Annual cycles in the behaviour and energetics of North Atlantic seabirds

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by Ruth Elizabeth Dunn.

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Abstract

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Energy is the central currency that drives biological processes at every hierarchical level of life and maintaining an energetic balance is therefore integral to an animal's survival. For iteroparous species, investigating how they manage their energy budgets throughout the annual cycle, in the face of seasonally varying intrinsic and extrinsic drivers, is critical to understanding the viability of populations. Although studying year-round energetics has previously been challenging, advances in biologging technology increasingly help to provide novel insights. Seabirds are a frequently investigated taxon within biologging studies; they are top marine predators that are often wide-ranging and many species are of high conservation concern due to a multitude of anthropogenic threats. However, despite an accumulation of knowledge regarding seabird movement and behaviour during their breeding seasons, our understanding of their year-round energetics remains fragmented. Within this thesis I therefore use a range of biologging and analytical approaches to investigate seabird behaviour and energetics throughout different key phases of the year, as well as across the entire annual cycle. Initially, using a global, multi-species, meta-analytical approach, I identify the large-scale drivers of seabird energetics during the breeding period. I demonstrate that seabird energy expenditure increases across the breeding season and also that it is higher for larger birds living at more extreme latitudes. I then focus on the North Atlantic marine ecosystem and compare the diving behaviour of common guillemots *Uria aalge*, razorbills *Alca torda* and Atlantic puffins *Fratercula arctica* during the period following the breeding season. Using biologging data, I identify interspecific, sex-specific and temporal differences in key dive metrics, driven

by differences in body mass, post-breeding strategy and environmental conditions. Next, I combine both biologging data and statistical modelling approaches to focus on temporal changes in the behaviour and energetics of common guillemots. I illustrate that seasonal variation in thermoregulatory costs, diving activity, colony attendance and associated flight all drive guillemot energy expenditure. Finally, I identify temporal and spatial patterns in year-round body mass, subsequent susceptibility to mortality and energy gain. By examining the year-round energetics of seabirds I have therefore been able to develop a more mechanistic understanding of the links between seabird behaviour, energetics and survival in the face of seasonal environmental variability. Due to my focus on energetics, these findings have conservation and management implications; I demonstrate novel approaches to not only increase our understanding of the year-round food requirements of the world's seabirds, but also the potential to identify times and locations throughout the year where seabirds might be susceptible to threats that may impede their survival.

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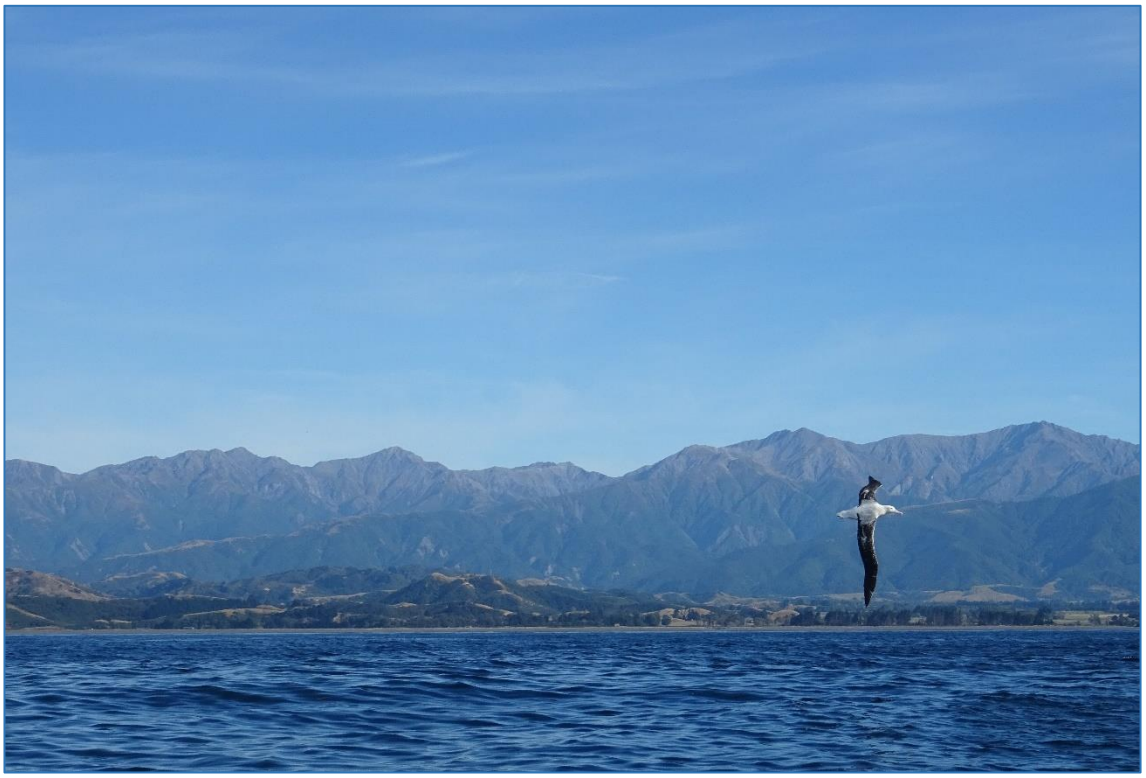
Chapter 1: General introduction



Full Annual Cycles

Numerous natural phenomena are ultimately driven by the Earth cycling the Sun on a tilted axis. Because of the Earth's tilt, many of its inhabitants are subject to seasonal variation in day length, temperature, precipitation, wind and sea ice coverage (Varpe, 2017). Animals with life cycles of over a year must therefore often adapt seasonal patterns of behaviour as they schedule annual life history activities (Russell et al., 2013). For example, yellow-bellied marmots *Marmota flaviventer* live in habitats with long, harsh, snowy winters and therefore hibernate for 8 months, timing their reproduction and the replenishment of fat reserves to occur during the shorter, more productive summer season (Paniw et al., 2020). Whilst the timings of different life history activities (e.g. hibernation, reproduction, migration and dispersal) are temporally and often spatially segregated, the events of each phase are inextricably linked with those of the previous and subsequent phases (Marra et al., 2015). Indeed, carry-over effects, whereby the events of one season influences an individual's performance in a subsequent period, are widespread in the animal kingdom (Harrison et al., 2011). Despite this, ecological research has had a strong bias towards the breeding period, a phase which, whilst critical, composes a relatively small proportion of the annual cycle for many species (Marra et al., 2015). As the drivers of animal ecology and physiology vary seasonally, it is challenging to extrapolate from studies that focus solely on the breeding season, to understand behaviour throughout the entire annual cycle (Ådahl et al., 2006). The study of full annual cycles is therefore critical to our understanding of animal ecology.

Full annual cycle approaches are particularly fundamental for migratory species that inhabit multiple environments or locations throughout the year, and which therefore face a diversity of climatic conditions (Small-Lorenz et al., 2013). These environmental conditions often play a key role in shaping the life-histories of migratory animals, with varying fitness consequences. For example, variations in primary productivity at key

wintering areas and staging sites influence the probability of common tern *Sterna hirundo* recruitment (Szostek and Becker, 2015) and migratory white stork *Ciconia ciconia* survival respectively (Schaub et al., 2005). Despite the importance of the environment on demographic parameters, the impacts of rapid, large-scale environmental change on annual cycles are not well understood (Culp et al., 2017). For migratory species in particular, this is important as they might be especially vulnerable to threats at certain times or whilst in certain areas. For example, variation in sea ice dynamics influences the timing of polar bear *Ursus maritimus* migration (Cherry et al., 2013) and sea level rise threatens the loss of nesting beach habitat for various species of sea turtle (Varela et al., 2019). Conservation strategies must therefore involve annual cycle approaches in order to interpret the year-round effects of environmental variability as well as anthropogenic-induced environmental change (Small-Lorenz et al., 2013).

Whilst previously we may have been limited in our ability to track what happens to individuals across whole annual cycles (Marra et al., 2015), the innovation, modernisation and miniaturisation of biologging devices over the last thirty years has increasingly enabled us to study previously enigmatic life history periods (Hussey et al., 2015; Kays et al., 2015; Wilmers et al., 2015). Combined with these technological advancements, the use of techniques such as stable isotope analyses (Rubenstein and Hobson, 2004), year-round citizen science approaches (Sullivan et al., 2014) and powerful analytical and modelling methods (Russell et al., 2013) are increasingly aiding the provision of novel insights into the year-round drivers of animal behaviour. The knowledge of animal annual cycles gained through these approaches, is intrinsically linked with our ability to develop an understanding of demography and population dynamics, this being a timely objective of ecological research, particularly in the face of environmental change (Reid et al., 2018).

Seabirds

Seabirds are a diverse, polyphyletic avian group, unified in their position as apex marine predators. Additionally, many seabirds typically share a number of life history traits such as their wide-ranging and long-lived nature. They must therefore survive numerous annual cycles, making them ideal taxon through which to research the influence of the environment on these cycles. Seabirds depend on land to breed but are reliant on marine habitats for large proportions of the year. Due to this existence at the interface of both the terrestrial and marine realms, seabirds are exposed to a potentially lethal cocktail of anthropogenic threats including invasive species, overfishing, bycatch, contaminants and pollution (Lewison et al., 2012). In particular, climate change transcends these threats, pervades all ecosystems and is altering marine conditions at unprecedented rates as the world's oceans are forced to absorb increasing quantities of heat (Harley et al., 2006). The influence of anthropogenic-induced changes on ocean dynamics, including increasingly severe weather conditions, are considered a substantial threat to almost a third of seabird species worldwide (Dias et al., 2019). Seabird populations are already exhibiting responses to anthropogenic changes and are more threatened than other comparable taxonomic groups, many species demonstrating marked population declines in recent decades (Croxall et al., 2012). Many of the effects of these changes are likely to be via bottom-up trophic dynamics; the species composition of primary producers is changing and the distributions and abundances of seabird prey species will consequently be affected (Grémillet and Boulinier, 2009; Sydeman et al., 2012). In addition to changes in prey availability, seabirds also experience threats from non-native species, overfishing, human disturbance, extreme weather events and bycatch (Croxall et al., 2012). Assessing the year-round impacts of the environment on this vulnerable group of

species, to then help better understand the influence of environmental change, is therefore a conservation priority (Daunt and Mitchell, 2013; Mitchell et al., 2020).

The breeding season

During their breeding seasons, many seabirds are central place foragers; they forage at sea whilst also being constrained to return to their colony site in order to mate, incubate eggs and provision chicks (Orians and Pearson, 1979). Indeed, during their breeding seasons, over 96% of seabird species are colonial, with colony sizes varying from a few pairs to thousands of individuals (Coulson, 2001). Colonial breeding can lead to increased risk of parasitism and disease as well as intra- and inter-specific competition for food (Brown and Brown, 2001). Despite this, breeding colonially is an advantageous strategy for many seabirds, offering defence from predators, high availability of social information and increased mating opportunities (Schippers et al., 2011).

Numerous studies over the last fifty years have been carried out at seabird breeding colonies across the globe, providing a wealth of information on parameters such as productivity, survival and feeding rates (e.g. Cannell and Maddox, 1983; Roby and Brink, 1986; Kampp, Meltofte and Mortensen, 1987). Additionally, over the last twenty years, their relative accessibility, large body sizes and the conservation concern surrounding them, have put breeding seabirds at the forefront of biologging research (Ropert-Coudert et al., 2010). Indeed, biologging developments have increasingly allowed us to integrate at-colony parameters with an accumulating understanding of at-sea seabird behaviour (Wilson and Vandenabeele, 2012). For example, deployments of global positioning system (GPS) loggers have revealed links between foraging behaviour, diet and breeding success in black-legged kittiwakes *Rissa tridactyla* (Ponchon et al., 2014) and between foraging location and diet in Cape gannets *Morus capensis* (Botha and

Pistorius, 2018). Furthermore, whilst metrics of diving behaviour were once obtained via capillary depth gauges and radio telemetry tags (e.g. Barrett and Furness, 1990; Grémillet, 1997), time depth recorders (TDRs) now increasingly allow further, more fine-scale research into seabird dive characteristics during the breeding season (Thaxter et al., 2009), as they collect data at greater resolutions, for longer durations. Indeed, technological advancements have greatly broadened our understanding of seabird ecology during the breeding season via a diversity of additional techniques: accelerometer loggers enabled the classification of behavioural states in imperial cormorants *Phalacrocorax atriceps* (Laich et al., 2010), video loggers provided insights into group foraging associations in little penguins *Eudyptula minor* (Sutton et al., 2017), oesophageal temperature and beak-opening sensors enabled the identification of prey capture events in king penguins *Aptenodytes patagonicus* (Hanuise et al., 2010) and surgically-implanted heart rate loggers provided estimates of energy expenditure in macaroni penguins *Eudyptes chrysolophus* (Green et al., 2007). As we broaden our knowledge of the behavioural ecology of particular seabird species and populations it is also vital that we examine what influences these top predators might be exerting on the marine ecosystems that they inhabit. Seabirds consume almost 100 million tonnes of food each year from a variety of shelf and offshore marine habitats (Karpouzi et al., 2007) and investigating their rates of prey capture and removal therefore has consequences for ecosystem management.

The non-breeding period

Seabirds exhibit a diversity of strategies upon release from the constraints of the reproductive season. Until comparatively recently these strategies have been difficult to research, although ringing studies have long provided descriptions of migration routes, wintering areas and locations of mortality (Wernham et al., 2002). Furthermore, insights into important wintering areas and the occurrences of seabird feeding

associations outside the reproductive period were gained via ship-based and aerial surveys (e.g. Camphuysen and Webb, 1999; Boertmann et al., 2004), whilst migration routes were also mapped by observers on cruise ships and through the recovery of dead birds (Salomonsen, 1967; Spear and Ainley, 1999). In addition to these methods, as with research during the breeding season, our understanding of non-breeding seabird ecology has also recently been revolutionised by the introduction of biologging technology with satellite tags (platform terminal transmitters; PTTs) and global location sensor (GLS) loggers now increasingly providing insights into seabird annual cycles (Fig. 1.1).

Due to methodological advancements, we now know that during the non-breeding period, seabirds undertake a highly varied diversity of moult and migratory strategies. For example, some seabirds, such as an Alaskan population of whiskered auklets *Aethia pygmaea*, remain close to their breeding colonies throughout the annual cycle (averaging 212 km from the colony; Schacter and Jones, 2018). Whiskered auklets may have adopted this residential strategy to enable foraging within shallow waters, and also to maintain proximity to land upon which they can roost (Schacter and Jones, 2018). Contrastingly, during their non-breeding periods, other species of seabird are known to engage in some of the longest migratory journeys recorded: Arctic terns *Sterna paradisaea*, sooty shearwaters *Puffinus griseus* and grey-headed albatrosses *Thalassarche chrysostoma*, use exceptionally long-distance migration strategies that stretch from pole to pole or circumnavigate the globe (Croxall et al., 2005; Egevang et al., 2010; Shaffer et al., 2006). In fact, the breeding cycles of grey-headed albatrosses *Thalassarche chrysostoma*, as well as those of many other albatross species, often extend to two years with birds taking an extended 'sabbatical' period from the constraints of breeding, during which they travel great distances (Warham, 1990). Furthermore, other species, such as Audubon's shearwaters *Puffinus iherminieri*, have

unusual breeding cycles that comprise of less than a year, the exact length of which varies between breeding locations, presumably driven by differences in the extent of seasonality at their tropical breeding sites (Bretagnolle et al., 2000).

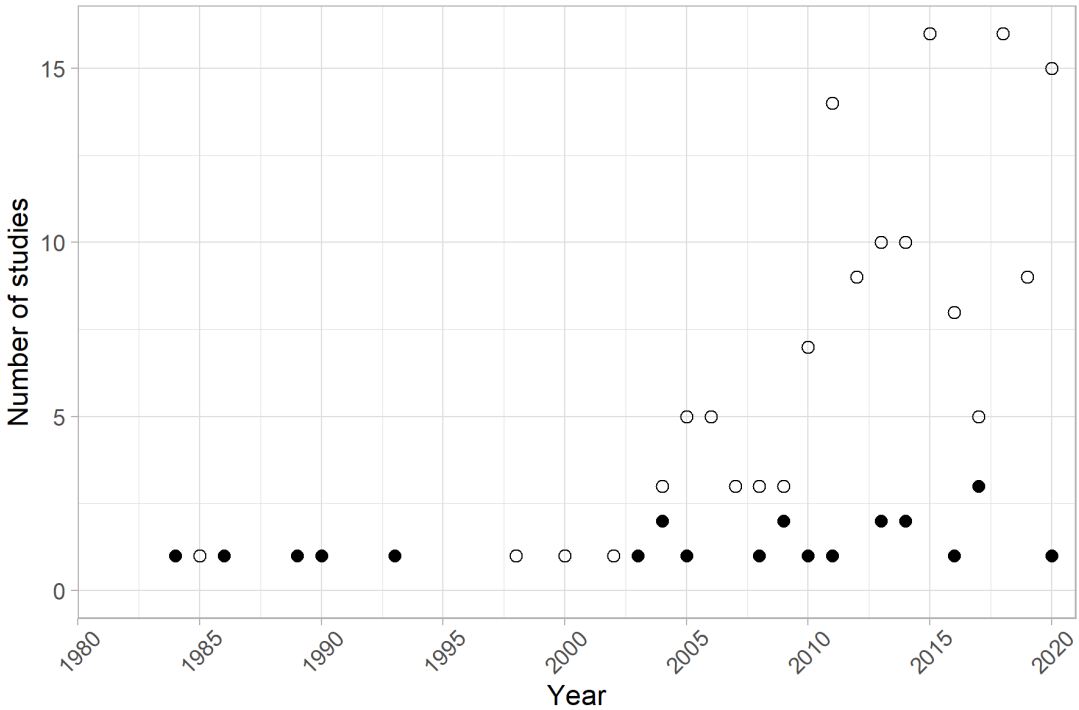


Figure 1.1. Annual number of studies published on non-breeding seabird activity (hollow points) and non-breeding seabird energetics (filled points). These figures are the result of a Google Scholar search, conducted between September 2016 and August 2020, for three keywords: "seabirds", "winter" and "non-breeding". Abstracts were scanned to identify whether each study contained information on i) seabird activity and ii) seabird energetics outside the breeding season.

Environmental and oceanographic conditions are often hypothesised to be key drivers of seabird migratory strategies. For example, sea surface temperature influences the non-breeding spatial segregation of sympatric southern Indian Ocean prion species (Quillfeldt et al., 2015), sea ice availability drives Arctic ivory gull *Pagophila eburnea* winter habitat preferences (Spencer et al., 2016) and during their non-breeding dispersive movements, Pacific Ocean brown skuas *Catharacta antarctica lonnbergi* target mixed subtropical-subantarctic shelf waters (Schultz et al., 2018). These environmental factors ultimately drive seabird migration and wintering location by influencing prey availability; seabirds make migratory movements in order to obtain prey resources that may otherwise be more challenging to access during the non-

breeding season, potentially due to changes in their accessibility within the water column or decreased marine productivity (Takahashi et al., 2015). Despite these insights, ultimately the influence of the environment on seabird ecology throughout certain periods of the annual cycle, such as the post-breeding, moult and winter months, currently remains largely unknown. Understanding the impacts of environmental influences on seabird behaviour across these key periods is important in expanding our knowledge as to how animals adjust their behaviour to balance the competing pressures that they face during these periods. Additionally, understanding environmental influences on year-round seabird behaviour is vital with regards to identifying where and when birds might be particularly vulnerable to mortality.

An Ecophysiology Approach

Energy is a central currency at every hierarchical level of life, underlying an animal's movement, behaviour and physiological functioning, including its growth, maintenance, reproduction and survival (Nagy, 2005; Pettersen et al., 2018). As well as being innately important, energy is a finite resource which animals must successfully manage in order to thermoregulate, move, forage and ultimately survive and maximise their fitness (Drent and Daan, 1980; Ellis and Gabrielsen, 2002). For long-lived organisms, such as seabirds, this necessity of balancing energetic budgets is superimposed on the task of successfully navigating seasonal environments and the differing physiological responses that this often invokes (Tomlinson et al., 2014). By researching the year-round energetic requirements of seabirds, I am therefore able to develop a more mechanistic understanding of the links between animal physiology and its environmental and ecological drivers.

Seabird breeding colonies tend to be located in close proximity to productive habitats, a relative abundance of prey and the potential for high energetic gains (Paredes et al.,

2012). It is likely that many species of seabird time their reproductive periods to coincide with optimal climatic conditions (Keogan et al., 2018), which will theoretically align with temporal patterns in food availability and energetic income (Perrins, 1970). Coinciding with these presumed energetic gains, the breeding season is also a time when seabirds are thought to expend high quantities of energy (Drent and Daan, 1980). Adult Brünnich's guillemots *Uria lomvia*, for example, have particularly high levels of energy expenditure during the chick-rearing period of the breeding season when they are required to provision offspring as well as build their own energy reserves (Elliott and Gaston, 2014). Indeed, due to their obligate foraging strategies, breeding seabirds must spend time and energy commuting between their breeding grounds and offshore foraging areas, capturing and transporting enough prey for themselves and their chicks (Langton et al., 2014). For example, whilst provisioning their chicks, blue petrels *Halobaena caerulea* alternate between long self-provisioning trips and shorter, energetically costly trips during which they maximise food delivery to their chicks (Weimerskirch et al., 2003). Additionally, despite the aforementioned benefits of colonial breeding, this strategy may also result in seabirds having to expend energy protecting their offspring from attacks from predators and conspecifics (Paredes and Insley, 2010). Furthermore, colonial breeding might incur other costs: Adélie penguins *Pygoscelis adeliae* that breed within larger colonies have been shown to experience higher energetic costs than those from smaller colonies due to depleted prey stocks forcing the penguins to engage in longer foraging trips (Ballance et al., 2009). Anthropogenic pressures can further exacerbate these potential energetic challenges in a number of ways, such as via depleted opportunities for energetic gains due to competition pressures exerted by fisheries (Ratcliffe et al., 2015) or by increased energy expenditure due to avoidance behaviour caused by wind farm developments (Dierschke et al., 2016). However, despite the importance of quantifying seabird energetics, and a

number of studies having sought to do this for certain species and populations of breeding seabird (e.g. Mehlum and Gabrielsen, 1993; Montevecchi et al., 1992; Sato et al., 2003), our knowledge of seabird energetic requirements, and their large-scale drivers, remains fragmented.

