Fine-scale foraging behaviour and energy expenditure of northern gannets: insights from accelerometry

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B309 (female) and O022 (male), of the 75000+ pairs you are my favourite.

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'Team gannet' (L to R: Chris Pollock, Keith Hamer, Jude Lane) taking a coffee break during fieldwork on Bass Rock.

Abstract

Animal-borne accelerometers allow body movement and behaviours to be recorded and identified. Quantifying these from free-living animals has many ecological applications, from identifying key behaviours in focal aspects of life history to estimating energy expenditure of locomotive patterns, all without direct observation. This is particularly valuable for species that are difficult to observe throughout their daily routines, such as those that utilise marine environments. Many seabirds navigate a three-dimensional landscape in unpredictable environmental conditions to find prey that are often patchy and widely distributed. Consequently, their foraging strategies, and utilisation of time and energy when foraging, are complex. Foraging effort and success determine the net energy gain by an organism and form an essential link between prey availability and reproductive success. Quantifying foraging energetics can be challenging, but aid in delivering sound conservation strategies in an era of intense environmental pressures and uncertainty.

By combining multifaceted data, principally accelerometers and GPS loggers, this thesis explored the at-sea movements of northern gannets, *Morus bassanus,* on a fine-scale individual basis. First, I examined associations between sexual dimorphism and sex differences. Within each sex, different facets of movements and behaviour were significantly related to body mass. However, the observed relationships were not consistent with the notion that sex differences were driven by sexual dimorphism. Secondly, I investigated the consistency in foraging behaviour and energy expenditure of individuals and the energy consequences of individual foraging site fidelity (IFSF). Birds were consistent in space use and energy expenditure but with varying degrees of repeatability among individuals and between sexes. The consequences of individuality were sex-specific, with greater IFSF associated with enhanced foraging success among females and elevated foraging effort among males. Third, I examined the effect of wind on fine-scale foraging behaviour and energy expenditure, finding that wind conditions strongly affected foraging behaviour, with contrasting effects of increasing wind speeds on females (lower take-off rates) and males (greater dive depths).

Overall, I demonstrate that not only do sexes and individuals differ in fine-scale behaviours and proxies of energy expenditure, but sex differences extend to the prevalence and consequences of individuality, and sexes respond differently to environmental conditions when foraging. This thesis highlights the need to consider sex differences and individuality when predicting the impacts of environmental change on populations of long-lived central-place foragers.

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Abbreviations

DBA	Dynamic body acceleration
GPS	Global positioning system
GLMM	General linear mixed effects model
IFSF	Individual foraging site fidelity
LMM	Linear mixed effects model
ODBA	Overall dynamic body acceleration
OWF	Offshore windfarms
TDR	Time-depth recorder
VeDBA	Vectoral dynamic body acceleration

Chapter 1 **Introduction**

Part of the colony accessible for study, known as the 'west chapel and path birds'

1.1 Movement, behaviour and foraging ecology

The field of movement ecology has expanded over recent decades alongside advancing technology from ‘where do animals go?’ to ‘what specifically are animals doing there?’ and ‘how could anthropogenic factors affect movement, and how do we manage that?’ Movement is a visible way behaviour is expressed, and an animal’s behaviour encompasses its responses to the environment and its own physiological condition (Shepard *et al.,* 2008). An ability to quantify movement accurately and in detail is therefore beneficial in understanding an animal’s requirements from its environment. Considerable innovation in technology over the past fifty years has revolutionised the study of the movement ecology of free-living animals (Ropert-Coudert and Wilson 2005). In particular, advances in the past decade have resulted in the miniaturisation of data-logging and tracking animal-borne devices which are able to record location, behaviour, environmental and physiological variables, the analysis of which is an ever-expanding field of research (e.g. Shaffer *et al.,* 2014; Wilmers *et al.,* 2015; Largey *et al.,* 2021).

Foraging is a fundamental component of animal behaviour, forming a vital link between prey availability and predator reproductive success (Boggs 1992). Thus, changes that affect foraging can contribute to population demographic rates (Duckworth *et al.,* 2021). Many species interact with anthropogenic factors on some scale whilst foraging, making an understanding of foraging behaviour imperative for informing conservation management (Lane *et al.,* 2020; O’Leary *et al.,* 2020).

Foraging behaviour encompasses all behaviours associated with the acquisition of food resources: searching, capture and consumption. Many animals search for food around a fixed site, such as a nest, den or food cache, and this is broadly referred to as central-place foraging (Andersson 1981). Central-place foragers are restricted by, and have to balance, the demands of searching for resources and returning to a fixed site (Orians and Pearson 1979) to achieve efficient foraging; the energy gained from food is higher than the energy expended to acquire it (MacArthur and Pianka 1966). Maximising foraging efficiency is even more important when feeding offspring (Kacelnik 1984). This can be on a relatively small scale, such as predatory mammals like stoats, *Mustela erminea L.,* returning a few kilometres to offspring confined to the safety of dens, or over much greater distances as often seen in colonial air-breathing marine predators like seals and seabirds that can travel hundreds of kilometres from breeding sites in search of food (Sandell 1989; Elliott *et al.,* 2009; Staniland *et al.,* 2010). These colonial central-place foragers face another pressure – local intraspecific competition, which can lead to localised prey depletion and individuals having to travel further to find food (Ashmole 1963; Elliott *et al.,* 2009).

Studying foraging behaviour at a fine-scale on free-living animals is difficult, particularly where behaviour cannot be directly observed or filmed, like those that utilise the marine environment (Hammond *et al.,* 2016). But classifying behaviour on a fine-scale provides the best information for broadscale understanding and implementation of effective management strategies (Ropert-Coudert *et al.,* 2004). For example, the study of flight patterns can provide information about foraging effort; flapping flight is one of the most energetically expensive forms of transport an animal can adopt, the costs of which are greatly influenced by wind conditions and theory predicts that flying animals will vary their foraging effort spatially and temporally to maximise energy efficiency across variable windscape (Taylor and Thomas 2002; Elliott *et al.,* 2013). Consequently the energetics of flight have great ecological importance and have been intensively studied across species in a comprehensive field of research (Taylor and Thomas 2002; Vandenabeele *et al.,* 2012; Amélineau *et al.,* 2014).

1.2 Sexual segregation and individuality in foraging behaviour

The energetic demands of foraging behaviour often increase during reproduction (Elliott *et al.,* 2014). Across many taxa, achieving reproductive success whilst maintaining individual fitness requires investment by both parents to rear offspring (Lack 1968; Gowaty 1996). This investment may not be equal between the sexes; individuals often face sex-specific physiological, behavioural and environmental constraints, or competing interests (Trivers 1972; Reynolds 1996). Consequently sexual segregation during parental duties often presents as foraging niche separation and may encompass spatial, temporal and diet differences (Lewis *et al.,* 2002; Elliott *et al.,* 2010; Clark *et al.,* 2021). In species with sexual dimorphism, sexual segregation may be driven by differences in physical traits, for example social dominance and competitive exclusion by the larger sex, often males over females (Isaac 2005). This was demonstrated experimentally in the downy woodpecker, *Picoides pubescens,* where females avoid the foraging microhabitat of the socially dominant males, but under malefree conditions females became malelike in their selection of foraging microhabitat (Peters & Grubb Jr. 1983). However this phenomenon is not exclusively explained by physical traits, and also occurs in species with little or no sexual dimorphism (Wearmouth and Sims 2008).

Understanding why sexual segregation arises and what each sex specifically requires from its environment is essential for the conservation of animal populations because these drivers and sex-specific requirements are likely to affect a population’s response to change (Bennett *et al.,* 2019). If sexual segregation occurs in habitat selection to reduce competition between the sexes, then it may be necessary to protect different habitats for males and females and environmental change could lead to one sex being more vulnerable to habitat loss and thus reduced fecundity due to sex-biased survival.

For example, it has only recently been found that for the endangered loggerhead turtle, *Caretta caretta*, sexual segregation contributes to higher mortality of males through increased interaction with anthropogenic threats in the coastal habitats they favour, compared to females that migrate further offshore, upon which previous adult survival estimates have been based (Rees *et al.,* 2016; Schofield *et al.,* 2020). Although sexual segregation is a common and important evolutionary phenomenon, it is still not regularly considered in environmental management despite having far-reaching consequences for population ecology (Bowyer *et al.,* 2001; Schofield *et al.,* 2020), with some researchers suggesting the sexes of certain large herbivores should be managed as if they were different species (Kie and Bowyer 1999).

In addition to sexual segregation, an important source of variation in foraging behaviour comes from consistent individual differences. For many long-lived species phenotypically similar individuals exhibit consistent differences in foraging behaviour, leading to individuals occupying distinct subsections of the foraging niche available to them (Bolnick *et al.,* 2003). Individuality in foraging behaviour has important implications for our understanding of animal ecology; individuality affects resource use, the level of intra-specific competition and niche partitioning (Phillips et al., 2004; de Grissac *et al.,* 2016). Individuality is also the foundation of carry-over effects whereby one season has consequences for following seasons (Harrison *et al.,* 2011). Therefore, the mechanisms behind individuality and the extent of individuality in populations determines the responses of individuals, and thus populations, to environmental factors and anthropogenic threats.

Individuality associated with foraging is generally thought to arise from different heritable phenotyes, such as genetic personality traits associated with differences in foraging areas (Patrick and Weimerskirch 2017), or through learning and culture as seen in several social mammalian groups (e.g. primates, dolphins and orcas Lefebvre 1995; Bender *et al.,* 2009; Foote *et al.,* 2016). There are also many instances where individuality occurs without obvious phenotypic markers and separately from group or parental learning (Arajuro *et al.,* 2011). These are hypothesised to be linked to individual trial and error of exploratory foraging behaviours, refined with age and experience (Guilford *et al.,* 2011; Votier *et al.,* 2017).

Individual foraging site fidelity (IFSF) is a common type of individual foraging specialisation that likely developed through one of these mechanisms (Votier *et al.,* 2017). IFSF is characterised by space use; whereby an individual is significantly more likely to consistently use a particular foraging area than that of the population (Wakefield *et al.,* 2015). This phenomenon can persist over long periods of time, and at different timescales and life history stages in a range of species (Guilford *et al.,* 2011; Baylis *et al.,* 2012; Wakefield *et al.,* 2015; Lescroël *et al.,* 2020). In a predictable environment, high fidelity to a site (high IFSF) may be advantageous with increased foraging efficiency associated with known foraging locations and specialised behaviours, but in unpredictable environments, low site fidelity (low IFSF) is thought to be adaptive due to behavioural plasticity (Candolin and Wong 2015; Patrick and Weimerskirch 2017).

Studies are beginning to demonstrate changes to foraging ranges of long-lived species may act disproportionately on some individuals and not be equal across the population, a vital consideration in species management (Owens *et al.,* 2019). However, the individual-level drivers and energetic, physiological and fitness-related consequences of individuality are poorly understood, and yet crucial to quantify in a rapidly changing world, as the degree of plasticity affects the capacity of populations to adapt (Phillips *et al.,* 2017; Harris *et al.,* 2019). One step towards understanding this is to quantify the energetic and fitness-related consequences of being consistent in foraging behaviours. If individuality is not consistently associated with efficient or successful foraging, that could suggest it is a constraint and not a flexible trait, potentially resulting in individuals that cannot learn and adapt to environmental change.

1.3 Measuring energy expenditure and fine-scale behaviours in free-living animals

Energy expenditure forms an essential link between foraging behaviour, physiology and individual fitness (Grémillet *et al.,* 2018). This has important implications for ecology and conservation; quantifying activity-specific energy expenditure clearly demonstrates how much energy an animal has to use to survive, and how this may be affected by environmental changes (Wilson *et al.,* 2020). For example, by determining the energy costs of different aspects of hunting behaviour and subsequent energy gains in African wild dogs, *Lycaon pictus*, Hubel *et al.,* (2016) showed African wild dogs to be more energetically robust than previously believed, and the factors associated with longer hunting time windows are the most likely to negatively impact energy management, such as lower prey density or greater periods of heat, as predicted with climate change.

Whilst energy expenditure can be measured directly, these methods have limitations in a field setting; the doubly-labelled water method provides a single estimate between two points in time where blood samples are collected, and the heart-rate method requires species-specific extensive calibrations and attachment methods can be sensitive to dives or involve surgical insertion (Green *et al.,* 2009; Speakman and Hambly 2016). Beyond direct measurements, proxies of energy expenditure can be derived from detailed body movement data, given that locomotion forms a large proportion of the energy used by an animal (Karasov 1992; Halsey *et al.,* 2011).

Accelerometers are bio-logging devices able to provide high resolution quantitative data on body movements and postures (e.g. Clutton-Brock *et al.,* 1999; Chimienti *et al.,* 2016). First used to study movement in sport and medical sciences in the 1950s (Morris 1973; Nokes *et al.,* 1984; Meijer *et al.,* 1992), it was not until the turn of the current century that accelerometers were used on free-living animals to identify behaviours, movement patterns and, more recently, to estimate energy expenditure (Wilson *et al.,* 2006, 2019; Ropert-Coudert *et al.,* 2016; Bennison *et al.,* 2022)**.**

Tri-axial accelerometers record acceleration (g) along three axes: surge, sway and heave (Figure. 1.1). This provides two types of acceleration data; static acceleration, originating from the force of the Earth's gravitational field, and dynamic acceleration from the movement of the animal (Shepard *et al.,* 2008). Both of these can determine an animal's posture and movement e.g., taking flight, landing and diving in imperial cormorants, *Phalacrocorax atriceps* (Wilson *et al.,* 2008).

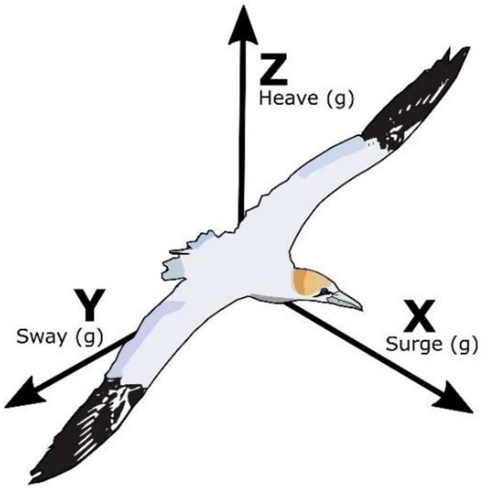


Figure 1.1. The directions and axes that tri-axial accelerometers record acceleration (g).

Static acceleration provides information on the posture of an animal, or more precisely, what the angle of the accelerometer is in relation to gravity (Shepard *et al.,* 2008). Postures may sometimes directly identify a behaviour. For example, an upright posture suggests that a meerkat, *Suricata suricatta*, is demonstrating vigilance behaviour (Clutton-Brock *et al.,* 1999). More commonly however, postures aid in the classification of particular behaviours, as it identifies suites of behaviour. For example, an upright gannet *Morus spp.* could be ascending a dive or standing at a nest, whereas a horizontal gannet may be flying, rafting on the water or swimming. In addition to the posture itself, how long it is held can refine the classification further. For example, the plunge dives of gannets are well documented, dives typically last between 3-5 seconds (Nelson 2002; Ropert-Coudert *et al.,* 2009; Green *et al.,* 2010). Therefore time spent upright beyond that range may be attributed to time on land. Of course, most behaviours are far more complex, and a whole array of behaviours can occur within the same posture. In these instances, dynamic acceleration can provide the level of detailed information necessary to identify these behaviours (Shepard *et al.,* 2008).

Dynamic acceleration refers to the changes in velocity due to the movement of the body across the sway, heave and surge axes (Wilson *et al.,* 2006). In its simplest form, dynamic acceleration is calculated by subtracting static acceleration from the total acceleration, thus when total acceleration is equal to the static acceleration there is zero dynamic acceleration (Wilson *et al.,* 2006). Therefore, dynamic acceleration is recorded as deviations from zero in the three axes of acceleration (g) over time (Wilson *et al.,* 2006). When interpreting dynamic acceleration data, one must adhere to Newton's third law of motion; for every action, there is an equal and opposite reaction (Newton 1687). For example, in the wingbeat cycle of a bird, a downward stroke causes the body to lift, and the upward stroke causes the body to drop, measured in the heave axis (Taylor and Thomas 2002). An example of locomotion in the sway axis would be the swimming pattern of many fishes, whereby as the tail moves laterally in one direction, the body moves in the other (Shepard *et al.,* 2008).

Dynamic Body Acceleration (DBA) is the sum of acceleration in the three axes, and derivatives of DBA can be used as proxies of energy expenditure (Wilson *et al.,* 2020). Overall Dynamic Body Acceleration (ODBA) is one example and is derived from the sum of the absolute dynamic acceleration of the sway, heave and surge axes combined (Wilson *et al.,* 2006). The simplicity of its calculation makes ODBA a popular metric to calculate from acceleration data (Wilson *et al.,* 2020). As body movement correlates closely with metabolism, ODBA has become a key tool to identify fine-scale behaviours and quantify energy expenditure of the unobservable (Elliott *et al.,* 2013; Wilson *et al.,* 2020).

Ideally, ODBA would be calibrated in order to be used as a proxy for energy expenditure. This has historically been achieved under laboratory conditions by simultaneously recording ODBA and the rate of oxygen consumption (VO_2) (Halsey *et al.,* 2011). However it is often not possible to carry out respirometry or facilitate a full range of behaviours of interest from study species, making laboratory calibration logistically challenging (Green *et al.,* 2009). In the field, ODBA has been shown to correlate closely with the metabolic rate of seabirds in a range of behaviours, including flight (Ropert-Coudert *et al.,* 2006; Hicks *et al.,* 2017). Even those with challenging foraging strategies like plunge-diving gannet species within the sulidae family, where derivatives of DBA have been validated for energy expenditure and behaviour classification with interesting insights into their ecology (Ropert-Coudert *et al.,* 2009; Elliott *et al.,* 2013; Angel *et al.,* 2015).

The limitations associated with estimating energy expenditure from ODBA have been assessed by several reviews (Rutz and Hays 2009; Gleiss *et al.,* 2011; Halsey *et al.,* 2011; Wilson *et al.,* 2020; Garde *et al.,* 2022). Two such limitations are important to consider for its application to foraging energy expenditure. Firstly, ODBA is a measure of activity, therefore it does not include energy expended whilst not moving, such as growth, production of eggs, thermoregulation and digestion (Green *et al.,* 2009). During chick rearing, seabirds can spend over 50% of the day resting (Héneaux *et al.,* 2007), therefore a large proportion of their time remains unaccounted for when estimating energy expenditure with ODBA. Secondly, the accuracy of ODBA-derived energy expenditure in diving birds has been disputed (Halsey *et al.,* 2011). Although ODBA has been found to be a good predictor of daily energy expenditure, validated by doubly labelled water and the heart rate method across different locomotion methods, it has been suggested that different equations for its calculation are needed for diving and swimming (Elliott *et al.,* 2013; Hicks *et al.,* 2017). These issues may be due to the complexities surrounding the effect of diving on the body; issues of intermittent breathing, lack of stable physiological state and the potential effects of temperature on metabolism (Halsey *et al.,* 2011).

Therefore, the application and suitability of ODBA as a proxy for energy expenditure should be taken as just that, an estimate. However, ODBA is an insightful metric in its own right and is often used alongside other data to study the effort associated with foraging behaviour. For example, using tri-axial accelerometers and GPS devices, an increase in ODBA of foraging trips has been linked to poor breeding years and increased time spent foraging by Australasian gannets, *Morus serrator,* without an increase in distance travelled during foraging trip (Angel *et al.,* 2015). These results suggest that individuals are limited by the range they are able to be foraging in whilst breeding (Angel *et al.,* 2015).

Without converting ODBA to energy expenditure, the patterns of movement are ecologically viable as a suggestion of effort; this has been illustrated in a comparison of the frequency distributions of ODBA for one cycle of foraging and resting in two species of seabirds with different foraging strategies (Halsey *et al.,* 2011). The frequency distributions are remarkably similar despite Magellanic penguins, *Spheniscus magellanicus,* foraging for 43% of the time and imperial shags, *Leucacarbo atriceps,* for only 25%. This approach can be used to measure the mechanical power output of comparable activities, providing a measure of effort relevant to the time and conditions under which data were recorded (Halsey *et al.,* 2011).

Given that accelerometers measure movement, the placement of the device is crucial in the accuracy and type of data that can be collected (Garde *et al.,* 2022). This is particularly prudent in species with energetically costly modes of locomotion and foraging. Flight is a costly mode of transport for birds (Ropert-Coudert *et al.,* 2006) and the addition of a device to the body not only adds weight but can increase drag and change the centre of gravity (Taylor and Thomas 2002; Vandenabeele *et al.,* 2012; Vandenabeele *et al.,* 2014). For flight, devices should be placed as close to the centre of gravity as possible i.e. on the back (Taylor and Thomas 2002). However, for diving birds it is recommended that devices be placed on the tail of the bird to reduce drag when underwater (Bannasch *et al.,* 1994). For birds that both fly and dive, such as gannets this could create a conundrum if device attachment influences flight efficiency, diving efficiency or both (Vandenabeele *et al.,* 2014). The possible impacts of device placement must therefore be carefully considered in conjunction with the species' life history and length of deployment.

When paired with location data, accelerometers can provide information on an animal's spatial use of its environment (e.g. Baylis *et al.,* 2012). Quantifying these from free-living animals has vast ecological applications; from identifying key behaviours in focal aspects of life history to estimating energy expenditure of locomotive patterns, all without having to directly observe the subject (Wilmers *et al.,* 2015). Marine predators, like seabirds and seals, navigate a three-dimensional landscape to locate prey that is often patchy and widely distributed (Ashmole 1971; Staniland *et al.,* 2004; Pettex *et al.,* 2010). Consequently, their foraging strategies, and how they utilise time and energy when foraging, are complex with much still to be unravelled, particularly when considering the response of species to environmental change (Elliott *et al.,* 2008; Wilson *et al.,* 2012; Nourani *et al.,* 2022).

1.4 Seabirds

Seabirds are an appropriate group of marine predators in which to investigate foraging behaviour; nesting on land, and often in colonies, seabirds are accessible for both productivity monitoring and the attachment of bio-logging devices (Bernard *et al.,* 2021). They are good indicators of environmental conditions over extensive spatial and temporal scales and provide an excellent example of how fitness can be related to foraging effort (Piatt, Sydeman and Wiese, 2007; Einoder 2009). As central-place foragers, the energy from food resources must exceed the energy used commuting to and from foraging areas and provisioning young (Schmid-Hempel 1988). Most seabirds utilise both the aerial and marine environment to forage for characteristically patchy and widely distributed prey, so there is a trade-off between adaptations for flight and prey capture, with potential consequences for the allocation of time and energy to these behaviours (Wiens 1976; Taylor and Thomas, 2002; Green *et al.,* 2010).

Though a popular group of animals to study, seabirds remain the most threatened group of birds, with a 70% decrease in global population numbers since 1950 (BirdLife International 2018; Grémillet *et al.,* 2018). In an extensive review of all seabird species, Dias *et al.,* (2019) determined that the three major anthropogenic factors that threaten seabirds are invasive alien species, fisheries bycatch and climate change, and though many species are in decline, the extent of anthropogenic impact can be species-specific. For example, invasive alien species that predate on eggs, chicks and sometimes adults will have the biggest impact on species that nest in only a few sites globally, like the Fiji Petrel *Pseudobulweria macgillivrayi* (Rodríguez *et al.,* 2019). Historically, increased competition with the rise in commercial fisheries was predicted to be the primary cause of seabird declines, e.g. the sandeel crash in the North Sea in the 1980s and associated declines in the breeding success of sandeel specialists in Shetland, the black-legged kittiwake, *Rissa tridactyla*, (Hamer *et al.,* 1993; Furness and Tasker 2000). Commercial fisheries also cause direct mortality of seabirds as bycatch; this particularly affects surface feeders such as albatrosses and shearwaters and can cause acute mortality, responsible for up to 60% of population declines (Pardo *et al.,* 2017). Climate change is now thought to be the biggest threat to seabird populations via three main pathways (Mitchell *et al.,* 2020); Firstly, climate change causes more severe weather events which can make foraging and flight difficult, leading to mass mortality events as well as steady reductions in body condition and subsequent breeding success (Harrison *et al.,* 2011; Newell *et al.,* 2015; Morley *et al.,* 2016). Second, increased sea surface temperatures and changing currents shifts prey distributions and abundance, meaning some seabirds are having to travel further and less efficiently to forage (Grémillet *et al.,* 2018). Finally, increasing offshore renewable energy production which can cause direct mortality in hitting blades, tidal turbines and other equipment, or by displacement and barrier effects leading to increased time and energy spent avoiding previously used foraging areas (Doney *et al.,* 2012; Furness *et al.,* 2013; Carroll *et al.,* 2019; Dias *et al.,* 2019; GWEC 2019).

1.5 Study species – the northern gannet

Northern gannets, *Morus bassanus*, (hereafter gannets) are the largest seabird in the North Atlantic, and during March-October over half of the global population breeds at various island and mainland colonies around the UK (Nelson 2002; Murray *et al.,* 2015). Gannets lay one egg per season, which is not usually re-laid if lost during the 6 week incubation or 13 week chick-rearing period (Nelson 2002). Despite the restrictions placed upon foraging time and range by the presence of a chick, gannets can travel hundreds of kilometres on a single foraging trip whilst chick-rearing (Hamer *et al.,* 2000). During these trips, gannets forage over wide ranges for patches of prey in frontal areas, principally lipid-rich shoaling fish such as mackerel, *Scomber scombrus*, sprats, *Sprattus sprattu*s, and sandeels, primarily *Ammodytes marinus*, but also fishery discards (Lewis *et al.,* 2003; Hamer *et al.,* 2007; Votier *et al.,* 2013; Grecian *et al.,* 2018).

Gannets have an exceptional primary foraging strategy, plunge-diving from heights of up to 40 metres to depths of up to 11 metres, and additional depth of up to 20m when propelled by their wings (Ropert-Coudert *et al.,* 2009). Previous studies using bio-logging devices, such as time-depth recorders and GPS loggers, have found that within their broad foraging strategy, individuals can adopt different, repeated foraging strategies (Wakefield *et al.,* 2015). These are broadly defined as U-shaped dives (longer in duration, often involve pursuing prey with wingbeats), V-shaped dives (shorter in duration without prey pursuit) and foraging from fishery discards (dives from the surface or extremely shallow dives) (Votier *et al.,* 2010; Stauss *et al.,* 2012; Cleasby *et al.,* 2015). Despite being monomorphic in appearance, male and female gannets utilise different foraging ranges and strategies, with males exhibiting more U-shaped dives and fishery discard foraging, and females more V-shaped dives (Votier *et al.,* 2013; Cleasby *et al.,* 2015), making them an excellent model species for the investigation of sexual segregation. Variation in foraging behaviour and range extends beyond sex differences, with gannets exhibiting a high degree of individual specialisation defined by foraging site fidelity, but with behavioural plasticity in some individuals and instances, denoting the complexity of foraging-related decision making (Kamil 1983; Hamer *et al.,* 2001; Wakefield *et al.,* 2015).

Gannet foraging behaviour can also be highly colony specific (Lewis *et al.,* 2001; Wakefield *et al.,* 2013; Clark *et al.,* 2021). Colony-specific behaviour may assist in identifying the function and origin of behaviours. For example, gannets at the world's largest breeding colony, Bass Rock, Scotland, have the longest foraging trips in duration and distance, suggesting an effect of density dependence (Hamer *et al.,* 2000). Indeed, the extent of sex differences differs between colonies and years too, suggesting extensive flexibility and adaptability within this species (Lane *et al.*, 2020; Clark *et al.*, 2021; Bennison *et al.*, 2022).

Though experiencing population growth and consistent breeding success in their North Sea range, more worrying trends are apparent in their Southern range, with population declines and lower inter-annual adult survival (Mavor *et al.,* 2006; Murray *et al.,* 2015; Grémillet *et al.,* 2020). The importance of quantifying energetics in relation to foraging is vital to both understanding foraging ecology and developing sound marine management strategies. In order to do this effectively, the first step is to provide more detailed behavioural data to link at-sea activities to energy expenditure and a more accurate account of the time spent exhibiting foraging behaviours.

1.6 Study site – Bass Rock

The research presented in this thesis was produced from data collected at Bass Rock, Scotland between June - August in 2017-2019. A volcanic plug approximately 2km off the coast in the Firth of

Forth, SE Scotland (56°6 ‘N, 2°36 ‘W), Bass Rock is the largest breeding colony of gannets in the world with 75000 breeding pairs in 2014 (Murray *et al.,* 2015). The Bass Rock gannet colony experienced intense population growth between 2004 and 2014 with apparently occupied nests increasing by over 50% (Mavor *et al.,* 2006; Murray *et al.,* 2015). The population has likely continued to increase in the years since 2014, with pairs breeding in previously unoccupied sites each year I visited between 2017 and 2021.

The study of gannets on Bass Rock has been an instrumental source of information and investigation for long-term behavioural and movement ecology, with bio-logging studies and adult survival monitoring for over 20 years and observational studies spanning 60 years (Hamer *et al.,* 2000; Nelson 2002; Wakefield *et al.,* 2013; Lane *et al.,* 2019; Pollock *et al.,* 2021), making birds at this colony an exceptional study species for investigating how seabird foraging behaviour may respond to a changing marine environment. Birds breeding here forage in the North Sea, utilising persistent ocean fronts during foraging in the chick-rearing season (Grecian *et al.,* 2018). Large offshore windfarm developments (OWFs) are increasing around the coast of Britain, and the North Sea surrounding the Firth of Forth is no different. Recent developments mean construction is currently underway within gannet foraging ranges, with more sites planned and consented to (Pollock *et al.,* 2021).

1.7 Thesis aim and objectives

The over-arching aim of this thesis is to contribute to the study of seabirds towards informing conservation and management efforts in times of environmental change. The motivation of this research is rooted in the belief that effective management is best achieved on a foundation of sound and empirical science. Therefore, this thesis intends to address some of the key knowledge gaps in the foraging ecology of gannets by investigating the potential energy consequences and drivers for known patterns of broad-scale behaviour and movement. In particular, I explore the variation and patterns in energy expenditure and fine-scale behaviours, and assess what variation can be attributed to sex, individuality and the environment. Whilst the focal species of this thesis is the gannet, the application of the ecological mechanisms broached and methods examined here are applicable to assessments of other seabirds and central-place foragers.

This thesis consists of three objectives and accompanying data chapters, each building on the previous, to provide distinct and yet sometimes connected investigations into the causes and consequences of variation in the foraging ecology of breeding gannets. To address the main aim of this thesis I needed to develop robust proxies of energy expenditure for at-sea behaviours, measures of fine-scale behaviours and an indicator of foraging success. The methodology and rationale for these are explained and justified in chapter 2, and also contribute to meeting the objectives of chapters 3 and 4.

Thesis objectives:

Objective 1: Examine the role of sexual dimorphism in the prevalence of sexual segregation and determine whether there are the sex-specific energy and behavioural consequences.

Gannets, like many other species, exhibit sexual segregation. The drivers behind sexual segregation determine how changes to foraging habitats and resources will affect populations and understanding the energy and behavioural consequences of sexual segregation provides an improved basis for impact assessments and management. So, in this chapter I firstly examine the role of sexual dimorphism as a potential driver in sexual segregation of gannets. I find that sexual dimorphism is more likely to be a consequence of segregation rather than a cause. Sexes differed in a number of traits associated with foraging, but I found that the overall effort associated with foraging trips did not differ between the sexes, suggesting niche divergence as a driver of segregation, not competitive exclusion by one sex over the other. The novel sex differences found in this chapter suggest there could be sex-specific consequences to changes in the foraging environment, and that within sex-specific foraging behaviour, there are likely to be other influencing factors.

Objective 2: Quantify measures of individuality in the foraging trips of gannets and assess the energy and behavioural consequences of individual foraging site fidelity (IFSF) to determine potential drivers of individuality and future responses to environmental change.

Individuality is common in long-lived species but is not often considered when informing a species' conservation and management. Individuality in terms of an individual's capacity to be flexible or consistent in behaviour is an important consideration for adaptability to a quickly changing climate. Therefore, it is crucial to not only accurately quantify the traits individuals are consistent or flexible in, but also whether there are consequences to being consistent or flexible. In addition, the effect of sex is rarely considered as a factor of individuality, and the results of chapter 2 suggest this is worth investigating for gannets. In this chapter I firstly define how consistent individual gannets are in different aspects of foraging behaviour and energy expenditure and assess this for each sex. I then explore the potential consequences of IFSF on other aspects of foraging behaviour. I find that gannets are highly consistent in some aspects of foraging behaviour, but individuals and sexes vary greatly in consistency. Most importantly, my findings suggest IFSF is of greater benefit to females than males, and conversely, females may be more vulnerable to negative impacts on foraging from environmental change.

Objective 3: Investigate how wind speed affects the foraging behaviour and effort of chick-rearing male and female gannets.

With a rapidly changing global climate, it is important to gather evidence of how species may respond to more unfavourable conditions and what causes these responses. Flying animals are highly adapted to the windscape, managing a delicate energy balance between conditions, flight costs and energy gain. These have been vigorously researched for commuting flight, but the consequences of wind conditions on foraging flight and behaviour are less well known. In chapters 2 and 3 there were inter-annual differences and variation remaining unexplained by sex and individuality that suggest the environment plays an important role in the energy expenditure and success of foraging trips. I brought together the wind conditions at foraging locations and the metrics developed in this thesis to investigate how wind affects foraging behaviour. I provide evidence that gannets spend more time foraging in windier conditions because prey is more difficult to detect, either by reduced visibility on a choppy surface, or prey moving deeper in the water column. I find that, once again, sexes respond differently, and this is likely due to differences in prey species and foraging strategy. The results of this chapter highlight that within ‘normal’ wind speeds, the effort and success of foraging can be affected by the wind, and that these need to be considered for more extreme weather events.

This thesis concludes in chapter 5 with a discussion of the key findings, how they enhance our understanding of seabirds to inform management and highlights areas for further study. As alluded to already, it is likely there are interactions between the effects of sex, individuality and the environment on energy expenditure and fine-scale behaviours, so I also synthesise these within the chapter. This thesis argues that the effect of sex and individuality should be considered in most, if not all, aspects of management strategies going forward, due to the potential of sex and individual-specific fitness and survival consequences.

1.8 References

Amélineau F, Péron C, Lescroël A, Authier M, Provost P, Grémillet D (2014) Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology* 217(6): 876–885, doi: 10.1242/jeb.097915.

Andersson M (1981) Central Place Foraging in the Whinchat, *Saxicola Rubetra*. *Ecology* 62(3), 538–544, doi: 10.2307/1937718.

Angel LP, Barker S, Berlincourt M, Tew E, Warwick-Evans V, Arnould JPY (2015) Eating locally: Australasian gannets increase their foraging effort in a restricted range. *Biology Open* 4(10): 1298-1305, doi: 10.1242/bio.013250.

Ashmole NP (1963) The regulation of numbers of tropical oceanic birds. *Ibis* 103b. 458 – 473, doi: 10.1111/j.1474-919X.1963.tb06766.x.

Ashmole NP (1971) Seabird ecology and the marine environment. *Avian biology* 1: 224–286

Bannasch, R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *The Journal of Experimental Biology* 194(1): 83–96, doi: 10.1242/jeb.194.1.83.

Baylis AMM, Page B, McKenzie J, Goldworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats. *Marine Mammal Science* 28(2): 276–294, doi: 10.1111/j.1748-7692.2011.00487.x.

Bender CE, Herzing DL, Bjorklund DF (2009) Evidence of teaching in atlantic spotted dolphins (*Stenella frontalis*) by mother dolphins foraging in the presence of their calves. *Animal Cognition* 12: 43-53

Bennett RE, Rodewald AD, Rosenberg KV (2019) Overlooked sexual segregation of habitats exposes female migratory landbirds to threats. *Biological Conservation* 240: 108266.

Bennison A, Giménez J, Quinn JL, Green JA, Jessopp M (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *Royal Society Open Science* 9: 210520, doi: 10.1098/rsos.210520.

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

BirdLife International (2018) The IUCN Red List of Threatened Species. e.T22696668A132587992. https://www.iucnredlist.org

Boggs CL (1992) Resource Allocation: Exploring Connections between Foraging and Life History. *Functional Ecology* 6(5): 508–518, doi:10.2307/2390047.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* 161(1) 1–28, doi: 10.1086/343878.

Bowyer T, Pierce BM, Dufft LK, Haggstrom DA (2001) Sexual segregation in moose: effects of habitat manipulation. *ALCES* 37(1):109-122

Candolin U and Wong BBM (2015) Behavioural responses to a changing world: Mechanisms and consequences, Behavioural Responses to a Changing World: Mechanisms and Consequences. *Oxford University Press* doi: 10.1093/acprof:osobl/9780199602568.001.0001.

Carroll MJ, Wakefield ED, Scragg ES, Owen E, Pinder S, Bolton M, Waggitt JJ, Evans PGH (2019) Matches and Mismatches Between Seabird Distributions Estimated From At-Sea Surveys and Concurrent Individual-Level Tracking. *Frontiers in Ecology and Evolution* doi:10.3389/fevo.2019.00333

Chimienti M, Cornulier T, Owen E, Bolton M, Davies IM, Travis JMJ, Scott BE (2016) The use of an unsupervised learning approach for characterizing latent behaviors in accelerometer data. *Ecology and Evolution* 6(3): 727–741, doi: 10.1002/ece3.1914.

Clark B, Cox SL, Atkins K, Bearhop S, Bicknell AWJ, Bodey TW, Cleasby IR, Grecian WJ, Hamer KC, Loveday BR, Miller PI, Morgan G, Morgan L, Newton J, Patrick SC, Scales KL, Sherley RB, Vigfúsdóttir, Wakefield ED, Votier SC (2021) Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. *Marine Ecology Progress Series* 661: 1–16, doi: 10.3354/meps13636.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick S, Newton J, Votier S, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series* 518: 1–12, doi: 10.3354/meps11112.

Clutton-Brock TH, O'Rain MJ, Bortherton PN, Gaynor D, Kansky R, Griffin AS, Manser M (1999) Selfish Sentinels in Cooperative Mammals. *Science* 284(5420): 1640 – 1644, doi: 10.1126/science.284.5420.1640.

de Grissac S, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile alba- trosses and petrels. *Sci Rep* 6:26103

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Croxall JP (2019) Threats to seabirds: A global assessment. *Biological Conservation* 237, 525–537.

