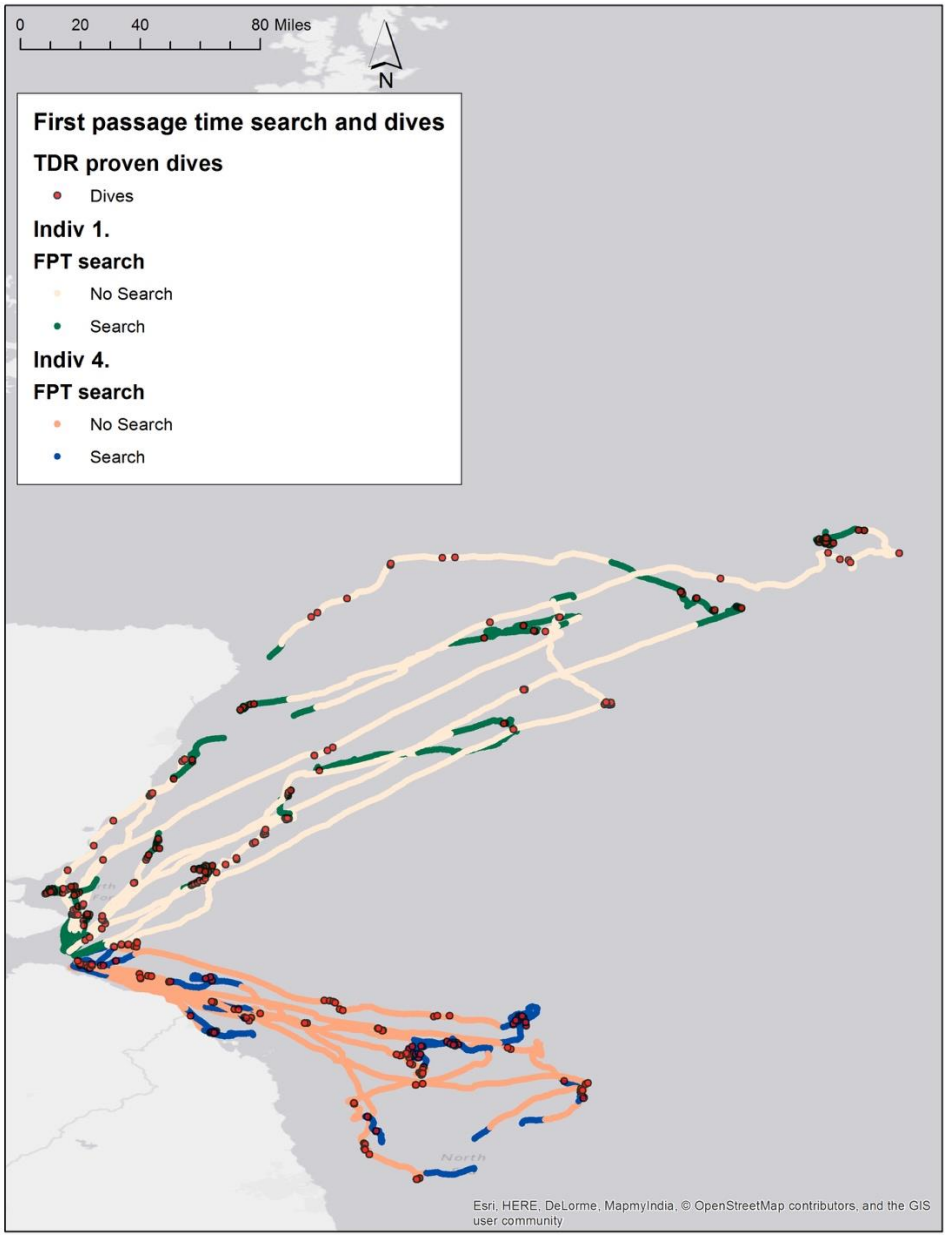

Figure S1. Example first passage time analysis of two complete random gannet tracks (multiple trips in one tracking session) at Bass Rock. Locations close to the colony and night-time have been removed.