Seabird behaviour outside the breeding season is intrinsically linked to the balancing of energy budgets, with many species migrating from their breeding grounds to exploit energetically beneficial habitats (Armstrong et al., 2016). Indeed, whilst being largely driven by prey availability and energetic gains, the migratory behaviour of seabirds does in turn incur energetic costs. For example, Atlantic puffins *Fratercula arctica* from higher latitude colonies experienced higher energetic expenditure due to the increased thermoregulatory costs associated with colder waters, than those from more southern colonies (Fayet et al., 2017a). Additionally, female puffins were likely to have higher costs than males due to divergent migratory routes and foraging strategies (Fayet et al., 2017b). Differential migratory strategies also had energetic consequences for northern gannets *Morus bassanus*; longer but more costly migratory journeys were energetically beneficial, due to offsets associated with lower thermoregulatory costs and foraging effort at their more distant wintering grounds (Pelletier et al., 2020). Ultimately, despite these insights into seabird energetics during key points during the year, the number of studies that investigate the energetics of these birds throughout their full annual cycles remains small, especially in comparison to increases in studies looking only at activity (Fig. 1.1).

Study System

This thesis uses data collected from three species of North Atlantic seabird from the Alcidae family: common guillemots *Uria aalge* (hereafter 'guillemots'; Fig. 1.2A; Chapters 3-5), Atlantic puffins *Fratercula arctica* (hereafter 'puffins'; Fig. 1.2B; Chapter

3) and razorbills *Alca torda* (Fig. 1.2C; Chapter 3). These three species of auk breed once per year in monogamous pairs and rear single chick broods at colonies around the coast of the North Atlantic, with some guillemots also breeding in the Pacific (Gaston and Jones, 1998). The demographic and biologging data used in this thesis were collected from the Isle of May National Nature Reserve, Scotland (56°11'N, 02°33'W; Fig. 1.2D) by the UK Centre for Ecology & Hydrology (UKCEH). On the Isle of May, guillemots breed upon densely packed cliffs whilst razorbills lay their eggs in cracks and crevices amongst these cliffs and puffins use burrows on the island's grassy slopes. Colony-based data on breeding success, diet and behaviour have been collected for puffins since the early 1970s (e.g. Harris, 1976, 1978) and for guillemots and razorbills since the early 1980s (e.g. Harris and Wanless, 1986, 1988, 1989). Biologging techniques, including GPS and TDR deployments, have also been used extensively, initially during the breeding season to identify important feeding areas and diving behaviour (e.g. Wanless et al., 2005; Thaxter et al., 2009) and more recently to determine wintering areas and trophic position (e.g. Harris et al., 2010; St John Glew et al., 2018) .

During their breeding seasons and across their breeding ranges, guillemots are single-prey loaders, bringing back just one prey item at a time to their young, whilst puffins and razorbills are multi-prey loaders, transporting numerous prey items from the marine environment to the nest-site in one trip in order to provision their chicks (Gaston and Jones, 1998). The flight that auks engage in to transport these prey items is extremely energetically costly as they have small wing areas relative to their body mass (i.e. high wing loading; Thaxter et al., 2010). The evolution of reduced wing areas means that all three species are well adapted to performing intensive wing-propelled diving bouts as they pursue their forage fish prey within the water column (Thaxter et al., 2010).

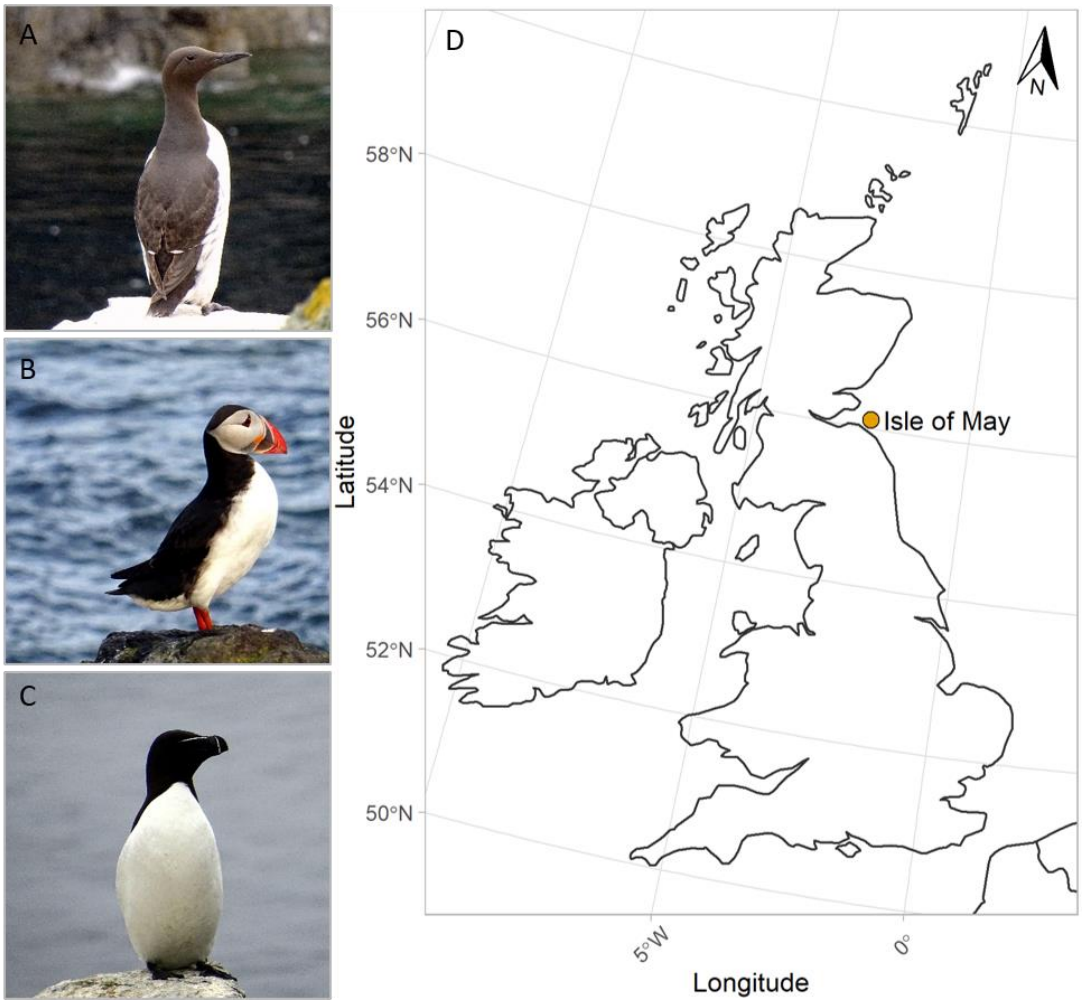


Figure 1.2. Photos of a A. common guillemot *Uria aalge*, B. Atlantic puffin *Fratercula arctica* and C. razorbill *Alca torda* taken on the Isle of May during the breeding season. The location of the Isle of May (illustrated by a yellow circle) in relation to the British Isles is shown in D.

There is variability in the departure strategies of the three auk species at the end of their breeding seasons; puffin fledglings can fly and depart the colony alone at night whilst male guillemot and razorbill parents accompany their flightless chicks in their departure from the colony as the chicks jump from the cliffs to the sea (Gaston and Jones, 1998). Following the breeding season, auks accumulate substantial fat reserves and also undertake a moult where they lose and subsequently regrow their primary flight feathers (Gaston and Jones, 1998). Guillemots, puffins and razorbills also disperse from the colony area and spend the winter primarily at sea. Specifically, auks from the Isle of May predominantly inhabit the North Sea and Northeast Atlantic waters during their non-breeding periods (Harris et al., 2015b, 2010; St. John Glew et al., 2019). During

this time, the different species exhibit inter-specific variation in their non-breeding diets, with guillemots feeding at higher trophic levels than puffins, as puffins adopt a more generalised, lower trophic level winter diet (St. John Glew et al., 2018). Additionally, auk winter diets differ in response to environmental conditions, with razorbills and puffins adjusting the trophic level that they foraged at between years of contrasting winter conditions (St. John Glew et al., 2019). Furthermore, whilst auks from other colonies have exhibited year-round dive depth differences (Linnebjerg et al., 2013) and intra-specific sex differences in foraging behaviour during the post-breeding period (Burke et al., 2015), many site- and species-specific knowledge gaps remain. By researching auk ecology and physiology outside the breeding season, I am not only broadening our understand of key periods in the life histories of Isle of May auks, I am also providing new behavioural insights into the interspecific and sex-specific differences that might exist during potentially critical periods of the annual cycle.

Many of the habitats that auks inhabit throughout their annual cycles are susceptible to degradation due to large-scale environmental changes as well as anthropogenic activities such as shipping routes and extractive industries (Fort et al., 2013a). As a result of these impacts, guillemots, razorbills and puffins are all species of conservation concern within the UK (Eaton et al., 2015). The UK populations of all three species have experienced declines in abundance and productivity over recent decades (Eaton et al., 2015) and razorbills are classed as near threatened on The IUCN Red List (BirdLife International, 2018a) with puffins classed as vulnerable (BirdLife International, 2018b). In particular, auks are susceptible to marine pollution, hunting, drowning in gillnets, harsh weather and climate-induced shifts in prey availability (McFarlane Tranquilla et al., 2013). Not only are they impacted by these factors, guillemots, razorbills and puffins are also essential, highly abundant components of the North Atlantic ecosystem;

changes in their ecology may also influence the wider marine community as they exert strong predatory pressure on lower trophic levels (Barrett et al., 2006). By studying the energetics of individual seabirds it is therefore possible to infer the food requirements of seabird populations, and ultimately the ecological influence that seabirds have on marine communities as a whole (Ellis and Gabrielsen, 2002; Ratcliffe et al., 2015).

A seabird's ability to balance its energetic budget, ultimately impacts individual survival (Fort et al., 2009). For seabirds, the winter months are thought to be particularly energetically challenging, with mortality often being concentrated during this time (Hatch, 1987; Wernham et al., 2002). Periods during which auks face challenges in balancing their energetic budgets, perhaps due to reduced foraging efficiency, may lead to energetic bottlenecks and mortality, with implications for population dynamics (Burke and Montevecchi, 2018). Identifying the drivers of mortality events is particularly vital for auk species, including guillemots, razorbill and puffins, which are a common component of winter 'wrecks': sporadically occurring events where large numbers of seabirds unexpectedly die (Harris and Wanless, 1996). The long-lived nature of auks, in addition to their small clutch sizes, reduces their populations' capacities to absorb mortality and recover from such events (Croxall et al., 2012). By researching seabird energetics throughout the annual cycle, we might therefore be able to identify the timings and locations of mortality which will aid us in better understanding the dynamics of future wreck events.

Thesis Outline

Within this thesis I investigate the drivers of seabird behaviour and energetics throughout the annual cycle. Initially I take a broad multi-species approach, investigating the drivers of energy expenditure across all species of seabird during the breeding season and consider this in the context of the energetic requirements of the

worlds' seabirds and the influences that they therefore exert on marine systems. I then focus on North Atlantic guillemots, razorbills and puffins and investigate the environmental, ecological and physiological drivers of their diving behaviour during the post-breeding period, moult and early-winter. Finally, I focus on the full annual cycles of guillemots, researching their movement, behaviour and energetics across the year in relation to the environments that they inhabit. For these analyses I use data from the Isle of May as a model system for understanding the associations between the environment and seabird annual cycles more broadly.

Chapter 2 details the large-scale determinants of the energy expenditure of free-ranging seabirds during their breeding seasons. I conducted a meta-analysis of the drivers of energetics from 64 studies of 47 different species and illustrate that body mass and colony latitude have a positive influence on rates of seabird daily energy expenditure. Additionally, I describe an increase in energy expenditure across the seabird breeding season.

- Chapter published: Dunn RE, White CR & Green JA (2018). A model to estimate seabird field metabolic rates. *Biology Letters*. 14: 20180190.

Chapter 3 features a comparison of the diving behaviour of guillemots, razorbills and puffins during the period immediately following the breeding season until midwinter. I demonstrate the interacting influences of species, sex and parental care and moult strategies on the dive depth, foraging effort and diurnal dive activity of the three species.

- Chapter published: Dunn RE, Wanless S, Green JA, Harris MP & Daunt F (2019). Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season. *Journal of Avian Biology*. 50: 02012.

Chapter 4 identifies patterns in diving activity, colony attendance and energy expenditure of guillemots throughout the annual cycle. I illustrate that the observed patterns of energy expenditure were driven by variation in thermoregulatory costs, diving activity, colony attendance and associated flight activity.

- Chapter published: Dunn RE, Wanless S, Daunt F, Harris MP & Green JA (2020). A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. *Scientific Reports*. 10: 5993.

Chapter 5 demonstrates the use of Bayesian state-space modelling to reconstruct year-round variation in guillemot body mass and energy gain. Using this modelling approach, I identify the times and locations throughout the annual cycle where Isle of May guillemots experienced higher susceptibility to mortality as areas of high energy gain.

- Dunn RE, Green JA, Wanless S, Daunt F, Harris MP & Matthiopoulos J. Modelling and mapping the mortality risk and energetic reward of a wild, mobile animal over its full annual cycle.

Chapter 6 discusses the main findings of my thesis and identifies new emerging questions that this work poses.

Chapter 2: A model to estimate seabird field metabolic rates

A model to estimate seabird field metabolic rates

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Author contributions:

RED participated in the study design, data collection, analyses and writing of the manuscript; JAG conceived the study, participated in data analysis and helped draft the manuscript; CRW participated in the design of the study and provided essential guidance with the analyses.

All authors contributed critically to the improvement of this paper and gave permission for the paper to appear within this thesis.

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Abstract

For free-ranging animals, field metabolic rate (FMR) is the sum of their energy expenditure over a specified period. This quantity is a key component of ecological processes at every biological level. We applied a phylogenetically informed meta-analytical approach to identify the large-scale determinants of FMR in seabirds during the breeding season, using data from 64 studies of energetics in 47 species, and use these data to create a model to estimate FMR for any seabird population. We found that FMR was positively influenced by body mass and colony latitude and that it increased throughout the breeding season from incubation to brood to crèche. FMR was not impacted by colony-relative predation pressure or species average brood size. Based on this model, we present an app through which users can generate estimates of FMR for any population of breeding seabird. We encourage the use of this app to complement behavioural studies and increase understanding of how energetic demands influence the role of seabirds as driving components of marine systems.

Introduction

Metabolic energy requirements drive biological processes at every hierarchical level of life. At the organismal level, field metabolic rate (FMR) is the total sum of energy that a free-ranging animal metabolises over a specified period of time. Understanding the determinants of interspecific FMR helps us to quantify the impact that free-ranging animals have on energy flows within the ecosystems that they inhabit (Nagy, 2005).

It has long been known that body size is a key determinant of FMR between organisms of the same taxonomic class, accounting for around 95% of within-class variation (Nagy, 2005). However, the magnitude of the remaining interspecific variation in metabolic rate can be considerable and is determined by a number of other physiological and ecological factors. For example, latitude (which encompasses variation in air temperature, sea surface temperature, productivity, day length and seasonality) positively influences FMR in small mammals due to cooler habitat temperatures and consequent increased thermoregulatory energetic costs (Speakman, 1999). Similarly, whilst energetic bottlenecks may occur at different points throughout the annual cycle, birds often exert high metabolic rates during the reproductive season due to the increased energetic costs associated with egg incubation and offspring provision (Bryant, 1997; Green et al., 2013; Shoji et al., 2015a). More recently, additional factors such as colony size and number of offspring have been suggested as drivers of FMR within free-ranging animals such as colonially breeding seabirds (Ballance et al., 2009; Ellis and Gabrielsen, 2002).

Studies on the metabolic rates of seabird species have increased dramatically in recent decades (Ellis and Gabrielsen, 2002). This is due both to their tractability and the need to better understand the food requirements of this important yet threatened group (Brooke, 2004). To date, the majority of studies have focused on the energetically

demanding reproductive period when seabirds are constrained by chick rearing to travel potentially large distances between the breeding colony and marine feeding areas (Burke and Montevecchi, 2009). Despite the need to understand the metabolic requirements of marine top-predators for conservation purposes, the FMR of many seabird species and populations remains unknown and the broad-scale determinants of interspecific variation in seabird FMR are unclear.

Here, we applied a phylogenetically informed meta-analytical approach to explore the large-scale determinants of seabird FMR during the breeding season, updating previous studies on the correlates of seabird FMR (Ellis and Gabrielsen, 2002). In addition, we present this model within a web-based app which can be used to make estimates of FMR for seabird species and populations where this has not previously been calculated.

Materials and Methods

Data compilation

A systematic search of the peer-reviewed literature was conducted between November 2016 and January 2018 inclusive, including all records until this time. We used a combination of the following keywords: "seabird*", "energ*", "field metabol*" and "rate" to search the Web of Science and Google Scholar. Abstracts were scanned for an indication that publications reported measurements of energy expenditure and where appropriate the full text was then consulted.

Values of FMR (n = 98), calculated using doubly labelled water, heart rate loggers or via the construction of time-energy budgets, were obtained from 64 original studies on 47 species of seabird. Additionally, values of mean bird mass, phase of breeding season (incubation, brood or crèche), colony name, latitude and number of breeding pairs at the colony were recorded. When these data were not available within the original studies, we contacted the authors or consulted further literature to obtain them.

Statistical analysis

Phylogenetic meta-analytic models to identify the large-scale determinants of seabird FMR and to make predictions of FMR were constructed in the *R* environment (R Core Team, 2020) using the *MCMCglmm* package (Hadfield, 2017). Models included combinations of the following fixed effects: log-transformed mean bird mass, species average brood size, phase of breeding season, colony latitude and colony-relative predation pressure (the log-transformed product of the number of breeding pairs and bird mass$^{2/3}$). We accounted for the potential non-independence of data due to shared ancestry by including a phylogenetic random effect alongside species and colony. To incorporate phylogeny we used the Ericson backbone tree downloaded from http://birdtree.org/ (Jetz et al., 2012). The tree was pruned to only include 313 seabird

species (Supplementary material A2.1). Log-transformed FMR was modelled as a Gaussian response variable and parameter-expanding priors were used for the random effects. The MCMC chains were run for a total of 260,000 iterations with a burn-in of 60,000 and thinning interval of 200. The best model (that which incorporated the optimum combination of fixed effects) was selected using the deviance information criteria (DIC; Spiegelhalter et al., 2002). Graphic diagnostics were used to assess for autocorrelation and jackknife analysis was used to resample the data and check the resulting model (Supplementary material Fig. A2.2). An estimate of phylogenetic heritability (H^2) was calculated to provide an index of the proportion of variance associated with the random effect of phylogeny (Hadfield and Nakagawa, 2010).

Meta-analysis data and phylogeny used are publicly hosted on figshare. The data are accessible at http://dx.doi.org/10.6084/m9.figshare.4765906 and the phylogeny is accessible at http://dx.doi.org/10.6084/m9.figshare.5972692 .

Results

All models were within two DIC values and were therefore considered to provide comparably good fits to the data (Supplementary material Table A2.3). All models showed similar positive effects of bird mass and absolute latitude on FMR in breeding seabirds (Fig. 2.1), with phase of the breeding season also having an impact. Conversely, models did not provide strong evidence to support that species average brood size or colony-relative predation pressure impacted FMR, and the phylogenetic heritability was low (Table 2.1).

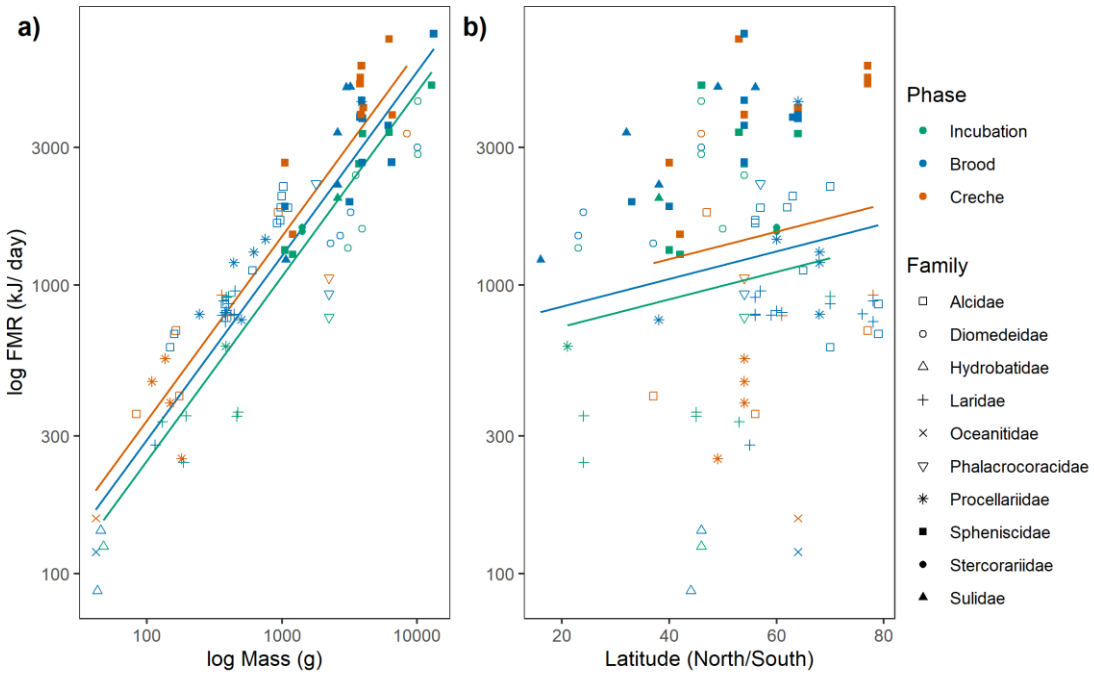

Figure 2.1. Breeding seabird field metabolic rate (FMR) was modelled as a function of a) bird mass and b) latitude. The colours of the points and model fit lines represents the stage of the breeding season, and the shape of the points corresponds with the family. Mass and FMR axes are displayed as a logarithmic scale.