Doney SC, Ruckelshaus M, Emmett Duffy J, Barry JP, Chan F, English CA, Galindo HM, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2012) Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4: 11-37

Duckworth J, O'Brien S, Peterson IK, Petersen A, Benediktsson G, Johnson L, Lehikoinen P, Okill D, Väisäen R, Williams J, Williams S, Daunt F, Green JA (2021) Spatial and temporal variation in foraging of breeding red-throated divers. *Journal of Avian Biology* 52(6): 1–12, doi: 10.1111/jav.02702.

Einoder LD (2009) A review of the use of seabirds as indicators in fisheries and ecosystem management. *Fisheries Research* 95: 6-13, doi: 10.1016/j.fishres.2008.09.024

Elliott KH, Woo K, Gaston A, Benvenuti S, Dall'Antonia L, Davoren G (2008) Seabird foraging behaviour indicates prey type. *Mar. Ecol. Prog. Ser.* 354:289–303.

Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK (2009) Central-Place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk* 126(3):613–625, doi: 10.1525/auk.2009.08245

Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behaviour by a monomorphic seabird represents risk partitioning. *Behavioural Ecology* 21:1024–1032, doi:10.1093/beheco/arq076

Elliott KH, Le Vaillant M, Kato A, Speakman JR, Ropert-Coudert Y (2013) Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology letters* 9(1): 20120919, doi: 10.1098/rsbl.2012.0919.

Elliott KH, Le Vaillant M, Kato A, Gaston AJ, Ropert-Coudert Y, Hare JF, Speakman JR, Croll D (2014) Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *Journal of Animal Ecology* 83(1): 136–146, doi: 10.1111/1365-2656.12126.

Foote AD, Vijay N, Ávila-Arcos MC, Baird RW, Durban JW, Fumagalli M, Hanson MB, Korneliussen TS, Martin MD, Robertson KM (2016) Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nature communications* 7(1): 1-12

Furness RW and Tasker ML (2000) Seabird-fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *MEPS* 202: 253-264

Furness RW, Wade HM, Masden EA (2013) Assessing vulnerability of marine bird populations to offshore wind farms. *Journal of Environmental Management* 119, 56–66.

Garde B, Wilson RP, Fell A, Cole N, Tatyah V, Holton MD, Rose KAR, Metcalfe RS, Robotka H, Wikelski M, Tremblay F, Whelan S, Elliott KH, Shepard ELC (2022) Ecological inference using data from accelerometers needs careful protocols. *Methods in Ecology and Evolution* 13(4):813-825, doi: 10.1111/2041-210x.13804.

Gleiss AC, Wilson RP, Shepard ELC (2011) Making overall dynamic body acceleration work: On the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* 2(1): 23–33, doi: 10.1111/j.2041-210X.2010.00057.x.

Gowaty PA (1996) Field Studies of Parental Care in Birds: New Data Focus Questions on Variation among Females. *Advances in the Study of Behavior* 25: 477–531, doi: 10.1016/S0065-3454(08)60341-1.

Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Interface* 15(143): 20180084, doi: 10.1098/rsif.2018.0084.

Green JA, Halsey LG, Wilson RP, Frappell PB (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *The Journal of Experimental Biology* 212(5): 745–746, doi: 10.1242/jeb.030049.

Green JA, White CR, Bunce A, Frappell PB, Butler PJ (2010) Energetic consequences of plunge diving in gannets. *Endangered Species Research* 10(1): 269–279, doi: 10.3354/esr00223.

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

Grémillet D, Péron C, Lescroël A, Fort J, Patrick SC, Besnard A, Provost P (2020) No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. *Marine Biology* 167(12): 1–10, doi: 10.1007/s00227-020-03801-y.

Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE 6* e21336, doi:10.1371/journal.pone.0021336

GWEC (2019) Global Wind Report 2019. Global Wind Energy Council, Brussels, Belgium

Halsey LG, Shepard ELC, Wilson RP (2011) Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 158(3): 305–314, doi: 10.1016/j.cbpa.2010.09.002.

Hamer KC, Monaghan P, Uttley JD, Walton P, Burns MD (1993) The influence of food supply on the breeding ecology of kittiwakes in Shetland. *Ibis* 135:255–263

Hamer KC, Phillips RA, Wanless S, Harris MP, Wood AG (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: Evidence from satellite telemetry. *Marine Ecology Progress Series* 200: 257–264, doi: 10.3354/meps200257.

Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets Morus bassanus at two North Atlantic colonies: foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series*, 224, 283–290.

Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295–305, doi: 10.3354/meps338295.

Hammond TT, Springthorpe D, Walsh RE, Berg-Kirkpatrick T (2016) Using accelerometers to remotely and automatically characterize behavior in small animals. *Journal of Experimental Biology* 219(11), 1618–1624, doi:10.1242/jeb.136135

Harris S, Descamps S, Sneddon LU, Bertand P, Chastel O, Patrick SC (2020) Personality predicts foraging site fidelity and trip repeatability in a marine predator. *J Anim Ecol.* 89:68–79

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

Héneaux V, Bregnballe T, Lebreton JD (2007) Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *Journal of Avian Biology* 38200: 44–57, doi: 10.1111/j.2007.0908-8857.03712.x.

Hicks O, Burthe S, Daunt F, Butler A, Bishop C, Green JA (2017) Validating accelerometry estimates of energy expenditure across behaviours using heart rate data in a free-living seabird. *Journal of Experimental Biology* 220(10): 1875–1881, doi: 10.1242/jeb.152710.

Isaac JL (2005) Potential causes and life-history consequences of sexual size dimorphism in mammals. *Mammal Review* 35: 101-115, doi: 10.1111/j.1365-2907.2005.00045.x

Kacelnik A (1984) Central Place Foraging in Starlings (*Sturnus vulgaris*). Patch Residence Time. *Journal of Animal Ecology* 53(1): 283–299, doi:10.2307/4357

Kamil AC (1983) Optimal foraging theory and the psychology of learning. *American Zoologist* 23(2):

291–302.

Karasov WH (1992) Daily Energy Expenditure and the Cost of Activity in Mammals. *American Zoologist* 32(2): 238–248

Kie JG and Bowyer RT (1999) Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80:1004-1020.

Lack D (1968) Ecological Adaptations for Breeding in Birds. *Oikos* 19(1): 1-9, doi: 10.2307/3564725.

Lane JV, Spracklen DV, Hamer KC (2019) Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series* 628: 183–193, doi: 10.3354/meps13089.

Lane JV, Jeavons R, Deakins Z, Sherley RB, Pollock CJ, Wanless RJ, Hamer KC (2020) Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research* 162: 105196, doi: 10.1016/j.marenvres.2020.105196.

Largey N, Cook ASCP, Thaxter CB, McCluskie A, Stockke BG, Wilson B , Masden EA (2021) Methods to quantify avian airspace use in relation to wind energy development. *Ibis* 163(3): 747–764, doi: 10.1111/ibi.12913.

Lefebvre L (1995) Culturally-transmitted feeding behaviour in primates: Evidence for accelerating learning rates. *Primates* 36:227–239

Lescroël A, Lyver POB, Jongsomjit D, Veloz S, Dugger KM, Kappes P, Karl BJ, Whitehead AL, Pech R, Cole TL, Ballard G (2020) Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series* 636: 189–205, doi: 10.3354/meps13208.

Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412(6849): 816–819 doi: 10.1038/35090566.

Lewis S, Sherratt TN, Hamer KC, Harris MP, Wanless S (2003) Contrasting diet quality of northern gannets *Morus bassanus* at two colonies. *Ardea-Wageningen* 91(2): 167–176.

MacArthur RH and Pianka ER (1966) On Optimal Use of a Patchy Environment. *The American Naturalist* 100(916): 603–609 doi: 10.1086/282454.

Mavor RA, Parsons M, Heubeck M, Pickerell G, Schmitt S (2006) *Seabird numbers and breeding success in Britain and Ireland, 2001*. Joint Nature Conservation Committee Peterborough.

Meijer GAL, Westerterp KR, van Hulsel AMP, ten Hoor F (1992) Physical activity and energy expenditure in lean and obese adult human subjects. *European Journal of Applied Physiology and Occupational Physiology* 65(6): 525–528, doi: 10.1007/BF00602359.

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

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

Morris JRW (1973) Accelerometry—A technique for the measurement of human body movements. *Journal of Biomechanics* 6(6): 729–736, doi: 10.1016/0021-9290(73)90029-8.

Murray S, Harris MP, Wanless S (2015) The status of the gannet in Scotland in 2013-14. *Scottish Birds* 35(1): 3–18

Nelson B (2002) *The Atlantic Gannet*. Published by Fenix Books Limited, Norfolk

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

Newton I (1687) *Mathematical Principles of Natural Philosophy*

Nokes L, Fairclough JA, Mintowt-Czyz WJ, Mackie I, Williams J (1984) Vibration analysis of human tibia: The effect of soft tissue on the output from skin-mounted accelerometers. *Journal of Biomedical Engineering* 6(3): 223–226, doi: 10.1016/0141-5425(84)90107-9.

Nourani E, Safi K, de Grissac S, Anderson DJ, Cole NC, Fell A, Grémillet D, Lerma M, McKee JL, Pichegru L, Provost P, Rattenborg NC, Ryan PG, Santos CD, Schoombie S, Tatyah V, Weimerskirch H, Wikelski M, Shepard ELC (2022) Extreme tolerable winds for seabirds are determined by morphology. *BioRχiv*, doi: 10.1101/2022.05.02.490292.

O’Leary BC, Hoppit G, Townley A, Allen HL, McIntyre CJ, Roberts CM (2020) Options for managing human threats to high seas biodiversity. *Ocean Coast Manag.* 187:105-110

Orians GH & Pearson NE (1979) On the theory of central place foraging. Analyses of ecological systems: 154–177. Ohio, USA: Ohio State University Press.

Owen E, Wakefield E, Hollinrake P, Leitch A, Steel L & Bolton M (2019) Breeding together, feeding apart: sympatrically breeding seabirds forage in individually distinct locations. *Marine Ecology Progress Series*, 620: 173-183

Pardo D, Forcada J, Wood AG, Tuck GN, Ireland L, Pradel R, Croxall JP, Phillips RA (2017) Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. *Proceedings of the National Academy of Sciences,* 114(50):829 – 837, doi:10.1073/pnas.1618819114

Paredes R, Orben RA, Suryan RM, irons DB, Roby DD, Harding AMA, Young RC, Benoit-Bird K, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky A (2014) Foraging responses of black-legged kittiwakes to prolonged food-shortages around colonies on the Bering Sea shelf. *PLoS ONE* 9(3): e92520, doi: 10.1371/journal.pone.0092520.

Patrick SC and Weimerskirch H (2017) Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *Journal of Animal Ecology* 86(3): 674–682, doi: 10.1111/1365-2656.12636.

Peters WD and Grubb Jr. TC (1983) An Experimental Analysis of Sex-Specific Foraging in the Downy Woodpecker, *Picoides pubescens*. *Ecology* 64(6): 1437–1443, doi: 10.2307/1937498.

Pettex E, Bonadonna F, Enstipp M, Grémillet D (2010) Northern gannets anticipate the spatio-temporal occurrence of their prey. *J Exp Biol* 213:2365–2371. doi:10.1242/jeb.042267

Phillips RA, Silk JRD, Phalan B, Catry P, Croxall JP (2004) Seasonal sexual segregation in two Thalassarche albatross species: Competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 271(1545), 1283–1291, doi:10.1098/ rspb.2004.2718

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

Piatt JF, Sydeman WJ, Browman HI (2007) Seabirds as indicators of marine ecosystems. *MEPS* 352: 199 – 204, doi: 10.3354/meps07070

Pollock CJ, Lane JV, Buckingham L, Farthe S, Jeavons R, Furness RW, Hamer KC (2021) Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea. *Marine Environmental Research* 17: 105457, doi: 10.1016/j.marenvres.2021.105457.

Rees AF, Alfaro-Shigueto J, Barata PCR, Bjorndal KA, Bolten AB, Bourjea J, Broderick AC, Campbell LM, Cardona L, Carreras C, Casale P (2016) Are we working towards global research priorities for management and conservation of sea turtles? *Endangered species research.* 31: 337 – 382

Reynolds J (1996) Animal breeding systems. *Trends in ecology and evolution* 11(2) 68-72.

Rodríguez A *et al.,* (2019) Future directions in conservation research on petrels and shearwaters. *Frontiers in Marine Science,* 6: doi:10.3389/fmars.2019.00094

Ropert-Coudert Y, Grémillet D, Kato A, Ryan P G, Naito Y, Le Maho Y (2004) A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour,* 67(5): 985–992, doi:10.1016/j.anbehav.2003.09.010

Ropert-Coudert Y and Wilson R (2005) Trends and perspectives in animal- attached remote sensing. *Frontiers in Ecology and the Environment* 3(8): 437–444, doi: 10.1890/1540-9295(2005)003[0437:TAPIAR]2.0.CO;2.

Ropert-Coudert Y, Wilson RP, Grémillet D, Kato A, Lewis S, Ryan PG (2006) Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. *Marine Ecology Progress Series* 328: 275–284, doi: 10.3354/meps328275.

Ropert-Coudert Y, Daunt F, Kato A, Ryan PG, Lewis S, Kobayashi K, Mori Y, Grémillet D, Wanless S (2009) Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology*, 40(4): 380–387, doi: 10.1111/j.1600-048X.2008.04592.x.

Rutz C and Hays GC (2009) New frontiers in biologging science. *Biology Letters* 5(3): 289–292, doi: 10.1098/rsbl.2009.0089.

Sandell M (1989) Ecological Energetics, Optimal Body Size and Sexual Size Dimorphism: A Model Applied to the Stoat, *Mustela erminea L*. *Functional Ecology*, 3(3): 315–324, doi: 10.2307/2389372

Schmid-Hempel P and Wolf T (1998) Foraging effort and lifespan of workers in a social insect. *J animal ecology* 57: 509 – 521

Schofield G, Klaassen M, Papafitsoros K, Lilley MKS, Kateselidis KS, Hays GC (2020) Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. 101(7): e03027

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

Shaffer SA, Clatterbuck CA, Kelsey EC, Naiman AD, Young LC, VanderWErf EA, Warzybok P, Bradley R, Jahncke J, Bower GC (2014) As the egg turns: Monitoring egg attendance behavior in wild birds using novel data logging technology. *PLoS ONE* 9(6): e97898, doi: 10.1371/journal.pone.0097898.

Shepard ELC, Wilson RP, Quintana F, Gómex Laich A, Leibsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C, MacDonald DW (2008) Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* 10(1): 47–60, doi: 10.3354/esr00084.

Speakman JR and Hambly C (2016) Using doubly-labelled water to measure free-living energy expenditure: Some old things to remember and some new things to consider. *Comparative Biochemistry and Physiology Part A : Molecular and Integrative Physiology* 202: 3–9, doi: 10.1016/j.cbpa.2016.03.017.

Staniland IJ, Reid K, Boyd IL (2004) Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Mar Ecol Prog Ser* 275:263–274

Staniland IJ, Gales N, Warren NL, Robinson SL, Goldsworthy SD, Casper RM (2010) Geographical variation in the behaviour of a central place forager: Antarctic fur seals foraging in contrasting environments. Mar Biol 157, 2383–2396, doi: 10.1007/s00227-010-1503-8

Stauss C, Bearhop S, Bodey TW, Garthe S, Gunn C, Grecian WJ, Inger R, Knight ME, Newton J, Patrick SC, Phillips RA, Waggitt JJ, Votier SC (2012) Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. *Marine Ecology Progress Series* 457: 151–162, doi: 10.3354/meps09734.

Hubel T, Myatt J, Jordan N, Dewhirst O, McNutt J, Wilson A (2016) Energy cost and return for hunting in African wild dogs and cheetahs. *Nat Commun. 7*: 11034, doi: 10.1038/ncomms11034

Taylor GK and Thomas ALR (2002) Animal Flight Dynamics II. Longitudinal Stability in Flapping Flight. *Journal of Theoretical Biology* 214(3): 351–370, doi: 10.1006/jtbi.2001.2470.

Trivers R (1972) Parental Investment and Sexual Selection. in *Sexual Selection and the Descent of Man* Aldine Publication Corporation, Chicago.

Vandenabeele SP, Shepard EL, Grogan A, Wilson RP (2012) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology* 159(1): 1–14, doi: 10.1007/s00227-011-1784-6.

Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, Wilson RP (2014) Excess Baggage for Birds: Inappropriate Placement of Tags on Gannets Changes Flight Patterns. *PLoS ONE* 9(3): e92657, doi: 10.1371/journal.pone.0092657.

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* 47(2): 487–497, doi: 10.1111/j.1365-2664.2010.01790.x.

Votier SC, Bicknell A, Cox SL, Scales KL, Patrick SC (2013) A Bird's Eye View of Discard Reforms: Bird-`Borne Cameras Reveal Seabird/Fishery Interactions. *PLoS ONE* 8(3): 4–9, doi:

10.1371/journal.pone.0057376.

Wakefield, ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green JA, Grémillet D, Jackson AL, Jessopp MJ, Kane A, Langston RHW, Lescroël A, Murray S, Le Nuz M, Patrick SC, Péron C, Soanes LM, Wanless S, Votier SC, Hamer KC (2013) Space Partitioning Without Territoriality in Gannets. *Science* 341(6141): 68–70, doi: 10.1126/science.1236077.

Wakefield ED, Cleasby IA, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity-why some gannets don't change their spots. *Ecology* 96(11): 3058–3074, doi: 10.1890/14-1300.1.

Wearmouth VJ and Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals. Behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology*, 54:107–170

Wiens JA (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics*, 7: 81-120

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V (2015) The golden age of bio-logging : how animal- borne sensors are advancing the frontiers of ecology. *Ecology* 96: 1741–1753, doi: 10.1890/14-1401.1.

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology* 75(5): 1081–1090, doi: 10.1111/j.1365-2656.2006.01127.x.

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* 4: 123–137, doi: 10.3354/esr00064.

Wilson RP, Quintana F, Hobson VJ (2012) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Biol. Sci.* 279:975–980

Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R, Hopkins L, Marks N, Geraldi NR, Duarte CM, Scott R, Strano MS, Robotka H, Eizaguierra C, Fahlman A, Shepard ELC (2019) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* 89(1): 161–172, doi: 10.1111/1365-2656.13040.

Chapter 2 **Sexual dimorphism and segregation in northern gannets: cause or consequence?**

A male exhibiting sex-specific behaviour by bringing his partner nesting material

2.1 Abstract

Like many other species, northern gannets, *Morus bassanus*, show sexual segregation. Gannets are monomorphic in appearance but sexually dimorphic in mass, with females around 9% heavier than males, leading to the suggestion that sexual dimorphism could be a driver of sexual segregation. Combining GPS, accelerometry and biometric data for chick-rearing gannets on Bass Rock in 2017 – 2019, I examined the associations between sexual dimorphism and differences between the sexes in foraging locations, fine-scale movements and behaviour and energy expenditure. I found that wing morphology did not differ between the sexes, and therefore females had significantly higher wing loadings than males. Subsequently, females made significantly longer trips than males, used flapping flight as opposed to gliding for a greater proportion of time than males during both outbound and inbound travel, with a significantly higher body amplitude than males during wingbeats, flew significantly faster than males on the inbound journey and had significantly higher ODBA per minute than males during outbound and inbound travel. In contrast, the rate of take-offs from the sea surface while actively foraging was significantly higher among males than females, and several lines of evidence suggested that higher take-off rates were associated with more successful foraging except in some cases at the highest take-off rates shown by males. Within each sex, different facets of the movements and behaviour of birds at-sea were significantly related to body mass. However, the observed relationships were not consistent with the notion that differences between sexes were driven by sexual dimorphism. I suggest that sexual dimorphism in body mass persists in spite of its effect on energy expenditure during flight, because heavier females gain an advantage in attaining greater depths during plunge dives. Hence I argue that sexual dimorphism in gannets is a consequence of sexual segregation and not a cause. The findings of this study emphasise the need to consider potential ecological consequences of sexual segregation during species management.

2.2 Introduction

In many bird species, both parents contribute to raising offspring (Lack 1968; Bennett and Owens 2002). This biparental care is often accompanied by differences between sexes in foraging niche, which arise in several ways including separation in space, time, habitat use and diet (Patrick and Weimerskirch 2014; Elliott *et al.,* 2010; Phillips *et al.,* 2004; Clark *et al.,* 2021). Sexual segregation is often associated with differences in physical traits, for example resulting in social dominance and competitive exclusion by the larger sex (often males, e.g. Peters and Grubb 1983). However, segregation is not exclusively explained by physical traits, and also occurs in species with little or no sexual dimorphism, in which the mechanisms for sex-specific foraging are less clear. Sex-specific foraging may reduce intraspecific competition or be a function of differences in birds' nutritional requirements, and hence likely play a key role in structuring species' distributions (Elliott *et al.,* 2010). Moreover, the extent of sexual segregation can vary unpredictably over time, making the drivers and function of sexual segregation more difficult to define (Cleasby *et al.,* 2015; Clark *et al.,* 2021).

The drivers and extent of sexual segregation are important to understand as anthropogenic factors are increasingly being shown to impact sexes differently, leading to demographic consequences and a call for sex-biased demography to be more frequently considered in conservation (Bugoni *et al.,* 2012; Gownaris and Boersma 2019). For example, an investigation into the decline of the megellanic penguin*, Spheniscus magellanicus,* found there to be sex bias in adults and juveniles with disproportionally higher female mortality from starvation during years of unfavourable conditions, and this was the greatest contributor to population declines, thus signifying a reduction in fisheries and changes in spatial management to slow the decline (Gownaris and Boersma 2019). Hence there is a need for further study of such species, by quantifying the extent of sexual segregation to define the needs of each sex from its environment, but also determining the consequences and therefore drivers of sexual segregation. For instance, by examining sex differences in finer-scale movements to assess the links between sexual segregation and individuals' time-activity budgets and energy expenditure.

Energy expenditure is a key ecological component linking animal behaviour, physiology and individual fitness (Wilson *et al.,* 2020). Energy balance is determined by the difference between energy expenditure and food acquisition, making the study of energy expenditure in far-ranging foraging animals particularly important (Shepard *et al.,* 2013). Yet the energy expenditure associated with foraging has rarely been studied in large and free-ranging animals, primarily because of the difficulties of simultaneously measuring energy expenditure and movements at sufficiently high spatial and temporal resolution, especially in flying animals (Wilson *et al.,* 2020). Some methods have been developed, for instance the doubly-labelled water method allows calculation of field metabolic rates but not over fine time-scales, while equipping animals with heart-rate loggers can be invasive where it requires surgical insertion (Speakman and Hambly 2016; Green *et al.,* 2009). An alternative is to equip animals with high resolution tri-axial accelerometers, enabling calculation of energy expenditure from dynamic body acceleration when the animal is active (Wilson *et al.,* 2006). The overall dynamic body acceleration (ODBA) and vectorial dynamic body acceleration (VeDBA) both correlate closely with field metabolic rate in a range of behaviours, including flight (Ropert-Coudert *et al.,* 2006; Hicks *et al.,* 2017; Wilson *et al.,* 2020). These two measures have each been validated for energy expenditure and behavioural classification in a number of bird species, providing important insights into their ecology (e.g. Shepard *et al.,* 2008; Elliott *et al.,* 2013; Pelletier *et al.,* 2020).

Seabirds are a useful model for studying sexual segregation, exhibiting biparental care under the constraints of central-place foraging, and are of high conservation interest (Grémillet *et al.,* 2018). Northern gannets, *Morus bassanus,* (hereafter gannets) are neritic seabirds that show slight sexual dimorphism; males and females are similar in appearance and overall body size, however females are ~9% heavier than males on average (Nelson 2002; Clark *et al.,* 2021; this study). This greater body mass could result in females having greater wing loading than males, with consequences for flight dynamics and energy costs, however to my knowledge this theory has not previously been examined. During chick-rearing, females have been shown to travel further and for longer than males on foraging trips, favouring stratified offshore waters over mixed coastal waters, flying higher than males during commuting and active foraging and diving to greater depths than males, culminating in consistent sex differences in isotopic niche (Lewis *et al.,* 2002; Cleasby *et al.,* 2015b; Lane *et al.,* 2020; Clark *et al.,* 2021). However, foraging behaviour also varies interannually, with sex differences discernible in some years but not in others (Clark *et al.,* 2021).

Despite this extensive body of research, the drivers of sexual segregation in gannets remain unclear, with potential drivers including sex-specific reproductive roles and requirements, competitive exclusion by one sex, and reducing intra-specific competition by niche divergence (Stauss *et al.,* 2012; Cleasby *et al.,* 2015; Giménez *et al.,* 2021). These drivers are likely to have different sex-specific energy consequences. There are few previous studies that have considered sex as a factor affecting energy expenditure in gannets (Amélineau *et al.,* 2014; Bennison *et al.,* 2022). Neither study identified a large difference between sexes in energy expenditure during foraging, although Bennison *et al.,* (2022) estimated that females had higher daily energy requirements than males, but a lower minimum dive success rate to meet these requirements.

Here, I aim to (a) examine the role of sexual dimorphism in the prevalence of sex segregation and (b) determine whether there are sex-specific energy and behavioural consequences of segregation. To do this, I first provide a baseline context of the sex differences in gannets at Bass Rock between 2017-2019 to compare to other years and colonies, using GPS data over a period of three years to examine sex differences in trip durations, distributions and time-activity budgets at-sea. I then combine bird biometrics and accelerometry data to address the first aim, whether or not the recorded sexual dimorphism in body mass affects wing-loading and flight characteristics of birds. To address the second part of the aim, I provide insight into sex differences in fine-scale foraging behaviour, with a focus on take-offs as the most energetically expensive activity during trips (Green *et al.,* 2010), using accelerometry data to identify take-offs from the sea surface during foraging trips. I then determine whether energy expenditure of trips and behaviours differs between the sexes and to shed light on the driver of sex segregation by quantifying the sex-specific energy expenditure of at-sea behaviours during foraging trips, using accelerometry data to calculate ODBA as a proxy for energy expenditure. By investigating these aims, I identify novel and pertinent information about gannet sexual segregation to better inform conservation management efforts and highlight the importance of this application to other seabirds.

2.3 Methods

2.3.1 Data collection

Movement data were obtained from June to August in 2017-19 at Bass Rock, Scotland (56^o 6' N, 2^o 36' W). In total, 35 male and 43 female chick-rearing gannets were captured at their nest-sites using a wire noose attached to a 4-6m telescopic pole, then restrained with a custom-made jacket. Where possible, birds were caught when changing over with their partner returning from the sea, to ensure chicks were not left unattended and birds did not regurgitate food during handling. Adults were caught when chicks were 2-8 weeks old and were therefore at a similar stage of the breeding cycle each year. All birds were weighed using a spring balance (± 10g) and were fitted with two leg rings: a British Trust for Ornithology numbered metal ring and a plastic ring with a unique alphanumeric code for individual identification at the study site. To test for a difference in wing area between sexes, following Wakefield *et al.,* (2019) I measured wing semi-span (from the spine to the wing tip, ± 1mm) of a sample of 49 birds (20 males and 29 females) and in each case photographed one wing, laid flat and fully extended on a board marked with a 5cm grid. I then geo-referenced the wing images in QGIS Desktop 2.14.3, digitised each outline (from root chord to wing tip) and calculated the partial wing area. I next calculated the total wing area as twice the partial wing area, plus the intervening body section (Pennycuick 2008). Some of the data for wing area were collected previously (2016) within the Bass Rock colony and used in addition to the data collected in 2017 and 2018 to increase the sample size for more robust analysis.

Two data loggers were attached to each captured bird using Tesa® tape (Beiersdorf AG, Hamburg, Germany). A calibrated accelerometer (X6 or HAM mini accelerometer, Gulf Coast Concepts LLC, Waveland, USA) weighing 16g and recording at 25Hz, was taped to feathers centrally on the lower back, close to the bird's centre of gravity (Taylor and Thomas 2002). In addition, a Global Positioning System (GPS) logger (i-gotU GPS Travel Logger GT-600, Mobile Action Technology) weighing 36g and recording at 1-minute intervals was taped to the dorsal side of the central two-three tail feathers. Birds were then released towards their nest-site and usually returned to it immediately. On a sub-sample of birds (seven individuals in 2019) a time-depth recorder weighing 2.7g (TDRs: G5, CEFAS Technology, Lowestoft, UK) was taped to the tail on the underside of the GPS logger, recording at 1-minute intervals and at 12Hz when submerged below 1m. Between 4-10 days after deployment, birds were recaptured using the same method, the loggers removed, and the birds weighed before release. In all cases, the handling time of birds was less than 20 minutes for logger deployment, and less than 10 minutes for logger retrieval. The combined weight of the data loggers was <2% of body mass, which was considered sufficiently small to minimise any adverse effects (Phillips *et al.,* 2003; Bodey *et al.,* 2018). Multiple loggers attached to the tails of gannets have been shown to change the angle of the tail during flight and increase the number of flap-glide cycles (Vandenabeele *et al.,* 2014). However, these effects were much lower for birds with individual loggers attached to the back and tail, as I did, and had no discernible impact on ODBA.

2.3.2 Trip metrics and at sea behaviours

Using the GPS data, I derived duration (hours), total distance travelled (km) and at-sea behaviours for each foraging trip using the 'adehabitatLT' package in R version 1.3.959 (Calenge 2006; R Team 2015). At-sea behaviours were defined as three broad categories: foraging, travelling, and resting. These were classified using the tortuosity (variation in turning angles between consecutive GPS locations) and step lengths (distance between consecutive GPS positions) to differentiate behaviours. Foraging was defined by high tortuosity and short step lengths, travelling by low tortuosity and long step lengths, and resting by low tortuosity and short step lengths (Wakefield *et al.,* 2013; Grecian *et al.,* 2015). These behaviour classifications have been validated using time-depth recorders (TDRs), with 99% of GPS positions defined as foraging locations occurring within 10 minutes of TDR detected dive occurrences (Wakefield *et al.,* 2013). Travelling was separated into outbound and inbound sections, defined as the GPS locations before and after the furthest recorded distance from the colony.

2.3.3 Spatial segregation of foraging areas

I used the utilisation distribution (UD) of GPS-defined foraging locations, estimated with kernel density analysis, to identify key foraging areas of individual birds. Locations identified as travelling or resting were therefore excluded from these estimations, as were locations during hours of darkness, as gannets do not forage at night (Hamer *et al.,* 2000; Furness *et al.,* 2018). Using the 'adehabitatHR' R package (Calenge 2006), I derived core foraging areas (50% UDs) and broad foraging areas (95% UDs) over a 1km^2 grid with a smoothing parameter of 10km. I then estimated the extent of within-year overlap between male and female UDs using Bhattacharyya's affinity (BA; Bhattacharyya 1943), which ranges from 0 (no overlap) to 1 (complete overlap). Following Cleasby *et al.,* (2015), I used a randomization procedure to test the null hypothesis that there was no difference in the spatial distribution of males and females each year. I created 1000 randomisations of the data by randomly assigning the sex of each bird's trip each year, following the same sex ratio as the observed data (0.3, 0.5 and 0.4 male in 2017-2019, respectively). P-values were calculated as the proportion of random overlaps that were smaller than the observed overlap (Cleasby *et al.,* 2015).

2.3.4 Fine-scale flight behaviour

To investigate differences in the flight characteristics of males and females, I sampled 10 minutes of continuous flight from the outbound and inbound segments of each foraging trip, when birds were >10km from the colony, therefore excluding ~15 minutes from the start and end of each trip. Birds were thus within similar air space and at the same stage of each trip, with a small payload (outbound after an extended period at the nest-site) or a large payload (inbound, presumably carrying food back to the chick). My rationale here was to attempt to reduce other variability that may have influenced flight characteristics, to compare the fundamental flight characteristics of each sex.

I analysed each ten-minute sample of accelerometry data during flight using IGOR Pro (version 8, Wavemetrics Inc., Portland, USA) to identify periods of flapping and gliding (see example of flap-glide cycle in Figure 2.1), and to measure wingbeat frequency (Hz) and body amplitude (m). Following established methods by Roberts and Gabaldón (2008), flapping flight was identified by bandpass filtering and then smoothing dynamic body acceleration to create an envelope from which a threshold value could be used to identify the start and end of each bout of flapping (here 0.4g; Figure 2.1). Wingbeat frequency (WBF) was then determined for each flight sample using a Fast Fourier Transform (FFT) of the X-dynamic acceleration, with WBF taken as the frequency where the magnitude of the FFT was highest (following Spivey and Bishop 2013). Body amplitude is the amount the body is displaced per wingbeat (m) and was derived from the dorso-ventral accelerations of the body. I also calculated the flight speed (m s^{-1}) for each flight sample from the corresponding GPS data as the average speed between the step lengths of each sample. Fine-scale flight behaviours were validated by firstly checking the corresponding GPS data derived behaviour classification (travelling in this case) and close inspection of the visual representation of accelerometry waves. Given the irrefutable nature of gravity, the angle of the accelerometer on the body is one reliable indicator of whether a bird is in flight and the changes in g for each axes correspond to the dedicated behaviour.

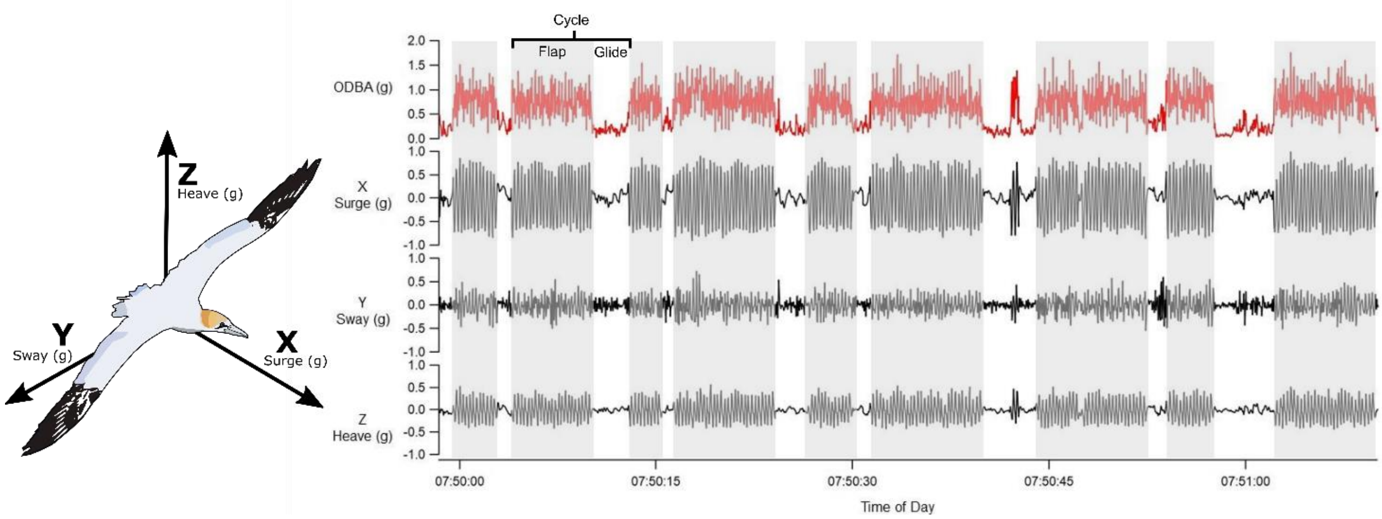


Figure 2.1. An example of X (surge), Y (sway), Z (heave) and overall dynamic body acceleration (ODBA) recorded during commuting flight of a chick-rearing northern gannet (*Morus bassanus*), consisting of flapping and gliding flight.

2.3.5 Proxies of energy expenditure

Accelerometry data were processed in R version 1.3.959 (R Team 2015) and IGOR Pro (version 8, Wavemetrics Inc., Portland, USA) to provide a proxy of energy expenditure during each foraging trip. The acceleration data for each trip were defined by the start and end time calculated from the GPS locations. Static acceleration was calculated for each of the axes by applying a two-band low-pass filter to the acceleration data for the corresponding axis (Shepard *et al.,* 2008). These were then subtracted from the total acceleration (comprising both static acceleration due to gravity and dynamic acceleration due to body movement) in each axis to give dynamic body acceleration (DBA) for surge, sway and heave. ODBA, the key metric in representing movement-based energy expenditure (Wilson *et al.,* 2006) was then calculated by summing the DBA of the three axes.

I chose to use the DBA derivative ODBA instead of VeDBA. ODBA has been shown to be slightly more sensitive than VeDBA to movement caused by logger attachment and placement but is a slightly better predictor of $\dot{V}O_2$ when attached centrally on the body (Qasem *et al.,* 2012; Wilson *et al.,* 2020). In this study, the sensitivity of ODBA to logger attachment was addressed by taping accelerometers at a precise point on the mid-lower back of the bird to minimise differences in position and attachment durability (Garde *et al.,* 2022). Accelerometers that became loose during deployment, due to apparent moulting of back feathers, were noted in the field and removed from the dataset (n=3).

To provide a measure of energy expenditure for at-sea behaviours a running total of ODBA throughout a foraging trip was calculated and interpolated with the GPS data at one-minute intervals, providing

ODBA for each minute of the trip and assigned behavioural category (foraging, travelling and resting at sea). Each trip's data were manually checked for incorrect behavioural categorisations because of time drift between the accelerometry data and GPS data and the maximum difference was found to be 30 seconds by the end of the deployment period. Given the broad behavioural categories and average time spent exhibiting each behaviour being > 3 hours, this error rate was deemed appropriate.

To give an average rate of energy expenditure during outbound travel, foraging and inbound travel, the ODBA of each activity was divided by the time spent in that activity. Resting was not included as a behaviour, as ODBA can overestimate the energy expenditure of resting at-sea, due to the movement of the bird caused by sea-state (Gómez-Laich *et al.,* 2015; Wilson *et al.,* 2020). Therefore, after the ODBA during resting was removed, the summation of the running total provided the ODBA of activity (travelling and foraging) per trip. I then calculated the average ODBA of activity (travelling and foraging) per minute of each trip by dividing by the trip duration (minutes) in each case. This trip-level metric combined the behaviour associated with flight and foraging behaviour into a single measure of energy expenditure in relation to how long the bird spent at sea.