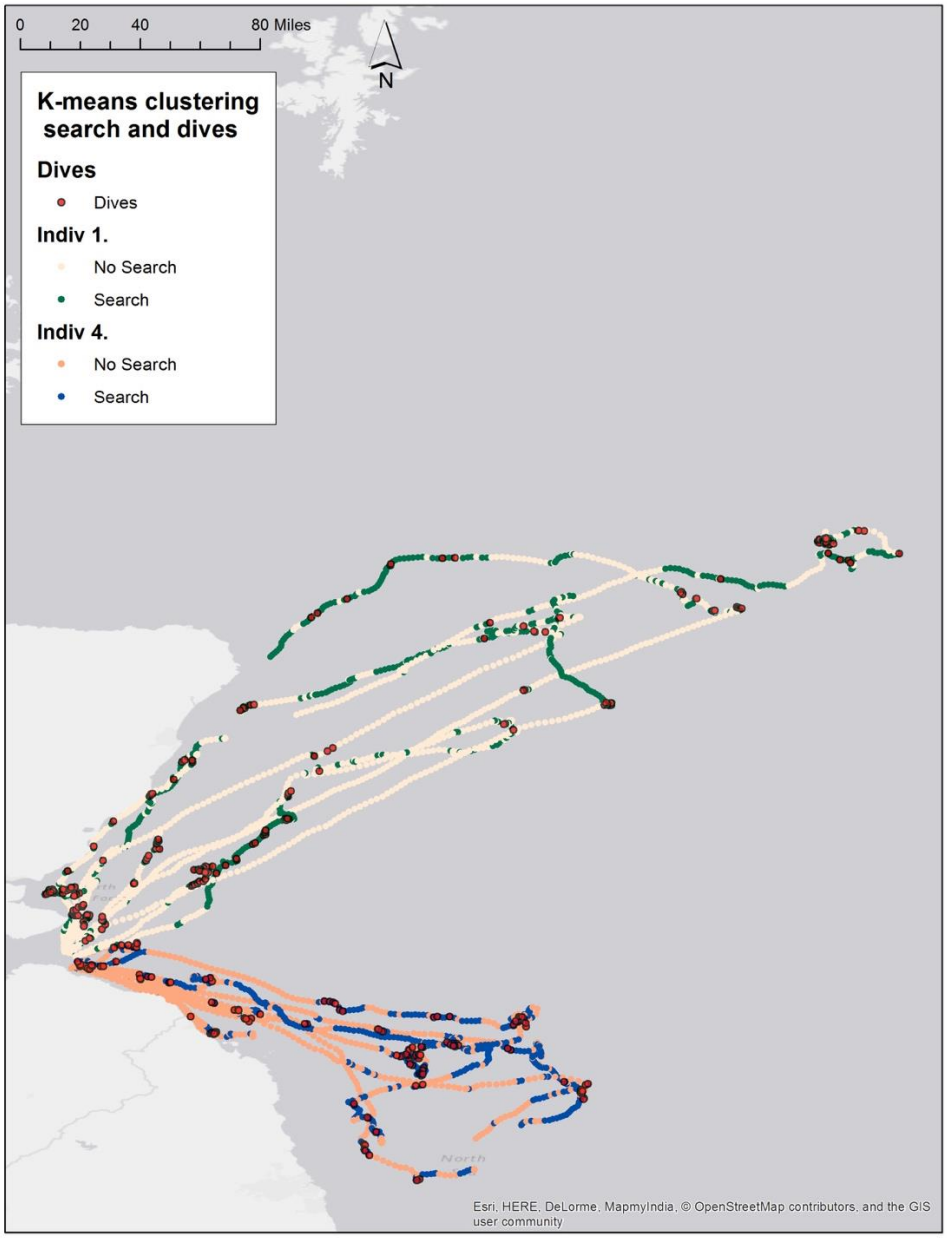

Figure S2. Example K-means clustering analysis of two complete random gannet tracks (multiple trips in one tracking session) at Bass Rock. Locations close to the colony and night-time have been removed.

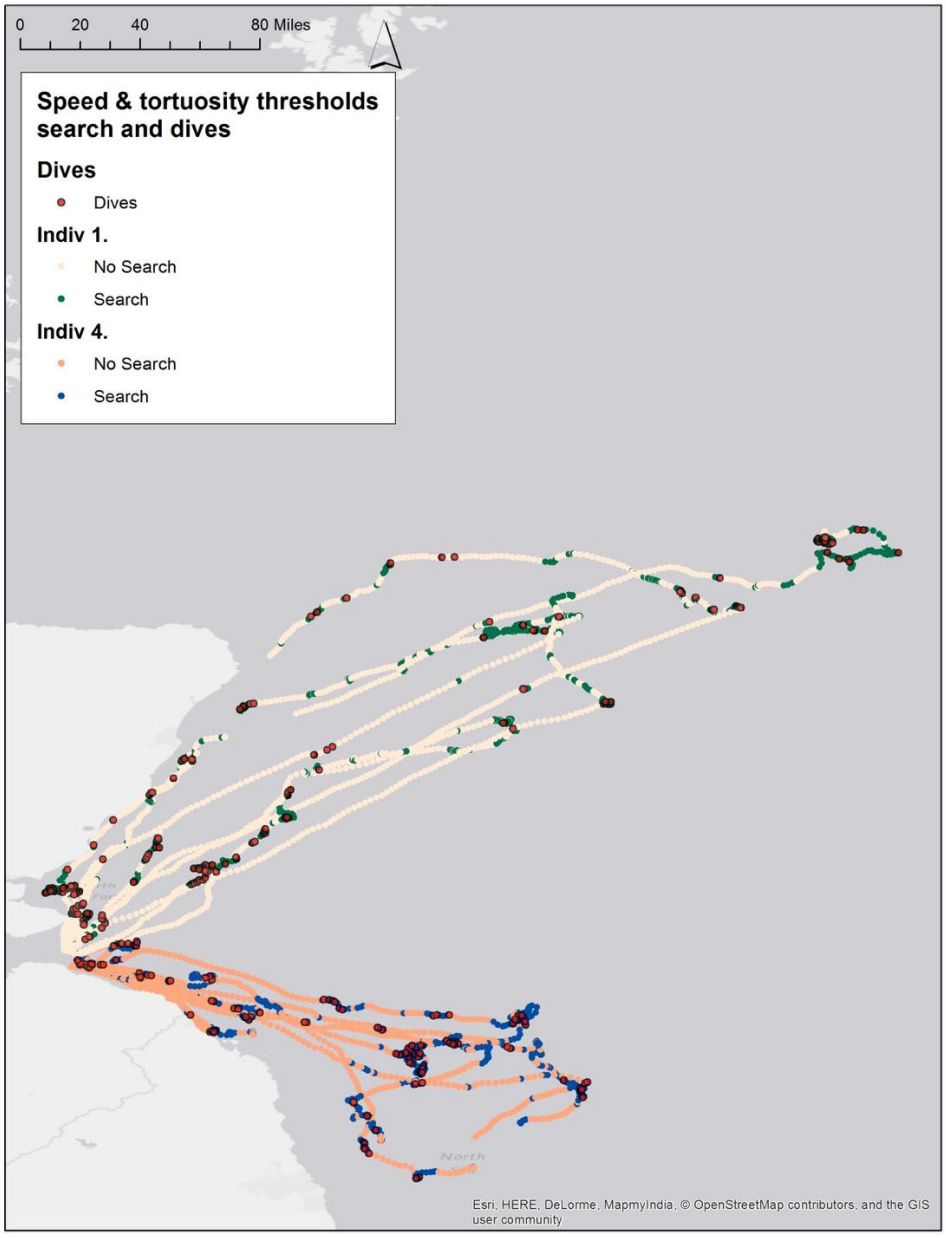

Figure S3. Example speed & tortuosity thresholds analysis of two complete random gannet tracks (multiple trips in one tracking session) at Bass Rock. Locations close to the colony and night-time have been removed.