Whilst all models were competitive and suggested similar results, the simplest model with the lowest DIC was considered the strongest (Supplementary material Table A2.3). This model was incorporated within the *R* shiny web framework (Chang et al., 2015) to create a web-based utility and user interface through which to generate estimates of seabird FMR. The app requires inputs of species, bird mass, colony latitude and breeding phase and returns a daily FMR estimate alongside highest posterior density

(HPD) confidence intervals, based on the optimal model. The 'Seabird FMR Calculator' web app is available at https://ruthedunn.shinyapps.io/seabird_fmr_calculator/.

Table 2.1. Results from the random-effects meta-analyses on the large-scale drivers of seabird field metabolic rate during the breeding season.

Effect	Posterior estimates	Lower 95% Credible Interval	Upper 95% Credible Interval	pMCMC
Intercept (brood)	0.92	0.62	1.21	<0.001
Breeding phase: incubation	-0.071	-0.12	-0.025	0.002
Breeding phase: crèche	0.068	0.027	0.11	0.006
Log bird mass	0.64	0.55	0.72	<0.001
Colony latitude	0.0048	0.0023	0.0073	0.002
H^2 heritability estimate	Mean = 0.035; Standard Deviation = 0.019			

Discussion

This study uses the most comprehensive methods available to provide the best and most up-to-date analyses into the large-scale determinants of seabird FMR during the breeding season. The results of our phylogenetically informed meta-analyses indicate a lack of evidence of a phylogenetic signal and therefore suggest that mean bird mass, absolute latitude and phase of the breeding period are more influential predictors of FMR in breeding seabirds than phylogeny.

We observed an increase in FMR across the breeding season from incubation to brood to crèche (Fig. 2.1). Although incubation can be an energetically costly period for seabirds, due to its intrinsic costs and those of its associated activities (Shoji et al., 2015a; Thomson et al., 1998), some species-specific studies have shown increased FMR later in the breeding season due to elevated basal metabolic rates and the energetic costs associated with offspring provision (Green et al., 2013; Grémillet et al., 1995). Our findings support these previous studies of energy expenditure in individual populations of seabird and extend them to identify a link between FMR and phase of the breeding period across a range of seabird species.

Whilst an organism's mass is well known to influence its energy expenditure, geographical relationships have been less frequently explored across such a breadth of taxa. Our study supports the hypothesis that, in response to adverse environmental conditions, seabirds breeding at high latitudes have higher FMR (Fig. 2.1). These increased rates of energy expenditure may be due to elevated metabolism and adjustments to metabolic rhythms in response to cooler temperatures, longer days, shorter breeding seasons and other climatic effects associated with high latitudes (Bryant, 1997; Bryant and Furness, 1987; Costa, 1991).

It has been proposed that seabird colonies may be surrounded by a 'halo' of depleted prey availability during the breeding season owing to increased feeding activities in the vicinity of the breeding colony (Ashmole, 1963; Birt et al., 1987). Local prey depletion might be greatest around large colonies, and this might require individuals at larger colonies to travel greater distances to forage (Wakefield et al., 2013). Whilst Adélie penguins *Pygoscelis adeliae* nesting in larger colonies therefore travel further to access prey resources, expending more energy in order to do so (Ballance et al., 2009), our cross-species analyses did not find general support for this hypothesis. Instead, we found that neither colony-relative predation pressure nor species average brood size influenced estimates of breeding seabird FMR. This lack of a distinguishable relationship may be due to the fact that the 'halo' argument has previously only been validated regionally, whereas our analyses include data that encompass a vast range of marine habitats and consequentially a high variance of prey availability. Furthermore whilst brood size might influence intraspecific FMR (Fyhn et al., 2001; Welcker et al., 2015), at the species-level FMR is set by life-history trade-offs for which the animal will have reallocated its energetic resources (Partridge and Harvey, 1988). Alternatively, our results might suggest a common optimal rate of FMR across taxonomic groups (Drent and Daan, 1980), given the internal demands of chick-rearing and the external influence of latitude.

We use our model to present a user-friendly web-based app (the 'Seabird FMR Calculator'). This app uses data on bird mass, colony latitude and phase of the breeding period, to calculate estimates and confidence intervals of FMR for any seabird population. Such estimates of FMR are essential when inferring the food consumption of populations of seabirds across multiple temporal scales (Brooke, 2004) and also when parametrising mechanistic models to make energetic predictions in a climate change context (e.g. Amélineau et al., 2018). We therefore envisage that outputs from the

'Seabird FMR Calculator' can be encompassed within future studies in order to increase understanding of the energetic demands of these top predators, their role within the wider marine ecosystem and how this might be influenced by climatic change. The creation of this app is particularly timely due to the competition pressures that seabirds, key driving components of marine systems, face from anthropogenic activities such as the depletion of marine stocks by global fisheries (Cury et al., 2011). The conservation of seabird populations is therefore of vital importance and we encourage that the 'Seabird FMR Calculator' is used as a key tool at the forefront of these efforts. In addition, we advocate the 'Seabird FMR Calculator' as a prototype for the development of similar apps which in turn can be used to make estimations of FMR for a wider range of taxa for which this information is available (e.g. marine mammals, marsupials, passerines and lizards; Nagy et al., 1999).

Chapter 3: Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season

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Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season

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Abstract

Information on seabird foraging behaviour outside the breeding season is currently limited. This knowledge gap is critical as this period is energetically demanding due to post-fledging parental care, feather moult and changing environmental conditions. Based on species' body size, post-fledging parental strategy and primary moult schedule we tested predictions for key aspects of foraging behaviour (Maximum Dive Depth (MDD), Daily Time Submerged (DTS) and Diurnal Dive Activity (DDA)) using dive depth data collected from three seabird species (common guillemot *Uria aalge*, razorbill *Alca torda* and Atlantic puffin *Fratercula arctica*) from the end of the breeding season (July) to mid-winter (January). We found partial support for predictions associated with body size; guillemots had greater MDD than razorbills, but MDD did not differ between razorbills and puffins, despite the former being 35% heavier. In accordance with sexual monomorphism in all three species, MDD did not differ overall between the sexes. However, in guillemots and razorbills there were sex-specific differences, such that male guillemots made deeper dives than females, and males of both species had higher DTS. In contrast, there were no marked sex differences in dive behaviour of puffins in July and August in accordance with their lack of post-fledging parental care and variable moult schedule. We found support for the prediction that diving effort would be greater in mid-winter compared to the period after the breeding season. Despite reduced daylight in mid-winter, this increase in DTS occurred predominantly during the day and only guillemots appeared to dive nocturnally to any great extent. In comparison to diving behaviour of these species recorded during the breeding season, MDD was shallower and DTS was greater during the non-breeding period. Such differences in diving behaviour during the post-breeding period are relevant when identifying potential energetic bottlenecks, known to be key drivers of seabird population dynamics.

Introduction

Intrinsic factors such as age, sex, reproductive status and body size are known to constrain foraging behaviour across a wide range of taxa and hence play a key role in shaping time activity budgets (King, 1974). In addition, a range of extrinsic factors, notably weather conditions and food availability, impact behavioural choices (Ellis and Gabrielsen, 2002; Humphries et al., 2004). In many cases both intrinsic and extrinsic effects exhibit temporal predictability e.g. in the timing of breeding or moult, changes in day length and likelihood of bad weather (McNamara and Houston, 2008). This interplay between intrinsic and extrinsic factors has helped elucidate how birds make decisions about reproduction during this crucial life history phase (Schlaepfer et al., 2002) and has been particularly well studied in long-lived birds (Phillips et al., 2017). However, in general, much less is known about how intrinsic and extrinsic factors influence foraging behaviour outside the breeding season, particularly in highly mobile species such as seabirds.

Most species of seabird are seasonal breeders and typically experience varying extrinsic conditions throughout their annual cycle. During the breeding season, individual seabird foraging strategies vary intrinsically depending on sex (Bearhop et al., 2006; Kato et al., 2000; Welcker et al., 2009), age (Grecian et al., 2018), parental role (Weimerskirch et al., 2000) and social dominance (González-Solís et al., 2000). The effect of sex on foraging strategy is often associated with size dimorphism, as size differences give rise to competitive exclusion and cause sex-specific niche specialization via trophic segregation or spatial partitioning (González-Solís et al., 2000; Phillips et al., 2017). In addition to size-driven sex-specific behavioural responses, monomorphic seabird species are also often subject to sex-role partitioning, particularly within their parental care strategies (Lewis et al., 2002). Sex-role

partitioning can lead to behavioural differences in foraging behaviour, time allocation, habitat preference and scheduling of migration (Phillips et al., 2017).

In addition to influencing behaviour among different categories of individuals within species, intrinsic drivers of variation in foraging behaviour are also key parameters with regard to the ecological segregation of different species of seabird. For example, sympatrically breeding species often forage at different depths in the water column and/or access different food resources in line with size-driven diving capacities; larger species tend to make longer, deeper dives and take larger prey items than smaller species (Halsey et al., 2006; Mori and Boyd, 2004; Schreer et al., 2001; Wilson, 1999). Additional interspecific differences in breeding season foraging ecology have been observed in sympatric species such as macaroni penguins *Eudyptes chrysolophus* and eastern rockhopper penguins *E. chrysocome filholi,* which forage at different trophic levels (Whitehead et al., 2017), and black-footed albatrosses *Phoebastria nigripes* and Laysan albatrosses *P. immutabilis,* which demonstrate interspecific segregation in their foraging habitats (Hyrenbach et al., 2002). Despite these intrinsically-determined breeding season behavioural differences, in the majority of cases it is not known whether such disparities persist into the post-breeding period when many species moult, migrate and experience seasonal differences in extrinsic environmental conditions.

Three diving species that often breed sympatrically in the north-east Atlantic, before wintering at sea, are the common guillemot (hereafter 'guillemot') *Uria aalge*, razorbill *Alca torda* and Atlantic puffin (hereafter 'puffin') *Fratercula arctica*. During the breeding season their diving capabilities scale allometrically: guillemots, the largest of the three species, make the deepest and longest dives, whilst dive depths and durations of razorbills exceed those of puffins which are the lightest species (Gaston and Jones,

1998). Further, guillemots have a higher foraging effort than razorbills during the breeding season (Thaxter et al. 2010). In general, it is not known whether these largely size-driven interspecific differences are maintained outside the breeding season, but Linnebjerg et al (2013) found that guillemots from the north-east Atlantic dived deeper than razorbills immediately after and prior to the breeding season. All three species are significantly heavier outside the breeding season compared to when they are breeding, due to the accumulation of fat reserves (Gaston and Jones, 1998). This morphological change could potentially impact the species' post-breeding diving capabilities, since changes in both body size and composition influence diving behaviour via their influence on drag and buoyancy (Halsey et al., 2006; Sato et al., 2003). However, while seasonal changes in body condition affect marine mammal diving behaviour (Richard et al., 2014), this aspect has not yet been investigated in seabirds.

Although guillemots, razorbills and puffins are all considered to be sexually monomorphic, sex-specific behavioural differences have been observed during the breeding season. For example, male razorbills have been found to dive deeper than females (Paredes et al. 2008, but see Linnebjerg et al. 2015) and there is evidence for sex-specific differences in the time budgets of guillemots, razorbills and puffins during the breeding season (Creelman and Storey, 1991; Thaxter et al., 2009). However, information on sex-specific foraging behaviour outside the breeding period (defined in this study as the departure of chicks from the breeding colony) is much scarcer. Sex-specific differences in foraging behaviour are predicted to be apparent in guillemots and razorbills where the male parent takes the partly grown chick to sea and continues to feed it for several weeks after the breeding season has ended until it completes its development and becomes independent (Gaston and Jones, 1998). In these species males would therefore be expected to spend longer diving per day during male-only parental care, and Paredes et al. (2008) and Burke et al. (2015) did indeed find that male

guillemots spent more time diving than females. Males may also adjust diving depth, either increasing it to access resources for chick provisioning, or decreasing it to maximise contact with the chick (Camphuysen, 2002; Linnebjerg et al., 2015). In contrast, puffin chicks are independent as soon as they leave the breeding burrow and the parents provide no further parental care (Harris and Wanless, 2011). Thus for this species no sex-specific behavioural differences are predicted.

Table 3.1. Morphological and behavioural characteristics of common guillemot, razorbill and Atlantic puffin populations on the Isle of May (other than puffin winter mass which was obtained from puffins killed in Faroese waters which is where some Isle of May puffins winter). Breeding mass obtained from the literature because mass was not taken from most study individuals to minimise disturbance.
[1] (Thaxter et al., 2010) [2] (Anker-Nilssen et al., 2018) [3](Harris et al., 2000) [4] (Gaston and Jones, 1998) [5] (Birkhead and Taylor, 1977) [6] (Harris and Wanless, 1990) [7] (Harris et al., 2014)

Species	Guillemot	Razorbill	Puffin
Breeding mass (g)	907 ± 55 SD [1]	600 ± 87 SD [1]	380.0 ± 0.71 SE [2]
Winter mass (g)	1107 ± 11 SD [3]	No data	497.7 ± 7.11 SE [2]
Sexual dimorphism	No	No	No
Post-fledging parental care	Yes	Yes	No
Post-fledging care parent	Male	Male	-
Timing of post-fledging parental care	July – August [4]	July – August [4]	-
Flightless moult	Yes	Yes	Yes
Timing of flightless moult	July – September [5,6]	July – September [6]	More variable schedule with peaks in October and March [7]

In addition to sex-specific differences associated with post-fledging care, auk diving behaviour could also be influenced by primary feather moult. Moult is an intrinsically

costly process requiring time, energy and nutrients (Bridge, 2006; Ellis and Gabrielsen, 2002), and the annual replacement of flight feathers is essential to ensure efficiency in both flight and thermoregulation (Murphy, 1996; Peery et al., 2008). In guillemots and razorbills, wing moult partially overlaps with the period of male-only post-fledging parental care and therefore the effects of these two phenomenon are likely to occur simultaneously (Gaston and Jones, 1998). The scheduling of moult in puffins seems much more variable, but typically occurs later than in guillemots and razorbills, with peaks in October and March (Harris et al., 2014). Due to the energetic constraints of moult, coupled with flightlessness (Bridge, 2006), moulting auks are thought to favour productive, sheltered areas with predicable prey (Linnebjerg et al., 2018; Peery et al., 2008). However, while it is known that auks continue to dive during their primary wing moult, how their diving capabilities are affected is currently equivocal (Elliott and Gaston, 2014). Some studies have concluded that there are likely to be small benefits because of reduced drag (Bridge, 2006; Lovvorn et al., 2004; Swennen and Duiven, 1991; Thompson et al., 1998). In contrast, a study of captive birds concluded that the smaller wing surface area of moulting birds requires more energy for efficient underwater propulsion and hence diving capability is reduced (Bridge, 2004).

Together, these intrinsic and extrinsic effects form a convenient framework for testing predictions about responses in diving behaviour associated with both intrinsic and extrinsic factors. Comparing these predictions with empirical data allows new insights into the drivers of diving behaviour outside the breeding season. We used this approach to investigate the diving behaviour of guillemots, razorbills and puffins breeding on the Isle of May, a major seabird colony in the north-western North Sea. Long-term studies at this colony have provided population level information on morphometrics, dive behaviour during the breeding season, and the breeding and moulting phenology of these species (Table 3.1). However, information on the diving behaviour of these

populations outside the breeding season is almost totally lacking. We used archival Time Depth Recorders (TDRs) to derive three indices of dive performance/activity for each species for each month between the end of the breeding season (July) and mid-winter (January): 1) Maximum Dive Depth (MDD), the maximum depth attained on a dive, 2) Daily Time Submerged (DTS), summed dive durations over a 24 h period, and 3) Diurnal Dive Activity (DDA), the proportion of individuals diving during each hour of the day. Specific predictions for these dive behaviour indices in response to intrinsic factors (body mass, sex-specific parental care strategies and moult schedule) and extrinsic drivers (seasonal environmental change) are summarised in Table 3.2.

Table 3.2. Predictions of hypotheses on the causes of differences in diving behaviour outside the breeding season in common guillemots, razorbills and Atlantic puffins from the Isle of May.

Hypothesis	Predictions		
	Maximum Dive Depth (MDD)	Daily Time Submerged (DTS)	Diurnal Diving Activity (DDA)
Interspecific and sex-specific body mass	Guillemot > Razorbill > Puffin; no sex-specific differences.	Higher foraging effort of guillemots than razorbills in breeding season to persist into non-breeding season. No specific predictions for puffins, or for sex differences.	No interspecific or sex differences.
Post-fledging parental care	Sex-specific differences in guillemots and razorbills in July/August, but not puffins. Alternative predictions: a) males reduce dive depth to maximise contact with chick; b) males increase dive depth to access particular prey.	Males > females in guillemots and razorbills, due to the costs of provisioning offspring. No specific predictions for puffins.	No interspecific or sex differences.
Primary wing moult	Change in guillemots and razorbills in August/September associated with dive efficiency and energetic costs; direction not clear because of equivocal evidence of dive efficiency at this time; no direct sex-specific differences expected. No specific prediction for puffins where timing of moult is more variable and unknown in these individuals.	As MDD.	No interspecific or sex differences.
Seasonal environmental change	Progressive change in dive depth with changing body composition and declining light levels.	Progressive increase between July and January as food availability changes and energetic costs increase.	Alternative predictions: a) greater use of night-time hours as season progresses in response to shortening day length and altered conditions; b) increasingly constrained to the middle of the day as daylight decreases.

Material and Methods

Data loggers

All fieldwork took place on the Isle of May National Nature Reserve, Scotland (56° 11'N, 02°33'W). During the 2005 breeding season, 30 adult guillemots brooding chicks were captured at the breeding site using a 7m noose pole and fitted with TDRs (LT2400, Lotek Wireless, St John's, Newfoundland, Canada, 36 mm x 11 mm) attached to Darvic leg-rings. During the 2008 breeding season, breeding razorbills (n = 24) were captured in the same way as guillemots and breeding puffins (n = 30) were caught in their burrows. For both species TDRs (G5, CEFAS, Lowestoft, UK, 31 mm x 8 mm) were again attached using Darvic leg-rings. In all cases the attachment process took <5 minutes. The mass of the TDR plus rings were 6.5 g, 3.3 g and 3.0 g, 0.7%, 0.6% and 0.8% of the breeding body mass of the respective species (Table 3.1). Three to five body feathers were collected from retrieved birds under UK Home Office Licence, to enable birds to be sexed using two CHD I genes (Griffiths et al., 1996). Birds were recaptured during the breeding season following deployment, i.e. 2006 for guillemots and 2009 for razorbills and puffins. The same methods as for deployment were used in order to recapture birds and the TDRs were removed. Retrieval rates were 43.3%, 54.2% and 40.0% for guillemots, razorbills and puffins, respectively.

Our original aim was to collect data over the entire non-breeding period (July – April for our study populations). However, this was only possible for guillemots for which all the TDRs were still recording data when they were retrieved. In the case of razorbills and puffins, some TDRs failed completely while others failed progressively during the autumn so that the number of individuals contributing data declined over time. We were thus only able to compare dive behaviour of the three species for the period July

– January. Details of the sampling periods and number of days of data are provided in Supplementary material A3.1.

To record data over an extended period, TDRs were set to take a depth reading every i) 16 seconds for a 24 h period every 30 days (guillemots, n = 9 retrieved birds), ii) 32 s for a 24 h period every 15 days (guillemots, n = 4), iii) 3 s for a 24 h period every 10 days (razorbills n = 7; puffins, n = 6) or iv) 30 s for a 24 h period every day (razorbills n = 6; puffins, n = 6). Two sampling rates were used for each species to balance resolution with number of days of data, due to the limited memory size of the TDRs. The memory size of the TDRs used on the guillemots was smaller, necessitating a 16/32 s protocol compared to the 3/30 s protocol used on razorbills and puffins.

Fledging dates were not known for any of the TDR birds. However, mean fledging dates for all three species were available from monitoring plots. We therefore used these population-level values to define the start of the non-breeding period as 10 July 2005 for guillemots, 30 June 2008 for razorbills and 18 July 2008 for puffins. Data collected prior to this were assumed to come from breeding birds (Supplementary material A3.2).

Data processing

A purpose-written script for IGOR Pro (Wavemetrics Inc., Portland, OR, USA, 2000, version 6.37) was used to determine values of dive depth and duration from all the TDR-recorded depth data from the 24 h sampling periods. After visually correcting for device drift (Elliott and Gaston, 2009), the dataset was filtered to remove values of <1 m that were likely to be associated with non-diving activities such as washing (Shoji et al., 2016). Maximum dive depth (MDD) was extracted for each derived dive. Thaxter et al. (2009) found strong bimodality in the dive depths of guillemots from the Isle of May during the breeding season. However, we found no evidence of bimodality outside the breeding season for any of the species and thus did not classify dives as shallow or deep

(Supplementary material A3.3). In addition to MDD, dive duration was also extracted for each dive and was summed to calculate a metric of daily time submerged (DTS). The loggers with lower sampling rates (30 and 32 s) will have missed some shorter dives, which could have resulted in an underestimate of DTS and/or an overestimate of MDD. However we expected the lack of short dives to be counteracted by an overestimation of dive duration, resulting in no overall effect of DTS. We investigated this potential issue in two ways. First, we compared the empirical estimates of MDD and DTS using the two sampling rates for each species and found that they did not differ significantly (Supplementary material A3.4). Second, we conducted a simulation exercise where we compared DTS at sampling intervals of 1, 2, 4, 8, 16 and 32 s and found that it was consistent across sampling frequencies (Supplementary material A3.4). We therefore concluded that these measures were robust to variation in sampling rate and so we excluded sampling rate from analyses. Because of these sampling issues, from hereon we refer to 'dive indices' as opposed to 'dives'.

To determine changes in patterns of Daily Dive Activity (DDA) for each species during the non-breeding period, the proportion of individuals recorded diving during each hour of the day was extracted for each month. An individual that showed evidence of one or more dives in a given hour in a given month was classified as having undertaken diving activity.