2.3.6 Take-offs from the surface

After processing the accelerometry data as described above, I used thresholds of changes in dynamic acceleration (g) in the heave axis, average body angle and variance of body angle to identify take-offs from the sea surface. The term body angle here refers to the angle of the accelerometer on the body, not the actual angle of the body. Accelerometry data were bandpass filtered and smoothed to create an envelope from which a threshold value would identify a shift in the dynamic X axis as a take-off. I calculated this threshold by manual inspection of 4 foraging trips (>100 take-offs) from two males, two females and the two generations of accelerometer, with accompanying dive data from TDRs. To ensure the following behavioural classifications were correct, I manually inspected the time points at which the TDRs had been triggered to record at maximum resolution (12Hz) – when submerged below 1m i.e. during a dive. A threshold of 0.5 ensured no take-offs were missed throughout a foraging trip, but also included other behaviours: dives, activity underwater and flight behaviour (sudden tilts upwards and downwards) (Figure S2.1). At the point a 'take-off' was identified, I calculated three measures of body angle that distinguished take-offs from other behaviours (Table S2.1). Behaviour that met all four thresholds were categorised as a take-off and resulted in an error rate of 0.89% for my data. I divided the number of take-offs per trip by the time spent foraging to give the take-off rate h^{-1} foraging (hereafter take-off rate).

I chose take-offs from the surface during foraging trips as the foraging behaviour to quantify to explore fine-scale foraging sex differences because although both dives and take-offs require extensive movement that can be detected through accelerometry (see Figure S2.1 as an example), the relationship between take-offs and energy expenditure is clear and well documented; taking off from the surface has been shown to be the most energetically costly behaviour during foraging for Australasian gannets, *Morus serrator,* and it appears likely this would follow for northern gannets too (Green *et al.,* 2010). Therefore, when exploring ODBA and fine-scale foraging behaviours, take-offs are likely to be a better indicator of the energetic consequences of differences in foraging behaviour.

2.3.7 Statistical analyses

To determine the extent of sexual segregation during 2017-2019 at the Bass Rock colony and whether there were previously untested fine-scale behavioural and energetic differences between the sexes, key foraging trip metrics (summarised in Table S2.2) were fitted as the response variable in linear mixed-effects models (LMMs) with restricted maximum-likelihood (REML) in the R package 'nlme' (Pinheiro et al. 2018). Thus, sex and year were included as fixed effects with an interaction between them. Year was included to account for any differences between the three breeding seasons of data collection, and a sex:year interaction was included to identify whether sex differences were consistent between years. LMMs were chosen due to the capacity to include random effects to account for the effect of repeated measures, that being multiple trips per bird within a year (1-5 trips). Thus, bird identity was included as a random factor. The data met the assumptions of LMMs; variables were normally distributed or were transformable to normality (sqrt-root transformations of trip duration, distance travelled, proportion of time spent foraging, travelling and resting and travelling ODBA per minute) leading to normally distributed model residuals, residuals had statistically equal variance and the factors were independent of one another. I modelled the responses variables associated flight characteristics and ODBA separately for outbound and inbound flight due to the expected difference in payload as a result of birds returning with prey during inbound flight and likely differences in wind conditions and direction at the beginning and end of each trip (Grémillet *et al.,* 2006; Lane *et al.,* 2019).

In addition to determining sex differences in key foraging trips, I wanted to explore how variation in energy expenditure might be related to the time-activity budgets and take-off rates for each sex. For these analyses males and females were modelled separately as sexes may have separate ecological consequences of their differences, and mass was included as an explanatory variable to account for within-sex differences in mass in relation to energy expenditure (Angel *et al.,* 2015). I two built more extensive LMMs with response variables of ODBA (foraging ODBA (g) per minute and active ODBA (g) per minute). Specifically, I wanted to investigate whether take-off rate affects the foraging ODBA of males and females differently (explanatory variables: mass and take-off rate) and explore what aspects of behaviour (explanatory variables: proportion of time spent foraging and travelling, take-off rate and mass) have the greatest effect on overall active ODBA. Again, year was included as a fixed effect to include potential inter-annual variation, and bird identity as a random effect. Models of best-fit were selected with Akaike's Information Criterion (AIC) using the dredge function in the MumIN package (Bartón 2009). The top model was determined by assessing the models with the lowest value of Akaike's information criterion corrected for sample sizes (AICc), ΔAICc >2 from the next ranked model and highest weight of raw AICc (Burnham and Anderson 2002).

When establishing whether take-off rate was a measure of foraging success, I wanted to see whether take-off rate explained any of the variation in key aspects of foraging behaviour. For example, if a high take-off rate was positively correlated with time spent foraging, that might indicate a low take-off rate is associated with successful foraging. Some relationships appeared non-linear upon visual inspection. I used GLMMs and model selection to determine if a non-linear relationship was a better fit for the data as GLMMs have the capacity to use non-normal data, whilst also accounting for the random effect of bird identity. I used a polynomial regression within the GLMM which included explanatory linear and non-linear terms (e.g. variable ^2, variable ^3) and then followed the model selection process explained above to determine if a non-linear relationship was a better fit than a linear one.

To investigate the fundamental relationship between mass and flight (Taylor and Thomas 2002), I wanted to determine whether or not any sex differences in trip metrics and flight characteristics were a function of body mass. There are some limitations to achieving this in this study's data. Due to the constraints of fieldwork, mass could only be measured at the beginning and end of deployment, and therefore not also between each foraging trip. In addition, the payload on the outbound and inbound stages of travel is assumed to be different, with birds likely 5-10% heavier carrying food for chicks on the inbound journey (Grémillet *et al.,* 2006; Machovsky-Capuska *et al.,* 2016). To account for these limitations, I used only the first trip and outbound section of flight for each bird, which had the most reliable measure of body mass. Linear models (LMs) were used to investigate the sex-specific relationships between body mass and trip duration, distance travelled, take-off rate and flight characteristics because I did not need to account for the effect of repeated measures in these analyses and so did not need a model with capacity for random effects.

2.4 Results

Females were significantly heavier than males (3103 ± 266g and 2808 ± 250g, respectively; $F_{63} = 20.7$, $P < 0.001$). Wing area however did not significantly differ between sexes (Table 2.1; $F_{46} = 0.26$, $P > 0.05$) and as a result females had significantly higher wing loading than males (119.3 ± 9.9Nm^{-2} and 112.7 ± 9.3 Nm^{-2}, respectively; $F_{46} = 5.42$, $P = 0.02$).

2.4.1 Spatial distributions of males and females

GPS data were obtained for 186 foraging trips from 28 males and 36 females, of which 110 foraging trips from 23 males and 22 females also had accelerometry data. Gannets covered a large area of ocean during foraging trips (~90,000 km^2), travelling mainly northeast or southeast from the colony and rarely in other directions (Figure 2.2). Spatial segregation between sexes was observed in 2017 and 2019 but not in 2018; in 2017, there was a significant difference in the broad foraging areas of males and females (Figure 2.2; 95% UD; BA = 0.623, $P = 0.025$) and in 2019, males and females occupied significantly different broad and core foraging areas (95% UD, BA = 0.609, $P = 0.004$; 50% UD, BA = 0.194, $P = 0.006$).

Foraging trips by females were of longer duration than those by males (30 ± 15 hours and 26 ± 14 hours, respectively; $\chi^2{}_1 = 5.57$, $P = 0.02$) and females travelled significantly greater distances than males during trips (634 ± 326 km and 487 ± 293 km, respectively; $\chi^2{}_1 = 10.75$, $P = 0.001$). Birds also travelled significantly shorter distances in 2019 than in 2017 (Table S2.2; Tukey test; $F_{60} = 2.70$, $P = 0.02$) or 2018 ($F_{60} = 3.13$, $P = 0.004$).

2.4.2 Time-activity budgets at sea

Females and males did not differ in their time-activity budgets at sea, with both spending on average 30% of a trip travelling, 54% resting on the sea surface and 16% foraging (Table 2.2; S2.3). Birds of both sexes spent significantly less time resting in 2017 than in 2018 (Table S2.2; Tukey test; $F_{120} = -2.60$, $P = 0.03$) or 2019 ($F_{60} = -3.78$, $P < 0.001$) and conversely spent significantly more time travelling in 2017 than in 2019 ($F_{60} = 3.71$, $P < 0.001$). There were no inter-annual differences in time spent foraging (Table S2.3).

2.4.3 Fine-scale flight behaviour and energy expenditure of outbound and inbound travel

Females utilised flapping flight as opposed to gliding for a greater proportion of time than males during both outbound and inbound travel (Table 2.2; $\chi^2{}_1 = 6.49$, $P = 0.01$ and $\chi^2{}_1 = 11.30$, $P < 0.001$, respectively). In addition, birds flapped significantly more on the outbound journey in 2018 than in 2017 (Table S2.2; Tukey test; $F_{38} = -0.07$, $P = 0.04$) or 2019 ($F_{38} = 0.08$, $P = 0.04$). Males and females did not differ in speed of travel during outbound flight, but females flew significantly faster than males on the inbound journey (Table 2.2; $\chi^2_1 = 4.44$, $P = 0.03$). Wingbeat frequency did not differ between sexes (Table S2.3), but the body amplitude of females was significantly higher than that of males during both outbound and inbound travel (Table 2.2; $\chi^2_1 = 6.33$, $P = 0.01$ and $\chi^2_1 = 4.08$, $P = 0.03$, respectively). The inbound body amplitude of both sexes was also significantly higher in 2018 than in 2019 (Tukey test; $F_{38} = 0.003$, $P = 0.02$). Over the course of a foraging trip, females had significantly higher ODBA per minute than males during outbound and inbound travel (Table 2.2; $\chi^2_1 = 7.45$, $P = 0.006$ and $\chi^2_1 = 8.90$, $P = 0.003$, respectively).

2.4.4 Take-offs and foraging behaviour

The rate of take-offs from the sea surface while actively foraging was significantly higher among males than females ($\chi^2_1 = 6.66$, $P = 0.01$; 22.5 ± 11.2 h^{-1} and 17 ± 6.4 h^{-1}, respectively) and take-off rate was significantly higher in 2019 than 2017 for all birds (Figure 2.3a; $F_{38} = 0.87$, $P = 0.01$). For females the higher the mean take-off rate during foraging bouts the lower the proportion of each trip spent foraging (Figure 2.3b; $\chi^2_1 = 23.82$, $P < 0.001$) and the absolute time spent foraging per trip (Figure 2.3d; $\chi^2_1 = 19.78$, $P < 0.001$), and the higher the proportion of each trip spent resting on the sea surface (Figure 2.3f; $\chi^2_1 = 5.17$, $P = 0.02$). For males the higher the mean take off rate while foraging, the lower the trip duration, distance travelled and absolute time spent foraging per trip (Figure 2.3; $\chi^2_1 = 10.10$, $P = 0.001$, $\chi^2_1 = 11.88$, $P < 0.001$, $\chi^2_1 = 14.26$, $P < 0.001$, respectively). In addition for males, there was a convex quadratic relationship between take-off rate and the proportion of each trip spent foraging (Figure 2.3e; $F_1 = 49.06$, $P < 0.001$; Table S2.4) and a concave quadratic relationship with the proportion of each trip spent resting on the sea surface (Figure 2.3f; $F_1 = 11.95$, $P = 0.001$). These data all suggest that higher take-off rates were associated with more successful foraging except in some cases at the highest take-off rates shown by males. ODBA per minute spent foraging was significantly higher in females than males (Table 2; $\chi^2_1 = 5.10$, $P = 0.003$), and take-off rate was a significant factor explaining foraging ODBA in males ($\chi^2_1 = 16.85$, $P < 0.001$) but was not included in the top model selection for females, where only bird identity significantly accounted for variation in ODBA per minute spent foraging (Table S2.5).

2.4.5 Trip energy expenditure

The ODBA per minute of activity (foraging plus travelling) during each trip did not differ between sexes (Table S2.3) but was significantly higher in 2019 than 2017 for all birds (Tukey test; $F_{38} = 0.47$, $P = 0.04$; Table S2.2). In contrast, the factors that influenced ODBA per minute of each trip did differ between the sexes (Table S2.5): model selection determined male ODBA per minute of activity of each trip to be best explained by increasing the proportion of time spent foraging, travelling and take-off rate ($\chi^2_1 = 142.01$, $P < 0.001$, $\chi^2_1 = 195.11$, $P < 0.001$ and $\chi^2_1 = 20.27$, $P < 0.001$, respectively) whereas female ODBA per minute of activity was best explained by increasing only the proportions of time spent foraging and travelling ($\chi^2_1 = 177.92$, $P < 0.001$ and $\chi^2_1 = 291.70$, $P < 0.001$, respectively).

2.4.6 Investigating sexual dimorphism

The time elapsed between measurement of body mass and recording of accelerometry data during each trip was 12 hours on average (range: 20 minutes – 2 days). Heavier females made significantly shorter trips than lighter females in both duration and distance travelled ($F_{36} = 5.21$, $P = 0.03$, $F_{36} = 4.77$, $P = 0.04$) whereas among males there was no significant relationship between body mass and trip duration or distance travelled ($F_{30} = 0.01$, $P > 0.05$, $F_{30} = 0.66$, $P > 0.05$) (Figures 2.4a; 2.4b). In contrast, heavier males flapped significantly more and had a higher body amplitude than lighter males ($F_{21} = 17.03$, $P < 0.001$, $F_{21} = 6.79$, $P = 0.02$) but there was no significant effect of body mass on flight characteristics of females ($F_{23} = 0.28$, $P > 0.05$, $F_{23} = 0.12$, $P > 0.05$) (Figure 2.4c; 2.4d). There was no relation with body mass for any ODBA metric or for take-off rate for either sex (Table S2.7).

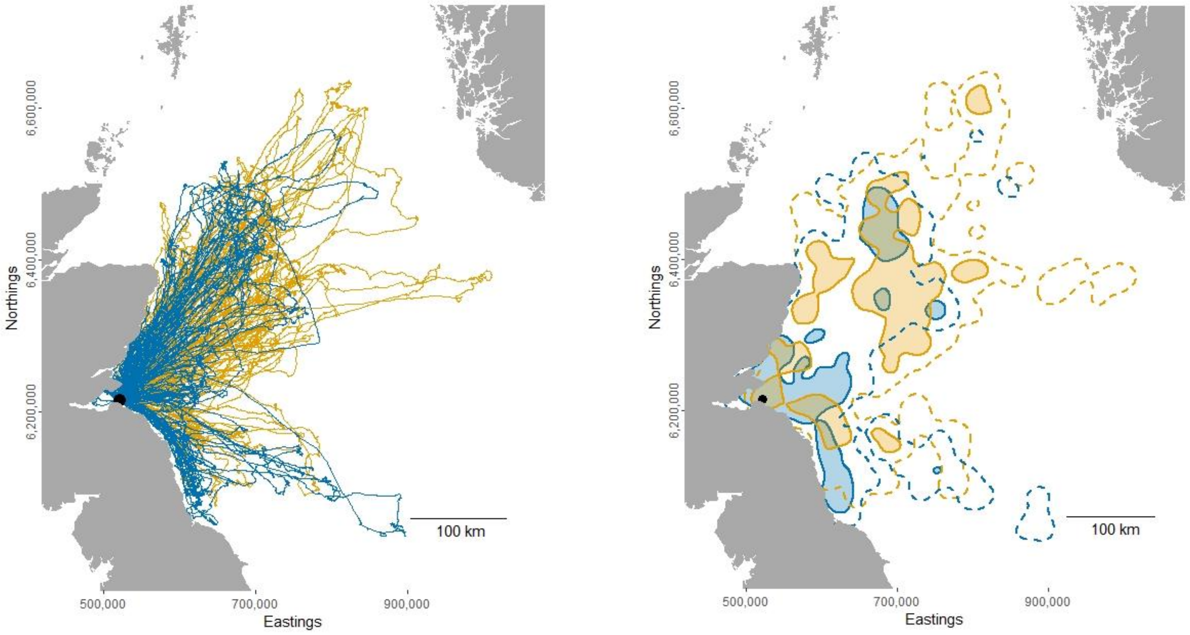
Table 2.1. Biometrics (mean ± SE) of male and female northern gannets (*Morus bassanus*) at Bass Rock, Scotland, measured between 2016 and 2019, with linear model statistics.

2017-2019	**Males (N=28)**	**Females (N=38)**	**F**	**df**	**P**
Wing (mm)	491.4± 1.83	495.1 ± 1.6	3.02	63	>0.05
Weight (g)	2807.7±46.8	3102.9 ± 44.2	20.70	63	<0.001
2016-2018	**Males (N=20)**	**Females (N=28)**	**F**	**df**	**P**
Wing area (m^2)	0.24±0.01	0.24±0.01	0.26	46	>0.05
Wing loading ($N\ m^{-2}$)	112.7±2.03	119.3±1.9	5.42	46	0.02

Table 2.2. Characteristics of foraging trips (mean ± SE) by male and female northern gannets (*Morus bassanus*) (N = number of trips, number of birds) at Bass Rock, Scotland, 2017 – 2019. ODBA (Overall Dynamic Body Acceleration) of activity included travelling and foraging but not resting on the sea surface.

	Female (N=95,36)	**Male (N=91,28)**
Duration (hours)	29.89 (1.48)	25.87 (1.06)
Distance (km)	633.76 (33.29)	486.72 (23.35)
Proportion of trip spent foraging	13.58 (0.60)	14.59 (0.53)
Proportion of trip spent travelling	31.33 (0.94)	27.10 (0.69)
Proportion of trip spent resting	53.26 (1.29)	56.43 (0.86)
	Female (N=55,22)	**Male (N=55,23)**
Proportion of outbound flight spent flapping	0.70 (0.02)	0.66 (0.02)
Proportion of inbound flight spent flapping	0.72 (0.02)	0.67 (0.01)
Outbound speed (m s^{-1})	16.41 (0.43)	15.57 (0.45)
Inbound speed (m s^{-1})	15.35 (0.49)	14.39 (0.32)
Outbound wingbeat frequency (Hz)	3.55 (0.02)	3.58 (0.01)
Inbound wingbeat frequency (Hz)	3.64 (0.01)	3.67 (0.01)
Outbound body amplitude (m)	0.037 (0.001)	0.035 (0.001)
Inbound body amplitude (m)	0.034 (0.001)	0.032 (0.001)
Outbound travelling OBDA (g) per minute	38.09 (0.50)	34.45 (0.51)
Inbound travelling ODBA (g) per minute	37.80 (0.60)	34.60 (0.51)
Foraging ODBA (g) per minute	40.27 (1.20)	35.66 (0.78)
ODBA of activity (g) per minute of the trip	18.20 (0.67)	16.40 (0.76)
Take-offs h^{-1} foraging	17 (0.91)	23 (1.49)

Overall



2017

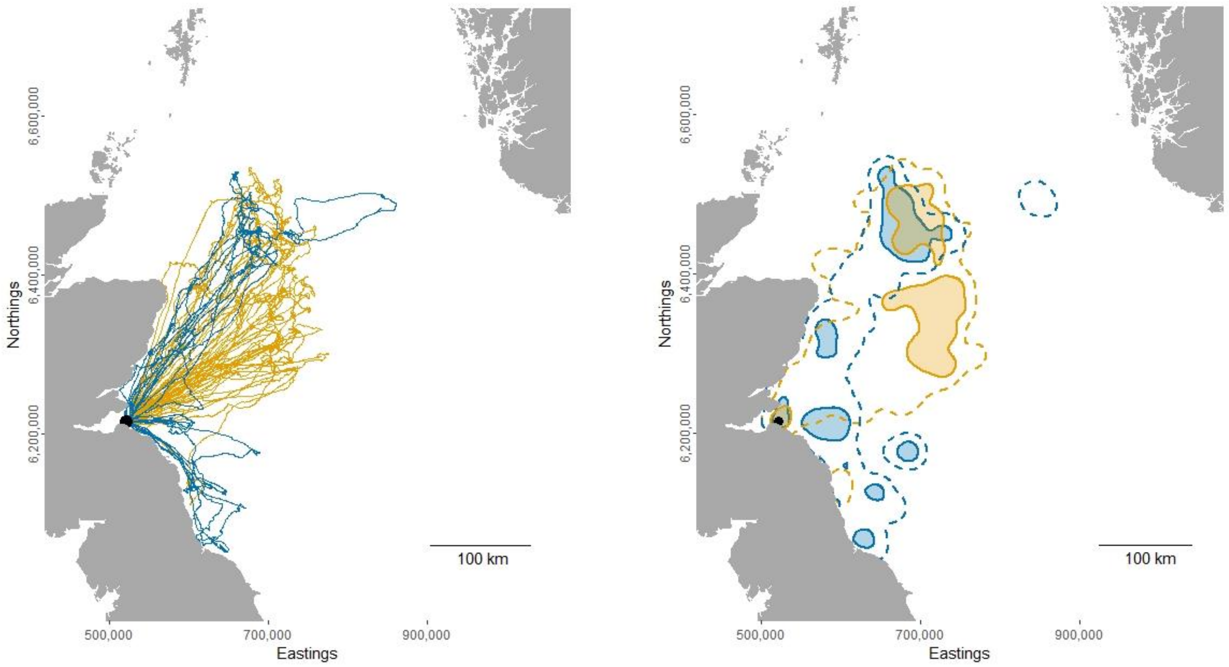
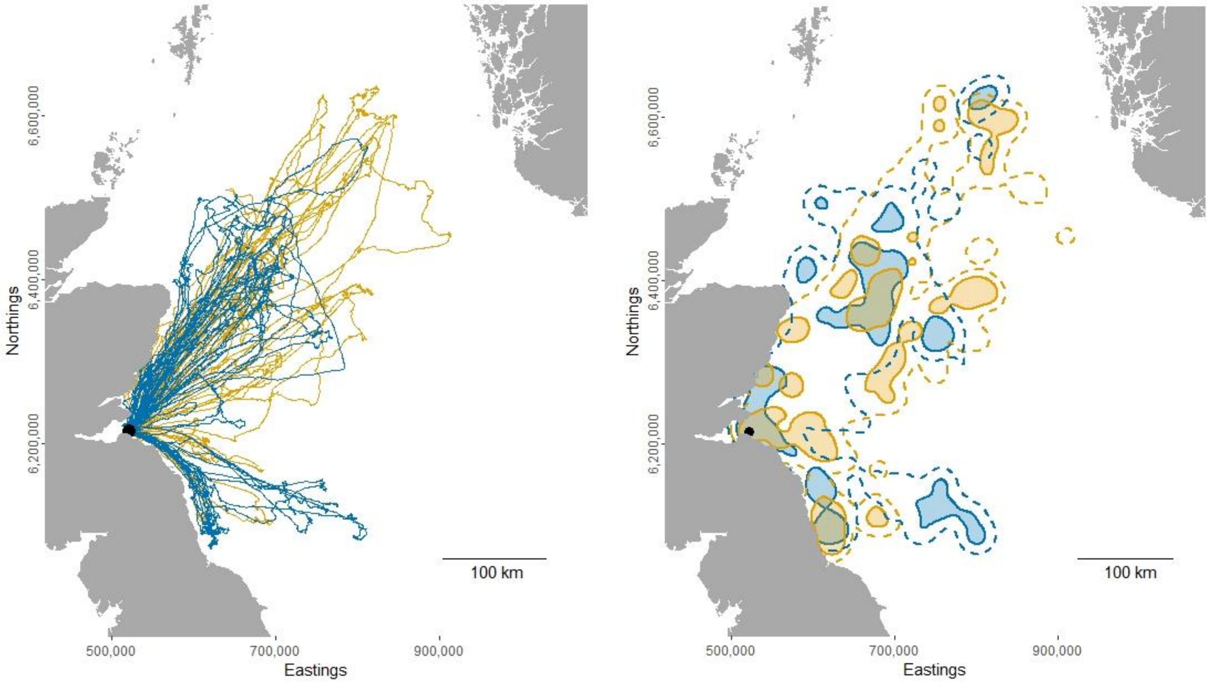


Figure 2.2. Foraging tracks (left) and utilisation distributions (UDs) (right) of male (blue) and female (orange) chick-rearing northern gannets (*Morus bassanus*) during 2017, 2018, 2019 and overall. No individuals were tracked for more than one year. UDs were calculated from active foraging locations and shading denotes UD contours (filled, 50%; unfilled, 95%) N= 186 trips, 64 birds. Black symbol shows the location of Bass Rock, Scotland

2018



2019

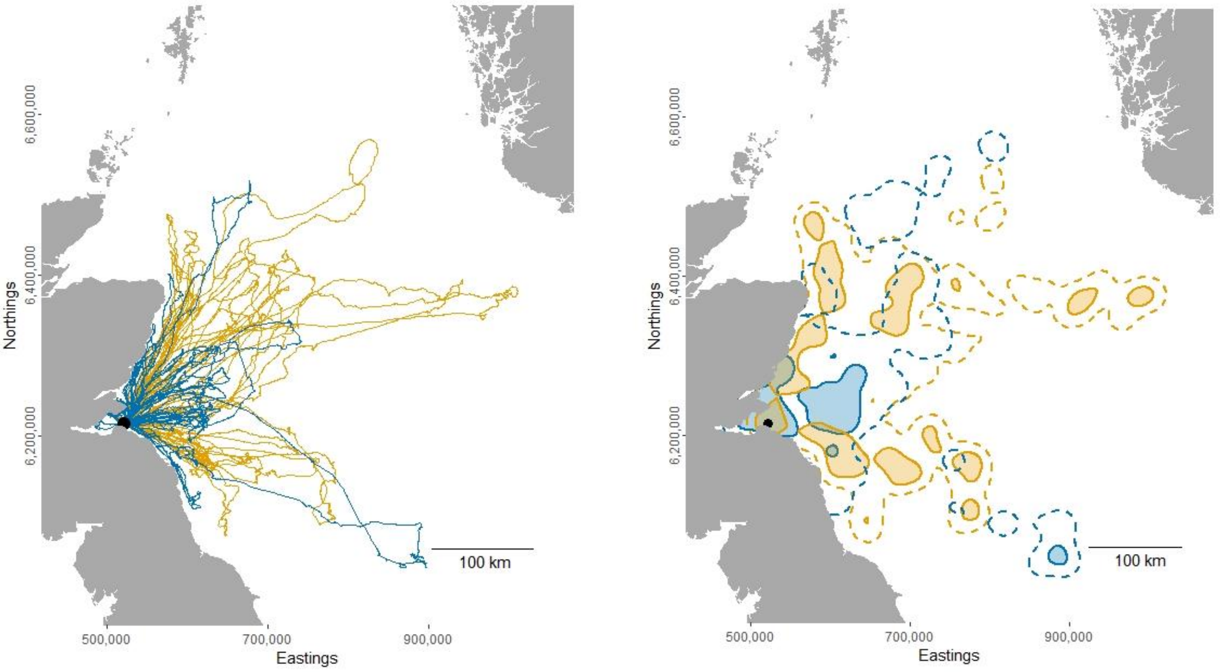


Figure 2.2 continued. Foraging tracks (left) and utilisation distributions (UDs) (right) of male (blue) and female (orange) chick-rearing northern gannets (*Morus bassanus*) during 2017, 2018, 2019 and overall. No individuals were tracked for more than one year. UDs were calculated from active foraging locations and shading denotes UD contours (filled, 50%; unfilled, 95%) N= 186 trips, 64 birds. Black symbol shows the location of Bass Rock, Scotland.

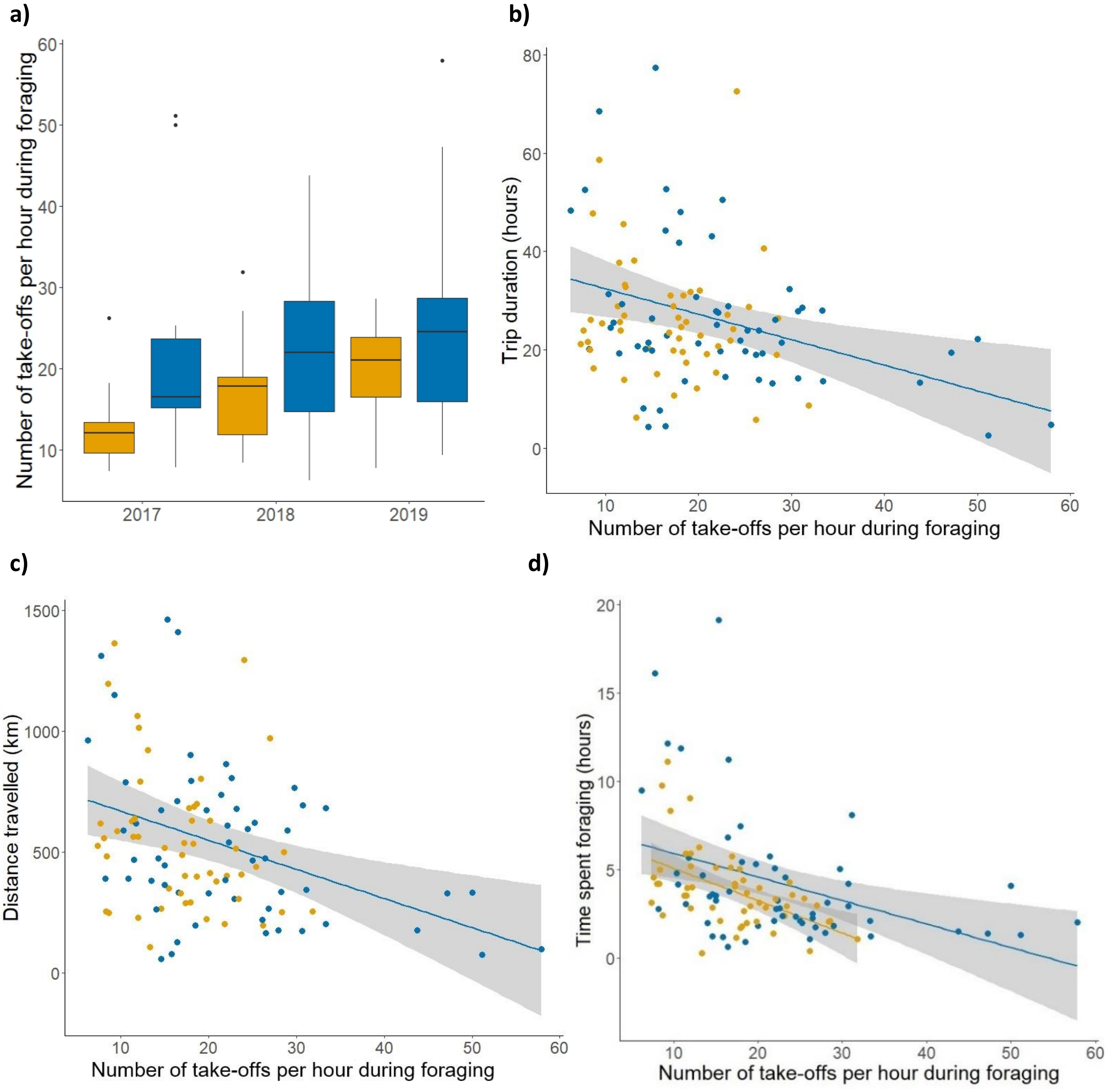


Figure 2.3. **(a)** The take-off rates h^{-1} foraging for male (blue) and female (orange) northern gannets (*Morus bassanus*) at Bass Rock, Scotland between 2017 and 2019 (mean ± SE, 95% confidence intervals and outliers), and the relationships between take-off rate h^{-1} foraging and: **(b)** trip duration; **(c)** distance travelled; **(d)** hours spent foraging; **(e)** proportion of time spent foraging**,** and; **(f)** proportion of time spent resting. Straight lines represent linear model predictions and curved lines represent quadratic model predictions, with 95% confidence regions in the shaded areas. N = 110 trips, 45 birds.

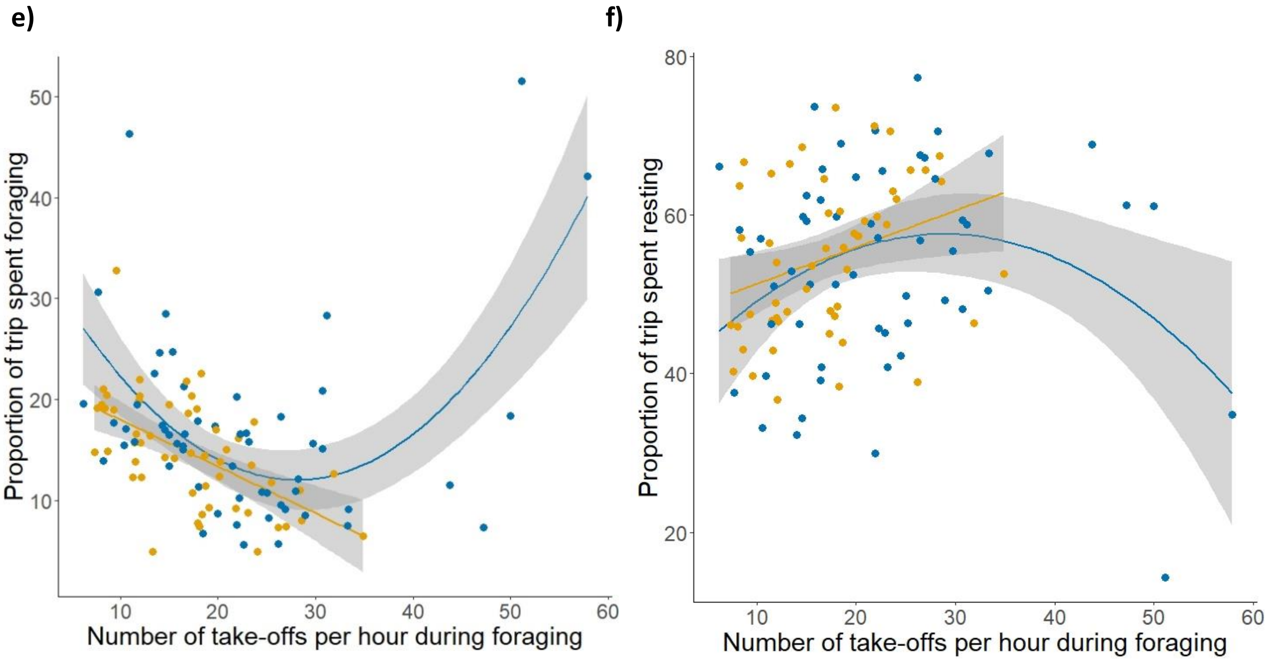


Figure 2.3. continued (a) The take-off rates h^{-1} foraging for male (blue) and female (orange) northern gannets (*Morus bassanus*) at Bass Rock, Scotland between 2017 and 2019 (mean ± SE, 95% confidence intervals and outliers), and the relationships between take-off rate h^{-1} foraging and: **(b)** trip duration; **(c)** distance travelled; **(d)** hours spent foraging; **(e)** proportion of time spent foraging**,** and; **(f)** proportion of time spent resting. Straight lines represent linear model predictions and curved lines represent quadratic model predictions, with 95% confidence regions in the shaded areas. N = 110 trips, 45 birds.

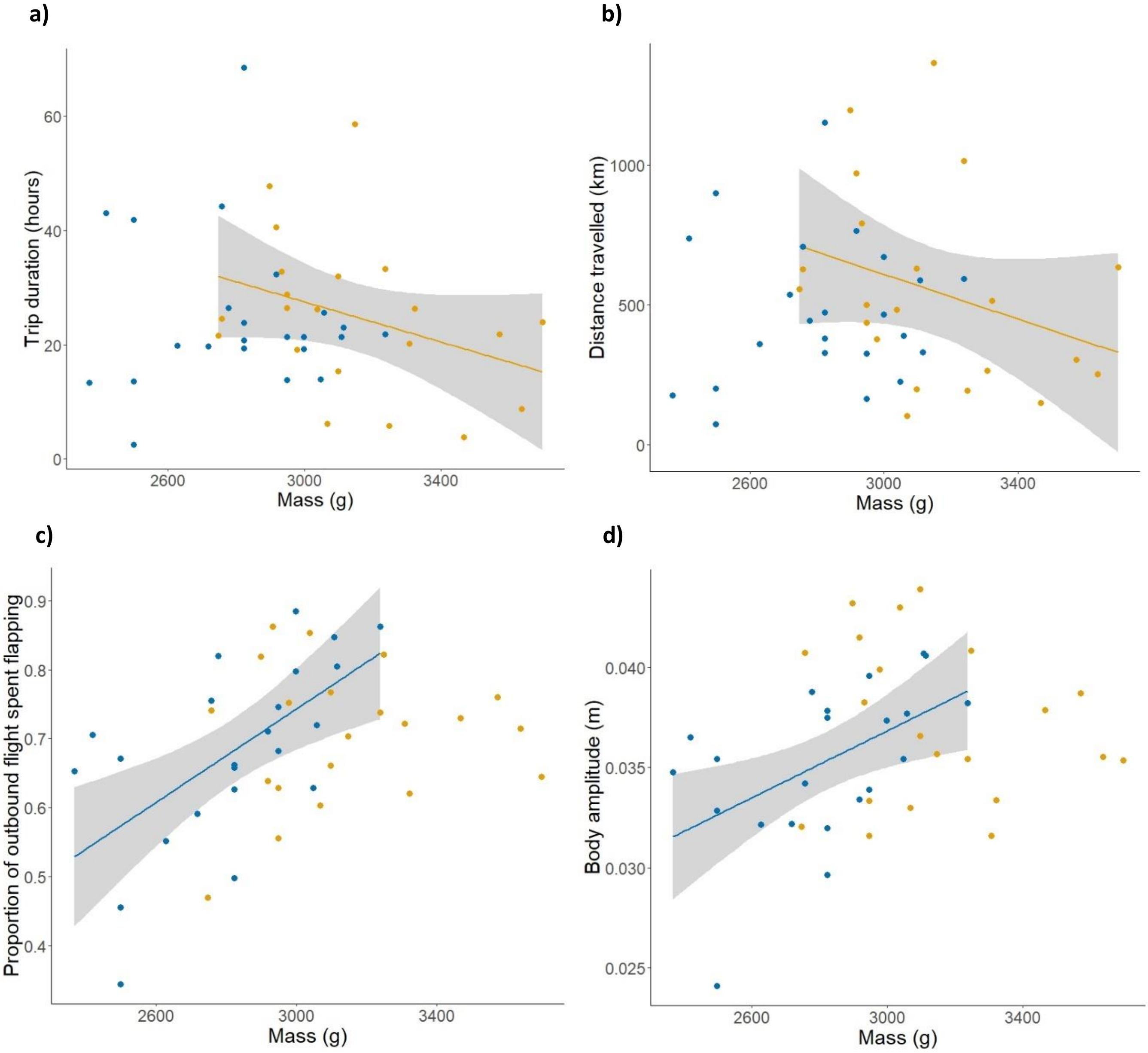


Figure 2.4. The relationship between body mass (g) and: **(a)** trip duration; **(b)** distance travelled; **(c)** the proportion of time spent flapping during outbound flight and; **(d)** body amplitude of chick-rearing male (blue) and female (orange) northern gannets (*Morus bassanus*) at Bass Rock, Scotland, between 2017 and 2019. Lines represent linear model predictions and shaded areas show 95% confidence regions. N = 110 trips, 45 birds.