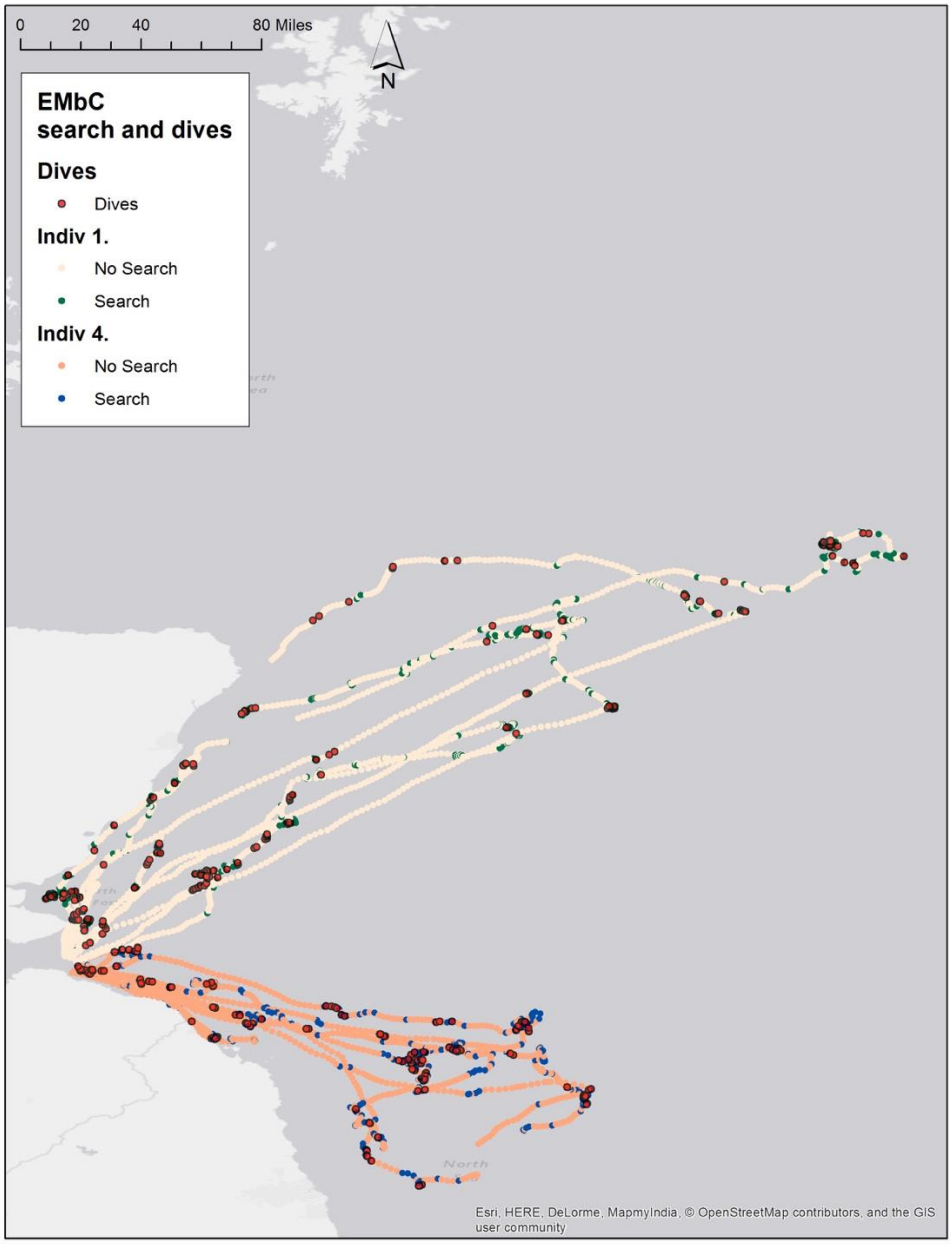

Figure S4. Example expectation-maximisation binary clustering (EMbC) analysis of two complete random gannet tracks (multiple trips in one tracking session) at Bass Rock. Locations close to the colony and night-time have been removed.