Statistical analyses

All analyses were computed within the R statistical Framework (R Core Team, 2020). Mixed models, performed using the lmer function in the *lme4* package (Bates et al. 2015), were used to evaluate species and sex-specific differences in MDD and DTS. Maximum dive depth data were log transformed to help approach normality prior to analyses. Initially, a three-way interaction between species, sex and month (where

month was an ordered categorical variable in order to allow for non-linear month-by-month responses) was tested for significance. This interaction allowed us to consider both interspecific and sex effects on temporal differences in MDD and DTS. Individual bird ID was included as a random factor to account for potential non-independence. When analysing MDD, day since deployment was also included as a random factor to account for a lack of independence between dives performed on the same day. To interpret the interaction terms, post hoc comparisons were performed using estimated marginal means statements with the *emmeans* package (Lenth, 2019). Based on the available information on the scheduling of post-fledging parental care and primary wing moult in the Isle of May populations, July and August were assumed to be the months when male guillemots and razorbills were predominantly engaged in post-fledging parental care and August and September were assumed to be the months when guillemots and razorbills (both sexes) moulted and regrew their primaries (Table 3.1). The non-breeding period was further divided into an autumn (July-September) and winter period (October-January) with environmental conditions in the latter assumed to be more severe.

Small sample sizes for razorbills and puffins, particularly from November onwards, precluded using formal analytical approaches such as GAMMs and GLMMs to investigate monthly changes in DDA. Instead, a visual approach was used to compare the proportion of birds recorded diving in each hour of the day. A similar approach has been adopted in studies of diurnal patterns in seabird commuting behaviour (Padget et al., 2017) and diving behaviour in turtles (Hays et al., 2001). Unless stated otherwise all values are means ± standard error and all times are GMT.

All data are available from the Environmental Information Data Centre: https://doi.org/10.5285/6ab0ee70-96f8-41e6-a3e3-6f4c31fa5372.

Results

Diving data

We recorded a total of 21,008 indices of diving from guillemots (mean 1,616 dive indices per individual, n = 13 individuals, range 1,043 – 2,551), 111,904 dive indices from razorbills (mean 8,606 dive indices per individual, n = 13 individuals, range 2,603 – 20,520) and 49,222 dive indices from puffins (mean 4,474 dive indices per individual, n = 12 individuals, range 686 – 11,470). Sample sizes for puffins and razorbills decreased progressively during the study due to TDR failures (see Supplementary material A3.1 for details). We note that the number of dives is probably an underestimate for all three species (Supplementary material A3.4).

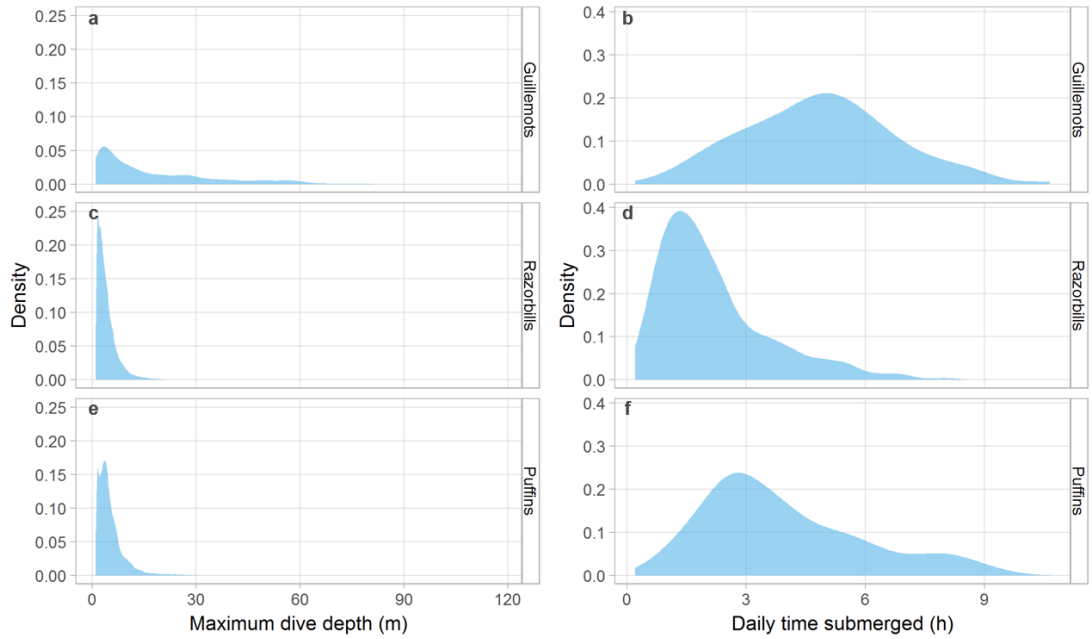

Figure 3.1. Density plots displaying the distribution of maximum dive depths (MDD; plots a, c and e) and daily time submerged (DTS, plots b, d and f) of common guillemots, razorbills and Atlantic puffins between July and January.

Overall frequencies for MDD and DTS outside the breeding season indicated that in all three species dive depths and daily diving effort were highly variable (Fig. 3.1). Deepest depths were 118.2 m, 47.4 m and 38.4 m for guillemot, razorbill and puffin respectively while 10.65 h, 8.15 h and 9.47 h per day were the maximum daily times submerged.

However, in general, MDDs outside the breeding season were relatively shallow with 59.8%, 98.9% and 97.0% dives <15 m in guillemots, razorbills and puffins respectively while average DTS was 4.86 ± 0.18 h, 2.10 ± 0.05 h and 4.07 ± 0.12 h for the three species (Fig. 3.1). The strong bimodality in MDD in guillemots recorded during the preceding breeding season (Supplementary material A3.2) was no longer present; MDD in all species was shallower than during the preceding breeding season, despite body mass increasing after the breeding season, but DTS was greater (Supplementary material A3.2).

Interspecific body mass effects

Based on interspecific differences in body mass we predicted that MDD outside the breeding season would be greater in guillemots than razorbills, and greater in razorbills than puffins (Table 3.2). Data from TDRs indicated that mean MDD for guillemots was indeed deeper than for razorbills (mean 17.6 ± 0.1 m c.f. 4.2 ± 0.1 m). However, mean MDD of razorbills was slightly shallower than that of puffins (4.2 ± 0.1 m c.f. 5.0 ± 0.1 m) (Fig. 3.1).

Table 3.3. Model outputs from linear mixed models investigating the factors influencing maximum dive depth (MDD) and daily time submerged (DTS) of common guillemots, razorbills and Atlantic puffins from the Isle of May during the non-breeding period (July – January).

Model Term	df	MDD		DTS	
		χ^2	p	χ^2	p
Species	2	77.61	<0.01	117.07	<0.01
Month	6	1375.29	<0.01	85.17	<0.01
Sex	1	0.50	0.48	2.09	0.15
Species × Month	11	2518.88	<0.01	151.82	<0.01
Species × Sex	2	3.71	0.16	4.09	0.13
Month × Sex	6	514.13	<0.01	127.03	<0.01
Species × Month × Sex	9	2964.46	<0.01	27.13	<0.01

We found support for our prediction that the higher foraging effort of guillemots than razorbills in the breeding season would persist into the non-breeding season. Thus, on average, DTS was higher in guillemots than in razorbills (4.86 ± 0.18 h and 2.10 ± 0.05 h respectively; Table 3.3). Mean DTS for puffins (4.07 ± 0.12 h) was similar to that of guillemots (Fig. 3.1).

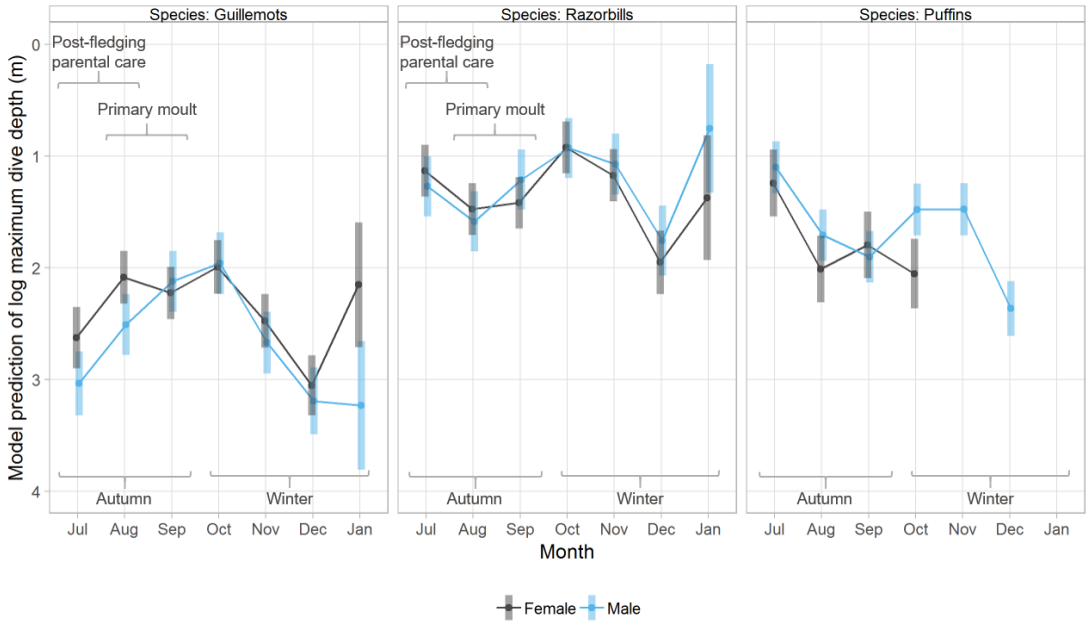

Figure 3.2. Estimated marginal means and 95% confidence intervals of log maximum dive depth (MDD) under the effect of the interaction of species, sex and month outside the breeding season. The y-axis has been inverted and 0 therefore equates to the water surface.

In accordance with our predictions that overall MDD and DTS would not differ between the sexes because all three species are sexually monomorphic, we found no evidence of a main effect of sex for any of the species (Table 3.3).

Post-fledging parental care

Sex-specific differences in guillemot and razorbill dive behaviour in July and August are predicted as a result of males providing post-fledging parental care of chicks during these months (Table 3.2). For MDD the predicted direction of the difference is unclear, since increased MDD would allow males to exploit a greater part of the water column while decreased MDD would minimise risks of males getting separated from their

chicks. The TDR data indicated a significant sex*month interaction (Table 3.3) and post hoc tests indicated that MDD was markedly deeper in male guillemots compared to females in July (mean 55.9 ± 1.4 m and 16.5 ± 0.6 m respectively) and August (mean 18.4 ± 0.5 m and 9.2 ± 0.2 m respectively), but there was no evidence of significant sex-related depth partitioning in razorbills (Fig. 3.2). DTS values are predicted to be greater in males than females because of additional effort required to provision the chick until it becomes independent (Table 3.2). In accordance with this, DTS of male guillemots in July was more than double that of females (10.65 h and 2.01 h respectively, although n = 1), but no difference was apparent in August (4.42 ± 0.57 h and 4.09 ± 0.54 h for males and females respectively), while in razorbills, DTS of males was longer in July (2.85 ± 0.22 h and 2.14 ± 0.13 h for males and females respectively) and markedly longer than females in August (2.98 ± 0.32 h and 1.20 ± 0.52 h for males and females respectively; Fig. 3.3). Puffins do not provide sex-specific, post-fledging parental care and we found no evidence of marked sex differences in either MDD or DTS in July (4.01 ± 0.36 h and 3.09 ± 0.21 h for males and females respectively) or August (2.99 ± 0.21 h and 2.76 ± 0.12 h for males and females respectively).

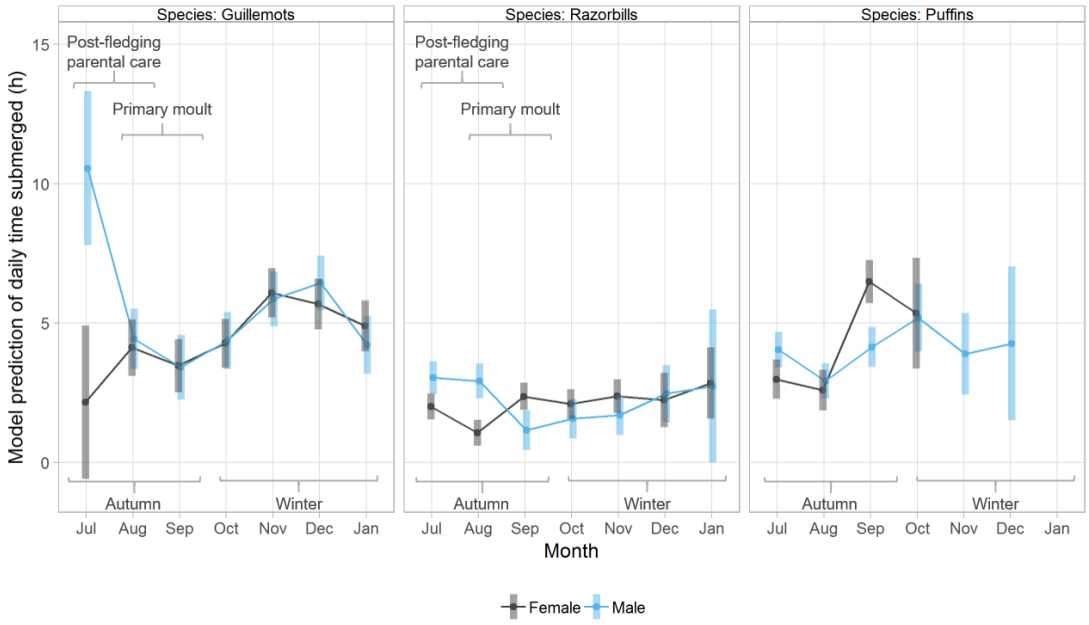

Figure 3.3. Estimated marginal means and 95% confidence intervals of daily time submerged (DTS) under the effect of the interaction of species, sex and month outside the breeding season.

Primary wing moult

The timing of primary moult in guillemots and razorbills overlaps with the period of post-fledging parental care but also extends into September. Unlike post-fledging parental care, no sex differences in dive behaviour are expected as a direct consequence of moult. However, inter-specific differences in MDD and DTS may arise from differences in diving efficiency and the energetic costs of moult. The direction of predicted differences are equivocal due to uncertainty in whether the loss of primaries increases or reduces diving efficiency (Table 3.2). As reported above, MDD did differ between male and female guillemots in July and August, suggesting that post-parental care effects were more important in this species. In contrast, no marked sex effects were apparent in razorbills. In both species, MDD in August and September was shallow relative to later in the season (Fig. 3.2), indicating that in general, birds were not making deep dives while they were moulting. However, MDD was lowest in October when most guillemots and razorbills should have completed their moult. Timing of primary moult in puffins is more variable than in guillemots or razorbills and was unknown in study

individuals but was most likely to have occurred in October. There was no evidence that puffin MDD in October was markedly different to other months (Fig. 3.2). Values for DTS in October were relatively high but sample sizes were small making comparisons difficult.

Seasonal environmental change

Predictions associated with changes in environmental conditions between the end of the breeding season and mid-winter are for MDD to change, DTS to increase and DDA to show changes (either more constrained use, or greater use of night-time hours; Table 3.2). These changes are predicted because day length shortens, light levels at depth are reduced due to the lower angle of the sun, and conditions change as a result of worsening weather within the North Sea and northeast Atlantic. We found that values of MDD for all three species increased rather than decreased between October and December, although values for puffin in November and December were based on a single bird (Fig. 3.2). Our prediction for DTS was partially supported since DTS was higher for guillemots in November and December (Fig. 3.3). DTS in razorbills increased slightly between October and December. No clear trend was apparent in puffins (Fig. 3.3), but sample sizes were too small to allow reliable comparisons.

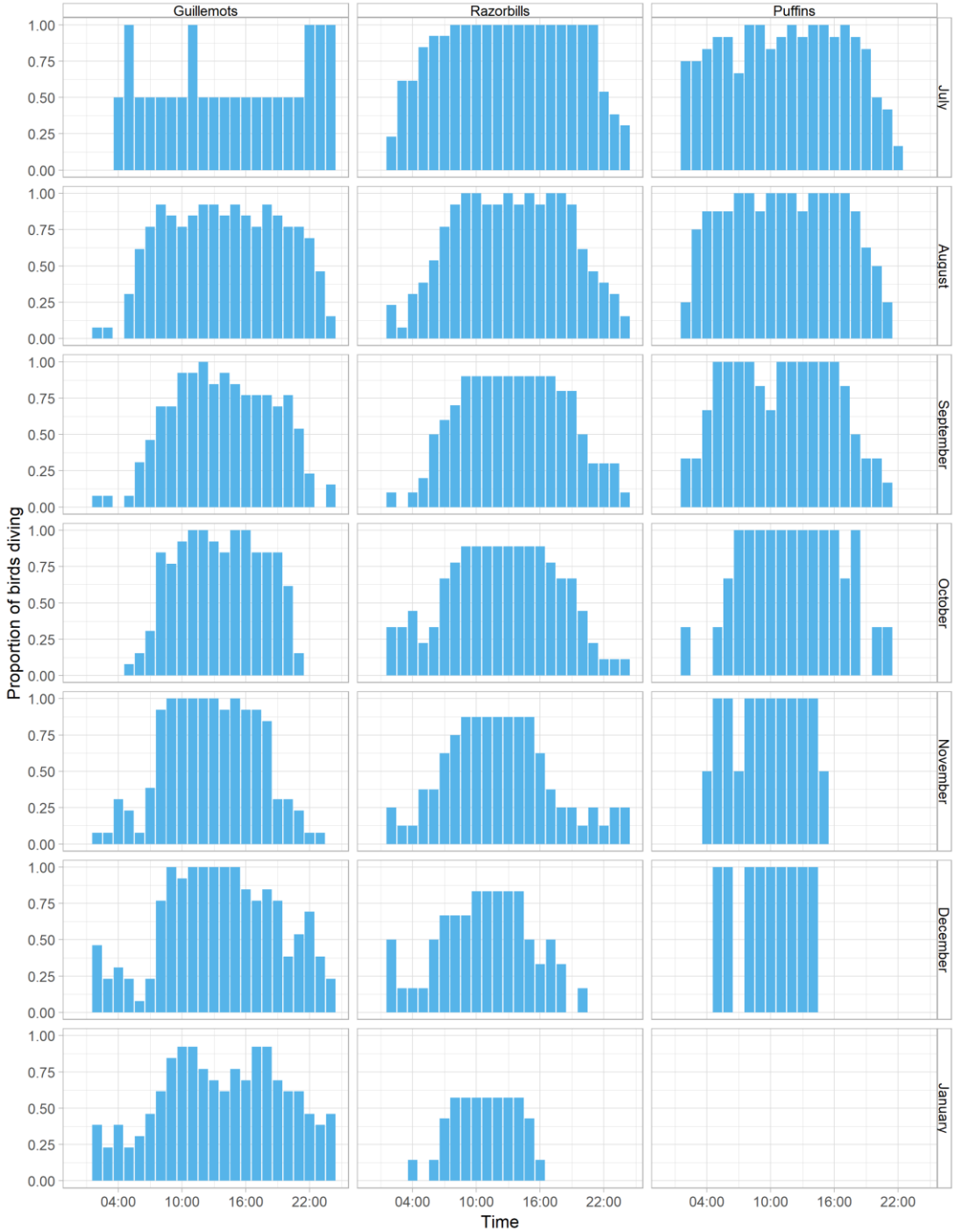

Figure 3.4. Changes in diurnal diving activity (DDA) of common guillemots, razorbills and Atlantic puffins from July to January.

There were seasonal changes in DDA, such that there was a gradual delay in the start time of diving and an advancement in the end time in razorbills and puffins as day length shortened (Fig. 3.4). In contrast, guillemots dived across the 24-hour period

throughout the winter, with 28% of diving occurring outside the hours of 08.00 – 20.00 (Fig. 3.4).

Discussion

Identifying the drivers of behaviour outside the breeding season and understanding their implications for energy budgets and energetic bottlenecks have recently been highlighted as research priorities (Cherel et al., 2016). Our study provides the first comprehensive assessment of the factors influencing key aspects of overwinter diving behaviour in three species of auk that together make up a major component of the seabird community wintering in the North Atlantic (Grandgeorge et al., 2008). We found that both intrinsic and extrinsic factors drive the diving behaviour of these species in ways which differ from those operating during the breeding season.

Interspecific differences

Overall, MDDs of all three species were well within their physiological capacities as indicated by maximum recorded dive depths of 138 m, 140 m and 68 m for guillemot, razorbill and puffin respectively (Burger and Simpson, 1986; Jury, 1986). However, studies elsewhere have recorded auks diving deeply outside the breeding season. For example, guillemots and razorbills from colonies in southwest Greenland had mean dive depths of 27.4 m and 8.6 m in September (Linnebjerg et al., 2013), compared to mean maximum depths of 10.9 m and 4.7 m for these species during the same month in our study. Guillemots, razorbills and puffins all show increases in body mass after the breeding season (Anker-Nilssen et al., 2018; Harris et al., 2000), presumably due to deposition of fat reserves. Increased fat deposits are likely to increase the diving costs required to overcome buoyancy (Lovvorn et al., 2004; Watanuki et al., 2006), especially given the shallow depths observed here. Thus the progressive increase in MDD outside the breeding season may suggest that increased buoyancy is driving deeper dives, but the general lack of deep diving indicates that diving behaviour of auks during the post-breeding period is predominantly driven by extrinsic factors such as light levels and

prey distribution as opposed to physiological constraints. Despite the wintering areas of guillemots, razorbills and puffins from the Isle of May having typical water depths of <100 m, and in many cases <50 m, there was no evidence that dive depth was restricted by the bathymetry in these relatively shallow areas, with dives by all species being concentrated mainly within the top 20 m of the water column.

When comparing our empirical data from bird-borne TDRs with predictions from different dive behaviour hypotheses, we found partial support for responses in accordance with interspecific differences in body mass and associated mass-specific oxygen stores (Paredes et al., 2008; Thaxter et al., 2010; Watanuki et al., 2006). Thus outside the breeding season, MDD of guillemots was markedly deeper than that of razorbills (Fig. 3.1). However, despite razorbills being 35% heavier than puffins, there was no significant difference in MDD between these two species with both making predominantly shallow dives (means of 4.2 ± 0.1 m and 5.0 ± 0.1 m respectively and >90% of records being <5m). Interspecific depth segregation in guillemots and razorbills has previously been recorded during the chick-rearing period on the Isle of May with the former making significantly longer, deeper dives (Thaxter et al., 2010). Contrastingly, on Skomer Island, Wales, puffins accessed deeper dive depths than razorbills during the breeding season despite their lower body mass (Shoji et al., 2015b).