2.5 Discussion

This study determined sexual dimorphism is unlikely to drive sexual segregation in gannets and is more likely to be a consequence of it. The results also revealed novel ways gannets sexually segregate: from fine-scale flight characteristics through to the effort attributed to travelling and foraging, but that these differences amounted to similar effort per unit time during foraging trips overall. These results, in conjunction with previous work, support the notion that sexual segregation is driven by niche divergence that benefits both sexes. Using gannets as a model, the results of this study demonstrate the importance of considering the foraging niche requirements of sexes separately for species management.

I began by providing measures of sexual segregation comparable to previous work to determine the extent of sexual segregation during the data collection period, before addressing the study aims with this baseline in mind. In keeping with other studies at Bass Rock, females made longer trips than males in terms of both duration and distance travelled, but the sexes did not differ consistently in all years studied (Lewis *et al.,* 2002; Wakefield *et al.,* 2015; Lane *et al.,* 2020). This pattern was also found in an eleven-year study of gannets in the Celtic Sea where the extent of spatial segregation varied across years, but sexes were consistently separate in habitat selection and isotopic niche (Clark *et al.,* 2021). These findings suggest that sexual segregation is driven by males and females targeting different prey, and therefore inter-annual variation in the extent of segregation in space could be due to changes in the distribution and availability of prey.

Female gannets are significantly heavier than males (e.g. Clark *et al.,* 2021) and this study shows females have a higher wing loading. Hence the first aim of this study was to investigate if sexual dimorphism could be a potential driver of sex differences in foraging behaviour, as found in other seabirds (e.g. two *Thalassarche* albatross species Phillips *et al.,* 2004). However, females made significantly longer trips than males and heavier females made shorter, not longer, trips than lighter females in both duration and distance (Figure 2.4a; 2.4b). Therefore these results suggests sexual dimorphism was not a driver of sexual segregation, in accordance with a study of gannets in the Celtic Sea (Clark *et al.,* 2021). Similarly, females spent a greater proportion of time flapping and had a higher body amplitude than males during both outbound and inbound travel, probably as a consequence of their greater body mass (Pennycuick 1987), and also flew faster than males on the inbound journey. However, while heavier males flapped significantly more and had a higher body amplitude than lighter males, there was no apparent effect of body mass on flight characteristics of females. These results imply that sexual dimorphism may not be the only driver of sex differences in flight characteristics and highlight the complexity and interacting drivers of sexual segregation. For instance, the higher inbound flight speed of females may be because they returned from greater distances than males so needed to do so more quickly in order to feed chicks (Hamer *et al.,* 2007), which can be achieved by increasing flapping flight and body amplitude, as seen in black-legged kittiwakes *Rissa tridactyla* (Taylor and Thomas 2002; Collins *et al.,* 2020). Payloads may also have differed between the sexes, and accurate and timely pre-and post-trip body mass measurements would allow a more detailed examination of how load carrying and chick-provisioning differ between sexes and whether or not there are sex-specific relationships between body mass and fine-scale flight characteristics, although this is difficult to achieve in practice (e.g. Grémillet *et al.,* 2006).

Sex differences in fine-scale flight characteristcs are likely to have sex-specific energy consequences. Flapping flight is more energetically expensive than gliding flight (Birt-Friesen *et al.,* 1989; Elliott *et al.,* 2013) and increases in body amplitude require more muscular effort to generate the additional lift for flight (Norberg 2012). This study supports that this is the pattern for gannets; within the 10 minute sample period there was a close positive relationship between ODBA of the sample and both the proportion of time spent flapping and body amplitude (Figure S2.2a; S2.2b), and the results reflect this relationship over the entirety of travel during a foraging trip; ODBA per minute of both outbound and inbound travel was ~9% higher in females than males (Table 2.2).

The flight characteristics and ODBA of outbound and inbound travel were not consistent between years. Birds flapped more on the outbound journey in 2018 than 2017 and had a higher body amplitude on the inbound journey in 2018 than 2019, perhaps suggesting 2018 had unfavourable wind conditions for flight. Indeed, wind direction and speed have been shown to affect gannet behaviour and energy expenditure of flight (Amélineau *et al.,* 2014; Lane *et al.,* 2019). My results add an additional element by identifying sex-specific flight characteristics and energy expenditure, an important factor for consideration of the effects of environmental change on central-place foragers that exhibit sexual segregation. For gannets, females may be more negatively affected by factors that lead to longer times in flight; for example barrier effects caused by offshore windfarm footprints and unfavourable wind conditions, such as more extreme and unpredictable weather events associated with climate change.

My measure of foraging energy expenditure - the ODBA per minute spent foraging was 12% higher for females than males, with no significant inter-annual variability (Table S2.4). Gannets plunge dive from heights of up to 40 m to catch prey in a deep V- or shallow U-shaped dive (Nelson 2002; Bennison *et al.,* 2022), with V-shaped dives more often associated with females and U-shaped dives with males, regardless of body mass, but heavier females dive deeper than lighter females (Cleasby *et al.,* 2015).

V-shaped dives require more height to achieve deeper depths (Garthe *et al.,* 2000; Cleasby *et al.,* 2015), and females fly higher than males during active foraging (Lane *et al.,* 2020). Flight associated with foraging is more energetically costly too; gannets spend more time in flapping flight when foraging than when commuting to and from the colony (Ropert-Coudert *et al.,* 2006; Amélineau *et al.,* 2014). Having higher wing loading, together with attaining greater heights between dives and the energy costs of flapping flight may explain the greater ODBA per minute of foraging for females found in this study. In contrast to Bass Rock, gannets at Great Saltee in the Celtic Sea had little difference between the dive types of males and females, and no significant sex differences in the energy expenditure of foraging (Bennison *et al.,* 2022). This highlights potential colony-specific differences that may influence the energy expenditure of foraging and the extent of sex differences in foraging behaviour, including local environmental conditions and the potential intensity of intra-specific competition. Thus also emphasising the need to replicate relevant analyses at different colonies, rather than assume continuity.

For both sexes the more take-offs per hour spent foraging the fewer hours were spent in foraging behaviour per trip. For females, the higher the take-off rate the lower the proportion of the trip spent foraging and the higher the proportion of time spent resting on the sea surface (Figure 2.3). For males, the situation was more complex because there was also a significant negative relationship between take-off rate and both trip duration and distance travelled. Hence very high take-off rates (equivalent to one presumed dive and subsequent take-off every 1.0 to 1.5 minutes, shown only by males; Figure 2.3) occurred during relatively short trips, resulting in quadratic relationships between take-off rates and the proportions of each trip spent in foraging or resting on the sea surface. Together, these data strongly suggest that a higher take-off rate from the sea surface during bouts of foraging, presumably indicating a higher frequency of dives, was associated with more successful foraging. An alternative possibility, that a high dive rate and subsequent take-off rate resulted from a high proportion of unsuccessful dives, would predict the opposite relationships to those found here, and hence is not supported by my findings.

Assuming that take-off rate during foraging bouts was at least broadly comparable to dive rate, my results may indicate differences in the foraging strategies of males and females. In Australasian gannets *Morus serrator*, a low plunge dive rate during foraging was attributed to high energy expenditure, measured by heart rate (Green *et al.,* 2010). This may partly explain why in this study females had a lower take-off rate than males, if there are higher energy costs associated with deeper V-shaped dives from greater heights compared to the shallower U-shaped dives from lower heights that males are more likely to perform (Cleasby *et al.,* 2015; Lane *et al.,* 2020).

Despite higher ODBA per minute of foraging and travelling for females than for males, the overall ODBA of activity (travelling and foraging combined) per minute of each trip did not differ between the sexes. Nor was there a sex difference in time-activity budgets. These findings seem to support the notion that sexual segregation in these birds derives from niche divergence to reduce intra-specific competition, to the benefit of both sexes, because an alternative explanation that segregation derives from sexual dimorphism through competitive exclusion of the smaller sex (e.g. Peters & Grubb 1983), might be expected to result in a sex difference in time-activity budgets and energy expenditure during trips.

For both sexes, the proportion of time spent foraging and travelling each significantly increased the overall ODBA of activity per minute of each trip (Table S2.5). This is of interest, as the time spent foraging is around half that of travelling for foraging trips at Bass Rock, and yet it is a significant factor in predicting trip energy expenditure. In this far-ranging species, the statistical significance of time spent foraging as well as the time spent travelling indicates the importance of what gannets encounter at foraging locations, in addition to the predictably high costs of getting there. There was significantly higher ODBA per minute of activity in 2017 than 2019 for all birds and conversely, lower take-off rate in 2017 than 2019. This might suggest an effect of environmental conditions on foraging success and overall trip effort.

ODBA per minute of activity during each trip was also significantly affected by take-off rate for males but not for females. This, along with the other sex-specific relationships between energy and behaviour, implies nuanced interactions between the energy expenditure of at-sea behaviours, environmental conditions and an individual's foraging strategy, in which males and females are likely to differ (Cleasby *et al.,* 2015; Wakefield *et al.,* 2015). In contrast to other seabirds in the UK, gannets have remarkably consistent breeding productivity, despite marked annual variation in environmental conditions (Mavor *et al.,* 2006; Lane *et al.,* 2019). This consistency seems to be related to high flexibility in foraging behaviour (Hamer *et al.,* 2007), and my results show that this also applies to fine-scale behaviours, as demonstrated in the inter-annual variation in flight characteristics and rate of take-offs during foraging.

This study identifies potential directions to further the study of sexual segregation and provides novel information towards identifying the drivers behind sexual segregation in gannets; sexual dimorphism is likely to be a contributing factor in fine-scale sex differences in flight characteristics but is not the only one. I suggest sexual dimorphism is a consequence of sex differences in foraging behaviour, rather than a cause. Overall trip effort is not detectably different between the sexes, suggesting niche divergence that benefits both sexes as a driver of sexual segregation, rather than competitive exclusion. These results contribute to growing evidence that knowledge and inclusion of sex-specific requirements and consequences are necessary for accurate management and assessment of seabird population trends.

2.6 References

Amélineau F, Péron C, Lescroël A, Authier M, Provost P, Grémillet D (2014) Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology* 217(6): 876–885, doi: 10.1242/jeb.097915.

Barton K (2009) Multi-model inference. Available at: http://r-forge.r-project.org/projects/mumin/

Bennett PM and Owens IPF (2002) The Evolutionary Ecology of Birds: Life Histories, Mating Systems, and Extinction. New York, NY: Oxford University Press.

Bennison A, Giménez J, Quinn JL, Green JA, Jessopp M (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *Royal Society Open Science* 9: 210520, doi: 10.1098/rsos.210520.

Bhattacharyya A (1943) On a measure of divergence betweentwo statistical populations defined by their probability distri-butions. *Bulletin of the Cacutta Mathematical Society* 35: 99–109.

Birt-Friese VL, Montevecchi WA, Cairns DK, Macko SA (1989) Activity-Specific Metabolic Rates of Free-Living Northern Gannets and Other Seabirds. *Ecological Society of America* 70(2):357-367.

Bugoni L, Griffiths K, Furness RW (2012) Sex-biased incidental mortality of albatrosses and petrels in longline fisheries: Differential distributions at sea or differential access to baits mediated by sexual size dimorphism? *Journal of Ornithology,* 152(2): 261-268, doi:10.1007/s10336-010-0577-x

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197: 516–519, doi: 10.1016/j.ecolmodel.2006.03.017.

Clark B, Cox SL, Atkins K, Bearhop S, Bicknell AWJ, Bodey TW, Cleasby IR, Grecian WJ, Hamer KC, Loveday BR, Miller PI, Morgan G, Morgan L, Newton J, Patrick SC, Scales KL, Sherley RB, Vigfúsdóttir, Wakefield ED, Votier SC (2021) Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. *Marine Ecology Progress Series* 661: 1–16, doi: 10.3354/meps13636.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick S, Newton J, Votier S, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series* 518: 1–12, doi: 10.3354/meps11112.

Collins PM, Green JA, Elliott KH, Shaw PJA, Chivers L, Hatch SA, Halsey LG (2020) Coping with the commute: behavioural responses to wind conditions in a foraging seabird. *Journal of Avian Biology* 51(4): 1–11, doi: 10.1111/jav.02057.

Elliott KH, Le Vaillant M, Kato A, Speakman JR, Ropert-Coudert Y (2013) Accelerometry predicts daily energy expenditure in a bird with high activity levels. *Biology Letters* 9(1): 20120919, doi: 10.1098/rsbl.2012.0919.

Elliott KH, Gaston AJ, Crump D (2010) Sex-specific behavior by a monomorphic seabird represents risk partitioning. *Behavioral Ecology* 21(5): 1024–1032. doi: 10.1093/beheco/arq076.

Garde B, Wilson RP, Fell A, Cole N, Tatyah V, Holton MD, Rose KAR, Metcalfe RA, Robotka H, Wikelski M, Tremblay F, Whelan S, Elliott KH, Shepard ELC (2022) Ecological inference using data from accelerometers needs careful protocols. *Methods in Ecology and Evolution* 13(4): 813–825, doi: 10.1111/2041-210x.13804.

Garthe S, Benvenuti S, Montevecchi WA (2000) Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*). *Proceedings of the Royal Society B-Biological Sciences* 267(1454): 1717–1722, doi: 10.1098/rspb.2000.1200.

Giménez J, Arneill GE, Bennison A, Pirotta E, Gerritsen HD, Bodey TW, Bearhop S, Hamer KC, Votier S, Jessopp M (2021) Sexual Mismatch Between Vessel-Associated Foraging and Discard Consumption in a Marine Top Predator. *Frontiers in Marine Science* 8: 636468, doi: 10.3389/fmars.2021.636468.

Gómez-Laich A, Yoda K, Zavalaga C, Quintana F (2015) Selfies of imperial cormorants (*Phalacrocorax atriceps*): What is happening underwater? *PLoS ONE* 10(9): e0136980, doi: 10.1371/journal.pone.0136980.

Gownaris NJ and Boersma PD (2019) Sex-biased survival contributes to population decline in a long-lived seabird, the Magellanic Penguin. *Ecological Applications.* 29(1)e01826, doi:10.1002/eap.1826

Green JA, White CR, Bunce A, Frappell PB, Butler PJ (2010) Energetic consequences of plunge diving in gannets. *Endangered Species Research*, 10(1): 269–279, doi: 10.3354/esr00223.

Grémillet D, Pichegru L, Siorat F, Georges JY (2006) Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. Marine Ecology Progress Series 319: 15–25, doi: 10.3354/meps319015.

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

Halsey LG, Green JA, Wilson RP, Frappell PB (2009) Accelerometry to Estimate Energy Expenditure during Activity : Best Practice with Data Loggers. *Physiology and Biochemical Zoology* 82(4): 396–404, doi: 10.1086/589815.

Hamer KC, Phillips RA, Wanless S, Harris MP, Wood AG (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: Evidence from satellite telemetry. *Marine Ecology Progress Series* 200: 257–264, doi: 10.3354/meps200257.

Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295–305, doi: 10.3354/meps338295.

Hicks O, Burthe S, Daunt F, Butler A, Bishop C, Green JA (2017) Validating accelerometry estimates of energy expenditure across behaviours using heart rate data in a free-living seabird. *Journal of Experimental Biology* 220(10): 1875–1881, doi: 10.1242/jeb.152710.

Lack D (1968) Ecological Adaptations for Breeding in Birds. *Oikos* 19(1): 1-9, doi: 10.2307/3564725.

Lane JV, Spracklen DV, Hamer KC (2019) Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series* 628: 183–193, doi: 10.3354/meps13089.

Lane JV, Jeavons R, Deakins Z, Sherley RB, Pollock CJ, Wanless RJ, Hamer KC (2020) Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research* 162: 105196, doi: 10.1016/j.marenvres.2020.105196.

Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B* 269: 1687–1693, doi: 10.1098/rspb.2002.2083.

Machovsky-Capuska GE, Senior AM, Benn EC, Tait AH, Schuckard R, Stockin KA, Cook W, Ogle M, BArna K, Melville D, Wright B, Purvin C, Raubenheimer D (2016) Sex-specific macronutrient foraging strategies in a highly successful marine predator: the Australasian gannet. *Marine Biology* 163(4): 1–14, doi: 10.1007/s00227-016-2841-y.

Mavor RA, Heubeck M, Schmit, S, Parsons M (2006) Seabird numbers and breeding success in Britain and Ireland. Peterborough: Joint Nature Conservation Committee.

Nelson B (2002) The Atlantic Gannet. Published by Fenix Books Limited, Norfolk

Norberg UM (2012) Vertebrate flight: mechanics, physiology, morphology, ecology and evolution. *Journal of Evolutionary Biology* 5(3):541-543, doi: 10.1046/j.1420-9101.1992.5030541.x.

Patrick SC and Weimerskirch H (2014) Consistency pays: Sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biology Letters* 10(10): 1-4, doi:

10.1098/rsbl.2014.0630.

Pelletier D, Seyer Y, Garthe S, Bonnefoi S, Phillips RA, Guillemette M (2020) So far, so good. . . Similar fitness consequences and overall energetic costs for short and long-distance migrants in a seabird. *PLoS ONE* 15(3): 1–23. doi: 10.1371/journal.pone.0230262.

Pennycuick CJ (2008) Modelling the flying bird. Elsevier Inc., Burlington, MA.

Peters WD and Grubb Jr TC (1983) An Experimental Analysis of Sex-Specific Foraging in the Downy Woodpecker, *Picoides Pubescens*. *Ecology*, 64(6): 1437–1443, doi:10.2307/1937498.

Phillips RA, Silk J, Phalan B, Catry P Croxall J (2004) Seasonal sexual segregation in two Thalassarche albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings. Biological Sciences* 271(1545): 1283–1291, doi: 10.1098/rspb.2004.2718.

Phillips RA, Xavier JC and Croxall JP (2003) Effects of Satellite Transmitters on Albatrosses and Petrels. *The Auk* 120(4): 1082-1090, doi: 10.1093/auk/120.4.1082.

Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss AC, Wilson R (2012) Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLoS One* 7(2): e31187, doi: 10.1371/journal.pone.0031187.

R Core Team. (2019) R: A language and environment for statistical computing. Vienna, Austria. Available from: https://www.r-project.org/.

Ropert-Coudert Y, Wilson RP, Grémillet D, Kato A, Lewis S, Ryan PG (2006) Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. *Marine Ecology Progress Series* 328: 275–284, doi: 10.3354/meps328275.

Shepard ELC, Wilson RP, Quintana F, Gómex Laich A, Leibsch N, Albareda DA, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C, MacDonald DW (2008) Identification of animal movement patterns using tri-axial accelerometry. *Inter-Research* 10: 47–60, doi: 10.3354/esr00084.

Shepard ELC, Wilson RP, Rees WG, Grundy E, Lambertucci SA, Vosper SB (2013) Energy landscapes shape animal movement ecology. *American Naturalist* 182(3): 298–312, doi: 10.1086/671257.

Speakman JR and Hambly C (2016) Using doubly-labelled water to measure free-living energy expenditure: Some old things to remember and some new things to consider. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology* 202: 3–9, doi: 10.1016/j.cbpa.2016.03.017.

Stauss C, Bearhop S, Bodey TW, Garthe S, Gunn C, Grecian WJ, Inger R, Knight ME, Newton J, Patrick

SC, Phillips RA, Waggitt JJ, Votier SC (2012) Sex-specific foraging behaviour in northern gannets *Morus bassanus*: incidence and implications. *Marine Ecology Progress Series* 457: 151–162, doi: 10.3354/meps09734.

Taylor GK and Thomas ALR (2002) Animal Flight Dynamics II. Longitudinal Stability in Flapping Flight. *Journal of Theoretical Biology* 214(3): 351–370, doi: 10.1006/jtbi.2001.2470.

Tibshirani, R (1996) Regression Shrinkage and Selection via the Lasso. *Journal of the Royal Statistical Society, Series B (Methodologica*l), 58(1):267–288

Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, Wilson RP (2014) Excess Baggage for Birds: Inappropriate Placement of Tags on Gannets Changes Flight Patterns. *PLOS ONE* 9(3): e92657, doi: 10.1371/journal.pone.0092657.

Wakefield ED, Bodey TW, Bearhop S, Blackburn J, Colhoun K, Davies R, Dwyer RG, Green JA, Grémillet D, Jackson AL, Jessopp MJ, Kane A, Langston RHW, Lescroël A, Murray S, Le Nuz M, Patrick SC, Péron C, Soanes LM, Wanless S, Votier S, Hamer KC (2013) Space Partitioning Without Territoriality in Gannets. *Science* 341(6141): 68–70, doi: 10.1126/science.1236077.

Wakefield ED, Cleasby IR, Bearhop S, Bodey TA, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fid–lity - why some gannets don't change their spots. *Ecology* 96(11): 3058–3074, doi: 10.1890/14-1300.1.sm.

Wakefield ED, Furness RW, Lane JV, Jeglinski JWE, Pinder SJ (2019) Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. *Journal of Avian Biology* 50(10): e02164, doi: 10.1111/jav.02164.

Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: The case of the cormorant. *Journal of Animal Ecology* 75(5): 1081–1090, doi: 10.1111/j.1365-2656.2006.01127.x.

Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R, Hopkins L, Marks N, Geraldi NR, Duarte CM, Scott R, Strano MS, Robotka H, Eizaguirre C, Fahlman A, Shepard ELC (2020) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology* 89(1): 161-172, doi: 10.1111/1365-2656.13040.

2.7 Supplementary materials S2

Table S2.1. The process of identifying take-offs from the surface from 4 thresholds in variables derived from accelerometry data for chick-rearing northern gannets (*Morus bassanus*).

Variable	**Threshold**	**Explanation**
Detection of change in dynamic X acceleration, marker at time point	0.5(g)	A change in the heave axis (up and down movement of the body). 0.5 ensures no take-offs are missed, but leaves other behaviours included.
Average body angle from detection to 10 seconds after	>0.31°	During flight, body angle is higher than when on water, so this removes any behaviour that is immediately followed by being on the water surface.
Variance body angle from detection to 5 seconds after	0.008 – 0.07°	Body angle can be >0.31 on average during underwater activity however, so having a variance window removes underwater behaviour.
Average body angle from detection to 2 seconds before	< 0.31°	This leaves behaviour during flight and take-offs, because body angle is lower when in the water, we can use the body angle average just before the 'take-off' to separate these.

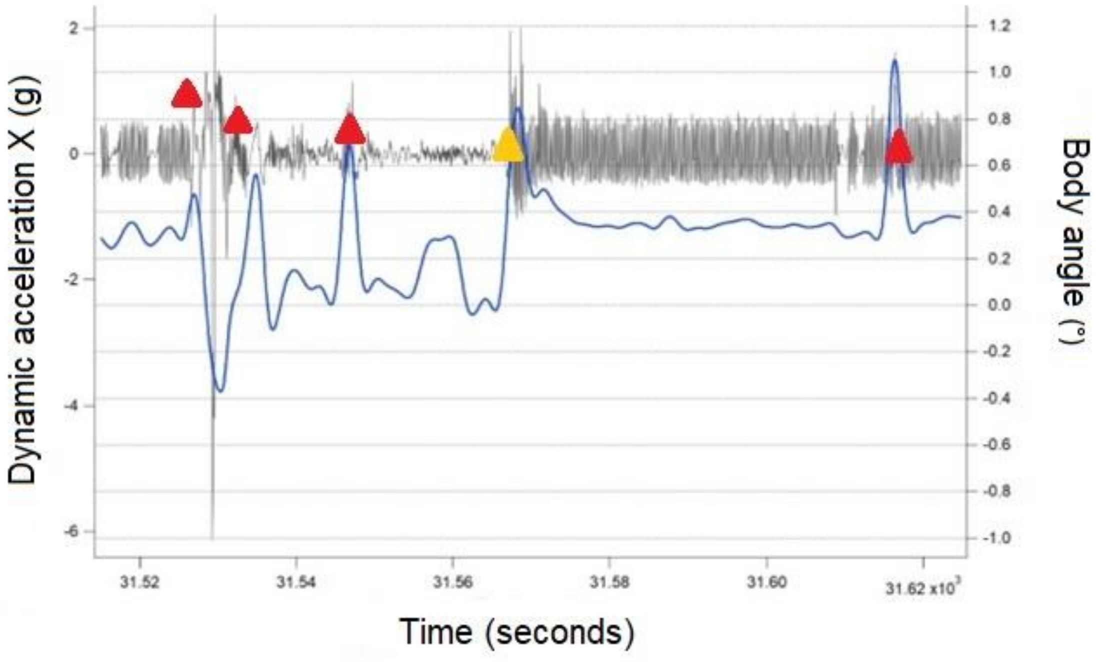


Figure S2.1. The dynamic X acceleration (black line) with triangle markers at the threshold of 0.5 (g) where orange = a true take-off and red = other behaviours (from left to right – a dive, surfacing from a dive, on the surface activity and in flight behaviour). The blue line shows the body angle (°) of the bird.

Table S2.2. Annual variation in foraging trip metrics (mean ± SE) of male and female chick-rearing northern gannets (*Morus bassanus*) (N=trips, individual birds) at Bass Rock, Scotland between 2017 and 2019.

	2017		**2018**		**2019**	
	Female (N=30,11)	**Male (N=14,6)**	**Female (N=33,13)**	**Male (N=45,13)**	**Female (N=33,13)**	**Male (N=31,10)**
Duration (hours)	28.39 (2.51)	27.64 (3.95)	32.51 (2.79)	28.78 (2.16)	28.62 (2.38)	20.86 (2.26)
Distance (km)	657.21 (52.55)	604.26 (103.02)	698.77 (65.14)	551.90 (40.63)	547.43 (51.67)	339.03 (38.71)
Proportion of trip spent foraging	13.40 (1.14)	18.90 (2.92)	13.20 (0.81)	13.51 (1.14)	14.14 (1.16)	14.20 (1.47)
Proportion of trip spent travelling	36.99 (1.66)	30.94 (2.02)	30.61 (1.52)	28.60 (1.51)	26.91 (1.25)	23.17 (1.26)
Proportion of trip spent resting	47.71 (1.95)	48.33 (3.39)	54.36 (1.60)	56.03 (1.77)	57.21 (1.95)	60.67 (1.98)
	Female (N=14,6)	**Male (N=14,6)**	**Female (N=24,8)**	**Male (N=25,9)**	**Female (N=16,8)**	**Male (N=16,8)**
ODBA (g) per minute of trip	20.92 (1.27)	19.01 (1.52)	18.26 (1.01)	16.53 (1.17)	15.27 (0.91)	13.90 (1.03)
Foraging ODBA (g) per minute	37.08 (1.21)	36.17 (1.16)	41.72 (2.50)	34.54 (1.60)	40.12 (0.89)	36.97 (1.71)
Outbound travelling OBDA (g) per minute	38.29 (1.13)	34.89 (0.95)	39.00 (0.71)	34.86 (1.45)	35.97 (0.68)	33.42 (1.51)
Inbound travelling ODBA (g) per minute	35.95 (1.23)	37.76 (0.68)	39.46 (0.74)	35.08 (1.20)	36.02 (1.08)	31.08 (1.40)
Outbound proportion spent flapping	0.69 (0.03)	0.59 (0.03)	0.74 (0.02)	0.68 (0.02)	0.66 (0.03)	0.68 (0.03)
Inbound proportion spent flapping	0.66 (0.04)	0.71 (0.03)	0.77 (0.02)	0.69 (0.02)	0.69 (0.03)	0.61 (0.03)
Outbound wingbeat frequency (Hz)	3.54 (0.04)	3.54 (0.03)	3.52 (0.02)	3.61 (0.02)	3.59 (0.02)	3.58 (0.03)
Inbound wingbeat frequency (Hz)	3.63 (0.04)	3.67 (0.04)	3.62 (0.02)	3.64 (0.02)	3.69 (0.02)	3.72 (0.02)

Outbound speed (m s^{-1})	15.97 (1.09)	16.81 (0.80)	17.47 (0.56)	15.32 (0.72)	15.13 (0.61)	14.89 (0.78)
Inbound speed (m s^{-1})	16.27 (1.07)	13.59 (0.79)	14.53 (0.62)	15.59 (0.50)	15.84 (1.00)	13.23 (0.74)
Outbound body amplitude (m)	0.038 (0.001)	0.034 (0.001)	0.038 (0.001)	0.035 (0.001)	0.035 (0.001)	0.036 (0.001)
Inbound body amplitude (m)	0.033 (0.001)	0.035 (0.001)	0.035 (0.001)	0.033 (0.001)	0.032 (0.001)	0.029 (0.001)
Take-off rate $^{h-1}$ foraging	13 (1.42)	21 (3.37)	17 (1.39)	22 (1.76)	20 (1.52)	25 (3.20)

Table S2.3. GLMM model estimates for sex-specific relationships of key foraging trip metrics and take-off rate h^{-1} foraging for chick-rearin northern gannets (*Morus bassanus*), Bass Rock, 2017-2019.

Parameter	**Estimate**	**SE**	**df**	**t**	**P**		**X^2**	**df**	**P**
Female duration (hours)									
Intercept -	5.85	0.80	31	7.33	<0.001				
Take-off rate	-0.22	0.19	31	-1.13	>0.05	**Take-off rate**	1.27	1	>0.05
Male duration (hours)									
Intercept -	7.27	0.77	32	9.40	<0.001				
Take-off rate	-0.52	0.16	32	-3.18	0.003	**Take-off rate**	10.10	1	0.001
Female distance (km)									
Intercept -	29.98	4.35	31	6.90	<0.001				
Take-off rate	-1.79	1.04	31	-1.72	>0.05	**Take-off rate**	2.95	1	>0.05
Male distance (km)									
Intercept -	34.29	3.79	32	9.05	<0.001				
Take-off rate	-2.75	0.80	32	-3.45	0.002	**Take-off rate**	11.88	1	<0.001
Female time foraging (hours)									
Intercept -	3.35	0.34	31	9.91	<0.001				
Take-off rate	-0.36	0.08	31	-4.45	<0.001	**Take-off rate**	19.78	1	<0.001
Male time foraging (hours)									
Intercept	3.36	0.39	32	8.58	<0.001				
Take-off rate	-0.31	0.08	32	-3.78	<0.001	**Take-off rate**	14.26	1	<0.001
Female proportion of trip spent foraging									
Intercept	5.88	0.45	31	13.19	<0.001				
Take-off rate	-0.52	0.11	31	-4.88	<0.001	**Take-off rate**	23.82	1	<0.001
Male proportion of trip spent foraging									
Intercept	7.10	0.57	32	12.38	<0.001				
Take-off rate 1	-3.44	0.48	32	-7.22	<0.001	**Take-off rate 1**	52.18	1	<0.001
Take-off rate ^{2}	3.12	0.43	32	7.22	<0.001	**Take-off rate ^{2}**	52.12	1	<0.001
Female proportion of trip spent resting									
Intercept -	6.36	0.46	31	13.88	<0.001				
Take-off rate	0.25	0.11	31	2.27	0.03	**Take-off rate**	5.17	1	0.02

Male proportion of trip spent resting									
Intercept	6.09	0.68	32	8.95	<0.001				
Take-off rate 1	1.57	0.56	32	2.78	0.009	**Take-off rate 1**	7.75	1	0.001
Take-off rate ^{2}	-1.48	0.51	32	-2.90	0.007	**Take-off rate ^{2}**	8.42	1	0.004

Table S2.4. The estimates from linear mixed models testing for differences between sexes, years and their interaction in key foraging trip metrics, with bird identity as a random factor to account for multiple trips per bird, of chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019, Bass Rock, Scotland

Parameter	**Estimate**	**SE**	**df**	**t**	**P**		**X^2**	**df**	**P**
Duration (hours)									
Intercept - 2017, Female	5.15	0.24	120	21.25	<0.001				
–Male - 2019	-0.73	0.54	60	-1.35	>0.05				
Distance (km)									
Intercept - 2017, Female	25.02	1.23	120	20.32	<0.001				
–Male - 2019	-3.43	2.76	60	-1.25	>0.05				
Proportion of trip spent travelling									
Intercept - 2017, Female	6.01	0.20	120	30.39	<0.001				
–Year - 2019	-0.81	0.27	60	-2.95	0.004	**Sex*Year**	0.49	2	>0.05
–Male - 2019	0.01	0.43	60	0.01	>0.05				
Proportion of trip spent foraging									
Intercept - 2017, Female	3.55	0.19	120	19.07	<0.001				
–Year - 2019	0.12	0.26	60	0.45	>0.05	**Sex*Year**	3.37	2	>0.05
–Male - 2019	-0.69	0.42	60	-1.65	>0.05				
Proportion of trip spent resting									
Intercept - 2017, Female	48.03	2.51	120	19.13	<0.001				
–Year - 2019	8.71	3.49	60	2.50	0.02	**Sex*Year**	0.49	2	>0.05

–Male - 2019	3.62	5.57	60	0.65	>0.05				
Outbound proportion of time spent flapping									
Intercept - 2017, Female	69.27	3.05	63	22.74	<0.001				
–Year - 2019	-3.37	4.15	37	-0.81	>0.05	**Sex*Year**	7.81	2	0.02
–Male - 2019	12.72	5.86	37	2.17	0.008				
Inbound proportion of time spent flapping									
Intercept - 2017, Female	66.33	3.85	63	17.25	<0.001				
–Year - 2019	3.06	5.60	37	0.61	>0.05	**Sex*Year**	0.92	2	>0.05
–Male - 2019	-12.26	7.10	37	-1.73	>0.05				
Outbound Speed (m s^{-1})									
Intercept - 2017, Female	15.95	0.96	63	16.56	<0.001				
–Year - 2019	-0.82	1.29	37	-0.64	>0.05	**Sex*Year**	3.71	2	>0.05
–Male - 2019	-0.97	1.81	37	-0.54	>0.05				
Inbound Speed (m s^{-1})									
Intercept - 2017, Female	16.27	0.83	63	19.51	<0.001				
–Year - 2019	-0.43	1.14	37	-0.38	>0.05	**Sex*Year**	6.56	2	0.04
–Male - 2019	0.07	1.61	37	0.05	>0.05				
Outbound wingbeat frequency (Hz)									
Intercept - 2017, Female	3.52	0.04	65	79.84	<0.001				
–Year - 2019	0.04	0.08	39	1.24	>0.05	**Sex*Year**	1.71	2	>0.05
–Male - 2019	-0.42	0.46	39	-0.61	>0.05				
Inbound wingbeat frequency (Hz)									
Intercept - 2017, Female	3.61	0.05	65	75.29	<0.001				
–Year - 2019	0.07	0.06	39	1.21	>0.05	**Sex*Year**	0.92	2	>0.05
–Male - 2019	-0.05	0.09	39	-0.61	>0.05				
Outbound body amplitude (m)									

Intercept - 2017, Female	0.04	0.01	63	34.06	<0.001				–
–Year - 2019	-0.01	0.01	39	-1.73	>0.05	**Sex*Year**	4.48	2	>0.05
–Male - 2019	0.01	0.01	39	1.75	>0.05				
Inbound body amplitude (m)									
Intercept - 2017, Female	0.03	0.01	63	23.06	<0.001				–
–Year - 2019	-0.01	0.01	39	-0.24	>0.05	**Sex*Year**	3.57	2	>0.05
–Male - 2019	-0.01	0.01	39	-1.76	>0.05				
Outbound ODBA (g) per minute									
Intercept - 2017, Female	6.06	0.18	65	34.53	<0.001				
–Male - 2019	-0.05	0.32	38	-0.16	>0.05				
Outbound ODBA (g) 10 minute sample									
Intercept - 2017, Female	0.81	0.01	65	60.67	<0.001				
–Male - 2019	0.03	0.02	38	1.39	>0.05				
Inbound ODBA (g) per minute									
Intercept - 2017, Female	6.09	0.18	65	33.28	<0.001				
Sex – Male	-0.07	0.25	38	-0.29	>0.05	**Sex**	8.90	1	0.003
Year – 2018	0.18	0.23	38	0.78	>0.05	**Year**	4.27	2	>0.05
–Male - 2019	-0.37	0.33	38	-1.13	>0.05				
Inbound ODBA (g) 10 minute sample									
Intercept - 2017, Female	0.78	0.02	65	51.53	<0.001				
–Male - 2019	-0.06	0.03	38	-2.20	0.03				
Take-off rate h^{-1} foraging									
Intercept - 2017, Female	3.54	0.25	65	14.27	<0.001				
–Year - 2019	0.87	0.32	38	2.69	0.01	**Sex*Year**	1.03	2	>0.05
–Male - 2019	-0.46	0.55	38	-0.83	>0.05				
Foraging ODBA (g) per minute									

Intercept - 2017, Female	6.02	0.21	65	28.34	<0.001				
Sex – Male	-0.17	0.29	38	-0.57	>0.05	**Sex**	5.10	1	0.003
Year – 2018	0.43	0.27	38	1.60	>0.05	**Year**	0.93	2	>0.05
Year – 2019	0.31	0.28	38	1.12	>0.05	**Sex*Year**	1.18	2	>0.05
–Male - 2019	-0.15	0.39	38	-0.39	>0.05				
Active ODBA (g) per minute									
Intercept	18.71	1.75	65	10.71	<0.001				
–Male - 2019	-0.89	3.17	38	-0.28	>0.05				

Table S2.5. The selection process for explanatory linear mixed models exploring factors that influence the ODBA per minute spent foraging and ODBA per minute of activity in each foraging trip for male and female chick-rearing northern gannets (*Morus bassanus*), between 2017 and 2019, Bass Rock, Scotland.