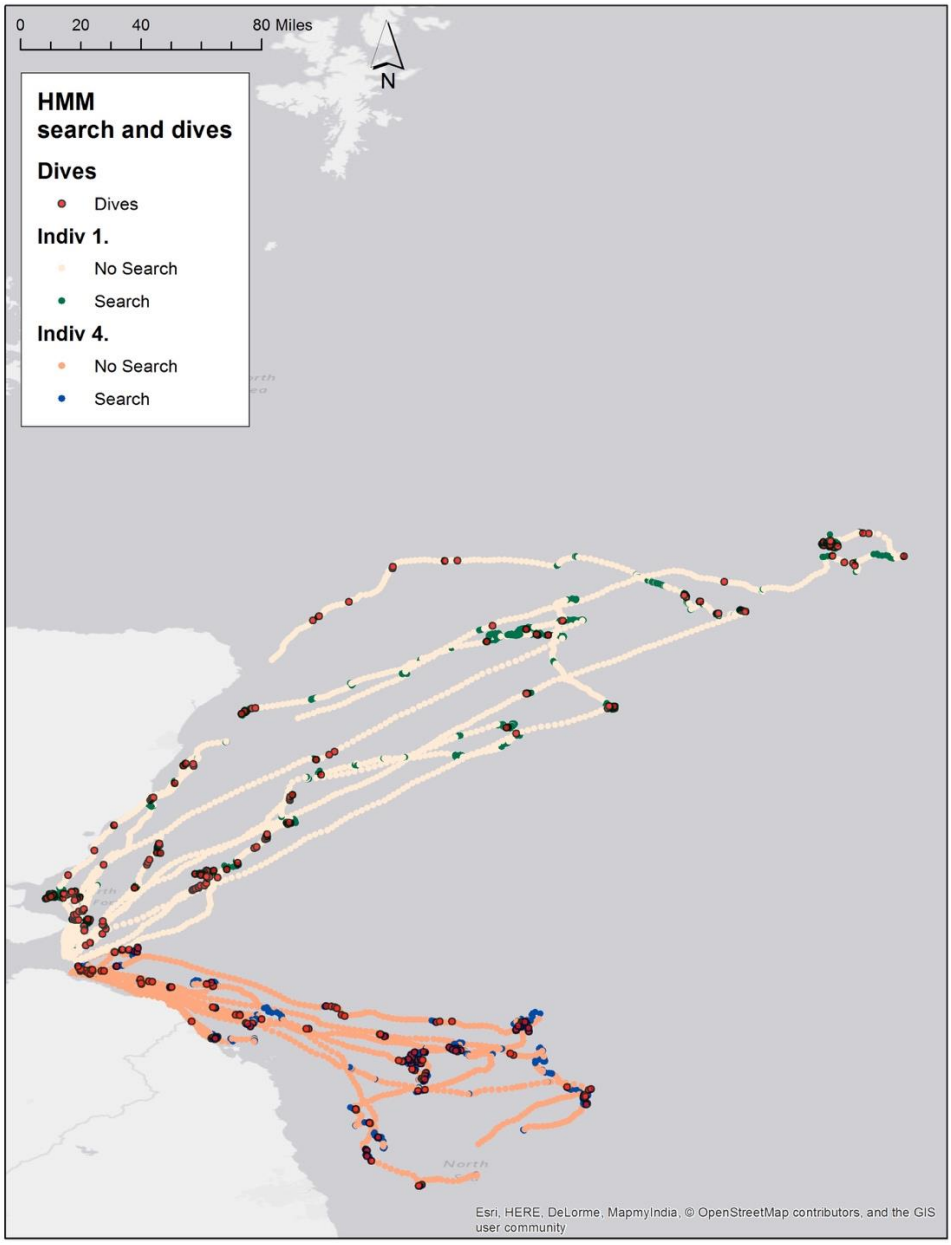

Figure S5. Example hidden markov model (HMM) analysis of two complete random gannet tracks (multiple trips in one tracking session) at Bass Rock. Locations close to the colony and night-time have been removed.