Interspecific differences in dive depth have been linked to differences in chick provisioning strategies: guillemots are obligate single-prey loaders and thus require larger prey items for their chicks than razorbills and puffins which are multiple-prey loaders and have the option of bringing back many smaller prey items (Wilson et al. 2004, Thaxter et al. 2010, Harris and Wanless 2011). Razorbills and puffins may therefore make shallower dives in order to target shoals of smaller sized but more numerous prey items (Chimienti et al., 2017; Ouwehand et al., 2004; Shoji et al., 2015b; Thaxter et al.,

2013, 2010). Although guillemot MDD decreased after the breeding season, greater depth usage compared to the other two species persisted through to January (Fig. 3.3). The evidence to date suggests that depth segregation among these species is maintained throughout the winter and that guillemots target different prey. In the case of the Isle of May auk community, these conclusions accord well with stable isotope analyses which indicate that guillemots consistently forage at a higher trophic level than razorbills and puffins during winter moult periods (St. John Glew et al., 2018).

In addition to the consistent difference in depth usage among species, razorbills also continued to have significantly lower DTS than guillemots outside the breeding season, matching interspecific differences in foraging effort during the breeding season (Thaxter et al., 2010). However, data from more populations and years are required to establish why guillemots have higher DTS than the other two auk species both during the breeding season and the subsequent non-breeding period.

Sex-specific differences

We also found support for the body mass hypothesis with respect to the overall absence of strong intraspecific sex differences in diving behaviour, consistent with the lack of sexual dimorphism in all three species. However, although sex was not significant as a main effect for either MDD or DTS for any of the species (Table 3.3), we did find evidence of intraspecific sex differences in some months. The timing of these sex differences accorded well with predictions based on interspecific differences in post-fledging parental care which occurs predominantly in July and August. Thus in guillemots and razorbills, the two species in which the male parent takes the partially grown chick to sea and provides it with food and protection for at least a month, MDD was deeper in male compared to female guillemots, while DTS was longer in male compared to female guillemots and razorbills (Fig. 3.3). Shallower dives have been

suggested as a way of maximising contact between males and their chicks thereby reducing risks of predation and/or the two getting separated in rough sea conditions (Camphuysen, 2002). However, we found no support for this, for guillemot MDD was deeper not shallower in males, particularly in July and August, suggesting that they may have dived deeper to access prey required for chick provisioning. Similarly Burke et al. (2015) found that male guillemots from colonies in Newfoundland, Canada made deeper dives than females whilst providing post-fledging parental care. Elevated DTS, which was recorded in both species, was consistent with the male providing for the additional nutritional demands of the growing chick (Burke et al., 2015; Paredes et al., 2008), although the timing of increased effort differed between the species with the sex difference being more marked for guillemots in July and for razorbills in August. Differences in sex-specific foraging effort during post-fledging parental care have previously been shown in both common and Brünnich's guillemots *Uria lomvia*, with male birds again spending more time diving at this time (Burke et al., 2015; Elliott and Gaston, 2014). An increase in DTS during the post-fledging period has not previously been demonstrated in razorbills. Clearly there is a need for more information on individual-level behaviour during this crucial period in this species. In puffins, where neither sex provides post-fledging parental care, the data matched our predictions such that there were no marked sex differences in either MDD or DTS in July or August.

Moult-driven differences

In guillemots and razorbills, the main moult, including the replacement of flight feathers when birds are flightless, is concurrent with the July/August post-fledging parental care period but also extends into September. In the Isle of May populations wing moult appears to be complete by early October because guillemots start attending the colony again in mid to late October (Harris and Wanless, 2016). Guillemots MDD and DTS was lower during August and September than it was later in the season. Such

patterns are consistent with guillemots having successfully located, and remained in, productive waters with abundant prey (Linnebjerg et al., 2018; Peery et al., 2008). In contrast, effects in razorbills were much less pronounced, with no clear changes associated with the moult period, further highlighting the need for more data on dive behaviour outside the breeding season for this species. Timing of moult in puffins appears to be much more variable than in guillemots and razorbills. The available evidence suggests that puffins from the Isle of May population are most likely to moult in October or March (Harris et al., 2014). The timing of moult was unknown in our study individuals, but as with razorbills, there was little evidence that moult had any marked effect on dive behaviour in terms of MDD or DTS.

Seasonal differences

Coinciding with seasonal changes in environmental conditions, we observed an increase in DTS within both guillemots and razorbills between October and January compared to between July and September (Fig. 3.3). Guillemots and razorbills were also found to increase MDD (Fig. 3.2), in keeping with our prediction that dive depth would increase with seasonal changes in body mass, and in accordance with other studies of guillemot winter diving behaviour (Burke and Montevecchi, 2018; Elliott and Gaston, 2014; Fort et al., 2013b). Deeper dives would allow birds to avoid the increased wave action and associated turbulence near the surface during storms (Finney et al., 1999). In addition, birds may have had to dive deeper in order to access energy-dense prey which remain at depth during the winter as surface waters cool (Burke and Montevecchi, 2018). Increases in DTS may also be due to birds working harder in order to capture potentially scarcer prey, particularly when light levels are lower. However, reasons for differences in DTS are difficult to interpret without independent data on the distribution of prey (Fayet et al., 2016). Further multidimensional studies are

therefore needed to disentangle the extrinsic influences on diving behaviour during the post-breeding period.

Progressive failures of TDRs on puffins meant that sample sizes from October onwards were very small, greatly hampering evaluation of dive behaviour during the winter period. Winter is thought to be a period of high mortality in puffins (Harris et al., 2010; Harris and Wanless, 2011) and future studies should therefore seek to address the links between foraging behaviour and survival during this time in this species.

The start of winter also signals an increasing restriction in terms of the temporal availability of daylight. Across all three species there was evidence that time of diving was increasingly constrained by daylight hours as the winter progressed, with the start of diving delayed in the morning and the end of diving advanced in the afternoon/evening (Fig. 3.4). This pattern was most obvious in puffins which apparently did not dive at night, suggesting they may have higher dependence on light to locate prey than the other two species (Martin and Wanless, 2015; Shoji et al., 2015b). This would accord with puffin diet outside the breeding season which is typically made up of small, often semi-translucent, prey items that are difficult to locate (Harris et al., 2015a; Hedd et al., 2010; Martin and Wanless, 2015). In contrast, several studies have recorded guillemots foraging across the 24-hour period (Hedd et al., 2009; Regular et al., 2011, 2010). We also found that some Isle of May guillemots continued to dive across the diel cycle, further demonstrating their ability to successfully forage under nocturnal light levels. Razorbill vision is more similar to that of guillemots than puffins (G.R. Martin pers. comm.) and razorbills have also previously been found to dive at night, although shallower depths were accessed in the late evenings and early mornings than during the middle of the day (Dall'Antonia et al., 2001; Linnebjerg et al., 2015). In our

study we also recorded evening and early morning diving in razorbills, but nocturnal dive behaviour was not as prevalent as in guillemots (Fig. 3.4).

Conclusions

In conclusion, we found evidence of interspecific, sex-specific and temporal segregation in maximum dive depth and daily time submerged across three auk species outside the breeding season. In combination these results demonstrate how intrinsic and extrinsic effects influence diving behaviour at this time. Such data are central to establishing when key energetic bottlenecks in the annual cycle in both sexes in different species occur. Quantifying when and where these bottlenecks occur will improve predictions of future climate impacts and assessments of the consequences of human activities such as offshore renewable developments on seabird species.

Chapter 4: A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle

Photo © Sam Langlois

A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle

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Author contributions:

SW, MPH and FD collected the data. Under the supervision of JAG, RED analysed the data and led the writing of the manuscript.

All authors contributed critically to the improvement of this paper and gave permission for the paper to appear within this thesis.

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Abstract

During their annual cycles, animals face a series of energetic challenges as they prioritise different life history events by engaging in temporally and potentially spatially segregated reproductive and non-breeding periods. Investigating behaviour and energy use across these periods is fundamental to understanding how animals survive the changing conditions associated with annual cycles. We estimated year-round activity budgets, energy expenditure, location, colony attendance and foraging behaviour for surviving individuals from a population of common guillemots *Uria aalge*. Despite the potential constraints of reduced day lengths and sea surface temperatures in winter, guillemots managed their energy expenditure throughout the year. Values were high prior to and during the breeding season, driven by a combination of high thermoregulatory costs, diving activity, colony attendance and associated flight. Guillemots also exhibited partial colony attendance outside the breeding season, likely supported by local resources. Additionally, there was a mismatch in the timing of peaks in dive effort and a peak in nocturnal foraging activity, indicating that guillemots adapted their foraging behaviour to the availability of prey rather than daylight. Our study identifies adaptations in foraging behaviour and flexibility in activity budgets as mechanisms that enable guillemots to manage their energy expenditure and survive the annual cycle.

Introduction

The annual cycles of seasonally breeding organisms are composed of life history events such as reproduction, post-breeding recovery, moult, migration, wintering, and preparation for the following breeding period (Marra et al., 2015). A multitude of ecological and physiological processes, that vary temporally, underpin these organismal annual cycles. For example, animals experience seasonally-driven fluctuations in resource availability and environmental conditions (Buehler and Piersma, 2008). To survive their annual cycles when faced with varying environmental conditions, animals must adjust their behaviour and balance their energy acquisition and expenditure (Karasov, 1986).

The reproductive season has previously been highlighted as an energetically costly period in an animal's annual cycle (Bryant, 1997; Thometz et al., 2016). High values of energy expenditure during the breeding period are incurred by parents making physiological and behavioural adjustments in order to invest in reproduction. During this time they incur costs through activities such as egg production and offspring provisioning, whilst also having to maintain their own body condition at a level that safeguards future survival and breeding (Drent and Daan, 1980; McBride et al., 2015). In species that adopt central-place foraging strategies during reproduction, high energetic costs are often driven by increased allocation of time to energetically expensive commuting behaviours (Boyd, 1999). Outside the breeding season many taxa adopt costly migratory strategies as an adaptive behavioural response to seasonal variation in environmental conditions, resource availability and subsequent energy intake (Dingle and Drake, 2007; Lennox et al., 2016). Animals may travel large distances to avoid energetically challenging areas and instead maximise energetic inputs, on the basis that the non-breeding location is sufficiently profitable to offset the costs of migration

(Braithwaite et al., 2015). Thus, an organism's movement, behaviour and external environment are all key factors in its energy expenditure during the annual cycle.

In addition to variation in migration strategies, many animals exhibit behavioural plasticity at hourly or daily scales in order to respond to variation in their environmental conditions. For example, basking sharks *Cetorhinus maximus* adopt a habitat-specific foraging strategy that is consistent with the daily vertical movements of their prey, to maximise energy intake versus expenditure (Sims et al., 2005). Additionally, animals might display differences in their behavioural budgets associated with their state or age, for example if one sex allocates more time to foraging or risk-averse behaviours due to sex differences in the time and energy required for reproduction (Williams et al., 2016). However, despite evidence of behavioural plasticity across numerous taxa, the energetic consequences of such plasticity over the annual cycle have rarely been assessed.

In this study, we present the first estimates of year-round daily energy expenditure (DEE) for surviving individuals in a population of free-ranging common guillemots (hereafter 'guillemots') *Uria aalge* and seek to understand the behavioural and energetic adaptations that they used in order to survive the annual cycle. Guillemots have the highest wing loading (mass per unit area of the wing) of any flying bird (Elliott et al., 2013) and are central place foragers during their summer breeding seasons (Davoren and Montevecchi, 2003). They therefore incur high energetic costs during the breeding period (Cairns et al., 1990), although these costs must remain below an optimal sustainable threshold (4 to 5 times their basal metabolic rate (BMR; Drent and Daan, 1980; Weathers and Sullivan, 1989) to ensure reproductive success and survival. Following the costly breeding season, guillemots moult and then spend the winter primarily at sea, although some populations also exhibit non-breeding colony

attendance (Harris et al., 2015b; Merkel et al., 2019). Previous studies have shown that guillemots exhibit behavioural plasticity in response to variation in the environmental conditions they encounter during the non-breeding period, with consequences for their energetic budgets and mortality. For example, those that wintered in the Norwegian, Barents and White Seas increased their foraging effort ahead of several weeks of polar night, potentially maximising prey intake prior to this period of intense environmental constraint (Fort et al., 2013b). Furthermore, guillemots that over-wintered on the Newfoundland Shelf increased their diurnal foraging effort in response to seasonally varying vertical distributions of prey resources (Burke and Montevecchi, 2018). Thus guillemots, as with other seasonally breeding diving birds, make good models to investigate behavioural and energetic responses to seasonally varying ecological drivers.

We investigated the year-round behavioural and energetic adjustments made by a temperate population of breeding guillemots that may face similar constraints to more northerly populations, but which also adopt a strategy of returning to their breeding colony outside the breeding season. Our data span a year that was marked by low survival and subsequent breeding success (Newell et al., 2013), hence increasing its optimality to investigate the strategies that surviving individuals exhibited. Therefore, within this study we investigated three questions. Firstly, how did the energy expenditure of surviving adult guillemots vary throughout the annual cycle? Secondly, how did these guillemots adjust their activity budgets and overwinter behaviour, in terms of migration and periodic returns to the colony, in order to balance their energy expenditure under varying environmental conditions? Thirdly, did guillemots adjust their diurnal diving behaviour in response to changes in daylight availability over the annual cycle?

Materials and Methods

Data collection

Fieldwork took place on the Isle of May National Nature Reserve, Scotland (56° 11'N, 02°33'W) from 2005-2006. The mean population fledging date (10th July 2005) and the first guillemot egg date (2nd May 2006) were obtained from long-term monitoring plots at the colony, using standardised methods (Newell et al., 2015).

During June 2005, we captured 30 adult guillemots that were brooding young chicks. We attached global location sensing (GLS) time depth recorder (TDR) devices (LT2400, Lotek Wireless, St John's, Newfoundland, Canada, 36 × 11 mm) to Darvic leg-rings under British Trust for Ornithology and Scottish Natural Heritage licences (licence numbers C/4671 and 5632 respectively). Device plus ring mass (6.5 g) was 0.69% of the birds' mean breeding body mass at recapture. During the 2006 breeding season, 13 adult guillemots were recaptured (43% retrieval rate; pre-breeding n = 3 and early chick-rearing n = 10) and the loggers were removed. We therefore obtained data from birds that survived the annual cycle. Three to five body feathers were collected from recaptured birds under UK Home Office Licence to enable birds to be sexed using two CHD I genes (Griffiths et al., 1996). All procedures were conducted in accordance with relevant UK guidelines and regulations and were approved under research licences issued by Scottish Natural Heritage.

Individuals from the Isle of May population are known to return to the colony after the autumn flightless period and during the winter, although they do not attend the colony during the night in the nonbreeding period (Harris and Wanless, 1990). We quantified population-level daytime non-breeding season colony attendance behaviour using daily time-lapse photography from 7th October 2005 to 20th May 2006. A camera was trained on a sub-colony of guillemots approximately 50 m north of the instrumented

birds. We assigned a daily density score of between zero and five, based on the number of individuals at the study plot (0 = no individuals; 1 = < 10 individuals; 2 = 10 – 20 individuals; 3 = 20 – 50 individuals; 4 = > 50 individuals; 5 = all ca. 100 breeding sites occupied).

Spatial data

Loggers employed internal processing algorithms to calculate daily location fixes; latitude and longitude were calculated on-board the devices based on estimates of day length and the timing of midday (Ekstrom, 2004). Locations were re-estimated using an iterative forward step selection framework through the *probGLS* package (Merkel, 2018). Improved location estimates were generated by calculating a cloud of possible locations (n = 1000) and weighting these according to 0.25° resolution NOAA optimally-interpolated sea surface temperature (SST) and daily median SST recorded by the logger (Merkel et al., 2016; Physical Sciences Division, 2019; Reynolds et al., 2007). Based on these weightings, 100 likely movement paths were computed and the geographic median for each location cloud was then selected. This method allowed estimations of locations around the equinoxes to be computed (Merkel et al., 2016). Despite the improved estimates generated using this algorithm, 6 days prior to each equinox were removed following visual inspection (locations between the 10th – 15th September 2005 and 11th – 16th March 2006). Next a cost-path analysis was conducted and fixes that indicated movements of over 750 km in 12 hours were removed (0.6% of all fixes; cut-off assigned based on a maximum flight speed of 60-70 kmh^{-1}; Pennycuick, 1987). These fixes typically resulted from light interference at dawn and dusk, perhaps caused by the logger being shaded e.g. if the leg was tucked into the feathers. Erroneous fixes were also frequent when the birds were thought to be at the breeding colony. Therefore, fixes that occurred prior to the 2005 mean fledging date and those that occurred after the date of the first guillemot egg in 2006 were assigned Isle of May coordinates.

Population-level monthly kernel home ranges for the non-breeding period, which was taken to be from 10 days after the mean fledging date to 30 days before the first egg date (i.e. 20th July 2005 – 2nd April 2006), were created using the *adehabitatHR* package (Calenge, 2006), using a least squared cross validation method and a 50 km grid size. Core use areas during the non-breeding period were represented by 50% kernel density contours.

Daily air temperature was extracted from either Lerwick (60° 14'N, 01°18'W), Leuchars (56° 38'N, 02°86'W), Bridlington (54° 1'N, 00°21'W) or Sandettie (51° 10'N, 01°80'W) weather stations (Met Office, 2012), depending on which was in closest proximity to the centroid of an individual's fortnightly GLS point cluster. These individual-specific fortnightly locations were also used in conjunction with the *maptools* package (Bivand and Lewin-Koh, 2018) to calculate location-specific times of sunrise, sunset and nautical twilight (when the sun was between 6 and 12 degrees below the horizon) for each day for each bird.

Activity data

Loggers recorded time, depth (to the nearest 0.01 m) and temperature (to the nearest 0.01°C). Due to the limited memory size of the loggers and to record data over an extended period of the annual cycle, loggers recorded a depth and temperature reading either every 16 s for a 24 h period every 30 days (n = 9) or every 32 s for a 24 h period every 15 days (n = 4). Dive and temperature data were available for all birds until March (n = 13), for 10 birds until April, 9 until May and 3 until June. The dive data were corrected for device drift using the *diveMove* package (Luque, 2007).

Days which did not have temperature and depth data for the entire 24 hour period were removed (n = 9) and the remaining data ($n_{\text{bird days}} = 179$) were used to derive daily time-activity budgets. Time-activity budgets were based on the identification of five key

activities: a. diving (T_d), b. flying (T_f), c. at the colony (T_c), d. active on water (T_a) and e. inactive on water (T_i; Burke and Montevecchi, 2018; Linnebjerg et al., 2014). Active on water (T_a) included intervals on the surface between dives and longer periods between dive bouts when activities such as swimming and preening were undertaken. Inactive on water (T_i) was taken to represent resting time when guillemots withdrew their leg and foot into their plumage (Linnebjerg et al., 2014).

Our behavioural classifications were based on a set of decisions appropriate to the resolution of the data at our disposal. Supplementary material Fig. A4.1 gives examples using this behavioural classification for representative periods of the annual cycle. Identification of different behaviours was made sequentially. First, times when loggers recorded depths of >1 m, were assigned as diving (T_d). We summed the time spent diving each day to give the daily time spent diving. We also calculated the proportion of time spent diving during daylight, night or nautical twilight during each 24 hour period, based on the location-specific times of sunrise, sunset and twilight. We extracted logger temperatures during these dives (T) to estimate the range of water temperature values that guillemots encountered whilst foraging on that day. Next, we classified all non-diving behaviours. We inferred that when the temperature recorded by the logger was greater than T – 0.2°C and less than the 75% quartile of T + 1°C, birds were active on the water (T_a; Elliott and Gaston, 2014).

We then split the annual cycle into different periods, based on the population-level phenology data, to further refine time-activity budgets based on a priori knowledge of sex- and period-specific drivers of guillemot activity in this particular population. As the mean population-level fledging date in 2005 was the 10th July, we assumed that instrumented birds could have been at the colony (T_c) until the 20th July and thus could have been engaged in any of the five behaviours during this time (Supplementary

material Fig. A4.1 A). Bouts of flight (T_f) were separated from bouts of inactivity (T_i) on the assumption that guillemots do not fly at night (Elliott and Gaston, 2014; Robertson et al., 2012) and logger temperature being less than daily air temperature + 4°C, as opposed to the higher temperatures expected during leg-tucking events (T_i; Burke and Montevecchi, 2018; Linnebjerg et al., 2014). We validated this classification of T_f and T_i by modelling the impact of behavioural state on the relationship between the duration of time spent in the activity and the maximum temperature recorded (Supplementary material Fig. A4.2). T_f was summed per day in order to calculate the daily time spent flying.

From 20th July until the assumed start of primary feather moult (15th August), female birds may have engaged in flight, but male birds were assumed to be at sea with their chicks and not to fly. We further assumed that all birds underwent primary feather moult between mid-August (15th) and the end of September (30th) during which time they were flightless. We therefore forced the data into three known activities during these periods (T_d, T_a or T_i; Supplementary material Fig. A4.1 B).

Based on previous studies, guillemots were assumed to be absent from the colony (no T_c) between the end of the breeding season (20th July) and November 15th. Previous studies of individually marked birds have not detected any difference between the sexes in return dates (Harris and Wanless, 1989b). Thus both males and females were assumed to be absent from the colony during this time and data were forced into the four other activities (excluding T_c) during this period. From the 2nd April (30 days prior to the date of the first guillemot egg in 2006) guillemots were assumed to be able to spend an increasing amount of time at the colony, based on previous intensive visual observations (Wanless and Harris, 1986). During this period we identified T_c activity as times when temperature recorded by the logger was less than the daily median

recorded during leg-tucking events (T_i; Supplementary material Fig. A4.1 C). Outside this period, when the logger temperature was elevated for over half an hour during the morning, we identified T_c activity as before. We classified periods of increasing logger temperature that occurred immediately before T_c events as T_f, and periods immediately after T_c as T_a, as birds fly to the colony before periods ashore and later land on the water immediately after departing from the colony (as also observed in Brünnich's guillemots *U. lomvia*; Linnebjerg et al., 2014).