Rank	**Model**	**df**	**LogLik**	**AICc**	**ΔAICc**	**AICc weight**
Male foraging ODBA (g) per minute						
1	Take-offs	4	-52.36	113.5	0.00	0.822
2	Mass + Take-offs	5	-53.35	117.9	4.39	0.092
3	Take-offs + Year	6	-52.78	119.3	5.76	0.046
4	-	3	-57.07	120.6	7.10	0.024
Female foraging ODBA (g) per minute						
1	-	3	-49.14	104.8	0.00	0.802
2	Year	5	-48.66	108.6	3.83	0.118
3	Take-offs	4	-50.34	109.5	4.74	0.075
4	Take-offs + Year	6	-50.70	115.2	10.44	0.004
Male active ODBA (g) per minute						
1	Prop. foraging + Prop. travelling + take-offs	6	-15.00	43.7	0.00	0.933
2	Mass + Prop. foraging + Prop. travelling + take-offs	7	-16.60	49.5	5.82	0.051
3	Prop. foraging + Prop. travelling + Take-offs + Year	8	-17.17	53.4	9.68	0.007
4	Prop. Foraging + take-offs	5	-21.12	53.4	9.72	0.007
Female active ODBA (g) per minute						
1	Prop. foraging + Prop. travelling	5	9.38	-7.5	0.00	0.944
2	Prop. foraging + Prop. travelling + Year	7	9.11	-1.7	5.75	0.053
3	Prop. foraging + Prop. travelling + take-offs	6	4.88	4.1	11.55	0.003
4	Prop. foraging + Prop. travelling + Take-offs + Year	8	4.65	10.0	17.45	0.000

Table S2.6. The estimates of the best fit linear mixed models determined by model selection in Table S2.5, with bird identity as a random factor to account for multiple trips per bird, for male and female chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019, Bass Rock, Scotland.

Male foraging ODBA (g) per minute									
Intercept	4.67	0.32	32	14.40	<0.001				
Take-offs	0.25	0.07	32	3.80	<0.001	**Take-offs**	14.43	1	<0.001
Male Active ODBA (g) per minute									
Intercept	0.25	0.23	30	1.09	>0.05				
Prop. foraging	0.41	0.03	30	11.92	<0.001	**Prop. foraging**	142.01	1	<0.001
Prop. travelling	0.05	0.01	30	13.97	<0.001	**Prop. travelling**	195.11	1	<0.001
Take-offs	0.13	0.03	30	4.50	<0.001	**Take-offs**	20.27	1	<0.001
Female Active ODBA (g) per minute									
Intercept	1.99	0.11	30	17.48	<0.001				
Prop. foraging	0.05	0.01	30	13.34	<0.001	**Prop. foraging**	177.92	1	<0.001
Prop. travelling	0.05	0.01	30	17.08	<0.001	**Prop. travelling**	291.70	1	<0.001

Table S2.7. The linear model estimates for the relationships between pre-deployment body mass (g) and first foraging trip metrics of male and female chick-rearing northern gannets (*Morus bassanus*), between 2017 and 2019, Bass Rock, Scotland.

Metric	**Residual SE**	**DF**	**R^2**	**adjR^2**	**F**	**P**
Male mass (g)						
Duration (hours)	1.24	30	0.0001	-0.04	0.004	>0.05
Distance (km)	5.98	30	0.02	0.01	0.66	>0.05
Prop. flapping	0.10	21	0.45	0.42	17.03	**<0.001**
Body Amplitude (m)	0.003	21	0.24	0.21	6.79	**0.02**
Take-off rate h^{-1} foraging	1.57	21	0.01	-0.04	0.18	>0.05
Outbound ODBA (g)	0.43	21	0.01	-0.03	0.27	>0.05
Inbound ODBA (g)	0.59	21	0.07	0.02	1.50	>0.05
Foraging ODBA (g)	0.73	21	0.02	-0.02	0.53	>0.05

Female mass (g)						
Duration (hours)	14.18	36	0.13	0.1	5.21	**0.03**
Distance (km)	340.8	36	0.12	0.10	4.77	**0.04**
Prop. flapping	0.10	23	0.01	-0.04	0.28	>0.05
Body Amplitude (m)	0.004	23	0.006	-0.05	0.12	>0.05
Take-off rate h^{-1} foraging	2.25	23	0.09	0.04	1.90	>0.05
Outbound ODBA (g)	0.32	23	0.08	0.03	1.71	>0.05
Inbound ODBA (g)	0.28	23	0.01	-0.04	0.24	>0.05
Foraging ODBA (g)	0.40	23	0.01	-0.05	0.01	>0.05

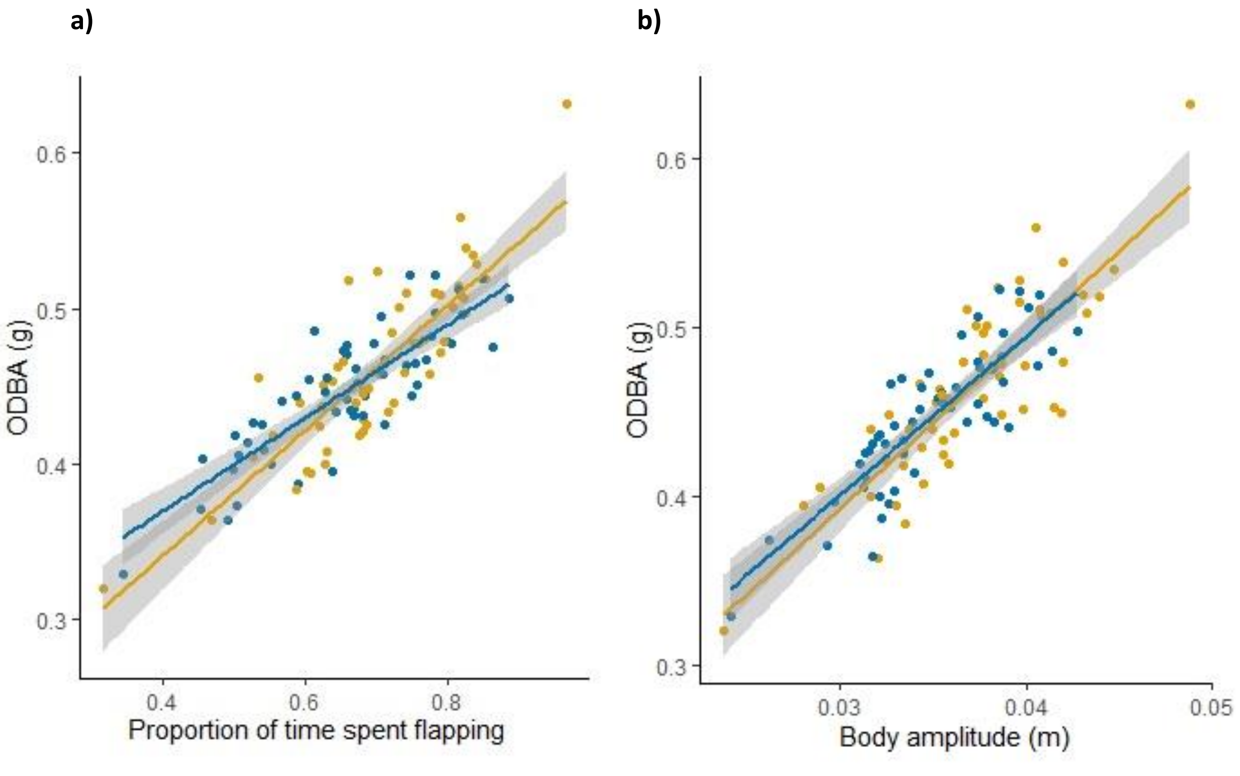
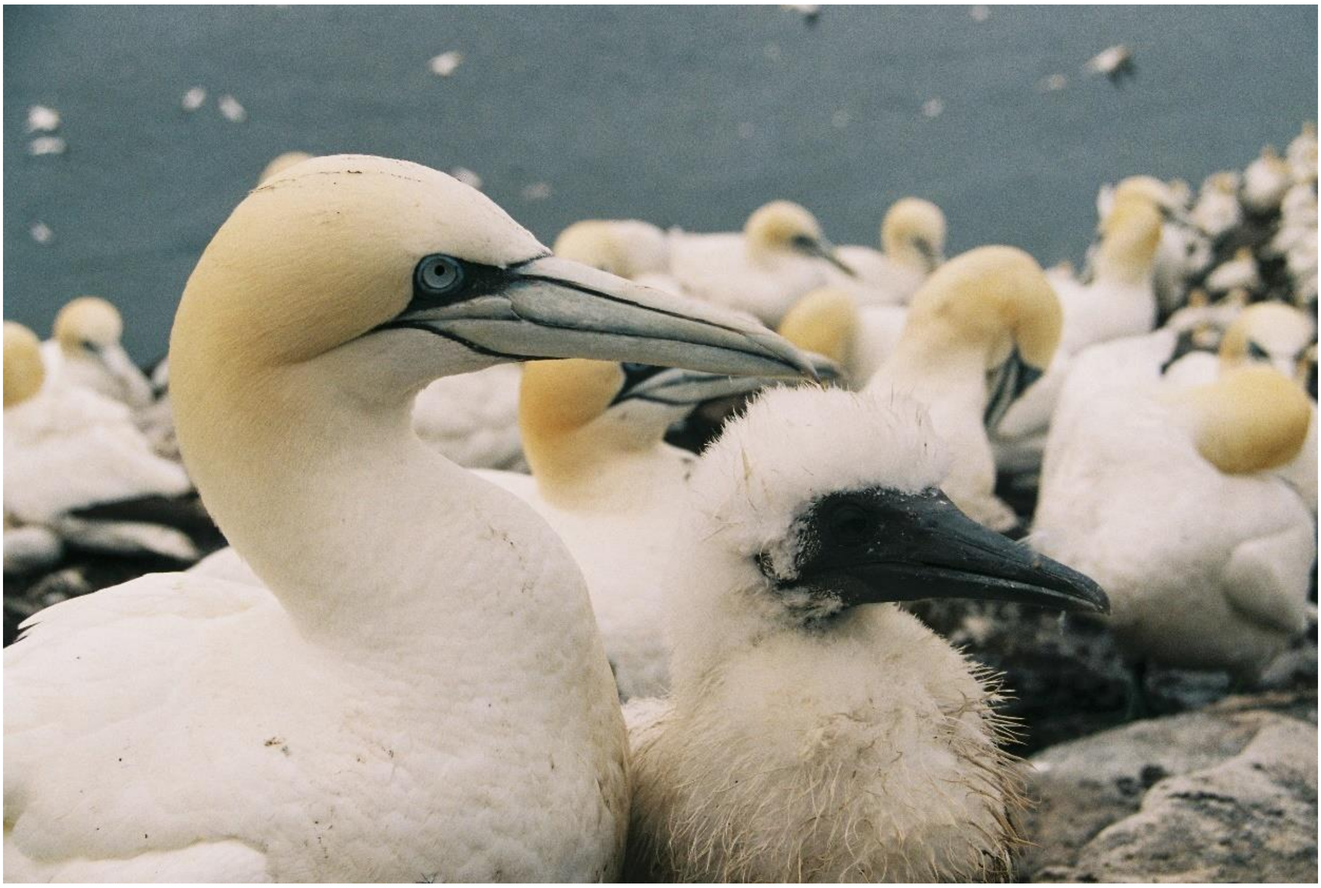


Figure S2.2. The relationship between the proportion of time spent flapping **(a)** and body amplitude (m) **(b)** with the ODBA (g) during a 10 minute sample of continuous flight of male (blue) and female (orange) chick-rearing northern gannets (*Morus bassanus*) on Bass Rock, Scotland, 2017-2019. Lines represent linear model predictions and 95% confidence regions in the shaded areas.

Chapter 3 **Individual differences in tri-axial movements and behaviour of northern gannets: incidence and implications**



A parent and chick await the return of the other on a damp day

3.1 Abstract

Individuality is prevalent across many taxa and is an important adaptation to consider in ecology. Individual differences during resource acquisition are common in marine central-place foragers, which often exhibit individual foraging site fidelity (IFSF). Yet it is unclear if IFSF is a consistent or flexible trait under different conditions, and therefore whether it is a constraint in a changing environment. Northern gannets, *Morus bassanus,* exhibit consistent individual differences in movements and behaviour with strong IFSF that persists across years. Using GPS loggers and accelerometers I investigated the consistency in foraging behaviour and energy expenditure of individual gannets and whether or not there were discernible energy and behavioural consequences of IFSF. I found that gannets were highly consistent in departure angle, return angle, foraging locations and energy expenditure (overall dynamic body acceleration) but with highly varying degrees of consistency among individuals and between the sexes. In females but not males, IFSF was significantly positively related to body mass and take-off rate during foraging bouts. In contrast among males, IFSF was significantly positively related to distance travelled, the proportion of each trip spent travelling, ODBA (overall dynamic body acceleration) per minute of trip and of inbound travel and was negatively associated with the proportion of each trip spent resting. These findings imply that the consequences of individuality were sex-specific, with greater IFSF being associated with enhanced foraging success among females but with elevated foraging effort among males. These results suggest individuals with more consistent foraging strategies may be more vulnerable to negative impacts of environmental change, and for this species, this could lead to sex-biased survival favouring males.

3.2 Introduction

Individual animals within populations vary considerably and consistently in their behaviour, which is often associated with group effects such as sex, breeding status and age (Durell 2000). Consistent behavioural differences that persist once the variation from such group effects are accounted for may be considered ‘individual specialisations’ (Bolnick *et al.,* 2003; Piper 2011). Within this field of study, individual specialisation is also referred to as individuality, individual consistency and individual differences (Votier *et al.,* 2010; Votier *et al.,* 2017; Morgan *et al.,* 2019). In the context of this research, they refer to the same phenomenon: behaviour that differs consistently among phenotypically similar individuals and can be characterised by the level of consistency at different time-scales, persistence or flexibility in different conditions, and the amount of flexibility within an individual (Bolnick *et al.,* 2003; Bell *et al.,* 2009). There has been a long-standing assumption in conservation that individuals are ecologically equivalent, but growing evidence suggests individuality has important implications for population management (Fretwell and Lucas 1969; Araújo *et al.,* 2011; Piper 2011; Boyd *et al.,* 2018). For example, a species’ resilience to habitat changes or loss may depend on the flexibility and extent of individual specialisations within the population (Owens *et al.,* 2019).

Given the significance of foraging to survival and fitness (Boggs 1992), individuality in traits related to resource acquisition are widely documented in a range of animals including sharks, small mammals, seabirds and bees (Kim *et al.,* 2012; Müller 2012; Ceia and Ramos 2015; Boone *et al.,* 2022). Individuality is often defined as the repeatability of metrics that represent behaviour, such as the foraging location, habitat selection, prey type and foraging strategy used by individuals (Bolnick *et al.,* 2003; Ceia and Ramos 2015; Wakefield *et al.,* 2015). To categorise a trait as repeatable there must be lower within-individual variance compared to among individuals. Thus, repeatability (r), measured by the ratio of variance within and among individuals, is commonly used to identify individual specialisations in foraging (Lessells and Boag 1987; Stoffel *et al.,* 2017).

Individual specialisation associated with foraging is common in generalist species and is understood to be adaptive, for instance by reducing competition among conspecifics (Bolnick *et al.,* 2003; Araújo *et al.,* 2011). Specialist individuals within a generalist species are thought to have an advantage when exploiting predictable resources due to increased foraging efficiency by reduced search time or higher prey capture rates (Patrick and Weimerskirch, 2017). Conversely generalism, or flexibility, within individuals is thought to be adaptive in unpredictable environments with the behavioural plasticity to switch prey or foraging environments (Candolin and Wong 2015). Identifying how individual specialisation manifests and discerning whether it persists when conditions are not predictable are crucial for predicting response to change in foraging habitat and to anthropogenic pressures (Durell 2000; Owens *et al.,* 2019).

A common form of individuality is the repeated use of the same foraging location, known as individual foraging site fidelity (IFSF). IFSF is prevalent in colonial central-place foragers across taxa e.g. ants (Beverly *et al.,* 2009), bats (Hillen *et al.,* 2010) and many air-breathing marine predators including pinnipeds and seabirds (Baylis *et al.,* 2012; Augé *et al.,* 2014; Lescroël *et al.,* 2020). In seabirds IFSF occurs in far-, mid- and short- ranging species and is described as the variation in foraging locations used by an individual but may also encompass how space is used more generally, for example by the bearing an individual departs the colony from (Hamer *et al.,* 2001; Patrick and Weimerskirch 2014; Morgan *et al.,* 2019).

How IFSF manifests can be species-specific and is crucial to determine for our understanding of the evolution and ecology of this phenomenon and its application to conservation measures (Owens *et al.,* 2019). One theory is the 'win-stay lose-shift' strategy (WSLS) which proposes individuals return to areas where foraging has been successful until it is not, when they will then seek a new area (Kamil 1983). Thus, species with this driver of IFSF may be more capable of adjusting to a changing environment. Conversely, IFSF may be driven by an 'always stay' strategy (Switzer 1993). This strategy assumes individuals develop 'site familiarity' which is thought to be a fitness advantage as individuals know where profitable resources areas are and target them repeatedly, increasing their foraging efficiency (Irons 1998; Piper 2011). This strategy would result in IFSF being consistent over longer timescales than a WSLS strategy, and both have been demonstrated in seabirds; e.g. site familiarity in northern gannets, *Morus bassanus*, and WSLS in breeding black-browed albatrosses, *Thalassarche melanophris,* (Wakefield *et al.,* 2015; Bonnet-Leburn *et al.,* 2021).

How an individual becomes familiar with a site, leading to IFSF, is also important to unravel when predicting population responses to change. If IFSF is determined intrinsically, as suggested by a study of animal personality, where boldness and shyness determined site fidelity in black-legged kittiwakes, *Rissa tridactyla*, (Harris *et al.,* 2019), or through exploration, learning, and subsequent memory for its continuation (Benhamou 1994; Ceia and Ramos 2015), individuals may not be able to adapt at the time-scales necessary to cope with changes to foraging habitats. Exploration as a mode of development of IFSF has been reported in several seabirds, with immature individuals occupying wider foraging niches than adults suggesting learning and experience over several years are a key process for IFSF development (Guilford *et al.,* 2011, Votier *et al.,* 2017, Owens *et al.,* 2019).

Beyond the drivers behind IFSF and how it develops in each indivudal, quantifying whether IFSF is beneficial to individuals is crucial for its application to conservation. To determine if IFSF may actually be a constraint, whereby individuals are unable to track changing conditions so are forced to return repeatedly to previously exploited spots, even if they're no longer as profitable, we need to determine the relationships between IFSF, key life history traits and measures of fitness. For example, if IFSF is persists under conditions with greater foraging effort or reduced breeding success, it could be hypothesised to be an inflexible trait and thus, a constraint. The extent of IFSF differs among individuals (e.g. Morgan *et al.,* 2019), suggesting there may be consequences to adopting IFSF, or interactions with other aspects of foraging behaviour. Consistency in other foraging behaviours and the relationships between these and IFSF are less well studied, though see Wakefield *et al.,* (2015) and Morgan *et al.,* (2019). Advances in bio-logging have opened up the study of energetics to free-ranging seabirds using proxies of energy expenditure from tri-axial accelerometers to bridge the gaps between foraging behaviour, physiology and individual fitness (Qasem *et al.,* 2012; Grémillet *et al.,* 2018; Wilson *et al.,* 2020). Yet few studies have considered the individual differences in the movement-based energy expenditure of behaviours or examined the relationship between IFSF and energy expenditure (Elliott *et al.,* 2014).

Here I focus on the individual differences in energy expenditure and relationships with IFSF in northern gannets, *Morus bassanus,* (hereafter gannets). Though considered generalists at a population level, gannets exhibit individual specialisations in departure direction from the colony, IFSF, search behaviour and diet during the breeding season and strong individuality in migration strategy and diet during the winter, which of both persist across years (Hamer *et al.,* 2001; Votier *et al.,* 2010; Patrick *et al.,* 2014; Wakefield *et al.,* 2015; Grecian *et al.,* 2019). Juvenile and immature gannets (fledging age to 5 years old) are less individually consistent in foraging areas and exhibit more flexibility, leading to the suggestion IFSF manifests as site familiarity through learning and experience for this species (Votier *et al.,* 2017).

Site familiarity may reduce energetic costs of finding food in mid- to long- ranging species like gannets (Piper 2011) but reducing costs through site familiarity is only part of the picture; individual skill and thus foraging success contribute to foraging efficiency (MacArthur and Pianka 1966). The extent of IFSF varies among individual gannets despite seemingly predictable foraging habitats and prey availability (Wakefield *et al.,* 2015; Grecian *et al.,* 2018), raising the question of whether or not there are consequences to IFSF and how these relate to fitness. If individuality is not consistently associated with efficient and successful foraging or individuals of better body condition, that could suggest it is a constraint and not a flexible trait, potentially resulting in individuals that cannot learn and adapt to environmental change.

Gannets at the world's largest colony, Bass Rock, Scotland, currently have high breeding success and are reaching capacity for available breeding sites (Mavor *et al.,* 2006; Murray *et al.,*2015; with pairs breeding in previously unoccupied sites each year I visited between 2017 and 2021). This provides an opportunity to study individual differences in time and energy and the consequences of IFSF in a seabird experiencing population growth and high intra-specific competition, that forages in relatively predictable and profitable habitats (Wakefield *et al.,* 2015; Grecian *et al.,* 2018).

In this chapter, I aim to explore potential consequences of individuality in the context of energy expenditure and fitness to consider future population responses to environmental change. I address this aim with the following objectives (1) quantify measures of individuality associated with energy expenditure and foraging effort in the foraging trips of gannets and (2) assess the energy and behavioural consequences of individual foraging site fidelity (IFSF). To accomplish these, I use GPS loggers and tri-axial accelerometers to calculate IFSF, time-activity budgets, take-off rates and proxies of energy expenditure to determine the IFSF and repeatability of trip and energy metrics of chick-rearing male and female northern gannets at Bass Rock in 2017 – 2019. I then use these metrics to identify whether or not there are consequential relationships between IFSF and key foraging trip metrics, energy expenditure and presumed correlates of fitness.

3.3 Methods

Data were collected in June-August 2017-2019 at Bass Rock (see Chapter 1 for description of site and Chapter 2 section 2.3.1 for data collection methods).

3.3.1 Trip metrics, energy expenditure and take-off rate

The calculation of distance travelled (km), duration (hours) and at-sea behaviours for each foraging trip were performed using the 'adehabitatLT' package in R version 1.3.959 (Calenge 2006; R Team 2015). At-sea behaviours were calculated using the tortuosity and step lengths to define foraging, travelling and resting whilst at sea, following Wakefield *et al.,* (2015) and explained in greater detail in section 2.3.2 in Chapter 2. Departure angle and return angle from the colony were calculated from the GPS data as the average bearing of the first 10 bearings >10km from the colony, and thus the last 10 bearings >10km from the colony.

Proxies of energy expenditure for foraging, travelling and overall activity during the trip were calculated from the accelerometry data processed following methods in section 2.3.5 of Chapter 2. Once processed, ODBA for foraging, travelling and overall activity were calculated by interpolating with the GPS behavioural classifications and assessed for error before being converted to rate per minute as described in section 2.3.5 of Chapter 2.

To investigate the potential benefits of IFSF I wanted to derive a metric of foraging success. I used the processed accelerometry data to calculate take-offs from the surface per trip, and then provide take-off rate h^{-1} foraging (hereafter take-off rate) by dividing the number of take-offs by the time spent foraging (details of methods in section 2.3.6 of Chapter 2). Take-off rate was determined to be a measure of foraging success, and Chapter 2 section 2.4.4. detail the results leading to the justification of take-off rate representing successful foraging.

I standardised the sample sizes for repeatability analyses by using the first three trips from individuals with three or more consecutive trips with both GPS and accelerometry data, resulting in a sample of 21 individuals (9 females and 12 males).

3.3.2 Individual repeatability within the population

To quantify the extent of individual consistency in different aspects of foraging behaviour and energy expenditure, I needed to calculate a measure of repeatability for each individual and the associated foraging trip metric. For each foraging trip metric, excluding departure and return angles, I used GLMMs in the R package "rptR" v.0.6.405 (Stoffel *et al.,* 2017) to calculate repeatability (r) values and P values from the ratio of within-group and between-group variance. GLMMs were used because they allow the calculation of variance with the inclusion of fixed effects (Carneiro *et al.,* 2017). In order to determine the variance due to individuals, I treated group effects (sex and year) as fixed effects and bird identity as a random effect. To investigate whether or not males and females had different repeatability in trip metrics, I also calculated r values for the sexes for the sexes separately, with year as a fixed effect and bird identity as a random effect. I reported the adjusted r values for bird identity, which accounts for the variance of fixed effects and thus leaves that within individuals. Trip duration, distance travelled, ODBA of inbound travel and proportion of time spent foraging were sqrt-transformed to meet the assumptions of normality in GLMM residuals and model residuals had equal variance and were independent of one another.

Departure and return angles do not meet the assumptions of a GLMM so I used circular ANOVAs in the R package “circular” v.0.4-7 (Agostinelli and Lund 2011) to calculate between and within subject variance, then calculated repeatability as the ratio of between-subject variance to total variance, following Lessells and Boag (1987). Associated standard errors for these measures were calculated using equation 1 (Becker 1984).

Equation 1:

$$\mathrm{SE}\sqrt{\frac{2(1-r)^2\{1+(k+1)r]^2}{k(k-1)(n-1)}}$$

n=number of individuals
r=repeatability
k= number of measurements per individual

3.3.3 Calculating individual consistency in space - IFSF

Following Chapter 2 section 2.3.3 I identified core foraging areas of each bird by kernel analysis of the utilisation distribution (UD) of foraging locations. Using ‘adehabitatHR’ package in R (Calenge 2006), I obtained foraging areas (95% UDs) over a 1km^2 grid with a smoothing parameter of 10km for each foraging trip. I then estimated the extent of spatial similarity in foraging locations for each individual using Bhattacharyya’s affinity (BA; Bhattacharyya 1943) of the foraging UDs, giving a measure of spatial similarity between 0-1 (where zero is no similarity, and 1 is complete overlap).

3.3.4 Behavioural and energetic consequences of IFSF

I wanted to investigate whether or not IFSF affects how gannets spend their time (trip duration, distance, time-activity budgets and take-off rate) and energy (ODBA of foraging, outbound travel, inbound travel and ODBA of activity during a trip) at-sea, and whether or not any such relationship has any consequence for a bird’s body mass. LMMs were used to investigate the relationships between IFSF and foraging trip metrics. I used the time and energy metrics listed above as the response variables, and individual BA scores as the explanatory, with bird identity as the random effect to account for repeated measures. The data met the assumptions of LMMs; variables were normally distributed or were transformable to normality (sqrt-root transformations of trip duration, distance travelled, proportion of time spent foraging, travelling and resting and travelling ODBA per minute) leading to normally distributed model residuals, residuals had statistically equal variance and the factors were independent of one another. Sexes were considered and modelled separately throughout due to the sex-specific foraging behaviour and energy expenditure identified in Chapter 2 could lead to sex-specific ecological consequences (Angel *et al.,* 2015).

In this study, body mass was used instead of size corrected mass (SCM) as an indicator of body condition. Body condition is often measured as mass of an individual relative to its size, for example by culmen, tarsus and wing length (Jacobs *et al.,* 2012). SCM would be preferable to absolute body mass as it allows the comparison of the relative size of energy reserves of individuals and avoids the assumption that morphologically larger individuals are of better body condition because of greater mass (Peig and Green 2009). This calculation was unfeasible in the scope of this study because of limitations in the field; some of the study birds had not had biometrics measured that season, and I chose not to re-measure individuals to reduce handling time and thus stress on the bird. In addition, measurements in the field were not taken by the same observer for every bird, leaving the potential of variation caused by human error. Therefore, inferences of body condition from mass alone should be taken as an estimation. However, it is also worth bearing in mind that SCM is only slightly better predictor of body condition than mass alone, explaining at most 5-10% more variation in lipid rich seabirds, of which this is highly species- and time-specific (Jacobs *et al.,* 2012).

3.4 Results

3.4.1 Individual consistency in foraging behaviours and energy expenditure

There was statistically significant repeatability within individual birds for a range of foraging trip metrics (Table 3.1), with return angle, proportion of trip spent travelling, ODBA per minute of activity during a trip, and ODBA per minute of outbound flight being particularly high ($r > 0.5$, $P < 0.01$ in each case). The proportion of each trip spent resting, ODBA per minute of inbound travel and per minute of foraging also had significantly higher within-group than between-group variance, although with lower mean repeatability ($r = 0.36 - 0.47$, $P < 0.05$ in each case). No significant individual repeatability was found for proportion of trip spent foraging, take-off rate, trip duration or distance travelled ($r < 0.1$, $P > 0.05$ in each case; Table 2).

There were some differences between the sexes in the repeatability of trip metrics (Table S3.1). When repeatability values were calculated separately for each sex, females were significantly repeatable within individuals and males were not for proportion of each trip spent resting and ODBA per minute of inbound travel ($r = 0.61$, $P = 0.007$ vs. $r = 0.35$, $P > 0.05$; $r = 0.66$, $P = 0.003$ vs. $r = 0.20$, $P > 0.05$, respectively). Conversely females were not repeatable and males were significantly repeatable within individuals in the proportion of each trip spent travelling and ODBA per minute spent foraging ($r = 0.43$, $P >0.05$ vs. $r = 0.56$, $P = 0.004$; $r = 0.32$, $P > 0.05$ vs. $r = 0.43$, $P = 0.03$, respectively). Both sexes were significantly repeatable in ODBA per minute of outbound travel and activity during a trip, but females were more so than males ($r = 0.71$, $P < 0.001$ and $r = 0.44$, $P = 0.03$, respectively, for outbound travel; $r = 0.74$, $P < 0.001$ and. $r = 0.45$, $P = 0.02$, respectively, for overall activity.

3.4.2 Individual consistency in space - IFSF

Gannets had relatively high consistency in foraging areas (BA score = 0.51 on average) and the extent of consistency varied greatly among individuals (range of BA scores = 0.27 – 0.79; Figure 3.1; Table 3.2). The spatial consistency in foraging areas of individuals did not differ between sexes ($W = 46$, $P > 0.05$) or among years (2017-2018; $W = 33$, $P >0.05$, 2017-2019; $W = 9$, $P >0.05$, 2018-2019; $W=24$, $P >0.05$).

3.4.3 Behavioural and energetic consequences of IFSF

There were sex-specific relationships between IFSF and time-activity budgets, energy expenditure, fine-scale foraging behaviour and body mass. Trip duration was not related to IFSF for either sex (females $F_{1,6} = 0.05$, $P > 0.05$, males $F_{1,10} = 0.81$, $P > 0.05$). Males with higher IFSF travelled greater total distances during foraging trips (Figure 2a; $F_{1,10} = 6.22$, $P = 0.03$), and thus spent a significantly higher proportion of each trip travelling, and significantly less time resting (Figure 3.2b and 2c; $F_{1.10} = 8.77$, P =0.01, $F_{1,10} = 0.03$). In contrast, these relationships were not significant for females ($F_{1,6} = 0.31$, P >0.05, $F_{1,6} = 0.19$, P >0.05 and $F_{1,6} = 0.27$, P >0.05, respectively). IFSF did not affect the proportion of a trip spent foraging for either sex (females $F_{1,6} = 0.32$, P >0.05, males $F_{1,10} = 0.45$, P >0.05). However, the number of take-off rate significantly increased with IFSF in females, whereas there was no such relationship in males (Figure 2d; females $F_{1,6} = 7.43$, P = 0.03, males $F_{1,10} = 3.23$, P >0.05).

The ODBA per minute spent foraging and during outbound travel were not significantly related to IFSF for either sex (females, $F_{1,6} = 0.73$, P > 0.05 and $F_{1,6} = 1.28$, P > 0.05, respectively; males, $F_{1,10} = 0.04$, P > 0.05 and $F_{1,10} = 0.96$, P >0.05, respectively). However, both ODBA per minute of activity during a trip and ODBA per minute of inbound travel significantly increased with IFSF for males, although neither was significant for females (Figure 3.2e and 2f; males, $F_{1,10} = 5.55$, P = 0.04 and $F_{1,10} = 13.11$, P = 0.005, respectively; females, $F_{1,6} = 0.01$, P > 0.05 and $F_{1,6} = 2.23$, P > 0.05, respectively). Figure 3.2g suggests a positive relationship between body mass and IFSF for both sexes, but while this relationship was statistically significant for females ($F_1 = 8.65$, P = 0.008) it was only marginally so for males ($F_1 = 4.08$, P = 0.05).

Table 3.1. Mean (SD) foraging trip metrics of chick-rearing northern gannets (*Morus bassanus*) at Bass Rock in 2017-2019 (N = 21 birds, 63 trips), with mean repeatability value (r), standard error (SE), 95% confidence intervals (CI) and P values of each metric, ordered from the most to the least repeatable.

	Mean (SD)	**r**	**SE**	**CI**	**p**
Return angle (°)	49.3 (0.2)	0.71	0.10	NA	NA
Proportion of trip spent travelling	30.6 (22.7)	0.59	0.12	0.34 - 0.77	<0.001
ODBA (g) per minute of activity during trip	17.9 (11.0)	0.58	0.11	0.33 - 0.76	<0.001
ODBA (g) per minute of outbound travel	37.4 (8.1)	0.54	0.13	0.24 - 0.72	<0.001
Proportion of trip spent resting	53.1 (24.9)	0.47	0.15	0.17 - 0.71	0.001
Departure angle (°)	49.3 (0.3)	0.43	0.11	NA	NA
ODBA (g) per minute of inbound travel	37.2 (8.7)	0.40	0.15	0.12 - 0.65	0.008
ODBA (g) per minute of foraging	37.9 (8.9)	0.36	0.15	0.08 - 0.60	0.02
Take-off rate h^{-1} foraging	20.0 (10.0)	0.09	0.13	0.00 - 0.39	>0.05
Proportion of trip spent foraging	16.1 (13.1)	0.03	0.11	0.00 - 0.37	>0.05
Duration (hrs)	23.1 (25.3)	0.02	0.05	0.04 - 0.18	>0.05
Distance (km)	492.2 (604.1)	<0.01	0.10	0.00 - 0.30	>0.05

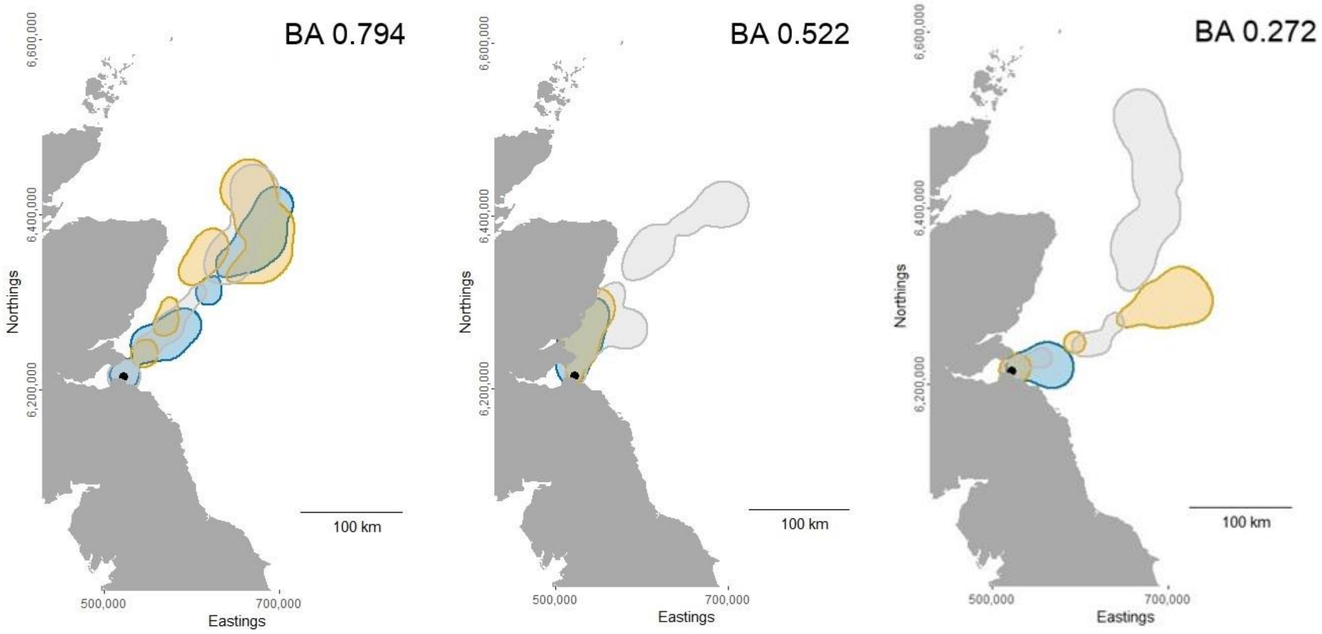


Figure 3.1. 95% utilisation distributions (UDs) of the most (left), mean (middle) and least (right) repeatable use of foraging areas by individual chick-rearing northern gannets (*Morus bassanus*). UDs were calculated from active foraging locations for three consecutive foraging trips (trip 1 = blue, trip 2 = orange and trip 3 = grey). Black shape shows location of Bass Rock.

Table 3.2. The similarity (BA scores) of 95% UD foraging areas for individual chick-rearing northern gannets (*Morus bassanus*) over three consecutive foraging trips, ordered from highest to lowest BA score.