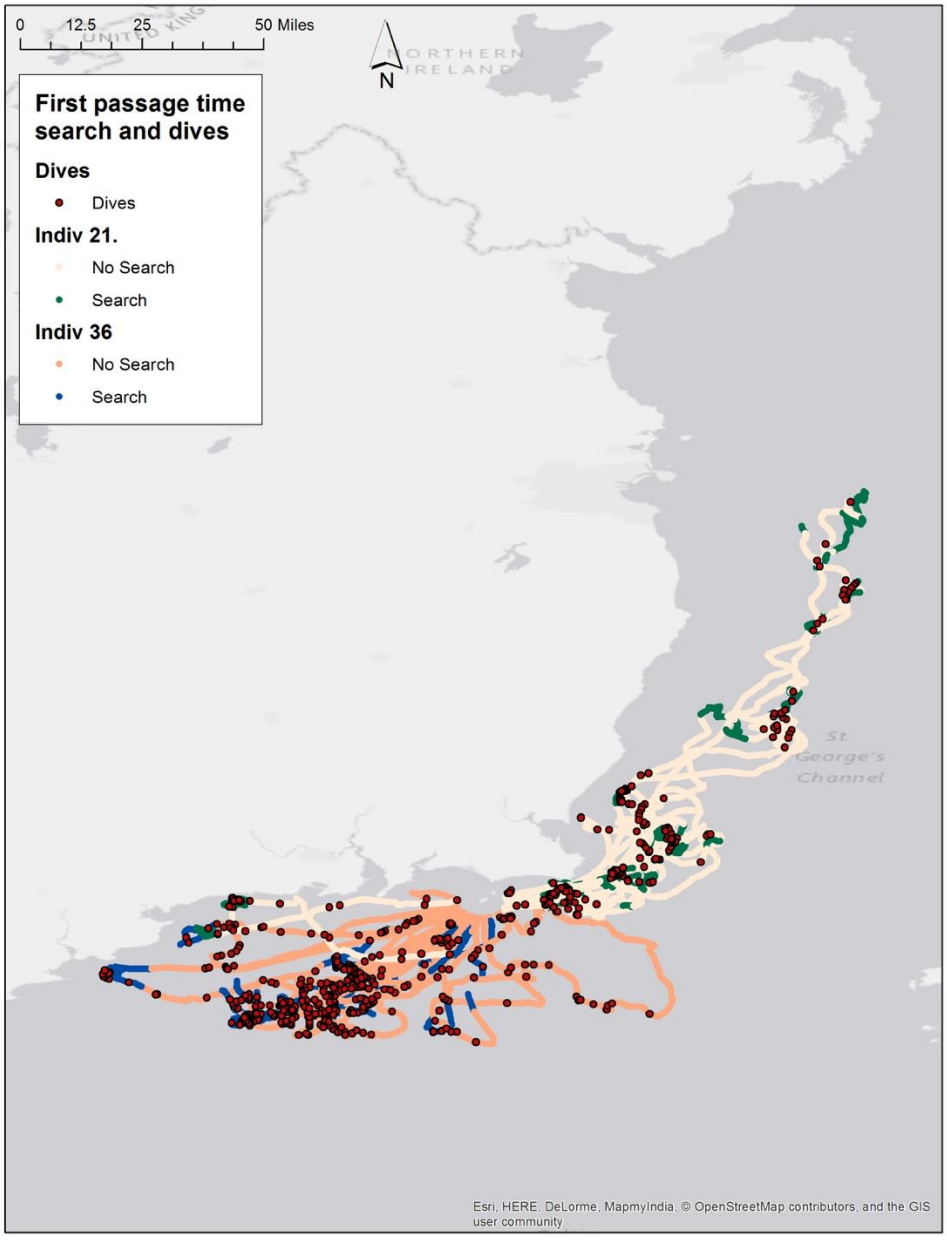

Figure S6. Example first passage time analysis of two complete random gannet tracks (multiple trips in one tracking session) at Great Saltee. Locations close to the colony and night-time have been removed.

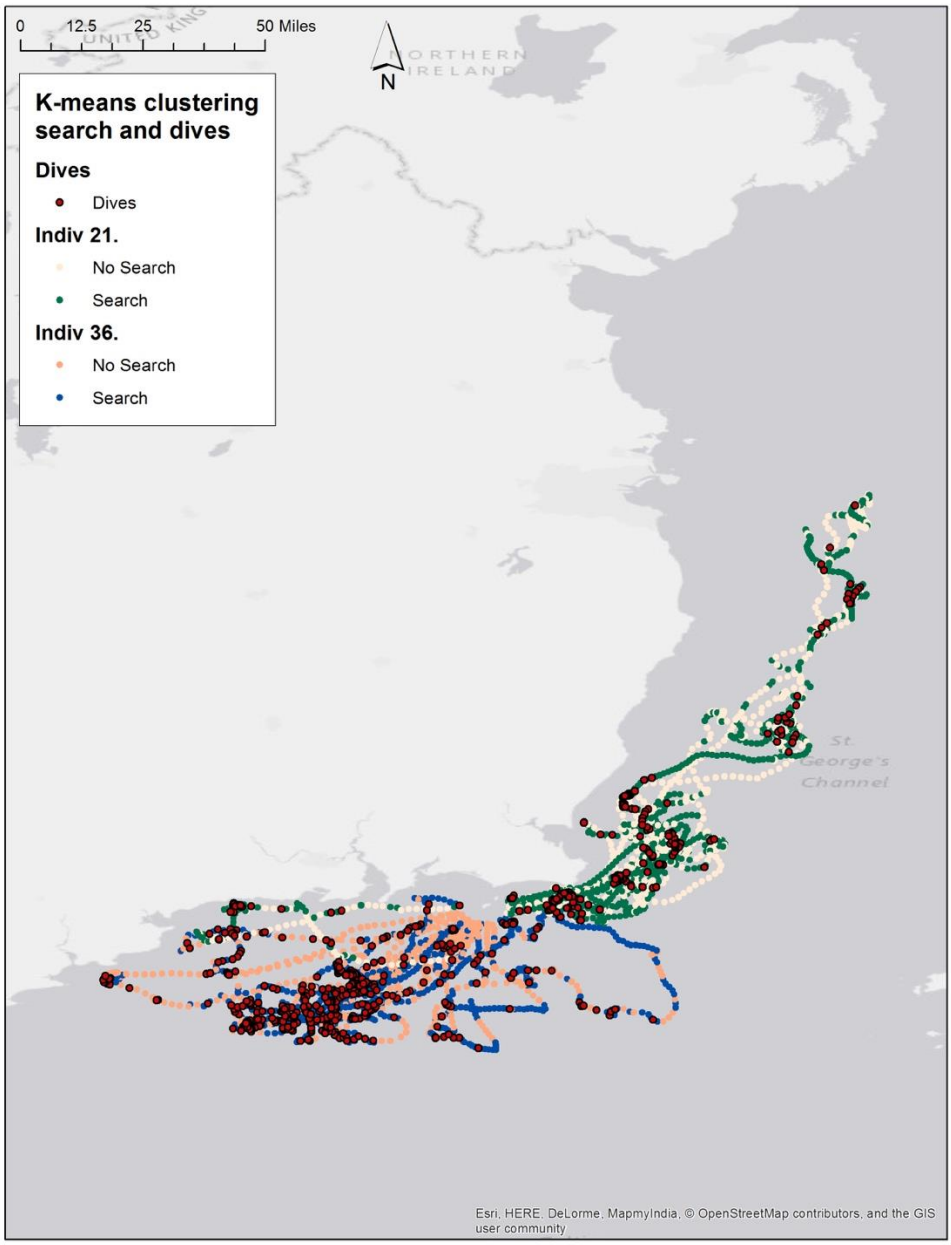

Figure S7. Example K-means clustering analysis of two complete random gannet tracks (multiple trips in one tracking session) at Great Saltee. Locations close to the colony and night-time have been removed.