Daily energy budgets

We combined daily time-activity budgets with estimates of activity-specific energy costs to determine the daily energy expenditure (DEE in kJ) using an equation based on Brünnich's guillemots (Burke and Montevecchi, 2018; Elliott et al., 2013; Elliott and Gaston, 2014):

$$DEE = 508\,T_f + 33\,T_c + 1.01\sum\left[1 - e^{\frac{-Td}{1.23}}\right] + (113 - 2.75\,SST)T_a + (72.2 - 2.75\,SST)T_i$$

eqn 4.1

where T_d represents individual dive durations in minutes (which were then summed for each day) and T_f, T_c, T_a and T_i represent hours in flight, at the colony, active on water and inactive on water respectively as previously defined. SST was the fortnightly mean recorded by the logger. We also calculated the daily energetic costs of flight and diving separately based on their relative contributions to equation 4.1.

Data analyses

Data exploration indicated potentially non-linear relationships in temporal patterns of guillemot DEE, SST, activity, activity costs and diving behaviour throughout the annual cycle and we therefore implemented generalised additive mixed models (GAMMs)

using the *gamm4* package (Wood and Scheipl, 2017). A similar approach has been adopted in studies of activity budgets of overwintering Laysan albatrosses *Phoebastria immutabilis* and black-footed albatrosses *P. nigripes* (Gutowsky et al., 2014), and migrating Cory's shearwaters *Calonectris borealis* (Ramos et al., 2018). We included day since logger deployment ('dDay') as a smoothing function because of its many levels, and sex as a fixed categorical factor. Individual bird was modelled as a random effect, with random intercepts, to account for the dependency structure present in the data (Zuur et al., 2014). We used a Gaussian distribution with an identity link function for GAMMs with the response variables of DEE, SST, daily time spent in flight, daily time spent diving, daily energetic cost of flight and daily energetic cost of diving (although sex was not included within the SST model). To model the proportion of total dive activity (daily time spent diving) that took place during daylight, night or nautical twilight we used a binomial distribution with a logit link function within three GAMMs. The predictor variables and random effects used within these binomial models were the same as those used in the previously described set of GAMMs. We validated the models by plotting the residuals against the fitted values and the model covariates (Zuur et al., 2014).

All analyses and plotting were conducted using R version 3.2.3 (R Core Team, 2020); all values are means ± standard error and all times are UTC.

All data is available from the Environmental Information Data Centre: https://doi.org/10.5285/bd24da1f-0761-4564-8dd8-dfd71a559a71.

Results

Daily Energy Expenditure (DEE) of guillemots showed clear temporal changes over the annual cycle but with no substantial effect of sex (Supplementary material Table A4.3). Values were relatively high at the end of the breeding season in July, but decreased markedly in August and September before showing a gradual and sustained increase over the non-breeding period (Fig. 4.1). DEE was lowest in September (generalised additive mixed model (GAMM) prediction = 1404 kJ) and highest in April (GAMM prediction = 2212 kJ).

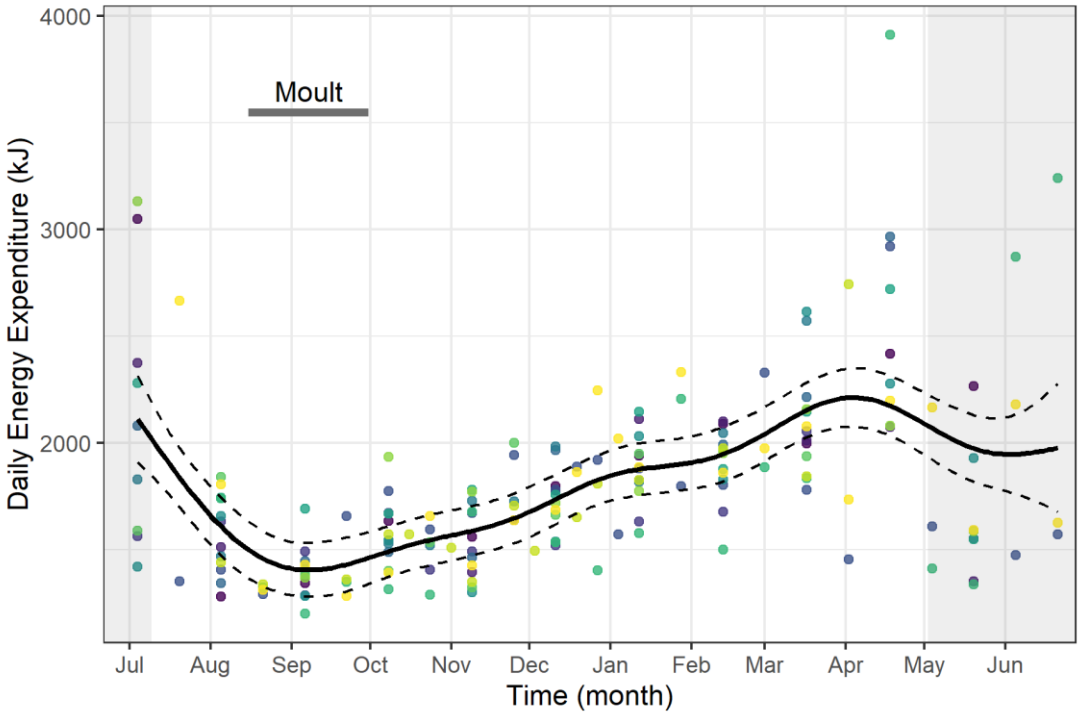


Figure 4.1. The daily energy expenditure of common guillemots from the Isle of May throughout the annual cycle (4th July 2005 – 21st June 2006). Mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (dashed lines) from generalized additive mixed models. We also present the raw data points, coloured by individual. The breeding season is shaded in grey and the horizontal dark bar corresponds to the moult period.

Thermal conditions, as indicated by sea surface temperature (SST), experienced by individual guillemots varied across the annual cycle (Supplementary material Table A4.3). Low values of DEE in August and September corresponded to high values of SST

during the same months (14.9 ± 0.3°C and 15.2 ± 0.3°C respectively; Fig. 4.2) while the April peak in DEE occurred shortly after minimum SST in March (5.7 ± 0.2°C; Fig. 4.2).

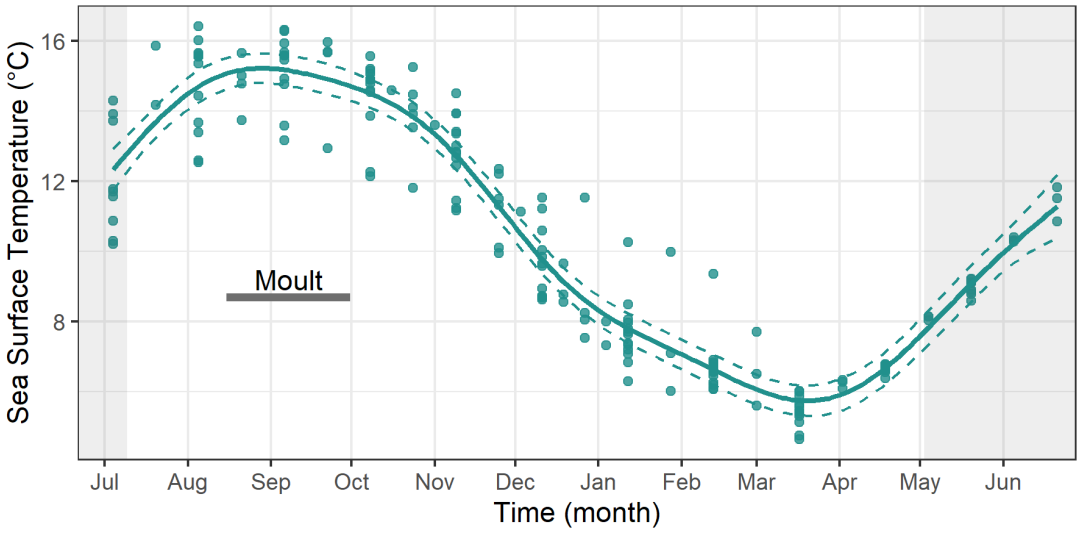


Figure 4.2. Logger-derived sea surface temperature (SST) throughout the annual cycle (4th July 2005 – 21st June 2006). Mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (dashed lines) from generalized additive mixed models. We also present the raw data points. The breeding season is shaded in light grey and the horizontal dark bar corresponds to the moult period.

Inspection of time-lapse camera data revealed that guillemots first returned to the colony after the breeding season on the 15th October but colony attendance remained low until early January (Fig. 4.3). Throughout the winter, low numbers of guillemots attended the colony during the early morning, with birds typically arriving just before dawn. The length of time that guillemots were ashore varied greatly from <1 hour to all day, but during November – January occupancy was usually <4 hours. From late January onwards there was a gradual increase in the proportion of guillemots that were at the colony (Fig. 4.3). Thus, by early April some birds were ashore every day and an increasing proportion of sites were occupied for a greater proportion of the day (Fig. 4.3). There was a continuation of this pattern into the breeding season, with birds found increasingly at the colony (Fig. 4.3).

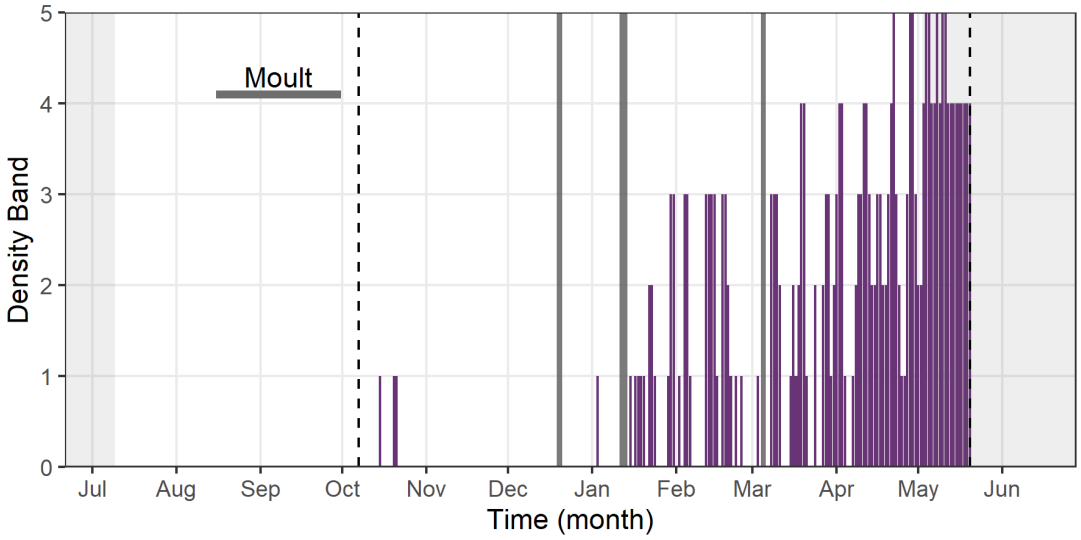


Figure 4.3. Population level non-breeding season colony attendance of a study plot of guillemots at the Isle of May, derived from camera data. Periods of no data during the non-breeding season are shaded in dark grey. The breeding season shaded in light grey and the horizontal dark bar corresponds to the moult period. Vertical dashed lines indicate the start and end dates of the camera data respectively.

Data from the activity loggers indicated that the time spent diving and flying each day varied over the annual cycle, with no substantial effect of sex (Supplementary material Table A4.3). During the period of the year that they were volant, the total time that guillemots spent flying per day was also generally low (Fig. 4.4 A), particularly between October and February (0.2 ± 0.03 h). During this winter period, flight time was less than 0.5 h for 90% of days and the maximum daily flying time was 1.52 h for an individual on 28th January. The longest individual flight that we identified during this winter period was 0.7 h on 13th February. Between March and June during pre-breeding, incubation and chick rearing, the GAMM predicted a gradual increase in average daily flight time from 0.72 ± 0.03 to 1.58 ± 0.07 h (Fig. 4.4 A). This resulted in a marked increase in flight-related energy expenditure (Fig. 4.4 B) and thus contributed to the rise in DEE across the non-breeding period (Fig. 4.1), although there was no substantial effect of sex (Supplementary material Table A4.3).

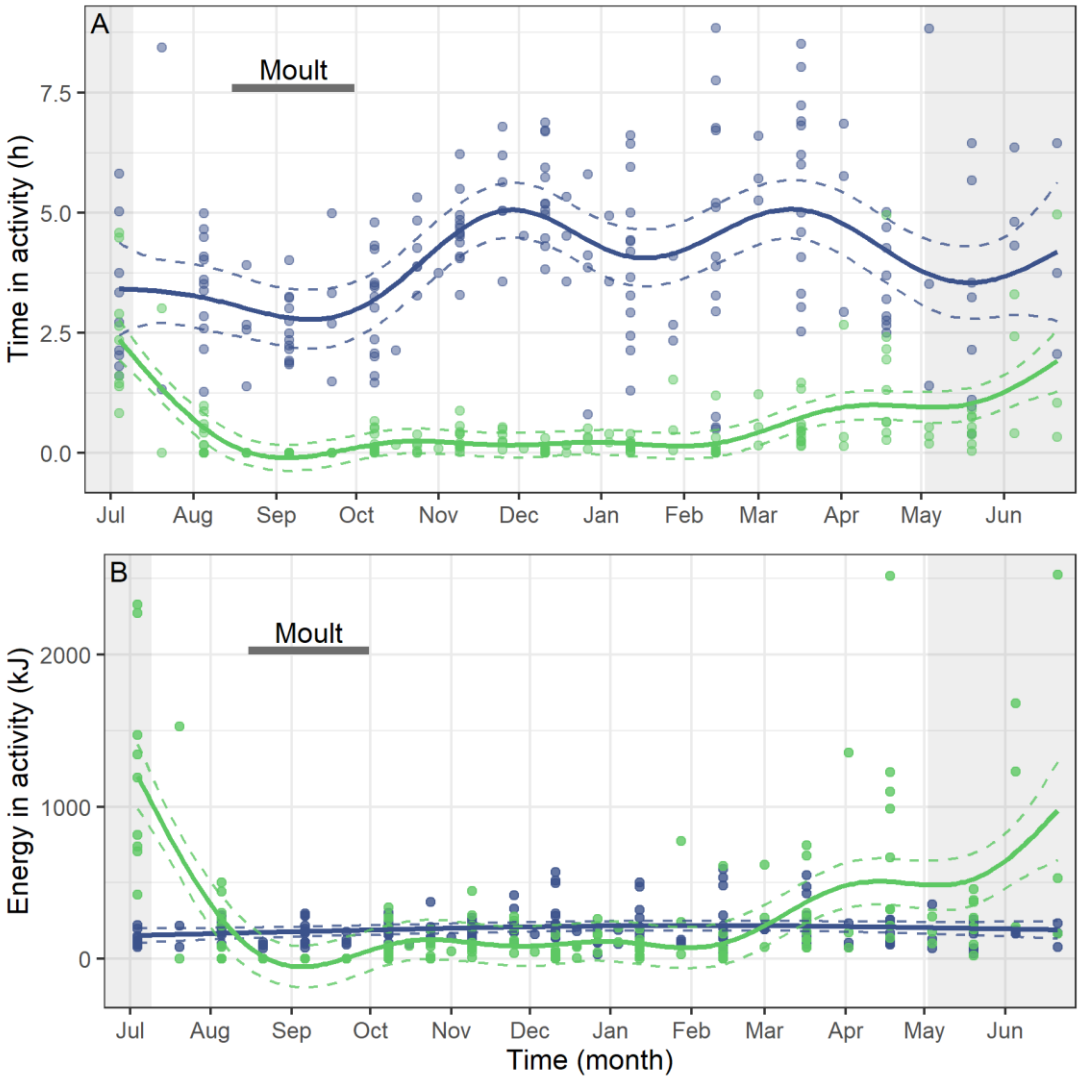


Figure 4.4. A. The daily time spent a) diving (blue) and b) flying (green) by common guillemots from the Isle of May. B. The daily energetic costs of a) diving (blue) and b) flying (green). For both panels, data span the annual cycle (4th July 2005 – 21st June 2006). Mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (dashed lines) from generalized additive mixed models. We also present the raw data points. The breeding season is shaded in grey and the horizontal dark bar corresponds to the moult period.

Guillemots spent considerably more time diving than flying throughout the annual cycle (mean dive time per day = 4.10 ± 0.13 h; Fig. 4.4 A). Time spent diving was high during the breeding season (May, June and July mean = 3.68 ± 0.43 h), but was even higher during the non-breeding period, particularly in November – December (4.85 ± 0.18 h) and in March (5.62 ± 0.43 h). Contrastingly, the GAMM predicted a minimum time spent diving per day of 2.78 h on 12th September. Despite large temporal fluctuations in daily dive time (Fig. 4.4 A), as the energetic costs of diving were

relatively low, this did not translate into large variation in the daily energetic cost of diving across the annual cycle, although this contribution was slightly higher in December – March than during the rest of the year (Supplementary material Table A4.3; Fig. 4.4 B).

Due to the temperate location of the guillemots, light availability varied greatly throughout the annual cycle with the proportion of daylight decreasing throughout the winter, corresponding with an increase in nocturnal conditions (Fig. 4.5 A). During June and July, higher proportions of the 24 hour period were subject to twilight as opposed to night than the rest of the year (Fig. 4.5 A). Throughout the year, the majority of dives occurred during daylight hours (proportion = 0.74 ± 0.02; Fig. 4.5 B). However, the proportion of total dive activity that occurred during daylight did vary temporally (Supplementary material Table A4.3) and was lowest in December – February (proportion = 0.57 ± 0.04). Nocturnal diving activity increased at this time (Fig. 4.4 B; mean annual night diving activity = 0.46 h ± 0.08; December – February diving activity = 1.18 h ± 0.23) and did not always coincide with a reduction in the total hours of available daylight (Fig. 4.5 A). The proportion of diving activity occurring during twilight also varied (Supplementary material Table A4.3), and was highest in July, when twilight composed a higher proportion of the 24 hour period, but not in June, when the daily proportion of twilight conditions was also high (Fig. 4.5 A). Sex did not have a substantial effect on the proportion of time spent diving during different daylight conditions (Supplementary material Table A4.3).

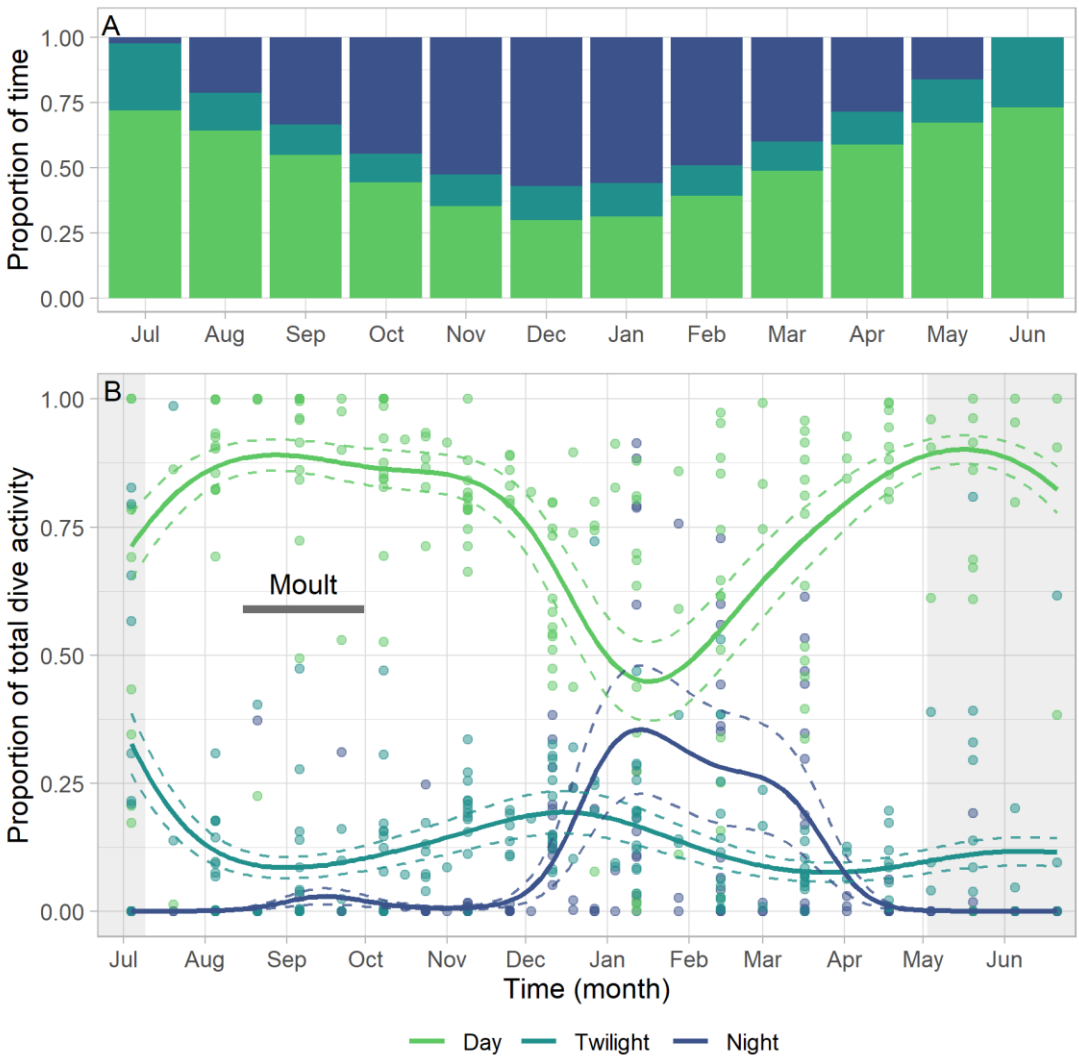


Figure 4.5. A. The proportion of the 24 hour period made up of day, twilight and night for each month, averaged across the individuals' locations and hence environmental conditions. B. The proportion of total dive activity that took place during day, night and twilight throughout the annual cycle (4th July 2005 – 21st June 2006). Mean estimated smoothing function (solid line) with upper and lower confidence intervals at two standard errors above and below the mean (dashed lines) from generalized additive mixed models. Data are from common guillemots from the Isle of May. We also present the raw data points. The breeding season is shaded in grey and the horizontal dark bar corresponds to the moult period.