Bird identity	**Sex**	**Year**	**BA score**
1	Male	2018	0.79
2	Male	2017	0.72
3	Male	2018	0.72
4	Male	2018	0.65
5	Male	2017	0.62
6	Female	2018	0.62
7	Female	2018	0.61
8	Female	2018	0.58
9	Female	2018	0.55
10	Female	2017	0.54
11	Male	2018	0.52
12	Male	2018	0.45
13	Female	2017	0.42
14	Female	2018	0.41
15	Male	2018	0.40
16	Male	2019	0.39
17	Male	2018	0.37
18	Male	2017	0.37
19	Female	2018	0.34
20	Male	2019	0.33
21	Female	2017	0.27

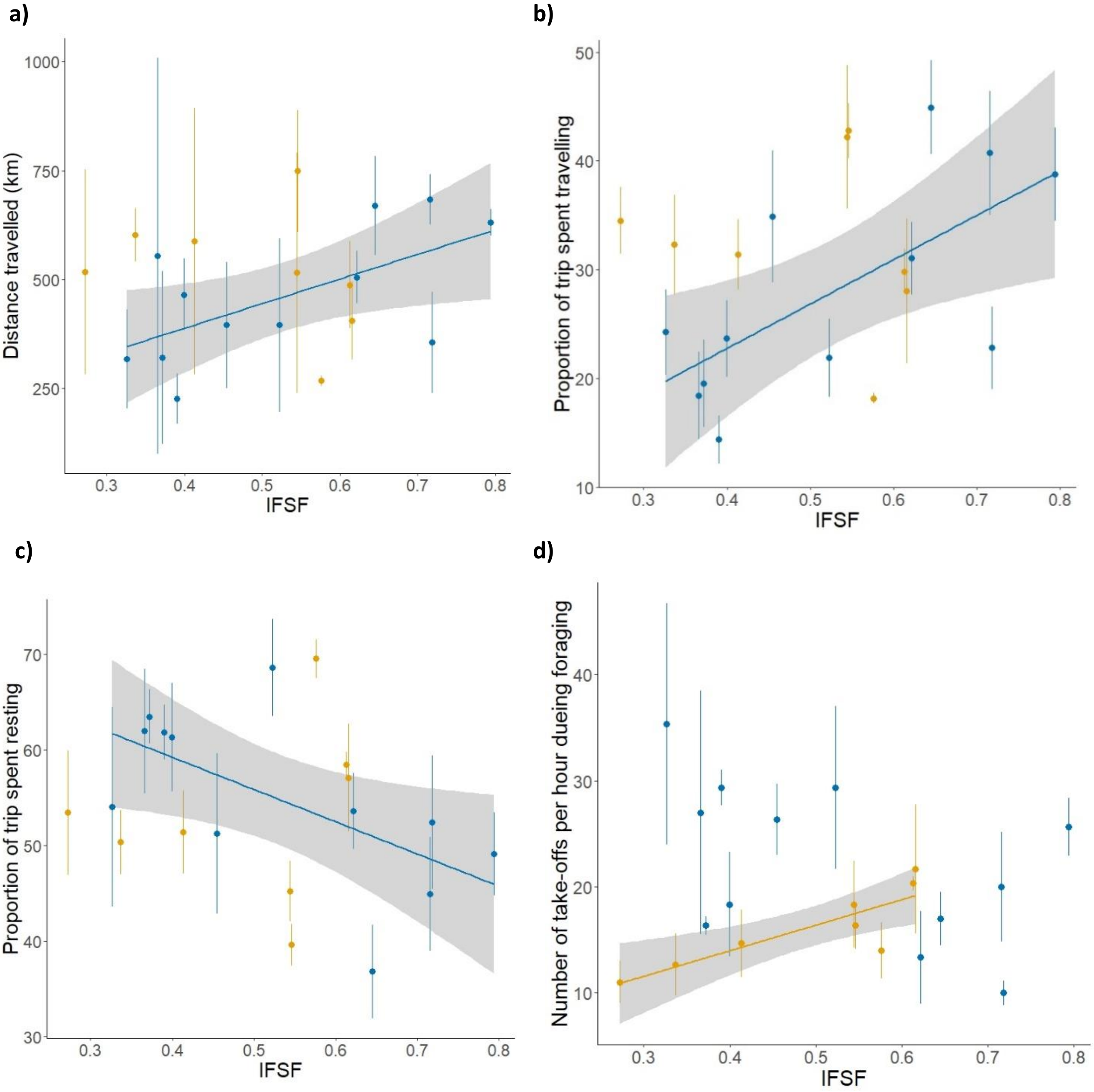


Figure 3.2. The sex-specific (blue = males, orange = females) relationships between IFSF (mean ± 1SE BA score for three consecutive foraging trips) and: (a) distance travelled (km); (b and c) proportion of each trip spent (b) travelling and (c) resting; (d) take-off rate per hour foraging; (e) ODBA per minute of activity during each trip (f) ODBA per minute of inbound travel, and; (g) bird mass for chick-rearing northern gannets (*Morus bassanus*). Lines represent linear model trends (solid = significant) with 95% confidence regions in grey. N = 21 birds, 63 trips.

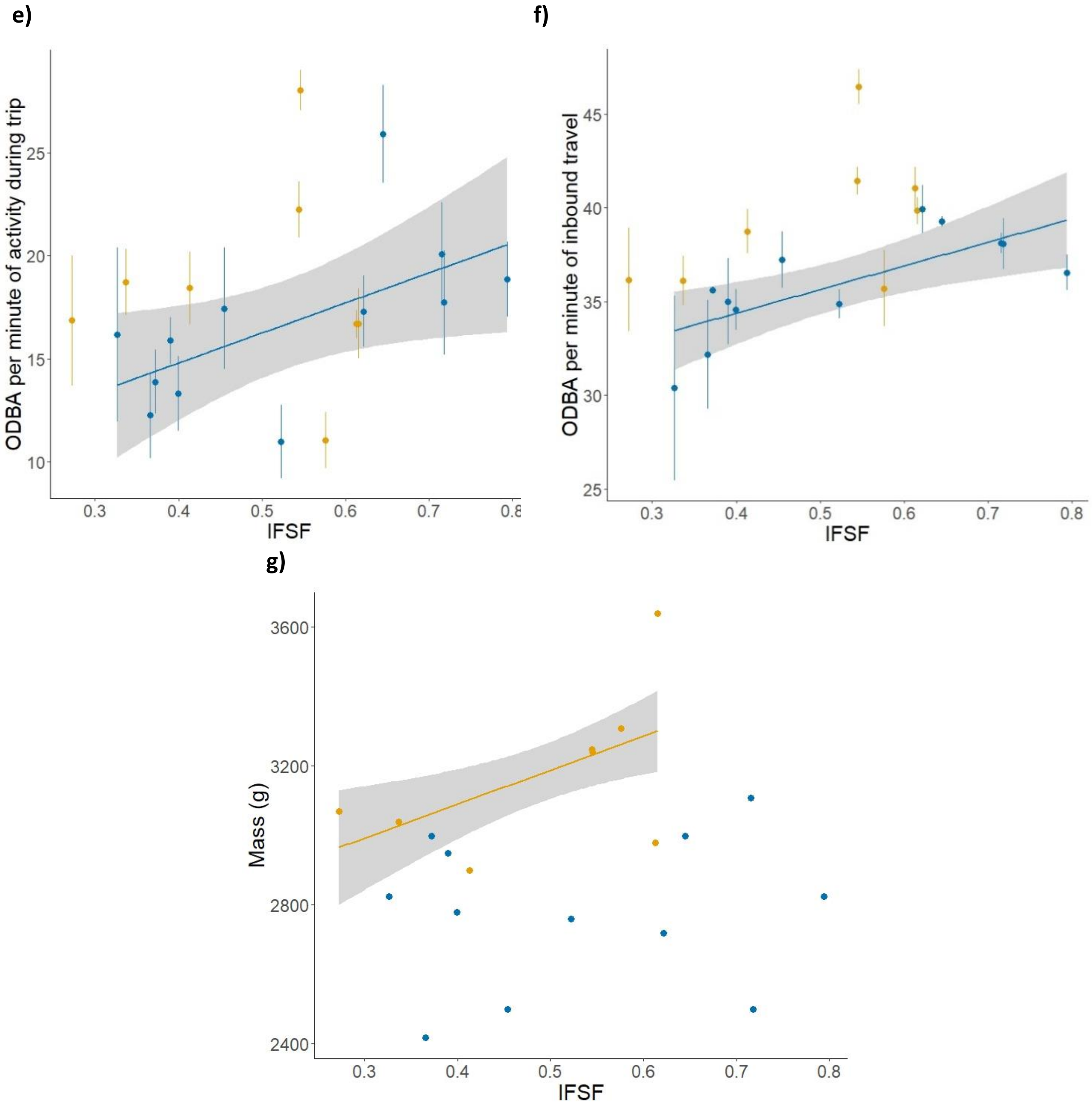


Figure 3.2. continued The sex-specific (blue = males, orange = females) relationships between IFSF (mean ± 1SE BA score for three consecutive foraging trips) and: (a) distance travelled (km); (b and c) proportion of each trip spent (b) travelling and (c) resting; (d) take-off rate per hour foraging; (e) ODBA per minute of activity during each trip (f) ODBA per minute of inbound travel, and; (g) bird mass for chick-rearing northern gannets (*Morus bassanus*). Lines represent linear model trends (solid = significant) with 95% confidence regions in grey. N = 21 birds, 63 trips.

3.5 Discussion

This study shows individuality in gannets extends to the energy expended for different behaviours and in trips overall, despite little consistency in trip duration, distance travelled and the metrics associated with foraging behaviour and success. These novel metrics applied to individuality suggest gannets could be at an energetic ceiling, whereby they are expending maximum effort available to them, but how that energy is expended behaviourally remains flexible. I found sex-specific consequences of spatial consistency; my findings indicate strong IFSF is advantageous to females but not for males, and conversely, females may therefore be more vulnerable to negative impacts of environmental change.

Before investigating the objectives of this study using novel metrics of individuality, I wanted to determine if the extent of individual consistency in space and time at Bass Rock 2017 – 2019 supports previous findings in gannets, thus allowing further conclusions to be considered in the context of typical levels of individual consistency for this species. In keeping with previous studies of individuality at Bass Rock (Wakefield *et al.,* 2015; Grecian *et al.,* 2018) and elsewhere (Patrick *et al.,* 2014), individuals were generally highly repeatable in foraging locations (Table 3.2) and departure angle, and not repeatable in trip duration or distance travelled (Table 3.1). Foraging paths of individuals were generally consistent but trips varied more in duration and distance, perhaps in response to local changes in environmental conditions, prey availability or individual energy requirements (Grecian *et al.,* 2018). Return angle was the most repeatable metric (Table 3.1), probably as a consequence of individuals returning in a straight line from foraging locations that were themselves repeatable. As discussed in Chapter 2, the costs of inbound flight are likely affected by the increased payload of carrying food, the need to return quickly to feed chicks, and in response to wind conditions faced from prevailing westerly winds on the return journey (Lewis *et al.,* 2004; Pennycuick 2008; Lane *et al.,* 2019). Significant individual repeatability of return angle may result from birds reducing these costs by using the most direct return route. Thus, barriers such as offshore windfarms could disrupt this inflexible aspect of an individual's foraging path should be carefully considered as a potential risk to gannets. This is particularly relevant for the Bass Rock breeding colony, where construction is underway within gannet foraging paths and more sites have been granted planning consent (Pollock *et al.,* 2021).

Despite little individual consistency of trip duration and distance travelled, individuals were highly consistent in the ODBA per minute of activity during a trip (Table 3.1). ODBA is an established proxy of energy expenditure (Hicks *et al.,* 2017; Wilson *et al.,* 2020), so statistical repeatability within individuals here suggests the effort an individual bird put into foraging trips per unit time was consistent. Seabirds can be highly individual and consistent in metabolic rate (Elliott *et al.,* 2014), so perhaps consistent effort during the trip reflected this. Other studies have shown birds to balance their own energy requirements and current body condition with those of their chick, which vary with chick age (Weimerskirch *et al.,* 1997). Consistency in a measure of effort over a trip may therefore represent successful regulation of effort. However, it could also indicate the presence of a limit, or energetic ceiling, on the effort each individual could put into trips during chick-rearing (Elliott *et al.,* 2014).

This is perhaps a limitation of quantifying individuality over three trips; it is a short time-scale in the context of a breeding season. Measuring body condition throughout a breeding season and quantifying measures of fitness to compare to individual repeatability in trip effort defined by ODBA would shed light on whether consistency in overall trip effort indicates energy regulation or an energetic ceiling. For example, higher IFSF in female European shags, *Phalacrocorax aristotelis*, was associated with earlier hatch dates and higher body condition (Morgan *et al.,* 2019). As gannets currently seem to have high and consistent breeding success in their northern range, the fitness consequences of consistency in trip effort could be more useful to explore in the southern part of their range, where gannets are experiencing declines in annual survival and population sizes (Murray *et al.,* 2015; Grémillet *et al.,* 2020).

Travel was a significantly consistent component of foraging trips for individual gannets in the proportion of each trip spent travelling and the ODBA per minute of outbound and inbound travel (Table 3.2). Individual consistency in time spent travelling was presumably related to IFSF, at least for males (Figure 3.2b, Table S3.1), while repeatability in metrics associated with flight effort may have resulted at least in part from consistent differences in flight efficiency related to differences in body mass, wing area and wing loading, as explored in Chapter 2. The ODBA per minute of inbound flight was more repeatable in individual females than for males (Table S3.1) likely related to greater body mass leading to a greater need for efficiency to reduce flight costs (Taylor and Thomas 2002).

There was less evidence of individual consistency in metrics associated with foraging behaviour than those associated with travelling; the proportion of time spent foraging and take-off rate had low individual repeatability, i.e. the within-individual variance was not significantly less than that of the population (Table 3.1). In other studies the individual consistency of the foraging behaviours in gannets has varied; dive depth and shape were significantly repeatable within individual gannets breeding at Grassholm Island, Wales, though the repeatability values (r) suggested less repeatability than other metrics (r = 0.18 for both metrics, Patrick *et al.,* 2014). In contrast, dive shape was not significantly repeatable for individual birds at Bass Rock, but mean dive depth and dive rate over the trip were, although there was significant inter-annual variation in repeatability values (r) in the two years studied for dive rate (2011, r = 0.5, P <0.05; 2012, r = 0.04, P >0.05; Wakefield *et al.,* 2015). Assuming take-off rate is broadly comparable to dive rate, our results differ from those previously found at Bass Rock. Gannets may have inter-annual variation in the level of individual consistency in dive rate, as suggested by the very different r values each year in Wakefield *et al.,* (2015) and lack of significant individual repeatability of take-off rate in the three years of this study. Therefore, consistency in dive rate may not represent individual specialisation, it may instead occur as a by-product of the foraging environment. In this study and within this thesis, take-off rate is likely equivalent to foraging success, thus also implying birds do not have the same degree of success whilst foraging between consecutive trips.

Although the proportion of time spent foraging and take-off rate were not significantly repeatable within individuals, ODBA per minute spent foraging was, suggesting individuals were consistent in the effort that could be dedicated to foraging behaviour (Table 3.1). This consistency could be indicative of individual specialisation as ODBA per minute spent foraging encompasses all behaviours and time spent exhibiting them. It may also represent the effect of body condition and individual metabolic rate on the effort that can be dedicated to foraging behaviour. Individual consistency in foraging effort with flexibility in foraging behaviours perhaps highlights the current success of this species, but also draws attention to a potential vulnerability – there is not individual flexibility in energy dedicated to foraging, whether because individuals function at capacity due to individual body condition and metabolic rate, or because this is an 'optimum' level needs to be determined when considering the vulnerability of this species to change.

The overarching conclusion from the investigation into the relationships between IFSF and foraging trip metrics is they were largely sex-specific (Figure 3.2a-g), suggesting that previously documented sex differences in gannet foraging behaviour, migration and demography (Cleasby *et al.,* 2015; Deakin *et al.,* 2019) extend to the consequences and drivers of individual differences. Distance travelled (km), proportion of time spent travelling, ODBA per minute of activity during a trip and ODBA per minute of inbound travel all significantly increased with IFSF for males, and the proportion of each trip spent resting significantly decreased with IFSF for males (Figure 3.2a-f), which may explain the lack of significant individual repeatability in the proportion of each trip spent resting for males, in contrast to females (Table S3.1). These results imply that males exhibiting greater IFSF expended greater effort during their foraging trips; they travelled further and expended more energy per unit time associated with return travel to the colony and over the whole trip than males with lower IFSF. These findings suggest that among males, IFSF may have resulted from birds inherently relying on memory to locate potential feeding areas (Switzer 1993; Piper 2011) rather than adopting a more flexible foraging strategy, echoing calls from previous studies (Weimerskirch 2007; Wakefield *et al.,* 2015) for a reappraisal of the view that-seabirds are necessarily highly flexible foragers (Lack 1968). Nonetheless there was a marginally significant positive relationship between IFSF and body mass for males, implying a potential benefit of IFSF, for instance through improved site familiarity (Irons 1998). If site familiarity is the underlying cause of IFSF in seabirds (e.g. Piper 2011; Wakefield *et al.,* 2015), then perhaps males follow a known path, exhibiting high individual repeatability in departure bearing, but if other resources are found along the way, they have the plasticity to switch, resulting in lower effort associated with travel and trip metrics. This 'trapline strategy' coined by Wanless *et al.,* (1990) has been suggested in other seabirds and gannets whereby individuals have no obligation to reach a particular patch and thus could engage in foraging opportunities when they arise on the outbound journey (Wakefield *et al.,* 2015; Borrmann *et al.,* 2019). This could support the notion that there are benefits to displaying flexibility represented by better body condition in individuals that switched diets in a previous study of gannets (Grecian *et al.,* 2019), or conversely better body condition allows individuals to adopt more risky behaviours (Geary *et al.,* 2019). This seems logical enough, but the lack of this pattern in females suggests there may be other factors involved; there may less flexibility in female foraging behaviour or that IFSF is of greater benefit to females than males.

In contrast to males, both body mass and take-off rate during foraging bouts significantly increased with IFSF for females. Assuming that take-off rate was related to foraging success (see Chapter 2) these findings indeed suggest a greater benefit of higher IFSF for females than for males. Isotopic niche separation between the sexes has been demonstrated at this colony and others (Cleasby *et al.,* 2015; Clark *et al.,* 2021) so perhaps the consequences of IFSF are a by-product of sex differences in prey availability; where the resources exploited by females were more consistent and predictable than those by males, as seen in other marine central-place foragers (Baylis *et al.,* 2012).

Under the assumption that higher body mass is an indicator of better body condition as described in the methods, IFSF is associated with females of better condition, and presumably fitness. In gannets, body mass has previously only been shown to be related to individual repeatability in trip duration (Wakefield *et al.,* 2015), but in other seabirds fitness has been correlated with individual specialisation, and in females only for the European shag (Patrick and Weimerskirch 2014; Morgan *et al.,* 2019). Therefore, it seems more likely that IFSF has different consequences for each sex, and the drivers of individual consistency are sex-specific; to reduce intra-specific competition by different foraging strategies and ensure breeding success.

Individual experience and exploration has been considered as a mechanism for the development of IFSF and individual consistency of foraging behaviour in gannets (Votier *et al.,* 2017). A factor not addressed in the scope of this study is the potential effect of age on individual consistency in foraging behaviours and energy expenditure. Age is known to have an effect on the degree of IFSF between immatures and adult gannets during the breeding and non-breeding seasons (Votier *et al.,* 2017; Grecian *et al.,* 2019). In European shags, older individuals have higher breeding success and are more efficient foragers with greater foraging success during the breeding season (Daunt *et al.,* 2007a; Daunt *et al.,* 2007b). Thus, differences and flexibility in individual consistencies may also be influenced by the age of breeding adults. Studying the age of adult gannets is difficult; there are currently no substantiated methods of determining the age of a breeding adult without the bird having been ringed as a juvenile or immature, when age is discernible from plumage (Nelson 2002). Due to the long pre-breeding period (5 years), well-established ringing and re-sighting efforts are required to have an individual of known age breeding within an accessible part of any breeding colony (Nelson 2002).

Previous studies have postulated that reducing intra-specific competition is not a driver of individuality in gannets (Votier *et al.,* 2017) but when viewed in the context of a partnership, having sex-specific individual specialisations may give gannet chicks improved chances of growth, survival and fledgling success under the varied conditions of the foraging environment and reduced competition between the sexes (e.g. Lane *et al.,* 2019). Partnership studies of breeding gannets are an under-explored area that could be key for developing greater understanding of sex-specific foraging during chick-rearing, particularly in relation to energy expenditure and the extent and purpose of individual specialisation. Such specialisations extend beyond the highly energetically demanding breeding season, and so any advantages seem likely to span longer time-scales than single breeding seasons, perhaps including carry-over effects for future breeding success (Grecian *et al.,* 2018).

The discussion within this study highlights the complexity of individuality in long-lived central-place predators. The key findings are that gannets are highly consistent in the effort they can give to foraging, travelling and trips overall, but how that energy is expended remains flexible, perhaps pointing to the current success of this species at this colony. However, metrics of lower effort were not always associated with IFSF, suggesting gannets cannot always ‘choose’ the optimal location to forage in. Thus, these results provide reasonable doubt to the assumption that foraging individuals choose the optimal habitat available, violating a key assumption of the Ideal Free and Ideal Despotic models (Fretwell & Lucas 1969), two of the main theories in foraging ecology used in conservation strategies (Boyd *et al.,* 2018; Owens *et al.,* 2019). An additional consideration in species management is the discovery that sexes differ in the consequences of IFSF. Though both sexes exhibit IFSF at similar levels, greater IFSF is associated with more effort in males compared to females. Therefore, when planning changes to foraging areas or predicting the impacts of change with population modelling, individuals cannot be assumed to be ecologically equivalent. Instead, the population-level consequences of anthropogenic factors and environmental change are determined through consistent individual differences, and this individuality can be sex-specific.

3.6 References

Agostinelli C and Lund U (2011) R package: Circular Statistics (version 0.4-3). Available from: https://r-forge.r-project.org/projects/circular/

Angel LP, Wells MR, Rodríguez-Malagón MA, Tew E, Speakman JR, Arnould JPY (2015) Sexual Size Dimorphism and Body Condition in the Australasian Gannet. *PLOSone* doi:10.1371/journal.pone.0142653

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecology Letters* 14(9): 948–958, doi: 10.1111/j.1461-0248.2011.01662.x.

Baylis AMM, Page B, McKenzie J, Goldsworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats. *Marine Mammal Science* 28(2): 276–294, doi: 10.1111/j.1748-7692.2011.00487.x.

Becker WA (1984) Manual of Quantitative Genetics. *4th edn.* Academic Enterprises, Pullman, WA.

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatabililty of behaviour: a meta-analysis. *Animal Behaviour* 77(4): 771–783, doi: 10.1016/j.anbehav.2008.12.022.

Bennison A, Giménez J, Quinn JL, Green JA, Jessopp M (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *Royal Society Open Science* 9: 210520, doi: 10.1098/rsos.210520.

Beverly I, McLendon H, Nacu S, Holmes S, Gordon DM (2009) How site fidelity leads to individual differences in the foraging activity of harvester ants. *Behavioral Ecology,* 20(3): 633–638, doi:10.1093/beheco/arp041

Bhattacharyya A (1943) On a measure of divergence betweentwo statistical populations defined by their probability distri-butions. *Bulletin of the Cacutta Mathematical Society* 35: 99–109.

Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist* 161(1): 1–28, doi: 10.1086/343878.

Bonnet-Lebrun AS, Collet J, Phillips RA (2021) A test of the win-stay–lose-shift foraging strategy and its adaptive value in albatrosses. *Animal Behaviour.* 182:145-51.

Boone SR, Brehm AM, Mortelliti A (2022) Seed predation and dispersal by small mammals in a landscape of fear: effects of personality, predation risk and land-use change. *Oikos* (2)

Borrmann RM, Phillips RA, Clay TA, Garthe S (2019) High foraging site fidelity and spatial segregation among individual great black-backed gulls. *Journal of Avian Biology* 50(12): 1–10, doi: 10.1111/jav.02156.

Boyd C, Barlow J, Becker EA, Forney KA, Gerrodette T, Moore JE, Punt AE (2018) Estimation of population size and trends for highly mobile species with dynamic spatial distributions. *Diversity and Distributions* 24:1-12

Calenge C (2006) The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516–519, doi: 10.1016/j.ecolmodel.2006.03.017.

Candolin U and Wong BBM (2015) *Behavioural responses to a changing world: Mechanisms and consequences*, *Behavioural Responses to a Changing World: Mechanisms and Consequences*. Oxford: Oxford University Press. doi: 10.1093/acprof:osobl/9780199602568.001.0001.

Carnerio APB, Bonnet-Lebrun A-S, Manica A, Staniland IJ, Phillips RA (2017) Methods for detecting and quantifying individual specialisation in movement and foraging strategies of marine predators. *MEPS .* 578: 151–166 doi:10.3354/meps12215

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick S, Newton J, Votier S, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series* 518: 1–12, doi: 10.3354/meps11112.

Daunt F, Afanasyev V, Adam A, Croxall JP, Wanless S (2007a) From cradle to early grave: Juvenile mortality in european shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. *Biol Lett* 3:371-374

Daunt F, Wanless S, Harris MP, Money L, Monaghan P (2007b) Older and wiser: Improvements in breeding success are linked to better foraging performance in european shags. *Functional Ecology* 21:561-567

Deakin Z, Hamer KC, Sherley RB, Bearhop S, Bodey TW, Clark BL, Grecian WJ, Gummery M, Lane J, Morgan G, Morgan L (2019) Sex differences in migration and demography of a wide-ranging seabird, the northern gannet. *Marine Ecology Progress Series*, 622:191-201.

Durell S (2000) Individual feeding specialisation in shorebirds: Population consequences and conservation implications. *Biological Reviews* 75(4): 503–518, doi: 10.1111/j.1469-185X.2000.tb00053.x.

Elliott KH, Le Vaillant M, Kato A, Gaston AJ, Ropert-Coudert Y, Hare JF, Speakman JR, Croll D (2014) Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *Journal of Animal Ecology* 83(1): 136–146, doi: 10.1111/1365-2656.12126.

Fretwell SD, Lucas HL (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica* 19:16-36

Geary B, Walter ST, Leberg PL, Karubian J (2019) Condition-dependent foraging strategies in a coastal seabird: Evidence for the rich get richer hypothesis. *Behavioral Ecology*, 30(2):356-63.

Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. *Journal of the Royal Society Interface* 15(143), doi: 10.1098/rsif.2018.0084.

Grecian WJ, Williams HJ, Votier SC, Bearhop S, Cleasby IR, Grémillet D, Hamer KC, Le Nuz M, Lescroël A, Newton J, Patrick SC (2019) Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. *Frontiers in Ecology and Evolution,* 7:214

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

Grémillet D, Péron C, Lescroël A, Fort J, Patrick SC, Besnard A, Provost P (2020) No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. *Marine Biology* 167(12): 1–10, doi: 10.1007/s00227-020-03801-y.

Guilford T, Freeman R, Boyle D, Dean B, Kirk H, Phillips R, Perrins C (2011) A dispersive migration in the Atlantic Puffin and its implications for migratory navigation. *PLoS ONE 6* e21336, doi:10.1371/journal.pone.0021336

Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets Morus bassanus at two North Atlantic colonies: Foraging trip duration and foraging area fidelity. *Marine Ecology Progress Series* 224: 283–290, doi: 10.3354/meps224283.

Hicks O, Burthe S, Daunt F, Butler A, Bishop C, Green JA (2017) Validating accelerometry estimates of energy expenditure across behaviours using heart rate data in a free-living seabird. *Journal of Experimental Biology* 220(10): 1875–1881, doi: 10.1242/jeb.152710.

Hillen J, Kiefer A, Veith M (2010) Interannual fidelity to roosting habitat and flight paths by female western barbastelle bats. *Acta Chiropterologica,* 12(1):187-95.

Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647–655, doi: 10.2307/176960.

Kamil AC (1983) Optimal foraging theory and the psychology of learning. *American Zoologist* 23:291–30

Kim SL, Tinker MT, Estes JA, and. Koch PL (2012) Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLOS ONE* e45068.

Lack D (1968) Ecological Adaptations for Breeding in Birds. *Oikos* 19(1): 1-9, doi: 10.2307/3564725.

Lane JV, Spracklen DV, Hamer KC (2019) Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series* 628: 183–193, doi: 10.3354/meps13089.

Lescroël A, Lyver POB, Jongsomjit D, Veloz S, Bugger CM, Kappes P, Karl BJ, Whitehead AL, Pech R, Cole TL, Ballard G (2020) Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series* 636: 189–205, doi: 10.3354/meps13208.

Lessells CM and Boag P (1987) Unrepeatable Repeatabilities: A Common Mistake. *The Auk* 104: 116–121, doi: 10.2307/4087240.

Lewis S, Benvenuti S, Daunt F, Wanless S, Dall'Antonia L, Luschi P, Elston DA, Hamer KC, Sherratt TN (2004) Partitioning of diving effort in foraging trips of northern gannets. *Canadian Journal of Zoology* 82(12): 1910–1916, doi: 10.1139/z05-005.

Mavor RA, Heubeck M, Schmit, S, Parsons M (2006) Seabird numbers and breeding success in Britain and Ireland. Peterborough: Joint Nature Conservation Committee.

Morgan EA, Hassall C, Pedfern CPF, Bevan RM, Hamer KC (2019) Individuality of foraging behaviour in a short-ranging benthic marine predator: Incidence and implications. *Marine Ecology Progress Series* 609: 209–219, doi: 10.3354/meps12819.

Müller HVT (2012) Individuality and consistency in foraging behaviour of the bumblebee *Bombus terrestris (*Doctoral dissertation, Queen Mary University of London)

Murray S, Harris MP, Wanless S (2015) The status of the gannet in Scotland in 2013-14. *Scottish Birds* 35(1): 3–18.

Nelson B (2002) *The Atlantic Gannet*. Published by Fenix Books Limited, Norfolk

Newton I (1998) *Population limitation in birds. Academic, London*

Owen E, Wakefield E, Hollinrake P, Leitch A, Steel L, Bolton M (2019) Breeding together, feeding apart: sympatrically breeding seabirds forage in individually distinct locations. *Marine Ecology Progress Series*. 620:173-83.

Patrick SC, Bearhop S, Grémillet D, Lescroël A, Grecian J, Bodey TW, Hamer KC, Wakefield E, Le Nuz M, Votier SC (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* 123(1): 33–40, doi: 10.1111/j.1600-0706.2013.00406.x.

Patrick SC and Weimerskirch H (2014) Consistency pays: Sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. *Biology Letters* 10(10): 1-4, doi: 10.1098/rsbl.2014.0630.

Patrick SC and Weimerskirch H (2017) Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. *Journal of Animal Ecology* 86(3): 674–682, doi: 10.1111/1365-2656.12636.

Peig J and Green AJ (2009) New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118, 1883–1891. doi: 10.1111/j.1600-0706.2009.17643.x

Pennycuick CJ (2008) Modelling the flying bird. Elsevier Inc., Burlington, MA.

Pollock CJ, Lane JV, Buckingham L, Farthe S, Jeavons R, Furness RW, Hamer KC (2021) Risks to different populations and age classes of gannets from impacts of offshore wind farms in the southern North Sea. *Marine Environmental Research* 17: 105457, doi: 10.1016/j.marenvres.2021.105457.

Piper WH (2011) Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology* 65(7): 1329–1351, doi: 10.1007/s00265-011-1195-1.

Qasem L, Cardew A, Wilson A, Griffiths I, Halsey LG, Shepard ELC, Gleiss AC, Wilson R (2012) Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE* 7(2): e31187, doi: 10.1371/journal.pone.0031187.

Stoffel MA, Nakagawa S, Schielzeth H (2017) rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution* 8(11): 1639–1644, doi: 10.1111/2041-210X.12797.

Switzer PV (1993) Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7: 533–555, doi: 10.1007/BF01237820.

Taylor GK and Thomas ALR (2002) Animal Flight Dynamics II. Longitudinal Stability in Flapping Flight. *Journal of Theoretical Biology* 214(3): 351–370, doi: 10.1006/jtbi.2001.2470.

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* 47(2): 487–497, doi: 10.1111/j.1365-2664.2010.01790.x.

Votier SC, Fayet AL, Bearhop S, Wodey TW, Clark BL, Grecian J, Guilford T, Hamer KC, Jeglinski JWE, Morgan G, Wakefield E, Patrick SC (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences* 284(1859): 20171068, doi: 10.1098/rspb.2017.1068.

Wakefield ED, Cleasby IR, Bearhop S, Bodey TA, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity - why some gannets don’t change their spots. *Ecology*, 96(11): 3058–3074, doi: 10.1890/14-1300.1.sm.

Wakefield ED, Furness RW, Lane JV, Jeglinski JWE, Pinder SJ (2019) Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. *Journal of Avian Biology* 50(10): 1–13, doi: 10.1111/jav.02164.

Wanless S, Harris MP, Morris JA (1990) A Comparison of Feeding Areas Used by Individual Common Murres (*Uria aalge*), Razorbills (*Alca torda*) and an Atlantic Puffin (*Fratercula arctica*) during the Breeding Season. *Source: Colonial Waterbirds*, 13(1): 16–24, doi: 10.2307/1521416.

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

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography* 54(3): 211–223, doi: 10.1016/j.dsr2.2006.11.013.

Weimerskirch H, Mougey T, Hindermeyer X (1997) Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: Natural variation and experimental study. *Behavioral Ecology* 8(6): 635–643, doi: 10.1093/beheco/8.6.635.

Wiese FK, Robertson GJ (2004) Assessing seabird mortality from chronic oil discharges at sea. *J Wildl Manag* 68:627–638

Wilson RP, Börger L, Holton MD, Scantlebury DM, Gómez-Laich A, Quintana F, Rosell F, Graf PM, Williams H, Gunner R, Hopkins L, Marks N, Geraldi NR, Duarte CM, Scott R, Strano MS, Robotka H, Eizaguirre C, Fahlman A, Shepard ELC (2020) Estimates for energy expenditure in free-living animals using acceleration proxies: A reappraisal. *Journal of Animal Ecology*, 89(1): 161–172, doi: 10.1111/1365-2656.130

3.7 Supplementary materials S3

Table S3.1. The mean repeatability value (r) standard error (se), 95% confidence intervals (CI) and P values of foraging trip metrics for male and female chick-rearing northern gannets (*Morus bassanus*) at Bass Rock in 2017-2019 (N = 12 males, 9 females, 3 trips for each individual).

Metric	Sex	r	se	CI	CI	p
Duration (hours)	Female	<0.001	0.127	<0.001 - 0.468		>0.05
	Male	<0.001	0.103	<0.001 - 0.383		>0.05
Distance (km)	Female	<0.001	0.157	<0.001 - 0.49		>0.05
	Male	<0.001	0.128	<0.001 - 0.433		>0.05
Proportion of trip spent foraging	Female	<0.001	0.147	<0.001 - 0.435		>0.05
	Male	<0.001	0.131	<0.001 - 0.402		>0.05
Proportion of trip spent travelling	Female	0.433	0.216	0.062 - 0.807		>0.05
	Male	0.56	0.167	0.175 - 0.809		**0.004**
Proportion of trip spent resting	Female	0.609	0.191	0.136 - 0.874		**0.007**
	Male	0.346	0.191	0 - 0.688		>0.05
ODBA (g) per minute of activity during trip	Female	0.738	0.175	0.257 - 0.943		**<0.001**
	Male	0.45	0.177	0.006 - 0.695		**0.02**
ODBA (g) per minute of foraging	Female	0.323	0.212	<0.001 - 0.718		>0.05
	Male	0.434	0.2	<0.001 - 0.729		**0.03**
ODBA (g) per minute of outbound travel	Female	0.713	0.2	0.13 - 0.907		**<0.001**
	Male	0.441	0.185	<0.001 - 0.726		**0.03**
ODBA (g) per minute of inbound travel	Female	0.659	0.21	0.125 - 0.87		**0.003**
	Male	0.201	0.189	<0.001 - 0.626		>0.05
Take-off rate h^{-1} foraging	Female	0.132	0.185	<0.001 - 0.546		>0.05
	Male	0.028	0.132	<0.001 - 0.417		>0.05

Chapter 4 **Effects of wind speed on foraging behaviour and energy expenditure in northern gannets**

In windy conditions, gannets seem to hover effortlessly above the colony

4.1 Abstract

Seabirds negotiate challenging environmental conditions, particularly when constrained as central-place foragers during the breeding season. For instance, wind direction and speed can strongly affect the energy costs of flight and time-activity budgets during chick-rearing. Increasing energy costs associated with flight relate to the increased mechanical effort required to fly in an unfavourable windscape, however it is not fully understood why some wind conditions cause birds to spend more time actively foraging. To this end, I used GPS loggers, tri-axial accelerometers and time-depth recorders to investigate how the foraging behaviour of northern gannets, *Morus bassanus*, was affected by the wind conditions encountered by birds at-sea and the consequences for time and energy expenditure. Although both sexes encountered the same wind speeds during foraging, I found that higher wind speeds were associated with lower rates of take-off from the sea surface during foraging bouts in females but not males. Females appeared to dive deeper than males and among the latter there was a significant positive effect of wind speed on dive depth, with the deepest dives by males attaining similar depths to those attained on average by females. These results suggest that wind conditions can strongly affect foraging behaviour, with contrasting effects of increasing wind speeds on females (lower take-off rates, presumably due to greater search times for prey and lower dive rates) and males (greater dive depths). The results of this study suggest that not only does weather likely impact the foraging effort of plunge-diving species, but that when considering the effect of weather we must also consider that sexes could be impacted differently.

4.2 Introduction

The breeding season is an energetically demanding time for seabirds (Elliott *et al.,* 2014a). During chick-rearing parents are constrained in space and time by the location of the nest and the presence of demanding offspring (Andersson 1981; Kacelnik 1984). This restricts the foraging areas available to parents and how long they can spend at sea (Elliott *et al.,* 2009). While many flying seabirds are highly adapted to travelling in the wind, they are not always able to avoid or compensate for extreme wind conditions encountered at-sea, making management of time and energy in relation to the conditions crucial to fitness (Spear and Ainley 1998; Nourani *et al.,* 2022). Moreover, extreme wind conditions at-sea are expected to increase in frequency and intensity with progressive climate change around UK coastal and marine environments, and globally (Young and Agustinus 2019; Wolf *et al.,* 2020). Hence there is a pressing need to better understand how the wind conditions encountered by birds at-sea affect key aspects of foraging behaviour during chick-rearing, particularly in relation to searching for and capturing prey.