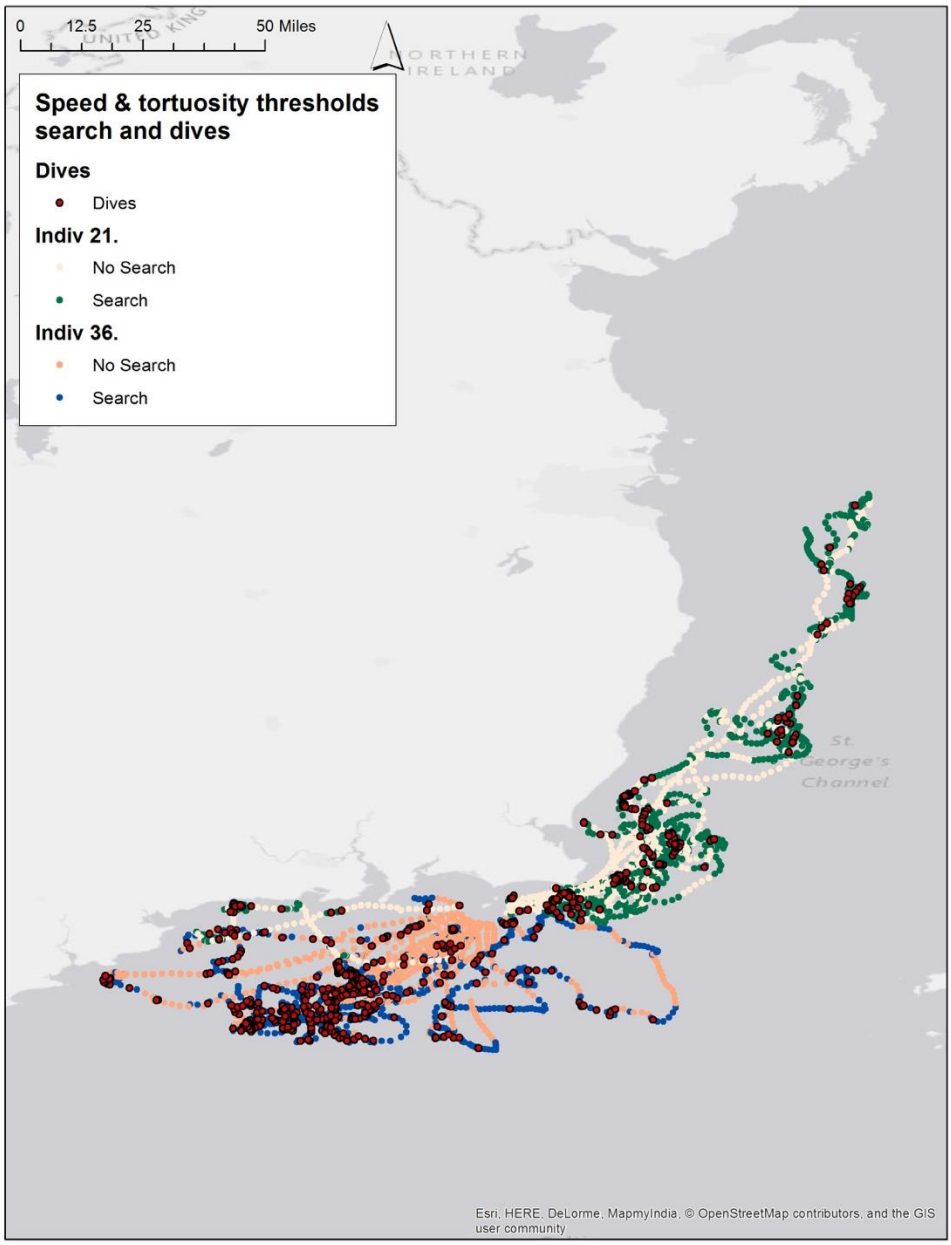

Figure S8. Example speed & tortuosity thresholds analysis of two complete random gannet tracks (multiple trips in one tracking session) at Great Saltee. Locations close to the colony and night-time have been removed.