Following the breeding season, guillemots moved away from the Isle of May and migrated to areas within the North Sea. Some individuals reached the English Channel and the Irish Sea (Fig. 4.6 A). Initially, after departing the breeding colony in July and August, as DEE began to decrease (Fig. 4.1), guillemots were widely distributed across the North Sea (kernel home ranges: 624,682 and 477,953 km² respectively). Their distribution was more restricted during December (Fig. 4.6 B) and January (Fig. 4.6 C; kernel home ranges: 163,436 and 158,863 km² respectively) when the majority of the

tracked population was concentrated within the western and northern North Sea. However, from January onwards, during the period of increasing DEE, guillemots moved progressively closer to the Isle of May (Fig. 4.6 C), still using the central part of the northern North Sea. These movements are consistent with the evidence that they were spending an increasing amount of time at the colony (Fig. 4.2), necessitating increasing commuting time between the feeding areas and the breeding sites (Fig. 4.4 A).

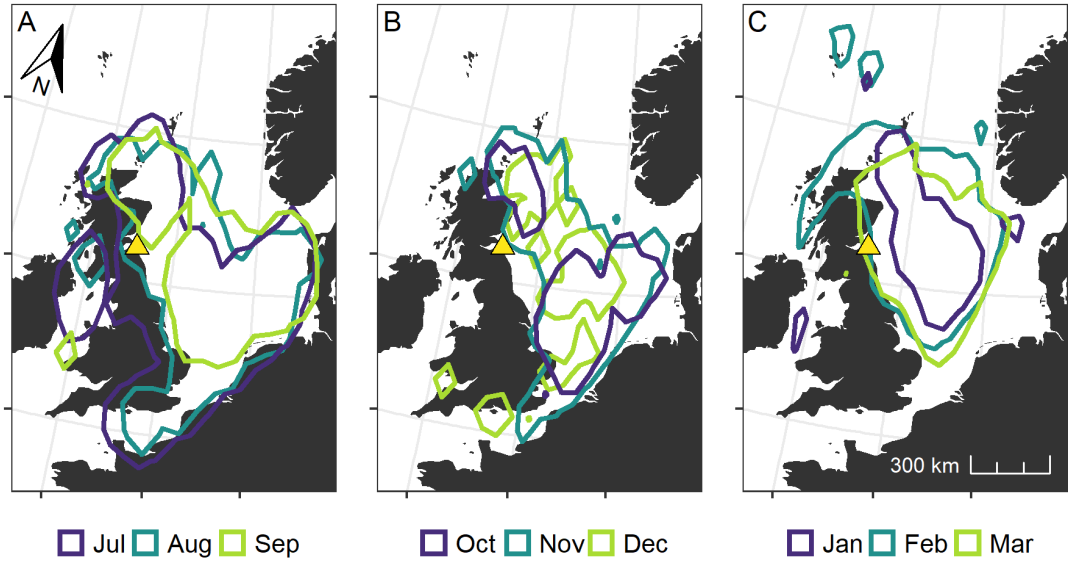


Figure 4.6. Core use areas (50% kernel density contours) of 13 common guillemots from the Isle of May (location illustrated with a yellow triangle) according to month and period of the non-breeding season.

Discussion

Animals must adapt their behaviour and energetic budgets in order to survive the seasonally varying environmental conditions that they face during their annual cycles. However, due to their challenging nature, the number of studies that have sought to investigate the behavioural and energetic strategies that free-ranging animals use to survive annual cycles is relatively small. We show that in this population, surviving guillemots managed their energy expenditure throughout the year by adjusting their activity budgets and demonstrating behavioural plasticity by foraging nocturnally. Daily Energy Expenditure (DEE) during the breeding season was largely higher than during the non-breeding period (Fig. 4.1) due to thermoregulatory costs and increased flight activity associated with colony attendance. However, despite heightened energetic costs, values of DEE remained below the proposed maximum sustainable threshold (4 to 5 × BMR Drent and Daan, 1980; Weathers and Sullivan, 1989), even at its peak (GAMM prediction of DEE during April = 2212 kJ; 3.8 × 580 kJ BMR; Gabrielsen, 1996).

Thermoregulatory costs can form large components of animal energy budgets (Boyles et al., 2011), particularly those of seabirds that spend large proportions of time within the marine environment, where thermoregulation provides a heightened energetic challenge (Croll and McLaren, 1993). The DEE equation (equation 4.1) that we used incorporated the seasonally varying thermodynamic costs of different values of SST during both the active and inactive periods on water. We therefore observed a year-round pattern in DEE that partially mirrored that of SST (Fig. 4.2). High values of SST corresponded to the main moult period when guillemots were flightless and both dive activity and DEE were low. During the moult period, kernel analyses indicated that guillemots were widely distributed throughout the North Sea (Fig. 4.6 A). This pattern of migration was likely to be representative of individuals targeting productive areas,

perhaps within multi-species flocks, where they could remain without making major flights (Camphuysen, 2002; Camphuysen and Webb, 1999). Using productive areas, particularly during times of higher SST which may in turn affect prey availability and quality, might therefore allow the repartitioning of energetic resources to the intrinsically costly process of feather renewal (Guillemette et al., 2007) and allow the accumulation of fat reserves (Harris et al., 2000). Indeed, it is likely that our values of DEE during the moult period are underestimates as they do not account for the intrinsic cost of moult (Lindström et al., 1993). For many migratory birds, primary feather moult takes place shortly after the breeding period (Bridge, 2006; De La Hera et al., 2010). The post-reproductive timing of moult might be particularly crucial for guillemots which need to replace feathers that have been physically abraded and in contact with guano whilst they were breeding on densely populated cliff ledges (Harris et al., 1997). Additionally, the occurrence of moult prior to a decrease in SST (Fig. 4.2) could also be advantageous in terms of acquiring high-condition plumage and subsequent decreased thermoregulatory costs (Croll and McLaren, 1993; Green et al., 2005).

Following the moult period, guillemot DEE gradually increased across the subsequent winter months before reaching a non-breeding season peak in April, followed by similarly high values during the breeding season (Fig. 4.1). Seabird energy expenditure is high during reproduction and generally increases across the breeding period (Dunn et al., 2018). Here, increasing values of guillemot energy expenditure throughout the non-breeding period were largely driven by heightened flight activity (Fig. 4.4), associated with increased colony attendance (Fig. 4.3). Whilst they are well adapted for wing-propelled diving, flight is an energetically costly activity for guillemot species, with Brünnich's guillemots *Uria lomvia* having the highest flight costs recorded for any vertebrate (Elliott et al., 2013). Contrastingly, in albatrosses flight is highly efficient

because they are able to use winds to soar and glide, as opposed to engaging in the costly flapping flight used by auks (Shaffer et al., 2001). Flight activity can therefore form high proportions of albatross time-activity budgets (e.g. 12.7 hours per day in incubating black-browed albatrosses *Thalassarche melanophris*) and yet result in relatively low values of mass-specific DEE (Shaffer et al., 2004). Guillemots, however, must adapt their behaviour and reduce their time spent flying in order to minimise its contribution to DEE. Guillemots from the Isle of May did reduce their flight activity from October to March, in comparison to the breeding season; it seems possible that the guillemots located productive North Sea foraging areas and stayed within these, likely making short commuting flights to optimal feeding patches, as opposed to extensive daily movements (Camphuysen, 1998). However, as the breeding season neared and birds became constrained to remaining in proximity to the colony to occupy and defend their breeding sites (Birkhead and del Nevo, 1987), flight activity and the associated energetic costs increased (Fig. 4.4), leading to heightened DEE (Fig. 4.1). Indeed, guillemots are under central-place foraging constraints during the pre-breeding and breeding periods, undertaking longer flights than during the winter, commuting to and from the colony on a daily or near-daily basis, with detrimental consequences for their energy expenditure. Contrastingly, energetically advantageous lower thermoregulatory costs may be likely whilst birds are at the colony as they will be exposed to warmer air temperatures, lower conductivity and increased body heat conservation through sharing warmth with conspecifics (Ancel et al., 2015). Overall, Isle of May guillemots chose to return to the colony outside the breeding season, indicating that despite its associated energetic costs, this must have been a beneficial strategy that local resources were able to support.

Coinciding with high values of DEE during the pre-breeding period (Fig. 4.1), guillemot dive activity showed a peak during this time (March), as well as during November –

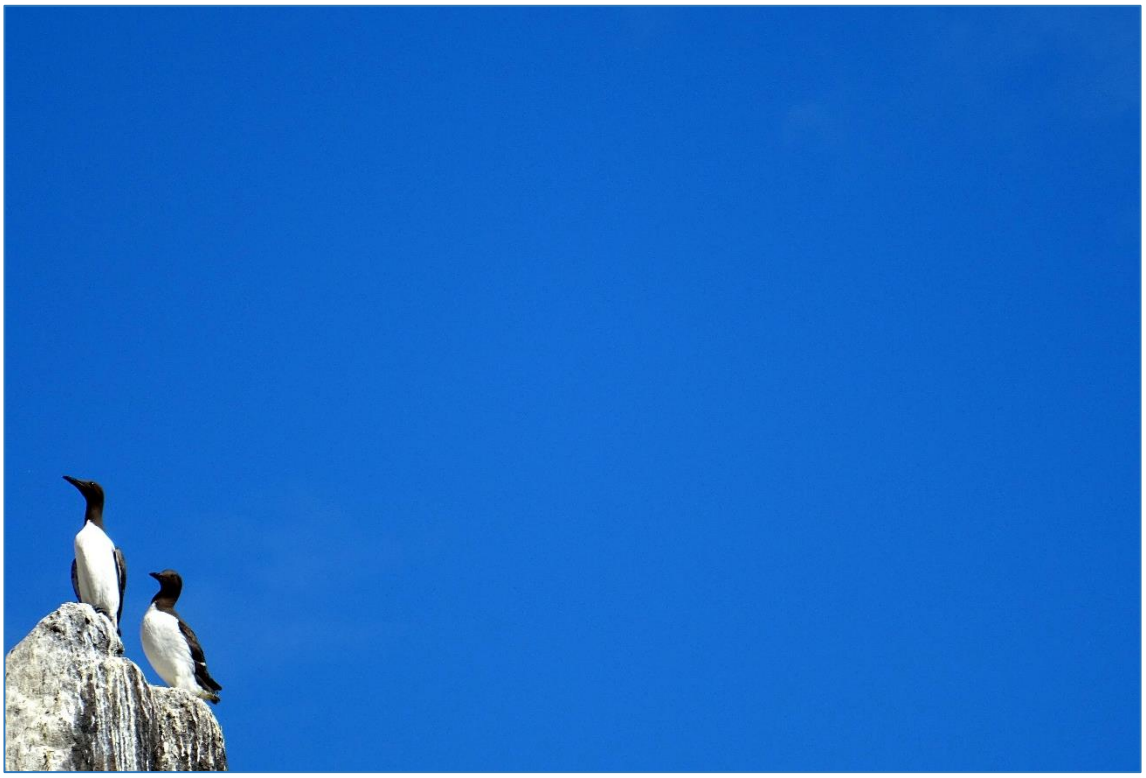
December (Fig. 4.4 A). These two non-breeding season peaks in dive activity may be due to increased foraging effort: the first peak a response to high thermoregulatory costs and winter storm events (Finney et al., 1999; Fort et al., 2009) and the second due to the nutritional requirements associated with attaining pre-breeding condition. Although, like penguins, guillemots are generally well adapted for diving, their efficiency at locating and capturing prey may be hindered by stormy conditions causing fish shoals to disperse and the daily vertical migrations of prey to be disrupted (Finney et al., 1999). Additionally, guillemots have relatively long wings and lighter body masses than penguins, which leads to increased drag, differences in buoyancy levels and dive costs being 30% higher than they would be in a similar-sized penguin (Elliott et al., 2013). These peaks in guillemot dive activity were therefore associated with a small increase in energetic costs (Fig. 4.4 B) and DEE (Elliott et al., 2014).

Had we observed an overlap in the timings of peak dive effort and peak nocturnal diving, this would have indicated that guillemots were under constraints and had to feed at night. Instead, there was a mismatch in the timings of two peaks in dive activity and a peak in nocturnal diving, which was highest during January – March (Fig. 4.5 B). This mismatch therefore suggests that guillemot foraging was not constrained by shorter days, and instead nocturnal diving may have been an active choice. Guillemots may have been influenced by moonlight availability whereby birds diversified from foraging largely on lesser sandeels (*Ammodytes marinus*) during the breeding season, to consuming nocturnally-available prey resources, such as bottom-dwelling and mid-water fish species, during the winter (Blake et al., 1985; Lorentsen and Anker-Nilssen, 1999). By adopting a seasonally optimal foraging strategy that tracks the availability of prey resources, guillemots may benefit from increased self-provisioning opportunities and the maintenance of high body condition throughout the non-breeding period (Hedd et al., 2010).

Despite our values of DEE being based on a number of assumptions (Burke and Montevecchi, 2018), we are confident in the patterns of guillemot behaviour and energetic expenditure that we have identified for this annual cycle. Although the pattern of DEE is different to those that have been recorded in guillemot populations breeding in Newfoundland, Canada (Burke and Montevecchi, 2018) and Svalbard, Norway (Fort et al., 2013b), our estimates are within the ranges reported within these studies. For each of these high latitude guillemot populations, the winter (January – February) was an energetically challenging period. Whilst we also found a gradual increase in energy expenditure throughout the late winter, we suggest that Isle of May guillemots adapted their behaviour in order to balance their energy budgets and maintain a reasonable level of DEE throughout the year, which also allowed them to return to the colony during the pre-breeding period. Indeed, our study provides estimates of guillemot DEE for a full year for the first time, hence enabling us to investigate the strategies used by birds that survived the entire annual cycle during a winter when the return rate of adult guillemots and their subsequent breeding success was extremely low (Newell et al., 2013). Furthermore, we describe a previously unidentified non-breeding season peak in DEE during the pre-breeding period, driven by low values of SST, central-place foraging constraints and high associated costs. We hypothesise that despite this pre-breeding peak in DEE and high values throughout the breeding period, surviving guillemots displayed adaptive measures to manage their energy budgets, under localised temperate conditions, and keep them below an energetically sustainable threshold. We therefore provide evidence to support the hypotheses that guillemots exhibit behavioural plasticity, identifying nocturnal foraging, non-breeding colony attendance and modulated flying and diving effort as responses to seasonally varying environmental conditions. By using guillemots as a model through which to investigate year-round responses to seasonal environmental

conditions, we emphasise the importance of understanding the interplay between energetic constraints and behavioural strategies and their links to survival and population dynamics.

Chapter 5: Modelling and mapping the mortality risk and energetic reward of a wild, mobile animal over its full annual cycle



Modelling and mapping the mortality risk and energetic reward of a wild, mobile animal over its full annual cycle

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Author contributions:

SW, MPH, MAN, MIB and FD contributed to the planning, collecting and management of the data. RED and JM analysed the data and RED led the writing of the manuscript under the supervision of JAG, JM and SW.

All authors contributed critically to the improvement of this chapter and gave permission for it to appear within this thesis.

Abstract

Investigating how individual animals balance their energy budgets and survive full annual cycles is important for understanding the viability of populations through environmental bottlenecks. However, due to the challenges associated with investigating the year-round movement, activity and energy expenditure of highly mobile animals in the wild, understanding how individuals manage their energy balances and avoid mortality throughout the year remains poorly understood. To improve our understanding of how energy budgets and mortality risk vary in time and space, we developed a hierarchical Bayesian state-space model for individual foragers. The model used estimates of activity budgets, locations and energy expenditure from biologging data to infer complete time series of animal body mass and energy gain throughout an annual cycle. Our study system was a population of common guillemots Uria aalge, breeding at a colony in the western North Sea. These seabirds manage their energy budgets by adjusting their behaviour and accumulating fat reserves, and yet are also periodically involved in 'wrecks' or large-scale mortality events, in which the proximate cause of death is starvation. Our estimates indicated that guillemot body mass varied throughout the annual cycle and that the majority of birds periodically experienced marked decreases in body mass to a threshold where mortality risk was high (critical mass declines). We were able to identify biologically interpretable locations of critical mass declines within the North Sea that varied in space throughout the year. Guillemot energy gain varied in both time and space and our model was able to account for scheduling of life history events and seasonality in extrinsic drivers such as sea surface temperature and daylength, whilst also allowing us to identify times and locations of high energy gain. By combining biologging data and Bayesian state-space modelling, we demonstrate a technique that can be used to identify times and areas of both high energetic reward as well as high mortality risk. This approach can be used to

address pure and applied scientific questions regarding the ecology, management and conservation of populations of wild, highly mobile animals that have previously been impossible to answer.

Introduction

Energy is a vital requirement in supporting an individual's basic functioning and daily activities and animals need to maintain a surplus in their annual energetic budget in order to survive and reproduce. Consequently, the distribution of energetic resources, as well as disruptions to acquiring them, are key drivers of biodiversity across both time and space (Bonn et al., 2004). Organisms that inhabit seasonal environments experience pronounced variation in climatic conditions, food availability, energetic demands and risk (Varpe, 2017). Additionally, overlaid on these seasonal variations in risk and reward, organisms must successfully allocate their annual energetic budgets in order to meet the demands of different life history priorities such as growth, maintenance and reproduction (Kozłowski and Wiegert, 1986). Finally, risks and their magnitudes may also vary in space and time due to variability in predator abundances, thermoregulatory costs, parasitism, extreme climatic events and other threats to survival (Gaynor et al., 2019). Yet despite its fundamental importance, few studies have investigated where and when wild animals extract energetic resources and experience risk throughout their annual cycles (Swift et al., 2020) as year-round data in particular have been lacking (Marra et al., 2015).

Advances in biologging technology have increasingly enhanced our ability to record locational and activity data for individuals over full annual cycles (Bograd et al., 2010). Biologging studies have been especially useful in marine systems, providing novel insights into the previously-obscure vertical and horizontal movements of animals across all ocean basins (Hussey et al., 2015). For example, leatherback turtles Dermochelys coriacea undertake trans-oceanic migrations to access zooplankton aggregations (Roe et al., 2014), narwhals Monodon monoceros move to safer habitats to avoid predation by orca Orcinus orca (Breed et al., 2017) and bowhead whales Balaena mysticetus dive to access prey at shallower depths during the spring and

summer than during the autumn and winter (Fortune et al., 2020). However, despite such advances we still know little about how the energy budgets and threats to survival of both marine and terrestrial organisms might vary in time and space throughout the annual cycle (Green et al., 2009; Swift et al., 2020). The current phenomenon of global environmental change has the potential to not only impact average temperatures at particular latitudes, but also to alter seasonal environmental patterns (Ernakovich et al., 2014). These changes may in turn lead to seasonal shifts in species distributions (Perry et al., 2005) and altered trophic interactions (Lauria et al., 2012), with consequences for individual survival and the viability of populations (Jenouvrier et al., 2009). Therefore, investigating animal energetics, potential environmental bottlenecks, and mortality risk across the full annual cycle is a key research priority (Lewison et al., 2012; Tomlinson et al., 2014).

Our understanding of the energetics of wild animals is limited primarily to measures of individual energy expenditure; recent analyses of year-round energetic balances focussing solely on energy expenditure as opposed to energy gain (Dunn et al., 2020; Pelletier et al., 2020). However, to fully understand both temporal and spatial variation in how animals either manage their energy budgets or face potential bottlenecks, it is also important to understand how they gain and store energy (Nwaogu and Cresswell, 2016). Measuring energy gain in wild animals, even over short timescales, can be challenging and there have been few previous attempts to empirically estimate and map energy consumption across annual cycles (although see Green et al., 2009; White et al., 2014). Now, however, analytical developments (such as hierarchical Bayesian state-space models) allow the reconstruction of hidden time series of ecological and physiological variables that are otherwise difficult to directly and continuously measure throughout animal annual cycles (Patterson et al., 2008; Russell et al., 2013). Here, for the first time, we use these models to reconstruct year-round variation in the energy

gain, body mass and consequent threats to survival of a wild, mobile population of animals.

We developed our approach using the common guillemot Uria aalge (hereafter 'guillemot'), a highly abundant, medium-sized (c1 kg), diving seabird that breeds once per year at colonies around the coast of the North Atlantic and Pacific oceans (Gaston and Jones, 1998). We studied guillemots from a major breeding colony on the Isle of May, Scotland. After the breeding season, Isle of May guillemots typically migrate into the North Sea and English Channel (Dunn et al., 2020), although one individual has been recorded making an extreme migratory journey to the Barents Sea (3,000 km from the breeding colony; Harris et al., 2015). Annual survival in this population is typically high (c90%; Reynolds et al., 2011) and individuals that survive the annual cycle do so by adjusting their migratory behaviour, making periodic returns to the colony and by managing their time-activity and energy budgets in the face of potential constraints such as reduced sea surface temperature and day length during winter (Dunn et al., 2020). Throughout their annual cycles, guillemots exhibit seasonal variations in body mass; healthy birds lose mass over the breeding season and accumulate fat reserves during the winter (Harris et al., 2000). Despite this, guillemots are periodically involved in large-scale mortality events or 'wrecks' that usually occur in the winter, during severe weather (Harris and Wanless, 1996). Birds dying in such wrecks are usually emaciated, indicating that they had been unable to feed for a long period and had progressively lost weight (Debacker et al., 2000).

Here, we used biologging data to estimate year-round daily time-activity budgets, locations and energy expenditure values of guillemot individuals. Next, we reconstructed time series of energy gain and body mass to investigate how energy budgets and mortality risk might vary in time and space during the course of an annual

cycle. We then developed a state-space model to reconstruct hidden time series of energy gain and body mass throughout the annual cycle and used this to address three key questions: 1) Where and when was the Isle of May population of guillemots exposed to increased mortality risk? 2) Where and when does variation in guillemot energy gain occur throughout the annual cycle? 3) How do relevant extrinsic drivers such as sea surface temperature, number of daylight hours, longitude, latitude and distance from the coast influence year-round energetic gain? By creating this model and addressing these questions we sought to develop an approach that can be used to identify times and areas of both high energetic reward as well as high risk in wild, mobile animals.

Materials and Methods

To address our aims, we created a hierarchical Bayesian state-space model that allowed us to supplement our biologger-derived estimates of location, activity and energy expenditure with prior information from other studies. The model reconstructed the hidden time series of adult guillemot energetic gain and body mass simultaneously at daily time units. Below, we provide an overview of the data used and describe the structure of the state-space model. All data processing and analyses were performed using R version 4.0.2 (R Core Team, 2020) and JAGS (Plummer, 2003).