The foraging trips of seabirds can be broadly separated into three stages: travelling to prey patches, foraging to capture sufficient prey for self-maintenance and to feed offspring, and returning to the colony. Most previous studies considering the effects of wind conditions on seabirds have focused on the travelling stages of trips, revealing how wind speed and direction in relation to the bird's direction of flight may affect energy expenditure, leading to adjustments in fine-scale flight behaviour (Amélineau *et al.,* 2014; Elliott *et al.,* 2014b; Collins *et al.,* 2020). Foraging behaviour can also be affected by wind conditions, although this is less well studied than travelling flight. Birds that forage under the water, such as kingfishers, dippers and penguins, are generally assumed to rely on vision to catch prey, so the foraging efficiency of such individuals varies with physical variables that affect prey visibility e.g. wind speed, light intensity and sun glare (Douthwaite 1976; O'Halloran *et al.,* 1990; Kooyman et al., 1992; Katzier *et al.,* 1989; Lovvorn *et al.,* 1991). For example Sandwich terns, *Sterna sandvicensis,* are a shallow plunge-diving species, and higher wind speeds make prey more difficult to capture due to reduced clarity through the water column (Baptist and Leopold, 2010). It has also been hypothesised that forage fish may move deeper in the water column in turbulent surface conditions (Parker-Stetter *et al.,* 2016) . If true, this puts the predators of these species at risk of reduced food availability, particularly if they cannot change foraging strategy. This includes surface-feeding and shallow-diving seabirds such as black-legged kittiwakes, *Rissa tridactyla,* that typically feed by dipping to the surface of the water (Furness & Monaghan 1987).

It is not only the conditions during breeding season that can affect seabird population trends and fitness; conditions at-sea during the inter-breeding season are an important factor in determining population trends and fitness (Grecian *et al.,* 2019; Grémillet *et al.,* 2020). For example, by studying the inter-breeding time-activity budgets of European shags, *Phalacrocorax aristotelis*, Daunt *et al.,* (2006) found foraging effort in February (~8 weeks before egg laying) was linked to the timing of breeding in the next season; females that spent more time foraging in February laid eggs later, suggesting they were of poorer body condition and lower quality individuals. In addition, this study linked these fitness effects with the weather; there were higher energy demands during onshore winds and decreased foraging efficiency at high wind speeds (Daunt *et al.,* 2006).

Beyond fitness and body condition, environmental conditions experienced outside of the breeding season directly affect survival; mass mortality events have been documented over the past century in a range of seabird families including shearwaters, cormorants and auks (Harris and Wanless 1996; Camphuysen *et al.,* 1999). There are many environmental variables that cause mass mortality events known as 'wrecks' of seabirds: oil spills, fishing activities, heatwaves and stormy weather (Camphuysen *et al.,* 1999; Barros *et al.,* 2014; Tavares *et al.,* 2020; Glencross *et al.,* 2021). Wrecks associated with adverse weather lead to food shortages and subsequent loss of body condition, but why weather causes starvation is unknown (Norman and Brown 1987; Piatt and Pelt 1997). Cyclonic conditions in the North Atlantic did not increase energy requirements in five species of seabird (little auk *Alle alle,* Atlantic puffin *Fratercula arctica,* common guillemot *Uria aalge,* Brunnïch's guillemot *Uria lomvia,* and black-legged kittiwake *Rissa tridactyla*) implying death was due to an inability to feed and/or inaccessibility to prey during cyclones (Clairbaux *et al.,* 2021).

Quantifying fine-scale foraging behaviour and thus foraging efficiency outside of the breeding season is unfeasible for many seabirds; birds don't regularly return to land, making device deployment and retrieval difficult for common attachment methods (Isaksen 1995; Shillinger *et al.,* 2012). To understand patterns, causes and consequences of climate variability on fitness, these factors must be measured accurately. Thus, investigating the effect of wind during the breeding season when high resolution data-logging devices can be deployed may provide insight into the causes of mass mortality events and thus steer conservation measures. It is becoming clear urgent shifts are needed in policies, and we must make sure not to focus on ineffectual factors (Grémillet *et al.,* 2020).

Some seabird species are more resilient to change than others; northern gannets, *Morus bassanus*, (hereafter gannets) are thought to be less susceptible to winter storms and oil spills than other seabirds inhabiting the north Atlantic (Wiese and Robertson 2004). However it is still crucial to determine the environmental conditions that even these seemingly resilient animals are affected by, both as indicators for the effects on other species, and for their own conservation interest (Grémillet *et al.,* 2020). Gannets are plunge-diving predators that can dive from heights of up to 40 metres to depths of up to 11 metres, and additional depth of up to 20m when propelled by their wings (Ropert-Coudert *et al.,* 2009). Within gannet foraging behaviour are two phases: location of prey within the patch and prey capture attempts. For seabirds that plunge-dive to catch prey this means every capture attempt will be proceeded by an energetically expensive take-off to gain the height needed to dive again (Green *et al.*, 2010). This must also be balanced with the searching flight associated with foraging, which is significantly more costly than travelling flight for this species (Amélineau *et al.*, 2014). Females dive significantly deeper than males in characteristic V-shaped dives, with shallower and U-shaped dives more frequently performed by males (Lewis *et al.,* 2004; Cleasby *et al.,* 2015). This sex-specific dive behaviour seems to be a function of isotopic diet niche separation between sexes (Clark *et al.,* 2021). Wind speed and direction have been shown to impact how gannets spend time at-sea and the energy expenditure of flight, though this has not been applied to fine-scale foraging behaviour or the energy expenditure associated with foraging (Amélineau *et al.,* 2014; Lane *et al.,* 2019).

Like other seabirds, gannets do not avoid extreme wind conditions, so they either make behavioural adjustments, or endure higher energy costs (Nourani *et al.*, 2022). Previous work at Bass Rock identified adverse effects of wind on the broad-scale foraging behaviour of gannets; strong winds increased the time spent foraging, and headwinds on the return journey slowed down flight speed, with gannets compensating for these by reduced time spent resting (Lane *et al.,* 2019). These data strongly suggest that increasing wind speeds adversely affected foraging, although it was not known whether or not stronger winds resulted in more unsuccessful prey capture attempts leading to more time actively foraging, or fewer prey capture attempts due to reduced visibility of prey and more time searching for prey in the air.

Data presented in Chapters 2 and 3 indicate significant annual variation in foraging behaviour, in addition to low individual repeatability in the proportion of each trip spent foraging and in the frequency of take-offs from the sea surface. These results imply that foraging behaviour was additionally affected by the environmental conditions encountered by birds at foraging locations, potentially including wind conditions. Given the consistent and stark sex differences in foraging behaviour and further sex-specific findings in Chapters 2 and 3, it is necessary to also consider the effect of wind on the foraging of each sex separately.

In this chapter, I aim to identify how wind speed affects the foraging behaviour and effort of chick-rearing male and female gannets with the following objectives: (1) establish what aspects of foraging behaviour lead to the relationship between wind speeds increasing time spent foraging, and (2) investigate how wind speed may affect the diving behaviour of male and female gannets. First, I combine GPS logger data with meteorological data to quantify the wind speeds encountered by males and females while engaged in foraging behaviour. Next, I use accelerometry data to explore the relationships between wind speed and take-off rate from the sea surface during foraging bouts for males and females. I then combine these data to examine how wind speed affected the time and energy birds spent foraging. Finally, I use time-depth recorders to investigate the sex-specific relationships between wind speed and dive depth to provide insight into how conditions above the sea surface may have affected behaviour below it.

4.3 Methods

4.3.1 Data collection

Collection of field data followed methods outlined in Chapter 2 section 2.3.1. In 2019 dive depth data from time-depth recorders (TDRs) were available for I 14 trips by 7 birds (3 males and 4 females). Maximum dive depth was automatically measured by the TDRs without need for further data processing or analysis.

4.3.2 Trip metrics, energy expenditure and take-off rate

To investigate the effect of wind speed on foraging behaviour and energy expenditure, I first needed to identify the locations used for foraging. I used the GPS data to classify at-sea behaviours of each location point following the methods outlined in Chapter 2 section 2.3.2. I then calculated absolute time spent foraging (hours) from the behavioural classifications at one minute intervals and the proportion of time spent foraging by dividing the timer spent foraging by the total trip duration (hours).

In order to establish what aspects of foraging behaviour contribute to the previously observed increase in time spent foraging during windy conditions (Lane *et al.,* 2019) I quantified metrics of energy expenditure and foraging success. By interpolating the GPS-defined behavioural classifications and processed accelerometry data I calculated a proxy of energy expenditure during foraging - the ODBA per minute spent foraging (processing and validation of methods in Chapter 2 section 2.3.5). I determined an estimate of foraging success using accelerometry data to identify the number of take-offs per trip, and then converted this into the rate of take-offs per hour spent foraging (hereafter take-off rate). Detailed methods of take-off rate calculation can be found in section 2.3.6 of Chapter 2 and justification as a measure of foraging success in Chapter 2 section 2.4.4 and discussion.

4.3.3 Wind speed

Wind speed during foraging trips were obtained from the ERA5 data set produced by the European Centre for Medium-Range Weather Forecasts (ECMWF) at the resolution available at the time of data analysis (hourly at 0.25 x 0.25°, or approximately 31 x 31km grid) (Dee *et al.,* 2011). This could be considered a limitation given the broad spatial scale of the data. However, the average scale of foraging behaviour in gannets, defined by area restricted search (ARS), is approximately 10km (Hamer *et al.,* 2009) and the time spent foraging per trip is approximately 3 hours, which is generally exhibited in two or more bursts of foraging in core areas (Figure 3.1 is a good example of this). Thus, the resolution of the wind data at the hourly temporal scale is likely as important to represent the conditions faced at sea during foraging.

For each bird location at-sea I extracted the closest wind data in time and space for zonal (west-east) and meridional (south-north) wind speeds (maximum time difference 29 minutes and maximum difference in distance is 15km) using the 'raster' and 'ncdf4' packages in R (Hijmans 2018; Pierce 2021).

I created an array of the time stamps, longitudinal and latitudinal points for each bird location and the wind data locations. I then identified the closest position in time and location to each bird location and extracted the wind data for that position from the array, before adding the nearest wind speed in time and space.

I then calculated wind speed (ms^{-1}) using equation 1:

Equation 1:

$$Wind\ speed = \sqrt{Uw^2 + V^2}$$

Uw = zonal wind component
Vw = meridional wind component

I determined the mean wind speed encountered by birds during foraging behaviour, as defined for each location (at 1-minute time intervals) by the GPS data. This process resulted in a measure of mean wind speed (±1.3 ms^{-1}) specifically during foraging behaviour for each trip – the average wind speed experienced by each bird at foraging locations.

4.3.4 Statistical analyses

Linear mixed models (LMMs) and generalised linear mixed-effects models (GLMMs) with restricted maximum-likelihood (REML) in the R package 'nlme' (Pinheiro *et al.,* 2018) were used to investigate the effects of wind speed on foraging behaviour and energy expenditure. GLMMs were used in some instances because of the potential of quadratic relationships and thus required the capacity of GLMMs to handle non-normal data unlike LMMs that assume normally distributed data.

To determine whether or not wind speed differed between sexes and years, I used a LMM to model wind speed as the response variable with sex, year and their interaction as fixed effects and bird identity as a random effect. To explore how wind speed affected foraging, I modelled metrics of foraging behaviour and energy expenditure of males and females separately as the response variables with wind speed as an explanatory variable, year as a fixed effect (except for dive depth, which was measured only in 2019) and bird identity as a random effect in each case. In some instances, relationships with wind conditions appeared non-linear, therefore in model selection I included quadratic metrics to test for this as justified in Chapter 2 section 2.3.7.

The data met the assumptions of LMMs; variables were normally distributed or were transformable to normality (sqrt-root transformations of trip duration, distance travelled, proportion of time spent foraging, travelling and resting and travelling ODBA per minute) leading to normally distributed model residuals, residuals had statistically equal variance and the factors were independent of one another.

Explanatory and linear or non-linear fit models were selected with Akaike's Information Criterion (AIC) using the dredge function in the MUmIN package (Bartón, 2009). The top model was determined by the lowest value of Akaike's information criterion corrected for sample sizes (AICc), ΔAICc >2 from the next ranked model and greatest raw AICc (Burnham and Anderson 2002). For analyses without a clear top model (ΔAICc <2 between top model and candidate model) I used model averaging to determine the relative importance of each parameter and associated estimates for models (ΔAICc <2) in MuMIn.

4.4 Results

4.4.1 Wind speed encountered by birds each year

Wind speed encountered by birds at sea differed significantly among years but not between sexes (Table S4.1). Wind speeds at foraging locations were significantly higher in 2017 than 2018 for all birds ($\chi^2_2 = 8.90$, $P = 0.01$, Tukey test; $F_{38} = 2.50$, $P = 0.04$) and females in 2018 encountered significantly lower wind speeds at foraging locations than females in 2019 ($\chi^2_2 = 6.40$, $P = 0.04$, Tukey test; $F_{38} = 3.28$, $P = 0.03$).

4.4.2 Take-off rate

As wind speed differed among years, an interaction between wind speed and year was included in model selection (Table S4.2). After model averaging, the take-off rate of females declined with increasing wind speed (Figure 4.1a) and examining each year separately, this relationship was strongest in 2019 (Figure 4.1b; $Z = 2.15$, $P = 0.03$, Table S4.3). For males, take-off rate was best explained by bird identity only (Table S4.2).

4.4.3 Energy expenditure

The ODBA per minute spent foraging was not directly affected by wind speed for either sex (Table S4.2). Male ODBA per minute spent foraging was best explained by take-off rate ($\chi^2_1 = 14.43$, $P < 0.001$) and the best model for females included only bird identity (Table S4.2). When wind speed was included in model selection for the proportion of trip spent foraging, the best model still only included take-off rate for both sexes (Table S4.2).

4.4.4 Dive depth

I obtained data from TDRs for 14 trips by 7 birds (3 males and 4 females). Take-off rate was not related to maximum dive depth (m) for females or males, ($\chi^2_1 = 1.04$, $P > 0.05$, $\chi^2_1 = 1.97$, $P > 0.05$), but there were sex differences detected in response to wind speed. Males dived deeper in higher wind speeds (Figure 4.2; $\chi^2_1 = 12.79$, $P < 0.001$) whereas female maximum dive depth did not change with wind speed ($\chi^2_1 = 0.21$, $P > 0.05$).

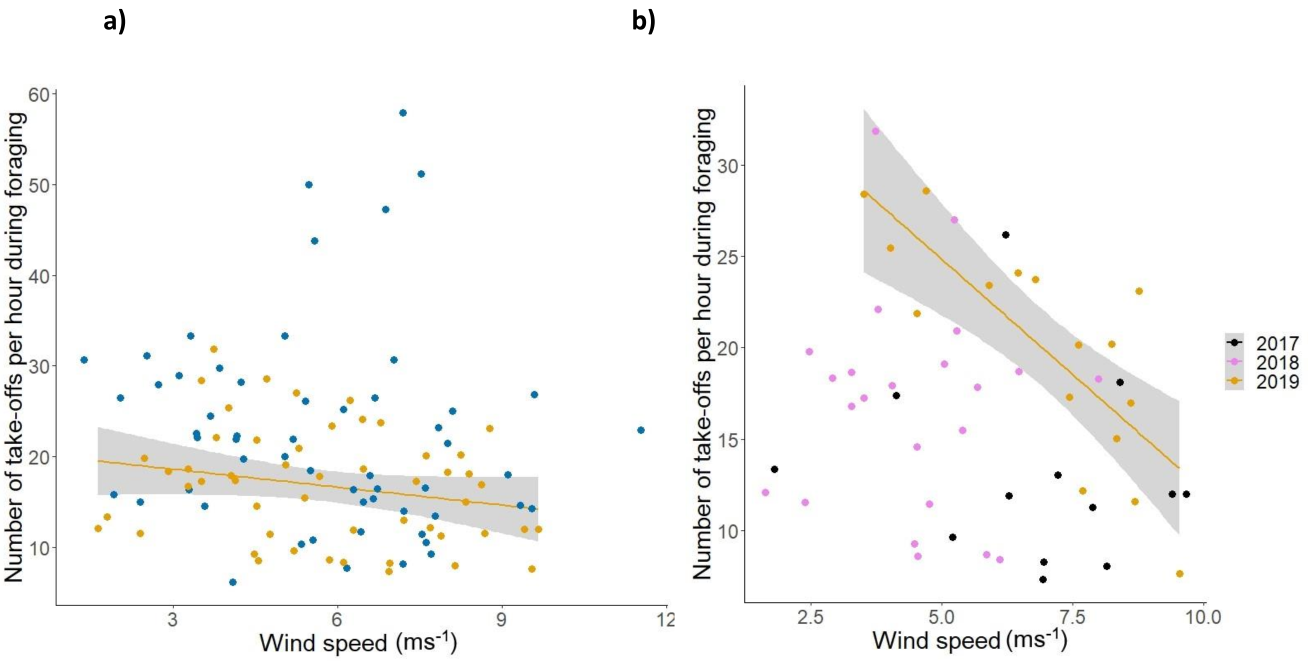


Figure 4.1. (a) The relationships between wind speed (ms^{-1}) and take-off rate h^{-1} foraging for females (orange) and males (blue) northern gannets, *Morus bassanus*, and; **(b)** inter-annual differences in this relationship for females. Solid lines show significant linear relationships and grey shading shows 95% confidence intervals. N = 110 trips, 45 individuals.

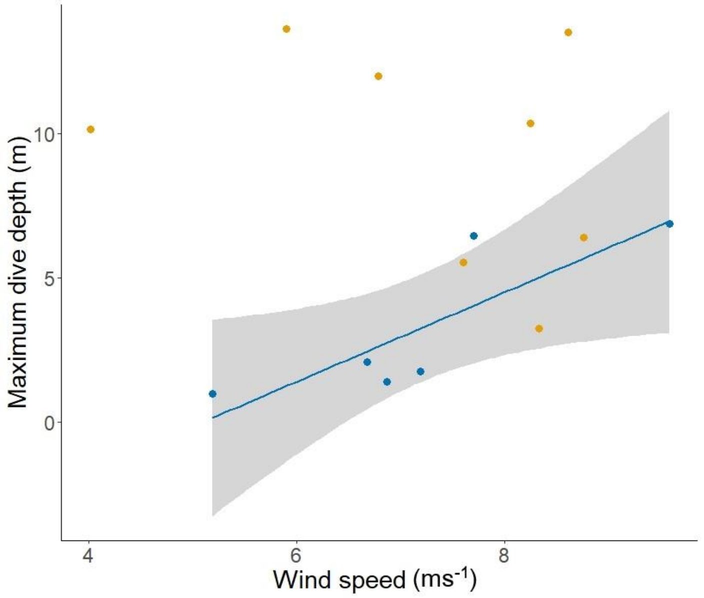


Figure 4.2. The sex-specific relationships between wind speed (ms^{-1}) and maximum dive depth for male and female chick-rearing northern gannets, *Morus bassanus,* at Bass Rock, Scotland in 2019. Solid line shows a significant linear relationship and grey shading shows 95% confidence intervals. N= 14 trips, 7 individuals.

4.5 Discussion

The aim of this study was to consider how wind speed affects the foraging behaviour and effort of chick-rearing male and female gannets. I found that in a seemingly resilient and flexible species wind speeds within a ‘normal’ range can reduce the success and increase the effort associated with foraging. Previous studies speculated the foraging efficiency of gannets declines in windier conditions due to inability to detect under the surface (Lane *et al.,* 2019) and the results here support this theory, though with different behavioural adjustments and effects for each sex. The take-off rate of females declined with increasing wind speed, particularly in 2019 (Figure 4.1b), whilst the take-off rate of males was not affected by wind speed but maximum dive depths of males increased with wind speed (Figure 4.2). It seems that in windy conditions, males do not lower their prey capture attempt rate as females do, but instead dive deeper for prey. The results of this study provide empirical evidence of how changing and more extreme weather events may impact the foraging abilities of seabirds due to changes in prey behaviour and visibility.

Wind speeds were not considered extreme in any of the three years of this study; mean wind speeds encountered by gannets during foraging bouts in 2017-2019 (2 – 12 m s^{-1}; Figure 4.1) were similar to those recorded for birds breeding near the species’ southern range margin, at Ile Rouzic, France, and previously at Bass Rock (Lane *et al.,* 2019, Figure 2 in Nourani *et al.,* 2022). Females and males experienced the same wind conditions while foraging (Table S4.1), so subsequent sex differences were not due to birds encountering different wind speeds. Hence, although wing loading differs between sexes (Chapter 2), it did not lead to sex-specific selection of foraging areas associated with particular wind conditions, as seen in some albatrosses with sexual dimorphism in wing loading, *Thalassarche melanophrys* and *T. chrysostoma* (Phillips *et al.,* 2004). It seems unlikely that males and females differ in visual acuity, or that a 10m difference between sexes in the averages heights attained prior to dives (34.6m for females and 25m for males Lane *et al.,* 2020) would significantly affect the visibility of prey. Therefore, my results suggest sex-specific behavioural adjustments and responses to wind conditions that may be related to differences associated with prey behaviour and capture attempts.

I found that wind speed likely affected the foraging success of females but not males, demonstrated by a lower take-off rate with increasing wind speeds for females. Low take-off rate could indicate a reluctance to dive if the conditions are not favourable, which would suggest diving and the subsequent take-off in poor conditions poses some sort of individual risk – whether by missed opportunity of no longer surprising prey, injury, or the time and energy costs of taking off and gaining height again (Nelson, 2002; Ropert-Coudert *et al.*, 2004; Green *et al.*, 2010). This seems particularly important for females; females put more effort into foraging per unit time (Chapter 2) and have a greater body mass (Clark *et al.,* 2021; Chapter 2), so the energy costs of taking off and gaining greater heights might lead to fewer capture attempts when prey are more difficult to see. For both sexes, take-off rate accounted for most of the variation in proportion of time spent foraging (Table S4.2), suggesting that reduced foraging success is what causes the proportion of time spent foraging during a trip to increase, rather than wind speed affecting other aspects of foraging behaviour.

My investigation into the effect of wind speed on maximum dive depth supports the notion that the forage fish exploited by males moved deeper in the water column when surface conditions were turbulent (Parker-Stetter *et al.,* 2016) and those exploited by females did not behave this way. Although based on a small sample size, these results support previous findings that males and females occupy distinct dietary niches (Wakefield *et al.,* 2015; Clark *et al.,* 2021), and that at this colony, females dive deeper on average than males (Lewis *et al.,* 2004; Cleasby *et al.,* 2015). Although sexual segregation in isotopic niche does not distinguish the prey species selected by each sex it does provide evidence that the prey of males are more likely to be associated with coastal waters, so may be comparable with other seabirds that forage coastally (Kelly 2000; Hobson *et al.,* 1994; Cherel and Hobson 2007). The regurgitations of breeding gannets (of unknown sex) showed that the diet of the study population consisted of 32% mackerel *Scomber scombrus*, 22% herring *Clupea harengus*, 23% sandeels *Ammodytes marinus* and 23% sprat *Sprattus sprattu*s (Hamer *et al.,* 2000). These are all important food species to many air-breathing marine predators (Furness & Monaghan 1987; Furness 1990; Bailey *et al.,* 1991). Thus both aspects of this study, fewer prey capture attempts and changes prey behaviour, have significant implications for the foraging efficiency of other species that target similar prey and/or have similar foraging strategies.

Some of the most vulnerable species are likely to be small surface-feeders, traits that are embodied by the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake) (Furness & Monaghan 1987). Kittiwake breeding productivity has been closely linked to anthropogenic and environmental factors influencing the growth and timing of life history changes of their primary prey, sandeels, with productivity varying across 3 years in accordance with prey availability (Lewis *et al.,* 2001). Therefore the potential shift in prey behaviour in relation to wind puts shallow-diving and surface feeding species are at real risk of food resources being out of reach in turbulent conditions.

This effect is likely to be more prominent in the inter-breeding season when weather conditions are less favourable (Bacon and Carter 1991; Stearns 1992; Newton 1998). These results may explain why extreme weather events in the inter-breeding season lead to wrecks of emaciated seabirds; starvation is likely due to reduced prey availability when prey move deeper in the water column, essentially making them inaccessible for some species, and fewer prey capture attempts because prey are more difficult to see, which may interact with prey moving deeper in the water column (Camphuysen *et al.,* 1999; Parker-Stetter *et al.,* 2016). Conservation efforts to protect seabirds in the inter-breeding season should be focused towards reducing the factors leading to extreme weather events, rather than, for example, attempting to mediate effects with fisheries restrictions or more protection during the breeding season. The inter-breeding season is vital to survival but it is also a crucial time for gaining condition for the following breeding season, thus carry-over effects will not be mediated within the breeding season (Trivers 1972; Harrison *et al.,* 2011; Salton *et al.,* 2015).

The inter-annual differences in the relationship between take-off rate and wind speed for females (Figure 4.2b) indicate something else within the environment contributes to the association between foraging success and wind speed. Prey exploited by females may have differed among years, either in spatial distribution or species targeted. In keeping with this notion, the diets of gannets at Bass Rock have previously shown marked annual variation, particularly in the proportion of sandeels, *Ammodytes marinus,* present (Table 1 in Hamer *et al.,* 2007) although the diet of birds were not recorded in this study. Conversely, prey patches may have been more densely or reliably aggregated in 2019. Indeed, the core and broad foraging areas of males and females were significantly segregated in 2019, suggesting this could be the case (Chapter 2 Figure 2). These ambiguities highlight the considerable gap between the scale of isotopic niche segregation and the actual prey species targeted by each sex (e.g. Clark *et al.,* 2021).

The extent of sex-specific behaviour, and potentially energy expenditure, differs among colonies and years (Cleasby *et al.,* 2015; Clark *et al.,* 2021; Bennison *et al.,* 2022), demonstrating the relationships between fine-scale foraging behaviour, the environment and prey behaviour and density are incredibly nuanced. This is a relatively small, but informative study. To ensure the robustness of patterns found here I would like to see the cohesion of data from different gannet colonies, particularly with respect to accelerometry, to provide further insights into behavioural plasticity and responses to varying environmental conditions across this species' range.

Previous studies have proposed the foraging success of gannets and other plunge-diving species declines in windier conditions due to a reduced ability to detect prey beneath the sea surface (Baptist and Leopold, 2010; Lane *et al.,* 2019). I found empirical evidence for this hypothesis; females had lower take-off rates while foraging, i.e. lower dive rates, in windier conditions. Take-off rate was a better predictor than wind speed of the proportion of a trip spent foraging and ODBA per minute spent foraging (Table S4.2), suggesting it was the effect of wind on foraging success by prey capture that contributed most to increases in the time and energy birds spent foraging. Further supporting this notion, males dived deeper in windier conditions, indicating prey remained deeper below the surface in turbulent surface conditions. These results strongly suggest the sexes are likely to respond differently when foraging in a changing climate, and thus should be considered separately when predicting the effects of climate change during and between breeding seasons. Overall, this work demonstrates that the foraging success and behaviour of one of the most resilient and successful generalist seabirds is likely affected by ‘normal’ wind conditions. Using gannets as an indicator for plunge-diving species and those that target similar prey, climate change will likely have a considerable impact on the foraging efficiency of this species and an even greater impact on others.

4.6 References

Amélineau F, Péron C, Lescroël A, Authier M, Provost P, Grémillet D (2014) Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology* 217(6): 876–885, doi: 10.1242/jeb.097915.

Andersson M (1981) Central Place Foraging in the Whinchat, *Saxicola Rubetra*. *Ecology* 62(3), 538–544, doi: 10.2307/1937718.

Bacon S, Carter DT (1991) Wave climate changes in the North Atlantic and North Sea. International Journal of Climatology, 11(5):545-58.

Bailey RS, Furness RW, Gauld JA, Kunzlik PA (1991) Recent changes in the population of the sandeel (*Ammodytes marinus Raitt*) at Shetland in relation to estimates of seabird predation. *ICES Marine Science Symposia*, 193: 209-216.

Baptist MJ and Leopold MF (2010) Prey capture success of Sandwich terns *Sterna sandvicensis* varies non-linearly with water transparency. *Ibis* 152(4): 815–825, doi: 10.1111/j.1474-919X.2010.01054.x.

Barros Á, Álvarez D, Velando A (2014) Long-term reproductive impairment in a seabird after the Prestige oil spill. *Biology Letters*, 10(4):20131041.

Barton K (2009) Multi-model inference. Available at: http://r-forge.r-project.org/projects/mumin/

Bennison A, Giménez J, Quinn JL, Green JA, Jessopp M (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *Royal Society Open Science* 9: 210520, doi: 10.1098/rsos.210520.

Camphuysen CJ, Wright PJ, Leopold M, Hüppop O, Reid JB (1999) A review of the causes, and consequences at the population level, of mass mortalities of seabirds. *ICES Coop Res Rep.* 232:51-66.

Ceia FR and Ramos JA (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. *Marine Biology* 162(10): 1923–1938, doi: 10.1007/s00227-015-2735-4.

Cherel Y and Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329: 281−287

Clairbaux M, Mathewson P, Porter W, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason HH, Bråthen VS, Merkel B (2021) North Atlantic winter cyclones starve seabirds. *Current Biology*. 31(17):3964-71.

Clark B, Cox SL, Atkins K, Bearhop S, Bicknell AWJ, Bodey TW, Cleasby IR, Grecian WJ, Hamer KC, Loveday BR, Miller PI, Morgan G, Morgan L, Newton J, Patrick SC, Scales KL, Sherley RB, Vigfúsdóttir, Wakefield ED, Votier SC (2021) Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. *Marine Ecology Progress Series* 661: 1–16, doi: 10.3354/meps13636.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick S, Newton J, Votier S, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series* 518: 1–12, doi: 10.3354/meps11112.

Collins PM, Green JA, Elliott KH, Shaw PJA, Chivers L, Hatch SA, Halsey LG (2020) Coping with the commute: behavioural responses to wind conditions in a foraging seabird. *Journal of Avian Biology* 51(4): 1–11, doi: 10.1111/jav.02057.

Daunt F, Afanasyev V, Silk JR, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology*. 59(3):381-8.

Dee DP, Uppala SM, Simmons AJ, Berrisford P, Poli P, Kobayashi S, Andrae U, Balmaseda MA, Balsamo G, Pauer P, Bechtold P, Neljaars ACM, van de Berg L, Bidlot J, Bormann N, Delsol C, Dragani R, Fuentes M, Geers AJ, Haimberger L, Healy SB, Hersbach H, Hólm EV, Isaksen L, Kållberg P, Köhler M, Matricardi M, McNally AP, Monge-Sanz BM, Morcrette JJ, Park BK, Peubey C, de Rosnay P, Tavolato C, Thépaut JN, Vitart F(2011) The ERA-Interim reanalysis: configuration and performance of the data assimilation system. *Quarterly Journal of the Royal Meteorological Society* 137(656): 553–597, doi: doi: 10.1002/qj.828.

Douthwaite RJ (1976) Fishing techniques and foods of the Pied Kingfisher on Lake Victoria in Uganda. *Ostrich* 47: 153–160

Elliott KH, Woo K, Gaston AJ, Benvenuti S, Dall'Antonia L, Davoren GK (2009) Central-Place Foraging in an Arctic Seabird Provides Evidence for Storer-Ashmole's Halo. *The Auk* 126(3):613–625, doi: 10.1525/auk.2009.08245

Elliott KH, Le Vaillant M, Kato A, Gaston AJ, Ropert-Coudert Y, Hare JF, Speakman JR, Croll D (2014a) Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *Journal of Animal Ecology* 83(1): 136–146, doi: 10.1111/1365-2656.12126.

Elliott KH, Chivers LS, Bessey L, Gaston AJ, Hatch SA, Kato A, Osborne O, Ropert-Coudert Y, Speakman JR, Hare JF (2014b) Windscapes shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. *Movement Ecology*, 2(1); 1–15, doi: 10.1186/s40462-014-0017-

2.

Frederiksen M, Daunt F, Harris MP, Wanless S (2008) The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, 77(5):1020-9.

Furness RW & Monaghan P (1987) *Seabird Ecology.* New York: Blackie.

Furness RW (1990) A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. *Ibis*, 132: 205±217

Furness RW and Tasker ML (2000) Seabird–fishery interactions: quantifying the sensitivity of seabirds to reductions in sandeel abundance, and identification of key areas for sensitive seabirds in the North Sea. *Mar. Ecol. Prog. Ser.,* 202: 253–264.

Glencross JS, Lavers JL, Woehler EJ (2021) A proposed framework for reporting mass mortality (wreck) events of seabirds. *ICES Journal of Marine Science*, 78(6):1935-42.

Grecian WJ, Williams HJ, Votier SC, Bearhop S, Cleasby IR, Grémillet D, Hamer KC, Le Nuz M, Lescroël A, Newton J, Patrick SC (2019) Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. *Frontiers in Ecology and Evolution,* 7:214

Green JA, White CR, Bunce A, Frappell PB, Butler PJ (2010) Energetic consequences of plunge diving in gannets. *Endangered Species Research*, 10(1): 269–279, doi: 10.3354/esr00223.

Grémillet D, Péron C, Lescroël A, Fort J, Patrick SC, Besnard A, Provost P (2020) No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. *Marine Biology* 167(12): 1–10, doi: 10.1007/s00227-020-03801-y.

Guéry L, Descamps S, Hodges KI, Pradel R, Moe B, Hanssen SA, Erikstad KE, Gabrielsen GW, Gilchrist HG, Jenouvrier S, Bêty J (2019) Winter extratropical cyclone influence on seabird survival: variation between and within common eider *Somateria mollissima* populations. *Marine Ecology Progress Series,* 627:155-70.

Hamer KC, Phillips RA, Wanless S, Harris MP, Wood AG (2000) Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: Evidence from satellite telemetry. *Marine Ecology Progress Series* 200: 257–264, doi: 10.3354/meps200257.

Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295–305, doi:

10.3354/meps338295.

Hamer KC, Humphreys EM, Magalhães, Garthe S, Hennicke J, Peters G, Grémillet D, Skov H, Wanless S (2009) Fine-scale foraging behaviour of a medium-ranging marine predator. *Journal of Animal Ecology 2009*, 78: 880–889

Harris MP, Wanless S (1996) Differential responses of Guillemot Uria aalge and Shag Phalacrocorax aristotelis to a late winter wreck. *Bird Study*, 43(2):220-30.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S (2011) Carry-over effects as drivers of fitness differences in animals. *Journal of Animal Ecology*, 80(1):4-18.

Hijmans RJ (2018) raster: Geographic Data Analysis and Modeling. R package version 2.8-4

Hobson KA, Piattt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63: 786−798

Isaksen KJ (1995) Distribution of seabirds at sea in the northern Barents Sea. Seabird populations in the northern Barents Sea: Source data for the impact assessment of the effects of oil drilling activity. *Norsk Polarinstitutt Meddelelser.* 135:67-78.

Kacelnik A (1984) Central Place Foraging in Starlings (*Sturnus vulgaris*). Patch Residence Time. *Journal of Animal Ecology* 53(1): 283–299, doi:10.2307/4357

Katzir G, Lotem A & Intrator N (1989) Stationary underwa- ter prey missed by Reef Herons, Egretta gularis: head posi- tion and light refraction at the moment of strike*. J. Comp. Physiol. A.* 165: 573–576.

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can J Zool* 78: 1−27

Kooyman GL, Cherel Y, Le Maho Y, Croxall JP, Thorson PH, Ridoux V, Kooyman CA (1992) Diving behavior and energetics during foraging cycles in King Penguins. *Ecol. Monogr.* 62: 143–163

Lane JV, Spracklen DV, Hamer KC (2019) Effects of windscape on three-dimensional foraging behaviour in a wide-ranging marine predator, the northern gannet. *Marine Ecology Progress Series* 628: 183–193, doi: 10.3354/meps13089.

Lane JV, Jeavons R, Deakins Z, Sherley RB, Pollock CJ, Wanless RJ, Hamer KC (2020) Vulnerability of northern gannets to offshore wind farms; seasonal and sex-specific collision risk and demographic consequences. *Marine Environmental Research* 162: 105196, doi: 10.1016/j.marenvres.2020.105196.

Lewis S, Wanless S, Wright PJ, Harris MP (2001) Diet and breeding performance of Black-legged Kittiwakes Rissa tridactyla at a North Sea colony, *Marine Ecology Progress Series*, 221:277-284

Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B* 269: 1687–1693, doi: 10.1098/rspb.2002.2083.

Lewis S, Benvenuti S, Daunt F, Wanless S, Dall'Antonia L, Luschi P, Elston DA, Hamer KC, Sherratt TN (2004) Partitioning of diving effort in foraging trips of northern gannets. *Canadian Journal of Zoology* 82(12): 1910–1916, doi: 10.1139/z05-005.

Lovvorn JR, Baduini CL, Hunt GLJ (2001) Modeling underwater visual and filter feeding by planktivorous shearwaters in unusual sea conditions. *Ecology* 82: 2342– 2356

MacArthur RH and Pianka ER (1966) On Optimal Use of a Patchy Environment. *The American Naturalist*, 100(916): 603–609, doi: 10.1086/282454.

Nelson B (2002) *The Atlantic Gannet*. Published by Fenix Books Limited, Norfolk.

Newton I (1998) *Population limitation in birds. Academic, London*

Norman FI, Brown RS (1987) Notes on Common Diving-Petrels *Pelecanoides urinatrix* found beach-washed in Victoria, 1985. *Emu,* 87(3):179-84.

Nourani E, Safi K, de Grissac S, Anderson DJ, Cole NC, Fell A, Grémillet D, Lerma M, McKee JL, Pichegru L, Provost P, Rattenborg NC, Ryan PG, Santos CD, Schoombie S, Tatyah V, Weimerskirch H, Wikelski M, Shepard ELC (2022) Extreme tolerable winds for seabirds are determined by morphology. *BioRχiv*, doi: 10.1101/2022.05.02.490292.