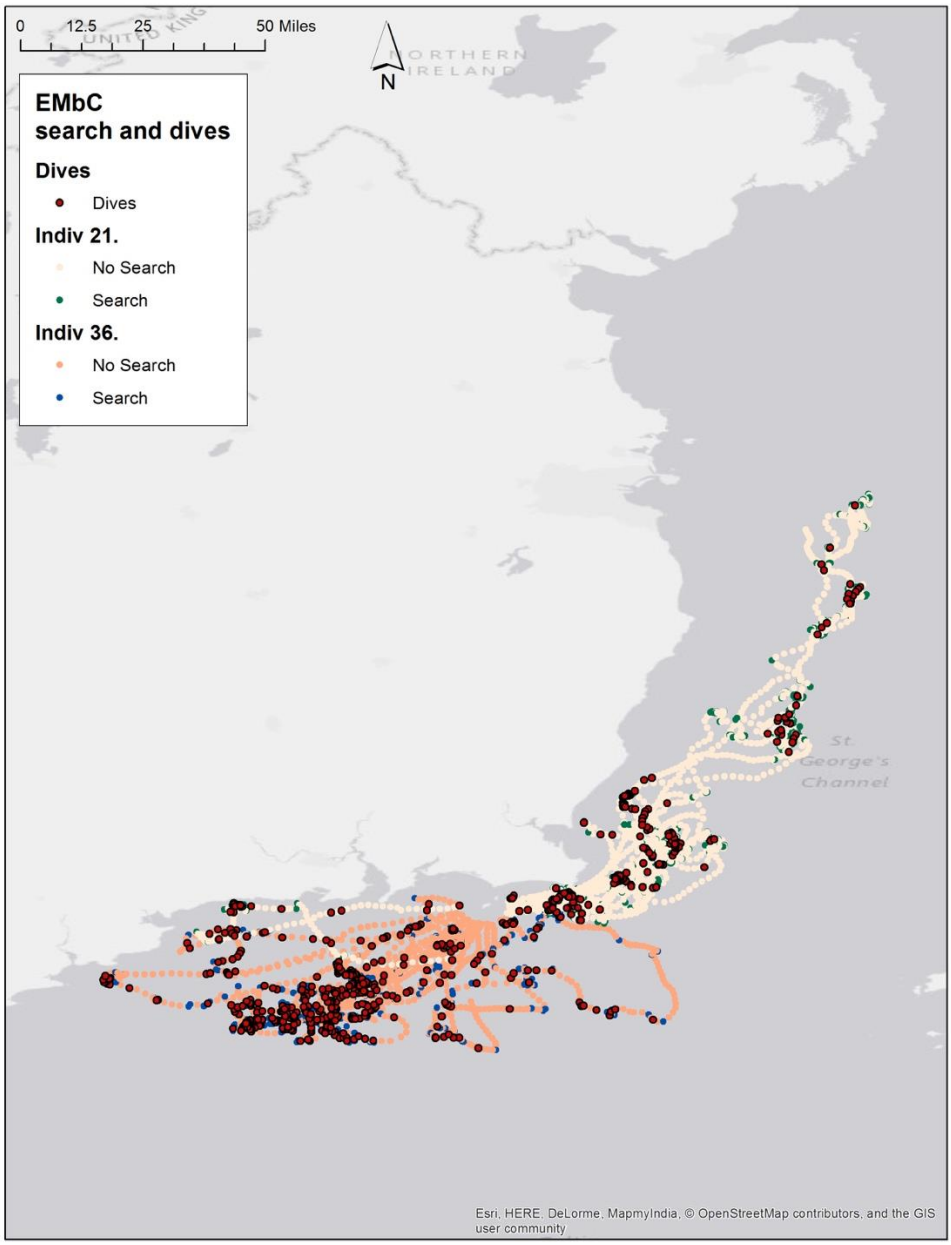

Figure S9. Example expectation-maximisation binary clustering (EMbC) analysis of two complete random gannet tracks (multiple trips in one tracking session) at Great Saltee. Locations close to the colony and night-time have been removed.

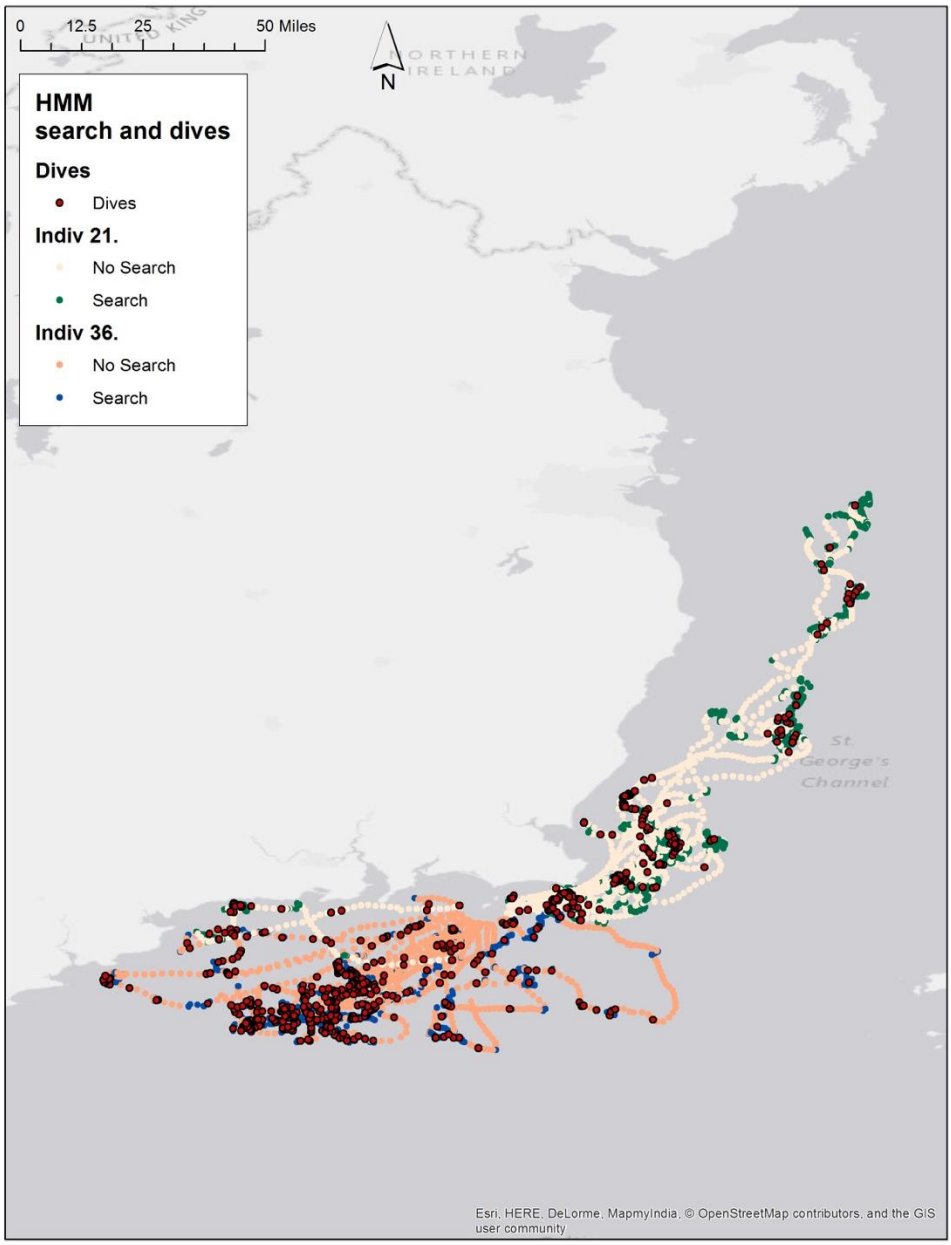

Figure S10. Example hidden markov model (HMM) analysis of two complete random gannet tracks (multiple trips in one tracking session) at Great Saltee. Locations close to the colony and night-time have been removed.

Appendix C Publications achieved during completion of this thesis

Whilst completing this thesis I have been able to publish both Chapters 2 and 3. Links to these are provided below:

Chapter 2: **Search and foraging behaviours from movement data: a comparison of methods.**

Citation:

Bennison, Ashley, Stuart Bearhop, Thomas W. Bodey, Stephen C. Votier, W. James Grecian, Ewan D. Wakefield, Keith C. Hamer, and Mark Jessopp. "Search and foraging behaviors from movement data: a comparison of methods." *Ecology and evolution* 8, no. 1 (2018): 13-24.

DOI access link: https://doi.org/10.1002/ece3.3593

Chapter 3: **Tidal drift removes the need for area restricted search in foraging Atlantic puffins**

Citation:
Bennison, Ashley, John L. Quinn, Alison Debney, and Mark Jessopp. "Tidal drift removes the need for area-restricted search in foraging Atlantic puffins." *Biology letters* 15, no. 7 (2019): 20190208.

DOI access link: https://doi.org/10.1098/rsbl.2019.0208

As well as publishing two chapters during this thesis, I have also been lucky enough to collaborate with various researchers throughout my department and beyond. These citations are included below:

Doyle, Thomas K., Damien Haberlin, Jim Clohessy, **Ashley Bennison**, and Mark Jessopp (2017) "Localised residency and inter-annual fidelity to coastal foraging areas may place sea bass at risk to local depletion." *Scientific reports* 7: 1-9.

Contribution: In this study, I was involved in the data collection (retrieval and exchange of monitoring stations). I also assisted with data analysis, producing several of the figures, and contributed to the manuscript.

Sydeman, William J., Sarah Ann Thompson, Tycho Anker-Nilssen, Mayumi Arimitsu, **Ashley Bennison**, Sophie Bertrand, Philipp Boersch-Supan et al (2017) "Best practices for assessing forage fish fisheries-seabird resource competition." *Fisheries Research* 194: 209-221.

Contribution: This publication was the culmination of a workshop held after the 2nd World Seabird Conference in Cape Town. The workshop provided an environment for researchers to produce the framework of a paper and they encouraged input from early career researchers. Following the workshop, a manuscript was produced and I also contributed to this.

Wischnewski, Saskia, Gavin E. Arneill, **Ashley W. Bennison**, Eileen Dillane, Timothée A. Poupart, Camilla A. Hinde, Mark J. Jessopp, and John L. Quinn (2019) "Variation in foraging strategies over a large spatial scale reduces parent–offspring conflict in Manx shearwaters." *Animal Behaviour* 151: 165-176.

Contribution: For this paper, I was heavily involved as a field worker, leading field teams whilst undertaking GPS tagging at two different sites. I also contributed to the manuscript.

Todd, Nicole RE, Michelle Cronin, Cian Luck, **Ashley Bennison**, Mark Jessopp, and Ailbhe S. Kavanagh (2020) "Using passive acoustic monitoring to investigate the occurrence of cetaceans in a protected marine area in northwest Ireland." *Estuarine, Coastal and Shelf Science* 232: 106509.

Contribution: For this publication, I helped the lead author during analysis of her MSc thesis which subsequently became this publication. I also had opportunity to contribute to the manuscript.

Critchley, Emma Jane, W. J. Grecian, **Ashley Bennison**, Adam Kane, Saskia Wischnewski, A. Cañadas, D. Tierney, John L. Quinn, and Mark J. Jessopp (2020) "Assessing the effectiveness of foraging radius models for seabird distributions using biotelemetry and survey data." *Ecography* 43, no. 2: 184-196.

Contribution: For this publication, I contributed previously unpublished puffin tracking data (which became Chapter 3) which acted as a comparison to the foraging radius model. I also had opportunity to contribute to the manuscript.

Breen, Patricia, Enrico Pirotta, Louise Allcock, **Ashley Bennison**, Oliver Boisseau, Paul Bouch, Aisling Hearty et al (2020) "Insights into the habitat of deep diving odontocetes around a canyon system in the northeast Atlantic Ocean from a short multidisciplinary survey." *Deep Sea Research Part I: Oceanographic Research Papers*: 103236.

Contribution: This study was the result of aerial surveys over the Irish Atlantic (for which I was an observer) which highlighted the prevalence of beaked whales. We

undertook a research cruise, for which I undertook marine mammal observation duties and I was also responsible for collating and processing sightings data. I also contributed to the manuscript.

Malvat, Z., S. A. Lynch, **A. Bennison**, and M. Jessopp (2020) "Evidence of links between haematological condition and foraging behaviour in northern gannets (Morus bassanus)." *Royal Society Open Science* 7, no. 5: 192164.

Contribution: This paper was the result of an MSc thesis, during which I collected some of the initial data and taught the student how to process blood slides from gannets in the field. I also helped to contribute to the manuscript.

Jessopp, Mark, Gavin E. Arneill, Milaja Nykänen, **Ashley Bennison**, and Emer Rogan (2020) "Central place foraging drives niche partitioning in seabirds." *Oikos*. doi: 10.1111/oik.07509

Contribution: This study was produced as part of the outcomes from aerial surveys across the waters of the Irish EEZ, for which I was an observer. I helped with initial analysis of the data and also contributed to the manuscript.

Kane, Adam, Enrico Pirotta, Saskia Wischnewski, Emma Jane Critchley, **Ashley Bennison**, Mark Jessopp, and John L. Quinn (2020) "Spatio-temporal patterns of foraging behaviour in a wide-ranging seabird reveal the role of primary productivity in locating prey." *Marine Ecology Progress Series* 646: 175-188.

Contribution: For this paper I was heavily involved as a field worker, leading field teams whilst undertaking GPS tagging at two different sites. I also contributed to the manuscript.