O'Halloran J, Gribbin SD, Tyler SJ, Ormerod SJ (1990) The ecology of Dippers *Cinclus cinclus* (L.) in relation to stream acidity in upland Wales: time-activity budgets and energy expenditure*. Oecologia* 85: 271–280

Parker-Stetter S, Urmy S, Horne J, Eisner L, Farley E (2016) Factors affecting summer distributions of Bering Sea forage fish species: Assessing competing hypotheses. *Deep-Sea Research Part II: Topical Studies in Oceanography* 134: 255–269, doi: 10.1016/j.dsr2.2016.06.013.

Pennycuick CJ (2008) *Modelling the Flying Bird*. Elsevier Inc., Burlington, MA.

Phillips RA, Silk J, Phalan B, Catry P, Croxall J (2004) Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings. Biological Sciences* 271(1545): 1283–1291, doi: 10.1098/rspb.2004.2718.

Piatt JF, Van Pelt TI (1997) Mass-mortality of Guillemots (*Uria aalge*) in the Gulf of Alaska in 1993. *Marine Pollution Bulletin*, 34(8):656-62.

Pierce D (2021) ncdf4: Interface to Unidata netCDF. R package version 1.19

Ropert-Coudert Y, Grémillet D, Kato A, Ryan P G, Naito Y, Le Maho Y (2004) A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds. *Animal Behaviour,* 67(5): 985–992, doi:10.1016/j.anbehav.2003.09.010

Ropert-Coudert Y, Daunt F, Kato A, Ryan PG, Lewis S, Kobayashi K, Mori Y, Grémillet D, Wanless S (2009) Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology*, 40(4): 380–387, doi: 10.1111/j.1600-048X.2008.04592.x.

Salton M, Saraux C, Dann P, Chiaradia A (2015) Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *Royal Society Open Science*, 2(1):140390.

Shillinger GL, Bailey H, Bograd SJ, Hazen EL, Hamann M, Gaspar P, Godley BJ, Wilson RP, Spotila JR (2012) Tagging through the stages: technical and ecological challenges in observing life histories through biologging. *Marine Ecology Progress Series,* 21;457:165-70.

Spear LB and Ainley DG (1998) Morphological differences relative to ecological segregation in petrels (Family: *Procellariidae*) of the Southern Ocean and tropical Pacific. *The Auk* 115: 1017–1033.

Stearns SC (1992) *The evolution of life histories. Oxford University Press, Oxford*

Tavares DC, Moura JF, Merico A, Siciliano S (2020) Mortality of seabirds migrating across the tropical Atlantic in relation to oceanographic processes. *Animal Conservation*, 23(3):307-19.

Trivers RL and Campbell B (1972) *Sexual selection and the descent of man. Aldinc Chicago,* 136-179.

Young IR and Agustinus R (2019) Multiplatform evaluation of global trends in wind speed and wave height. *Science* 364(6440): 548–552, doi: 10.1126/science.aav9527.

Wakefield ED, Cleasby IR, Bearhop S, Bodey TA, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity - why some gannets don’t change their spots. *Ecology*, 96(11): 3058–3074, doi: 10.1890/14-1300.1.sm.

Wiens JA (1976) Population responses to patchy environments. *Annual Review of Ecology and Systematics*, 7: 81-120

Wolf J, Woolf D, Bricheno L (2020) Impacts of climate change on storms and waves relevant to the coastal and marine environment around the UK. *MCCIP Science,* 15;2020:132-57.

4.7 Supplementary materials S4

Table S4.1. Model estimates testing for differences in the mean wind speed (ms^{-1}) encountered during foraging behaviour by male and female northern gannets (*Morus bassanus*) rearing chicks at Bass Rock, Scotland in 2017-2019.

Wind speed (ms^{-1}) at foraging locations ~ Sex and Year									
Intercept - 2017, Female	6.86	0.65	65	10.58	<0.001				
Sex – Male	-0.77	0.89	38	-0.87	>0.05	**Sex**	0.003	1	>0.05
Year - 2018	-2.46	0.81	38	-3.02	0.005	**Year**	8.90	2	0.01
Year - 2019	0.06	0.85	38	0.07	>0.05	**Sex*Year**	6.40	2	0.04
Male – 2018	2.04	.12	38	1.82	>0.05				
Male - 2019	-0.41	1.19	38	-0.34	>0.05				

Table S4.2. Model selection tables for GLMMs investigating the influencing factors and interactions of wind speed and foraging behaviour of male and female chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019, Bass Rock, Scotland.

Rank	**Model**	**df**	**LogLik**	**AICc**	**ΔAICc**	**AICc weight**
Female Take-off rate ~ Year* Wind speed						
1	Year	5	-56.13	123.6	0.00	0.472
2	-	3	-59.09	124.7	1.11	0.271
3	Wind speed + Year	6	-55.75	125.4	1.79	0.193
4	Wind speed	4	-59.61	128.1	4.51	0.050
Male Take-off rate ~ Year* Wind speed						
1	-	3	-86.21	178.9	0.00	0.807
2	Year	5	85.79	182.8	3.89	0.116
3	Wind speed	4	-87.51	183.8	4.92	0.069
4	Wind Speed + Year	6	-87.12	188.0	9.07	0.009
Female ODBA per minute spent foraging ~ Wind speed*Year*Take-off rate						
1	-	3	-20.25	47.0	0.00	0.849
2	Year	5	-20.33	52.0	4.96	0.071

3	Take-off rate	4	-21.92	52.7	5.68	0.050
4	Wind speed	4	-22.86	54.6	7.55	0.019
Male ODBA per minute spent foraging ~ Wind speed*Year + Take-off rate						
1	Take off rate	4	-52.36	113.5	0.00	0.850
2	Take-off rate + Year	6	-52.78	119.3	5.76	0.050
3	Wind speed + Take-off rate	5	-54.56	120.3	6.82	0.029
4	Year	3	-57.07	120.6	7.10	0.026
Female Proportion of trip spent foraging ~ Wind speed*Year*Take-off rate						
1	Take-off rate	4	-48.87	106.6	0.00	0.829
2	Take-off rate + Wind speed	5	-49.83	111.0	4.38	0.093
3	Take-off rate + Wind speed + Year	6	-49.54	112.9	6.35	0.035
4	Take-off rate + Year + Take-off rate*Year	8	-47.45	114.3	7.67	0.018
Male Proportion of trip spent foraging ~ Wind speed*Year + Take-off rate + Take-off rate^{2}						
1	Take-off rate + Take-off rate ^{2}	5	-74.02	159.2	0.00	0.863
2	Take-off rate + Take-off rate ^{2}	6	-75.43	164.6	5.34	0.060
3	Take-off rate + Take-off rate ^{2}	7	-74.23	164.8	5.56	0.054
4	-	3	-80.53	167.5	8.30	0.014

Table S4.3. Estimates of averaged models as determined in model selection (Table S4.2) investigating the relationships between foraging behaviours and wind conditions of chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019 at Bass Rock, Scotland.

	Estimate	**SE**	**Adj.SE**	**Z**	**P**		**2.5%**	**97.5%**
Female Take-off rate ~ Wind speed*Year								
Intercept	3.86	0.43	0.43	8.93	<0.001	**Intercept**	3.01	4.70
2018	0.42	0.32	0.34	1.23	>0.05	**2018**	-2.25	1.08
2019	0.87	0.29	0.32	2.77	0.006	**2019**	0.26	1.49
Wind speed	-0.12	0.05	0.05	2.15	0.03	**Wind speed**	-0.23	-0.01

Table S4.4. Estimates for the model of best fit selected in table S4.2, investigating the relationships between foraging behaviours and wind conditions of chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019, Bass Rock, Scotland.

Intercept	**Estimate**	**SE**	**df**	**t**	**P**		χ^2	**df**	**P**
Male ODBA per minute spent foraging ~ Take-off rate									
Intercept			32	14.40	<0.001				
Take-off rate	0.25	0.07	32	3.80	<0.001	**Take-off rate**	14.43	1	<0.001

Table S4.5. Estimates for the models investigating the relationships between dive depth (m), take-off rate h^{-1} foraging and wind conditions of chick-rearing northern gannets (*Morus bassanus*) between 2017 and 2019, Bass Rock, Scotland (N=14 trips, 7 individuals).

Intercept	**Estimate**	**SE**	**df**	**t**	**P**		χ^2	**df**	**P**
Female maximum dive depth (m) ~ Wind speed									
Intercept	12.28	6.55	3	1.88	>0.05				
Wind speed	-0.40	0.87	3	-0.46	>0.05	**Wind speed**	0.21	1	>0.05
Male maximum dive depth (m) ~ Wind speed									
Intercept	-1.19	0.89	2	-1.35	>0.05				
Wind speed	0.41	0.12	2	3.56	>0.05	**Wind speed**	12.79	1	<0.001
Female take-off rate ~ maximum dive depth (m)									
Intercept	4.19	0.40	3	10.62	<0.001				
Max. depth	0.04	0.04	3	1.02	>0.05	**Max. depth**	1.04	1	>0.05
Male take-off rate ~ maximum dive depth (m)									
Intercept	6.57	1.02	2	6.47	>0.05				
Max. depth	-0.35	0.25	2	-1.41	>0.05	**Max. depth**	1.97	1	>0.05

Chapter 5 **Discussion**

An incoming rain shower from the mainland, with The Law above North Berwick in the distance.

5.1 Summary of aim and objectives

The marine environment is changing under anthropogenic influences (Young and Agustinus 2019; Wolf *et al.,* 2020). During these rapid changes, it is crucial to understand the impacts and drivers of foraging behaviour in the species at risk, and direct findings towards predicting the consequences of ongoing and future climate change on populations (Mitchell *et al.,* 2020). The primary of aim of this thesis has been to contribute to the study of seabirds towards informing conservation and management efforts by investigating the potential energy consequences and drivers for known patterns of broad-scale behaviour and movement of chick-rearing northern gannets, *Morus bassanus.* Through this thesis I have investigated the variation and patterns in energy expenditure and fine-scale behaviour associated with the sexes, individuality and the environment. I found that when predicting the effects of anthropogenic change on populations we should include the effect of sex and individuality within our studies because sexes and individuals are likely to respond differently. Seabirds share many life history traits (Furness and Monaghan 1987), so considering these factors will improve and refine predictions of anthropogenic impacts going ahead, to help provide robust management and conservation strategies for this enigmatic and ecologically important group of animals.

Objective 1: Examine the role of sexual dimorphism in the prevalence of sexual segregation and determine whether there are the sex-specific energy and behavioural consequences.

In Chapter 2 I showed that wing loading differs between the sexes as a consequence of greater body mass in females than males. From samples of comparable outbound and inbound flight, I found the fine-scale flight characteristics of the sexes differed, with the results suggesting females put more effort into flight than males. These fine-scale differences in flight characteristics likely explain the higher ODBA per minute during flight of females over a trip. I determined that take-off rate h^{-1} foraging is likely associated with foraging success and found that males have a higher take-off rate than females. Movements and behaviour of birds within each sex were related to body mass but in a way that was not consistent with the notion that differences between sexes were driven by sexual dimorphism. Rather, sex differences in body mass are likely a consequence of the different foraging strategies of males and females, with heavier females gaining an advantage in attaining greater depths during plunge dives.

Objective 2: Quantify measures of individuality in the foraging trips of gannets and assess the energy and behavioural consequences of individual foraging site fidelity (IFSF) to determine potential drivers of individuality and future responses to environmental change.

In Chapter 3 I found gannets were highly individually consistent in space and energy expenditure, but how this energy was expended in time and behaviours, were flexible. Individual foraging site fidelity (IFSF) was associated with enhanced foraging success in females and higher foraging effort for males. Hence the consequences of individuality were sex-specific.

Objective 3: Investigate how wind conditions affect foraging success by examining fine-scale behaviour and energy expenditure during foraging under different wind speeds.

In Chapter 4 I focused on how foraging behaviour and energy expenditure were affected by the wind conditions encountered by birds while foraging. The results of this chapter suggest that like shallow diving seabirds, wind conditions affect the foraging success of gannets (Baptist and Leopold 2010). Interestingly, there were sex-specific interactions with wind conditions, with females apparently foraging less successfully in windier conditions and males diving deeper for prey.

5.2 Key findings and implications

Accelerometry and methods

At the beginning of this PhD project, there were eight scientific publications using accelerometers to investigate the foraging behaviour and effort of the three species of gannet *Morus sp.* (searching “gannet” and “acceleromet” *Web of Science*, 23/08/2017). During the process of this PhD nine further papers have been published, none of which examine gannets at Bass Rock (Web of Science 25/05/2022). Whilst progress is evident, estimating effort and energy expenditure is still relatively novel, with researchers often creating unique approaches to handle the complex and ‘big’ accelerometery data (e.g. Shaffer, Costa and Weimerskirch 2003; Green *et al.,* 2010; Amélineau *et al.,* 2014; Grémillet *et al.,* 2018). This has been crucial to the development of methods, but it is time to bring these approaches together to better utilise the wealth of data that accelerometers can produce. As accelerometers become more affordable, lighter and smaller with longer battery life, the potential application and understanding can expand to different aspects of the breeding season, and ideally to annual cycles. Within Chapter 4 I discussed the vulnerability of seabirds to extreme weather events during the inter-breeding season and the impacts on foraging efficiency and subsequent fitness and survival (Grecian *et al.,* 2019; Grémillet *et al.,* 2020). Quantifying energetic effort and identifying behaviours on a finer-scale than ‘time spent’ during the winter could bring the energy budgets and thus stressors on seabirds to the full annual cycle, providing a clearer understanding of the interactions between them and fitness (Harrison *et al.,* 2021; Elliott *et al.,* 2014).

The novel metrics developed in Chapter 2 and used throughout this thesis have broad implications to other seabirds and central-place foragers. Bringing together metrics of foraging behaviour to determine take-off rate can be used as a measure of foraging success in species that physically enter the water to feed. The calculation of take-offs are not bound to accelerometers and could be determined using time-depth recorders, geolocators or any bio-logging device that has a saltwater switch or even thermometer, depending on the resolution (Mattern *et al.,* 2015; Wilmers *et al.,* 2015). The potential application with geolocators is exciting; geolocators are generally smaller devices, with a battery life that can span years, as well as having a more durable attachment method on leg rings (Wilmers *et al.,* 2015). These characteristics could produce estimates of foraging effort and success over wintering periods and open up the study of foraging effort to smaller and more difficult to access species, such as shearwaters (e.g. Ramos *et al.,* 2019).

There is considerable scope for answering increasingly complex species-specific and broader ecological questions with the methods created in this thesis, to aid in determining the consequences of change on population dynamics. Much of our current efforts to determine these come in the form of predictive modelling, such as population viability analysis (PVA) and individual-based models (IBMs) (Beissinger and McCullough 2002; Railsback and Grimm 2019). IBMs are becoming an integral part of predicting the impacts of change and are also capable of improving ecological theory and synthesising empirical findings to identify broad trends (Evans *et al.,* 2013). Regularly used in academia, there is mounting pressure to include IBMs within environmental impact assessments due to the current lack of consideration of the effect of individuality on populations (Warwick-Evans *et al.,* 2017; Stelzenmüller *et al.,* 2018). IBMs are a ‘bottom-up’ approach, identifying individuals as distinct entities, with individual characteristics and plasticity, derived from the available literature (Railsback and Grimm 2019). Thus, for IBMs and other ‘big data’ management efforts there must be a foundation of empirical science, with as few assumptions as possible to ensure their accuracy. The results of this thesis suggest strong individuality in the effort and energy expenditure of breeding gannets, which very likely applies to other seabirds that exhibit individual consistencies in foraging behaviour and space. Energy expenditure is a vital link between behaviour and fitness consequences, and thus would be a valuable addition to IBMs (Grémillet *et al.,* 2018).

Bringing together the three themes of this thesis

This thesis worked towards identifying how sex, individuality and the environment might contribute to the variation in fine-scale foraging behaviour and energy expenditure of chick-rearing gannets. Though investigations into these themes were conducted in three distinct chapters, they clearly interacted with one another. Many seabirds share life history traits exhibited by gannets – biparental care, monogamy, individual site fidelity and long lives with slow maturity periods (Furness and Monaghan 1987). These results call for research towards the conservation of these species to consider populations at an individual and sex-based level, rather than ecologically equivalent individuals.

Within each chapter, some assumptions and gaps used in conservation management are resolved. Gannets are sexually dimorphic, if only in body mass (Nelson 2002; this study). The effect of this on behaviour has been varied or overlooked, so to finally reveal the relationships between mass, sex and the finest scales of behaviour, e.g. individual wingbeats, provides a baseline for the other relationships observed (Clark *et al.,* 2021; Bennison *et al.,* 2022). The rest of this chapter broadens the perspective on how we study sex differences in species with sexual segregation. Quantifying energy expenditure and a measure of foraging success provide new evidence to suggest sexual segregation likely persists to reduce intra-specific competition and improve breeding success. Sex differences identified in all three data chapters support the notion that perhaps we should consider sexes separately, as long-standing sexual segregation research has called for in other animals (Kie and Bowyer 1999).

The effect of sex also plays a role in the consequences of individuality in gannets, something that has not been investigated this way in seabird foraging ecology. IFSF is a measure of individual spatial consistency and is frequently quantified in central-place foragers (e.g. Baylis *et al.,* 2012; Wakefield *et al.,* 2015; Lescroël *et al.,* 2020). The findings of this chapter indicate high IFSF is advantageous to females but not for males, and conversely, females may therefore be more vulnerable to negative impacts of environmental change. Individuality has been given little regard in environmental impact assessments, an oversight when considering anthropogenic developments within foraging ranges, such as offshore wind farms or tidal developments. The results of this chapter highlight that the effect of sex on the individual consequences of IFSF is important when considering population dynamics during environmental change and in the context of our understanding of the evolution and persistence of individuality. Supporting a growing body of work calling for individuals to be considered separately (Ceia and Ramos 2015), with the addition of sex-specific consequences.

The results of Chapter 3 found little individual consistency in metrics associated with foraging, suggesting a stronger effect of environmental conditions on these aspects of behaviour. The sex differences in response to wind bring the results of the three chapters together. These findings again seems to be due to sex differences in foraging strategies – as discovered in Chapter 3, males may have a more variable strategy with more variable consequences. It appears when males forage earlier in a foraging trip (in distance and time) they can put more effort into foraging with a higher take-off rate perhaps because the cost of travel will be less, so more energy can be spent exploiting profitable areas, and the consequences of this are seen when males travel further afield with less efficiency. As surmised in Chapter 3, females may target more reliable and consistent prey patches and be adapted to do so with heavier body mass allowing greater depths to be reached (Lewis *et al.*, 2002).

It seems to me that these differences between sexes, and individuals within each sex, may be driven by ensuring reproductive success. Female gannets put very little investment in eggs – one of the lowest relative yolk to egg mass of all birds, with low lipid and energy content (Ricklefs and Montevecchi 1979; Birkhead 2016). Consequently the incubation and chick-rearing period are long, with seemingly equal parental care (Nelson 2002). This pattern of rearing offspring suggests that although gannets have incredibly high breeding success rates, it really does take two for the additional effort of feeding a chick for this species. Results in Chapter 3 may support this; individual consistency in metrics associated with energy expenditure could suggest gannets are at an energetic ceiling. The consequences of this hypothesis have been shown at the southern range of gannets, where populations have declined in recent years due to prey shortages in warming waters, and the effects of poor winter conditions (Grémillet *et al.,* 2020; Clairbaux *et al.,* 2021; d'Entremont *et al.,* 2022). The results of this thesis only apply to the breeding season, but the persistence of sex differences and individuality continue in inter-breeding dietary niche, migration routes and wintering locations (Deakin *et al.,* 2019; Grecian *et al.,* 2019). Persistence of individuality over the annual cycle makes sense if established by site familiarity through exploring, experience and learning (Piper 2011; Votier *et al.,* 2017). However, the persistence of sex differences outside the breeding season suggest another driver of sexual segregation. Perhaps sex differences are due to different nutritional requirements as previously hypothesised (Morehouse *et al.,* 2010), though the low investment in egg production by females doesn't support this. Clearly there is more to uncover in the mechanisms behind sexual segregation in gannets.

In regard to conservation measures in the face of climate change, and anthropogenic responses to the climate crisis, the results of these three chapters suggest females are likely to be at more risk of reduced fitness and survival; energy costs associated with flight are higher for females, they make longer foraging trips during the breeding season, and the energy costs of foraging are higher too. Remove the yet undetermined benefit that comes from the foraging strategy of females, and this sex is more vulnerable to change. IFSF is a greater benefit to females than males, suggesting factors that make prey less predictable will affect them more negatively than males that have an association with less effort and low IFSF. Applying the results of Chapter 4 to the inter-breeding season, and females may have reduced foraging success, and thus lower foraging efficiency when exposed to more frequent extreme weather events, leading to potential carry-over effects (Harrison *et al.,* 2011).

5.3 Considerations and future directions

The research presented here builds on studies to date working towards developing our understanding of seabird ecology using gannet behaviour, energy expenditure and the application of the methods created for this thesis. It should be noted that this thesis is to be viewed in the context of timescale and location; I discuss inter-annual differences, but make no conclusive inferences given the three years of data collection because three seasons may not be long enough to represent some patterns as consistent (Hamer *et al.,* 2007; Clark *et al.,* 2021). Bass Rock is the largest gannet colony in the world, so density dependence and intra-specific competition are more likely to act upon gannet behaviour here (Lewis *et al.,* 2001; Murray *et al.,* 2015). In addition, birds have access to different food resources at different colonies, both in the availability of common prey species and proclivity to target fishery discards (Lewis *et al.,* 2003; Votier *et al.,* 2010). Thus, some aspects of these results and, more widely, gannet foraging ecology are likely to be colony-specific (Nelson 2002; Lewis *et al.,* 2001; Wakefield *et al.,* 2013).

The methods developed in this thesis, and their application to identifying sources of variation in the energy expenditure and fine-scale behaviour of individual gannets bridge some of the assumptions made within gannet and wider seabird ecology. The areas of research suggested below address small, but significant gaps in our knowledge of seabird foraging ecology that have become apparent throughout the process of this PhD.

To enhance our understanding of the relationships among fitness, body condition and foraging behaviour, I think it’s time for a revival of at-colony studies. There are gaps and assumptions unable to be addressed in this thesis that are a crucial component of biparental care and the consequences of it; how much food does each parent provision the chick? This area remains insufficient in our understanding of the consequences of sex differences in gannets and other seabirds. During data collection for this thesis, accelerometers were attached to birds during periods of nest attendance, and with further deployments and at nest validation (via direction observation or video recordings) these data could be used to quantify chick feeding rates as seen in other birds (Yang *et al.,* 2021) and investigate sex-specific effort at the nest, which has been speculated but is yet to be quantified (Nelson 2002; Clark *et al.,* 2021). In other species of seabird, personality at the nest (whether individuals are bold or shy) plays a role in determining foraging behaviour and IFSF (Harris *et al.,* 2019). With the long-term data available for some individuals at the Bass Rock colony for the breeding season and migration, personality studies could shed light on the origin of IFSF in seabirds and the potential of sex-specific personalities suggested in this thesis.

Chapter 2 and 3 highlighted differences between sexes in energy expenditure and consequences of IFSF. Thus, a partner's behaviour may change in response to the other's effort and under different environmental conditions. These interactions are important to consider for conservation, as there may be fitness consequences to sex-related differences in foraging effort that have not yet been considered. Partnership studies of breeding gannets and other seabirds are an under-explored area, partly due to logistical difficulties of deploying tags on a pair, however scientific progress in this area could be significant for developing understanding of sex-specific foraging during chick-rearing, particularly in relation to energy expenditure and the extent and purpose of sex-specific individuality. Divorce rates are generally low in northern hemisphere seabirds, but it has been demonstrated in response to breeding failure in a number of species including black-legged kittiwakes, *Rissa tridactyla,* and northern gannets (Mercier *et al.,* 2021; Pelletier and Guillemette 2022). In northern gannets divorce rates have been linked to breeding failure of the previous season but partner replacement can also have fitness costs; whereby partner retention in the closely related Australasian gannet, *Morus serrator,* had consistently higher reproductive success compared to those that replaced partners (Ismar *et al.,* 2010). This phenomenon and fitness consequences provide further evidence towards the importance of pair effort and behaviour. Quantifying traits of foraging on pairs simultaneously would address a frequently made assumption; that individuals in a pair act independently of one another, but perhaps they are co-operating, and responding to each other on a trip-by-trip basis, as one unit. Using the proxies of energy expenditure and foraging success developed in Chapter 2 and applying them to pairs instead of individuals could open up a whole new approach to studying seabird foraging ecology during the chick-rearing season.

Chapter 4 identified adverse effects of wind speed on foraging success and dive behaviour. Gannets occasionally adopt underwater wingbeats as a strategy to reach greater depths after the initial plunge-dive, and this strategy is likely to more energetically costly and time-consuming than plunge-diving without using wingbeats underwater (Ropert-Coudert *et al.,* 2009; Green *et al.,* 2010). Underwater wingbeats allow gannets to increase dive depths and pursue prey not caught upon immediate entry to the water (Ropert-Coudert *et al.,* 2009). The circumstances of underwater wingbeats are relatively unknown in this species and the results of Chapter 4 brought forth a hypothesis; gannets might use the more costly underwater wingbeats in windier conditions to compensate for inaccurate dives due to reduced visibility and perhaps in other unfavourable conditions, such as a high density of conspecifics targeting the same prey patch. Underwater wingbeats are identifiable from accelerometry data, and on a less fine-scale by the time spent underwater with time-depth recorders (Ropert-Coudert *et al.,* 2009; Cleasby *et al.,* 2015). Thus, it could be determined if underwater wingbeats are associated with unfavourable diving conditions and inaccurate dives. Then, as I did for take-off rate, it could be established if the prevalence of underwater wingbeats has trip wide consequences by relating it to energy expenditure and other trip metrics. This would likely apply to other seabirds that target prey sensitive to surface turbulence and improve our understanding of the associations between prey and predator behaviour below the surface.

5.4 Conclusion

The marine environment is highly likely to continue to change significantly in the coming years (Young and Agustinus 2019; Wolf *et al.,* 2020). To manage seabird populations it is vital to develop a deeper understanding of how common life history phenomena affect populations. Proxies of energy expenditure and examining behaviour on a fine-scale have enormous potential to bridge the gaps between identifying behaviour and determining the consequences of it. Throughout this thesis I advocate for the increased inclusion of sex and individuality within the assessment of environmental change on seabird populations. I argue that the results of this thesis demonstrate that even one of the most resilient seabirds will likely be affected by anthropogenic constraints upon its populations, and thus gannets are strong ecological indicators for the effects on other seabirds. Without further consideration of the variation in the energy expenditure and fine-scale behaviour between individuals and sexes, our understanding and reliance on assumptions may limit our capacity to effectively conserve seabird populations and the habitats they rely on.

5.5 References

Amélineau F, Péron C, Lescroël A, Authier M, Provost P, Grémillet D (2014) Windscape and tortuosity shape the flight costs of northern gannets. *Journal of Experimental Biology* 217(6): 876–885, doi: 10.1242/jeb.097915.

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. *Ecology Letters* 14(9): 948–958, doi: 10.1111/j.1461-0248.2011.01662.x.

Baptist MJ and Leopold MF (2010) Prey capture success of sandwich terns *Sterna sandvicensis* varies non-linearly with water transparency. *Ibis* 152(4): 815–825, doi: 10.1111/j.1474-919X.2010.01054.x.

Baylis AMM, Page B, McKenzie J, Goldworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: Continental shelf vs. oceanic habitats. *Marine Mammal Science* 28(2): 276–294, doi: 10.1111/j.1748-7692.2011.00487.x.

Beissinger SR and McCullough DR (2002) *Population Viability Analysis. University of Chicago Press*

Bennison A, Giménez J, Quinn JL, Green JA, Jessopp M (2022) A bioenergetics approach to understanding sex differences in the foraging behaviour of a sexually monomorphic species. *Royal Society Open Science* 9: 210520, doi: 10.1098/rsos.210520.

Birkhead TR (2106) *The most perfect thing: the inside and outside of a bird's egg. Bloomsbury USA*

Ceia FR and Ramos JA (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. *Marine Biology* 162(10): 1923–1938, doi: 10.1007/s00227-015-2735-4.

Clairbaux M, Mathewson P, Porter W, Fort J, Strøm H, Moe B, Fauchald P, Descamps S, Helgason HH, Bråthen VS, Merkel B (2021) North Atlantic winter cyclones starve seabirds. *Current Biology*. 31(17):3964-71.

Clark B, Cox SL, Atkins K, Bearhop S, Bicknell AWJ, Bodey TW, Cleasby IR, Grecian WJ, Hamer KC, Loveday BR, Miller PI, Morgan G, Morgan L, Newton J, Patrick SC, Scales KL, Sherley RB, Vigfúsdóttir, Wakefield ED, Votier SC (2021) Sexual segregation of gannet foraging over 11 years: movements vary but isotopic differences remain stable. *Marine Ecology Progress Series* 661: 1–16, doi: 10.3354/meps13636.

Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick S, Newton J, Votier S, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Marine Ecology Progress Series* 518: 1–12, doi: 10.3354/meps11112.

d'Entremont KJ, Guzzwell LM, Wilhelm SI, Friesen VL, Davoren GK, Walsh CJ, Montevecchi WA. Northern Gannets (*Morus bassanus*) breeding at their southern limit struggle with prey shortages as a result of warming waters (2022) *ICES Journal of Marine Science*, 79(1):50-60.

Deakin Z, Hamer KC, Sherley RB, Bearhop S, Bodey TW, Clark BL, Grecian WJ, Gummery M, Lane J, Morgan G, Morgan L (2019) Sex differences in migration and demography of a wide-ranging seabird, the northern gannet. *Marine Ecology Progress Series*, 622:191-201.

Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Crozall C (2019) Threats to seabirds: A global assessment. *Biological Conservation* 237: 525–537, doi: 10.1016/j.biocon.2019.06.033.

Durell S (2000) Individual feeding specialisation in shorebirds: Population consequences and conservation implications. *Biological Reviews of the Cambridge Philosophical Society* 75(4): 503–518, doi: 10.1111/j.1469-185X.2000.tb00053.x.

Elliott KH, Le Vaillant M, Kato A, Gaston AJ, Ropert-Coudert Y, Hare JF, Speakman JR, Croll D (2014) Age-related variation in energy expenditure in a long-lived bird within the envelope of an energy ceiling. *Journal of Animal Ecology* 83(1): 136–146, doi: 10.1111/1365-2656.12126.

Evans MR, Grimm V, Johst K, Knuuttila T, De Langhe R, Lessells CM, Merz M, O'Malley MA, Orzack SH, Weisberg M, Wilkinson DJ (2013) Do simple models lead to generality in ecology? *Trends in ecology & evolution*, 28(10):578-83.

Furness RW and Monaghan P (1987) *Seabird Ecology.* New York: Blackie.

Grecian WJ, Williams HJ, Votier SC, Bearhop S, Cleasby IR, Grémillet D, Hamer KC, Le Nuz M, Lescroël A, Newton J, Patrick SC (2019) Individual spatial consistency and dietary flexibility in the migratory behavior of northern gannets wintering in the northeast Atlantic. *Frontiers in Ecology and Evolution,* 7:214

Green JA, White CR, Bunce A, Frappell PB, Butler PJ (2010) Energetic consequences of plunge diving in gannets. *Endangered Species Research*, 10(1): 269–279, doi: 10.3354/esr00223.

Grémillet D, Lescroël A, ballard G, Bugger KM, Massaro M, Porzig E, Ainley DG (2018) Energetic fitness: Field metabolic rates assessed via 3D accelerometry complement conventional fitness metrics. *Functional Ecology* 32(5): 1203–1213, doi: 10.1111/1365-2435.13074.

Grémillet D, Péron C, Lescroël A, Fort J, Patrick SC, Besnard A, Provost P (2020) No way home: collapse in northern gannet survival rates point to critical marine ecosystem perturbation. *Marine Biology* 167(12): 1–10, doi: 10.1007/s00227-020-03801-y.

Hamer KC, Humphreys EM, Garthe S, Hennicke J, Peters G, Grémillet D, Phillips RA, Harris MP, Wanless S (2007) Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. *Marine Ecology Progress Series* 338: 295–305, doi: 10.3354/meps338295.

Harris SM, Descamps S, Snddon LU, Bertrand P Chastel O, Patrick S (2020) Personality predicts foraging site fidelity and trip repeatability in a marine predator. *Journal of Animal Ecology* 89(1): 68–79, doi: 10.1111/1365-2656.13106.

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

Ismar SM, Daniel C, Stephenson BM, Hauber ME (2010) Mate replacement entails a fitness cost for a socially monogamous seabird. *Naturwissenschaften*, 97(1):109-13.

Kie JG and Bowyer RT (1999) Sexual segregation in white-tailed deer: density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy* 80:1004-1020.

Lescroël A, Lyver POB, Jongsomjit D, Veloz S, Bugger CM, Kappes P, Karl BJ, Whitehead AL, Pech R, Cole TL, Ballard G (2020) Inter-individual differences in the foraging behavior of breeding Adélie penguins are driven by individual quality and sex. *Marine Ecology Progress Series* 636: 189–205, doi: 10.3354/meps13208.

Lewis S, Sherratt TN, Hamer KC, Wanless S (2001) Evidence of intra-specific competition for food in a pelagic seabird. *Nature* 412(6849): 816–819 doi: 10.1038/35090566.

Lewis S, Benvenuti S, Dall-Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society B* 269: 1687–1693, doi: 10.1098/rspb.2002.2083.

Lewis S, Sherratt TN, Hamer KC, Harris MP, Wanless S (2003) Contrasting diet quality of northern gannets *Morus bassanus* at two colonies. *Ardea-Wageningen* 91(2): 167–176.

Mattern T, Masello JF, Ellenberg U, Quillfeldt P (2015) Actave. Net–a web-based tool for the analysis of seabird activity patterns from saltwater immersion geolocators. *Methods in Ecology and Evolution,* 6(7):859-64.

Mercier G, Yoccoz NG, Descamps S (2021) Influence of reproductive output on divorce rates in polar seabirds. *Ecology and Evolution*, 11(19):12989-3000.

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

Morehouse NI, Nakazawa T, Booher CM, Jeyasingh PD, Hall MD (2010) Sex in a material world: why the study of sexual reproduction and sex-specific traits should become more nutritionally-explicit. *Oikos* 119: 766−778

Murray S, Harris MP, Wanless S (2015) The status of the gannet in Scotland in 2013-14. *Scottish Birds* 35(1): 3–18.

Nelson B (2002) *The Atlantic Gannet*. Published by Fenix Books Limited, Norfolk

Paredes R, Orben RA, Suryan RM, irons DB, Roby DD, Harding AMA, Young RC, Benoit-Bird K, Ladd C, Renner H, Heppell S, Phillips RA, Kitaysky A (2014) Foraging responses of black-legged kittiwakes to prolonged food-shortages around colonies on the Bering Sea shelf. *PloS ONE* 9(3): e92520, doi: 10.1371/journal.pone.0092520.

Piper WH (2011) Making habitat selection more “familiar”: a review. *Behavioral Ecology and Sociobiology* 65(7): 1329–1351, doi: 10.1007/s00265-011-1195-1.

Pelletier D and Guillemette M (2022) Times and partners are a-changin’: relationships between declining food abundance, breeding success, and divorce in a monogamous seabird species. *PeerJ,* 10:e13073.

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

Ramos R, Morera-Pujol V, Cruz-Flores M, López-Souto S, Brothers M, González-Solís J (2019) A geolocator-tagged fledgling provides first evidence on juvenile movements of Cory’s Shearwater *Calonectris borealis*. *Bird Study*, 66(2):283-8.

Ricklefs RE, Montevecchi WA (1979) Size, organic composition and energy content of North Atlantic gannet Morus bassanus eggs. *Comparative Biochemistry and Physiology Part A: Physiology,* 64(1):161-5.

Ropert-Coudert Y, Grémillet D, Ryan P, Kato A, Naito Y, Le Maho Y (2004) Between air and water: The plunge dive of the Cape Gannet *Morus capensis. Ibis*, 146(2): 281–290, doi: 10.1111/j.1474-919x.2003.00250.x.

Ropert-Coudert Y, Daunt F, Kato A, Ryan PG, Lewis S, Kobayashi K, Mori Y, Grémillet D, Wanless S (2009) Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology*, 40(4): 380–387, doi: 10.1111/j.1600-048X.2008.04592.x.

Shaffer SA, Costa DP, Weimerskirch H (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* 17(1): 66–74, doi: 10.1046/j.1365-2435.2003.00705.x.

Stelzenmüller V, Coll M, Mazaris AD, Giakoumi S, Katsanevakis S, Portman ME, Degen R, Mackelworth P, Gimpel A, Albano PG, Almpanidou V (2018) A risk-based approach to cumulative effect assessments for marine management. *Science of the Total Environment*, 612:1132-40.

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* 47(2): 487–497, doi: 10.1111/j.1365-2664.2010.01790.x.

Votier SC, Fayet AL, Bearhop S, Wodey TW, Clark BL, Grecian J, Guilford T, Hamer KC, Jeglinski JWE, Morgan G, Wakefield E, Patrick SC (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proceedings of the Royal Society B: Biological Sciences* 284(1859): 20171068, doi: 10.1098/rspb.2017.1068.

Wakefield ED, Cleasby IR, Bearhop S, Bodey TA, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity - why some gannets don’t change their spots. *Ecology*, 96(11): 3058–3074, doi: 10.1890/14-1300.1.sm.

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

Web of Science. Available at: www.webofknowledge.com (Accessed: 23 August 2017).

Wilmers CC, Nickel B, Bryce CM, Smith JA, Wheat RE, Yovovich V (2015) The golden age of bio-logging : how animal- borne sensors are advancing the frontiers of ecology. *Ecology* 96: 1741–1753, doi: 10.1890/14-1401.1.

Wolf J, Woolf D, Bricheno L (2020) Impacts of climate change on storms and waves relevant to the coastal and marine environment around the UK. *MCCIP Science,* 15;2020:132-57.

Yang X, Zhao Y, Street GM, Huang Y, Filip To SD, Pursell JL (2021) Classification of broiler behaviours using triaxial accelerometer and machine learning. *Animal* 15(7): 100269, doi: 10.1016/j.animal.2021.100269.

Young IR and Agustinus R (2019) Multiplatform evaluation of global trends in wind speed and wave height. *Science* 364(6440): 548–552, doi: 10.1126/science.aav9527.id