Study site, biologging and extrinsic data

Fieldwork took place on the Isle of May National Nature Reserve, Scotland (56° 11'N, 02°33'W; Supplementary material A5.1). In June 2016, 30 adult guillemots that were brooding young chicks were captured at their breeding sites using a noose pole. Global location sensing loggers (GLS; Mk3006 from Biotrack, UK) were attached to the birds using Darvic leg-rings (combined mass 3.5 g, or <0.4% of the mass of the adults on which they were deployed). During the subsequent breeding seasons, birds were recaptured using the same method and the loggers removed (80% retrieval rate; n_{2017} = 21; n_{2018} = 3). We therefore only obtained data from birds that survived the annual cycle. Nearly all individuals were weighed (to the nearest g) when loggers were deployed and retrieved ($n_{deployment}$ = 29; $n_{retrieval}$ = 24) and the handling process took < 5 minutes each time.

Daily energy expenditure in guillemots varies throughout the annual cycle based on daylight hours experienced and sea surface temperature (Dunn et al., 2020). Additionally, different migratory strategies and wintering areas can vary in their associated energetic costs (Pelletier et al., 2020). We therefore extracted sea surface temperature, number of daylight hours, daily location and distance to the closest point

on the coastline for the 17 loggers (71%) that recorded data for the entire annual cycle using previously described approaches for this species and study site (Supplementary material A5.2). Daily activity budgets and energy expenditure (E) were also estimated from saltwater immersion data, using approaches developed for this species and study site (Supplementary material A5.3).

Bayesian state-space modelling

A Bayesian state-space model was developed to estimate the unobserved (latent) time series of adult guillemot daily energy gain and body mass. We were ultimately interested in estimating $M_{i,t}$ and $G_{i,t}$, the mass M and daily energy gain G of individual i at day t, where t ranges from 1 – 364 and corresponds to a time series from 26th June 2016 to 24th June 2017.

An individual's mass on a given day $M_{i,t+1}$ was defined as follows:

$$M_{i,t+1} \sim N\left(\mu_{i,t+1}, \tau_{i,t+1}\right) \qquad \text{eqn 5.1}$$

Here, the precision implied by τ is the physiological variation around the expectation μ which we assumed to be ±1% of body mass, as there is no evidence to suggest that individuals would adjust conversion rates between food, energy and body mass at a daily timescale (Halsey, 2018); the prior distribution is defined in Table 5.1. An individual's mass on a given day was equivalent to its mass the previous day plus a change in mass and therefore the expectation μ was dependent on whether there was an energy surplus or deficit during the previous day and was therefore formulated as follows:

$$\mu_{i,t+1} = M_{i,t} + V\left(G_{i,t} - E_{i,t}\right) \qquad \text{eqn 5.2}$$

We assumed that excess lipids were transferred to body reserves whilst excess protein was excreted or used in other metabolic pathways (Green et al., 2007). In the closely related Brünnich's guillemot *Uria lomvia*, lipids accounted for 35.25% of mass lost

across a breeding season (Elliott et al., 2008). The energetic density of lipid is 39.3 kJ g^{-1}. Assuming that when birds are in deficit they use fat stores as the primary source of metabolic energy, then this would equate to a mass change value (V) of 0.072 g lost per kJ. We also assumed that birds experiencing an energetic surplus put excess lipid into their fat stores and therefore gained mass at the same rate. The prior distribution for V is defined in Table 5.1. We generated $G_{i,t}$ from a gamma distribution, suitable for a continuous, non-negative variable that offers parametric control over dispersion, such that:

$$G_{i,t} \sim gamma(r_{i,t}, \lambda_{i,t}) \qquad \text{eqn 5.3}$$

Both shape r and rate λ were calculated from values of mean $\bar{U}$ and precision φ, where φ was the unexplained environmental stochasticity around $\bar{U}$; the prior distribution of φ is defined in Table 5.1. In its most parameterised form, $\bar{U}_{i,t}$, a linear function of extrinsic covariates that describe daily energy gain, was formulated as follows:

$$\bar{U}_{i,t} = D exp(r_0 + r_1 T_{t,i} + r_2 L_{t,i} + r_3 X_{t,i} + r_4 Y_{t,i} + r_5 C_{t,i}) \qquad \text{eqn 5.4}$$

Here, parameter r_0 corresponds to the intercept of the energy gain per hour which was then scaled up by the hours per day spent foraging D. We estimated a prior distribution of r_0 by summing the number of prey items caught per minute foraging (0.8 ± 0.4 items; Thaxter et al., 2013), the energetic density of prey items (5.8 ± 6.6 kJ; Wanless et al., 2005), the amount of time per hour foraging that was spent actively engaged in prey capture (40 minutes when accounting for inter-dive intervals) and the nitrogen-corrected metabolisable energy coefficient of lesser sandeels *Ammodytes marinus* (77.52 ± 1.60%; Hilton et al., 2000). Guillemots feed at a consistently high trophic level throughout the annual cycle (St. John Glew et al., 2018), justifying our assumption that they consumed a high quality diet throughout the year and our subsequent use of these breeding season prey values. Additionally, r_1, r_2 , r_3, r_4 and r_5 correspond to the slopes

on the linear scale of the response of energy gain to sea surface temperature T, number of daylight hours L, longitude X, latitude Y and distance to coastline C respectively. The priors of all coefficients (Table 5.1) were centred at 0, expressing the null hypothesis of no effect.

The model outlined in equation 5.1 is effectively a random walk through the state-space of mass. This means that although changes in mass are constrained by the biological priors on an incremental basis, the overall mass is in principle unconstrained. However, we know that there are biological constraints on both minimum and maximum mass that we also wanted to impose as additional prior information to help the model with the fitting process. We therefore wanted to penalise the likelihood when the overall mass of the animal went above or below a certain maximum and minimum mass respectively. Attempting this in conjunction with equation 5.1 did not work during model fitting, due to needing a smooth central tendency, rather than a truncation. We therefore introduced an additional constraint to $M_{i,t}$:

$$M_{i,t} \sim N(\mu_p, \tau_p) \qquad \text{eqn 5.5}$$

Here, μ_p was the midpoint between the heaviest guillemot mass recorded M_{max} (1450 g; Harris, Wanless and Webb, 2000) and the lightest sustainable body mass M_{min} (600 g; Grogan et al., 2014) and τ_p was defined as follows:

$$\tau_p = \frac{1}{{\sigma_p}^2}, \text{where } \sigma_p = \frac{(M_{max} - M_{min})}{4}$$

Table 5.1. Prior distributions for the parameters used to model guillemot mass and daily energy gain throughout the annual cycle. Gamma distributions are expressed in terms of shape and rate and normal distributions are expressed in terms of mean and precision.

Output	Variable	Parameter	Prior
Mass	Precision	τ	$\sim gamma(2.35, 51.11)$
	Mass change value	V	$\sim gamma(20793.64, 288400)$
Energy gain	Environmental stochasticity	φ	$\sim N(500, 0.0001)$
	Intercept	r_0	$\sim gamma(4.65, 0.94)$
	Sea surface temperature	r_1	$\sim N(0, 0.01)$
	Daylight length	r_2	$\sim N(0, 0.01)$
	Latitude	r_3	$\sim N(0, 0.01)$
	Longitude	r_4	$\sim N(0, 0.01)$
	Distance to coastline	r_5	$\sim N(0, 0.01)$

All models were fitted using JAGS (Plummer, 2003) using the *runjags* interface in R (Denwood, 2016). Whilst we estimated daily time series of adult daily energy gain G and body mass M, we extracted values of these parameters at weekly intervals. We ran our models with a burn-in of 20,000 and for 30,000 iterations to achieve convergence. The JAGS code is presented in Supplementary material A5.4.

To investigate the effect of the extrinsic variables (sea surface temperature, daylight hours, longitude, latitude and distance to coastline) on year-round energetic gain, we used the Deviance Information Criterion (Burnham and Anderson, 2002) to perform model selection (via backward elimination) on models containing variations of the linear predictor $\bar{U}_{i,t}$ (equation 5.4; see Supplementary material Table A5.5). Convergence was evaluated via visual inspection of the chains. We used our selected model to reconstruct time series of $M_{i,t}$ and $G_{i,t}$. We identified times and locations where the birds experienced high susceptibility to mortality, hereafter 'critical mass declines', as periods in the $M_{i,t}$ time series where the lower 95% Bayesian credible

interval (CRI) fell below 800 g, the lowest mass recorded during breeding season weighing. We also mapped energy gain using the $G_{i,t}$ time series and R packages *sp, raster* and *plotKML*.

Results

Our model reconstructed hidden time series of body mass and energy gain of 17 adult guillemots throughout the 2016/17 annual cycle. We found that estimates of guillemot body mass indicated substantial individual variation in year-round body mass trajectories (Fig. 5.1A). All 17 individuals experienced at least one critical mass decline, and many individuals experienced multiple critical mass declines (max = 7; Fig. 5.1A). These periods occurred throughout the year but in 2016/17 were most frequent in July, September and March (Fig. 5.1B). Critical mass declines were in short duration, typically lasting about a week (Fig. 5.1A). The largest critical mass decline recorded was 215 g over the seven day period preceding 20th July 2016.

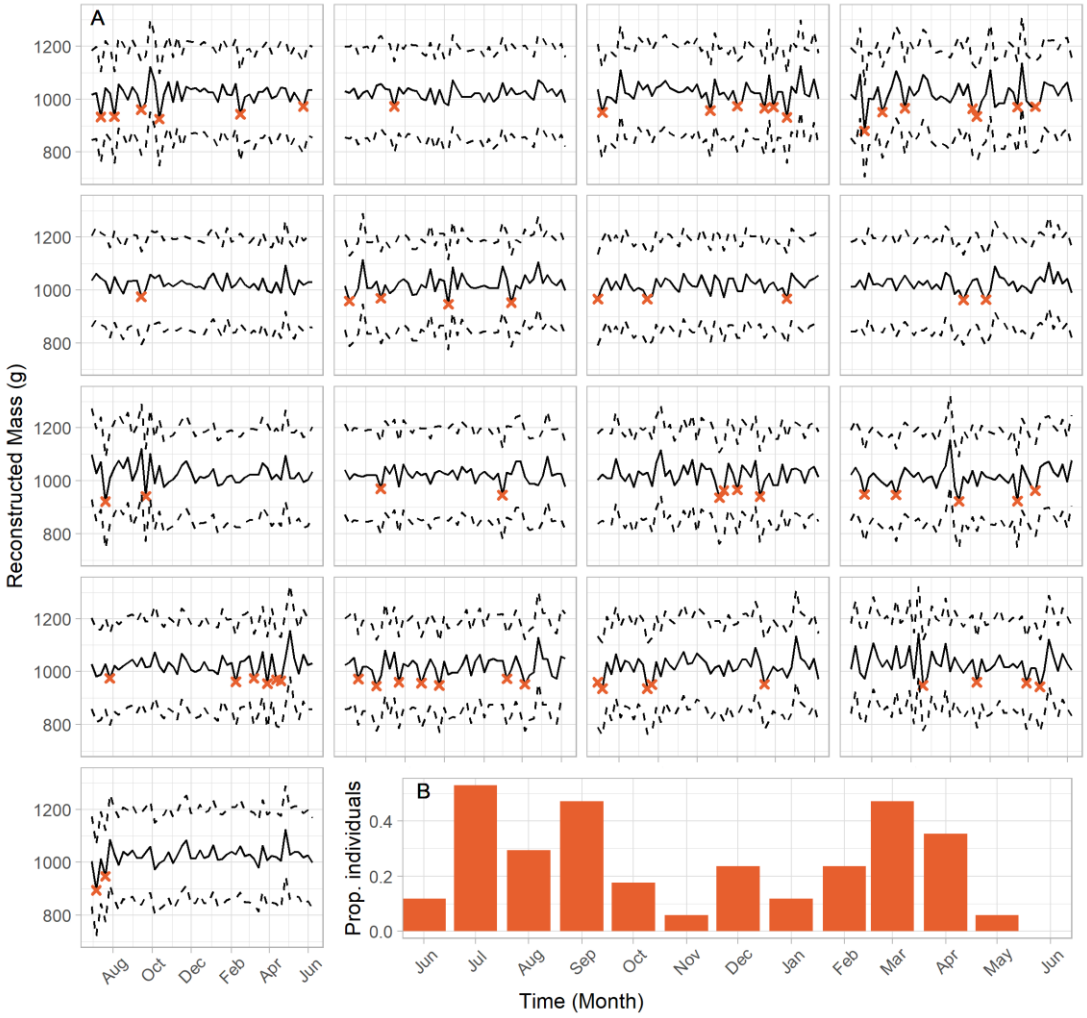


Figure 5.1. A: Reconstructed fluctuations in the body mass of 17 common guillemots from the Isle of May at weekly intervals across the 2016-17 annual cycle. The solid lines show the posterior median daily body mass and the dashed lines show its associated uncertainty (95% Bayesian credible intervals). Critical mass declines are indicated with an orange cross. B: The proportion of individuals that experienced critical mass declines each month, across the annual cycle.

Over the annual cycle, guillemots from the Isle of May were distributed widely in the North Sea and critical mass declines occurred across the full range of this spatial distribution (Fig. 5.2). Throughout the annual cycle, birds were at high risk of mortality whilst in the northwestern North Sea, including the waters around the Orkney and Shetland archipelagos to the north east of the UK mainland (Fig. 5.2 A-D). The critical mass decline areas were not fixed in space throughout the annual cycle however, and included areas between the North and Baltic Seas to the east, and the central and eastern North Sea during the autumn and winter (Fig. 5.2 A-C).

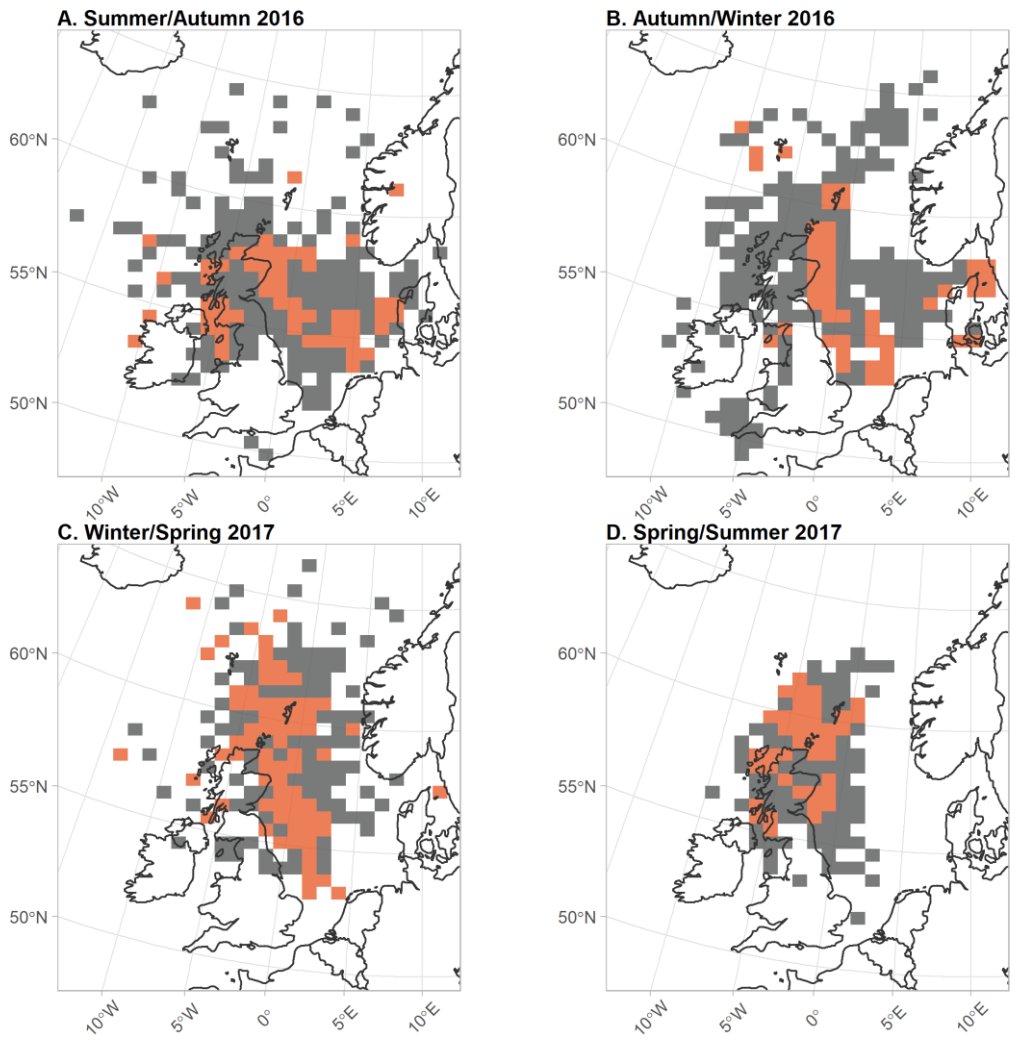


Figure 5.2. Where did common guillemots encounter high risk of mortality? Distribution of locations (100 km resolution) where birds were located (shown in grey) and where they were estimated to experience critical mass declines in A. 01/07/2016 – 30/09/2016, B. 1/10/2016 – 31/12/2016, C. 01/01/2017 – 31/03/2017 and D. 01/04/2017 – 07/06/2017.

Estimates of guillemot energy gain varied temporally over the course of the annual cycle, these patterns varying among individuals (Fig. 5.3A). Daily energy gain estimates ranged from 743 kJ for one individual on 31st May 2017 to 3605 kJ by another individual on 27th July 2016. Despite high inter-individual variability, estimated mean daily energy gain per week at the population level remained fairly stable across the course of the annual cycle. This being said, values were lower during May and June, when guillemots incubate their eggs and rear their chicks, and were higher during July and August, immediately following the breeding season (Fig. 5.3B).

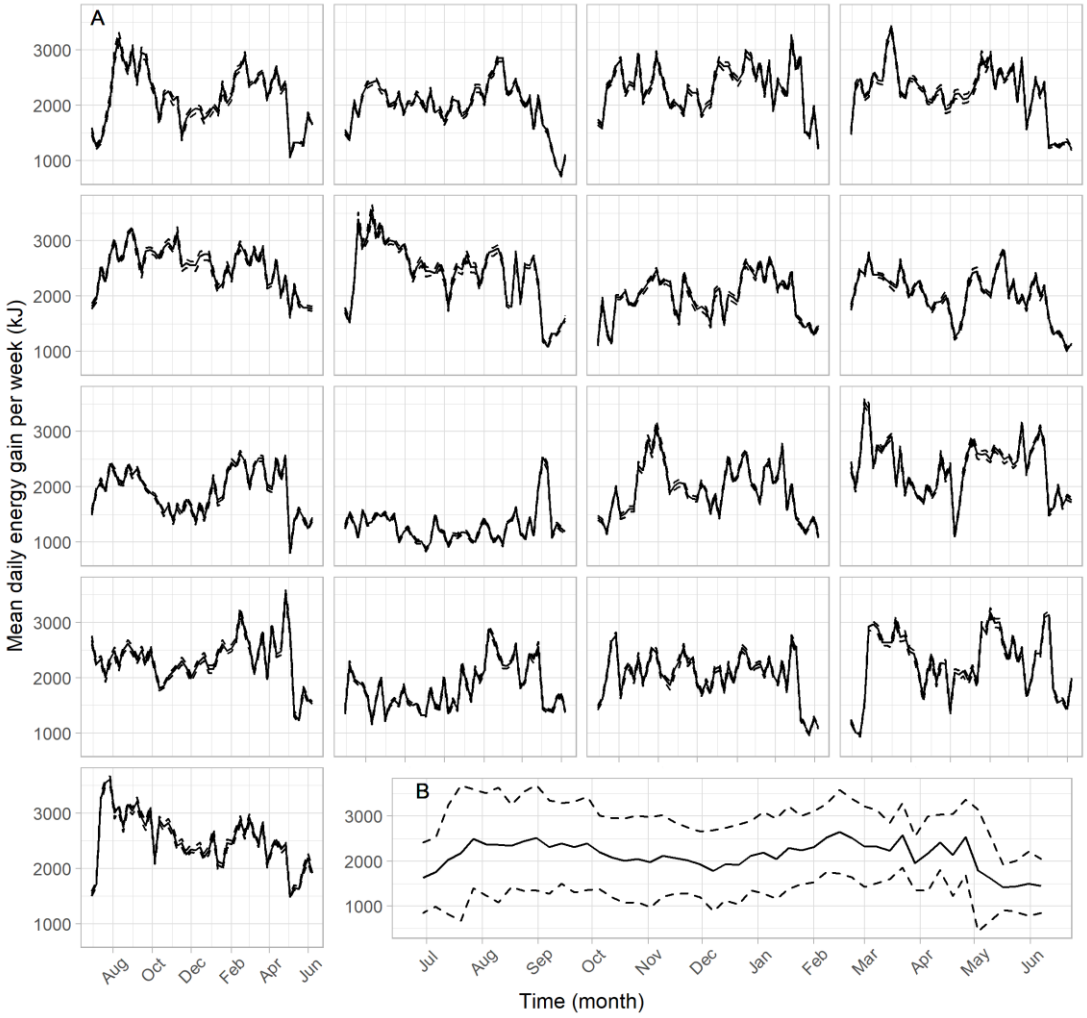


Figure 5.3. A: Reconstructed fluctuations in the daily energy gain per week of 17 common guillemots from the Isle of May throughout the 2016-17 annual cycle. The solid lines show the posterior median daily energy gain and the dashed lines show its associated uncertainty (95% Bayesian credible intervals). B: The population mean daily energy gain per week with the standard deviation indicated with dashed lines.

In addition to varying temporally, energy gain by guillemots also varied spatially (Fig. 5.4). Although guillemots gained energy from a large area that extended across the North Sea, areas of high energy gain were also evident (Fig. 5.4). These high energy gain areas were predominantly located in the north-western North Sea, close to the coasts of eastern Scotland and north-east England (Fig. 5.4). Seasonal changes in the spatial distribution of total energy gain were largely driven by changes in the time that birds spent foraging within the different areas (Supplementary material Fig. A5.6).

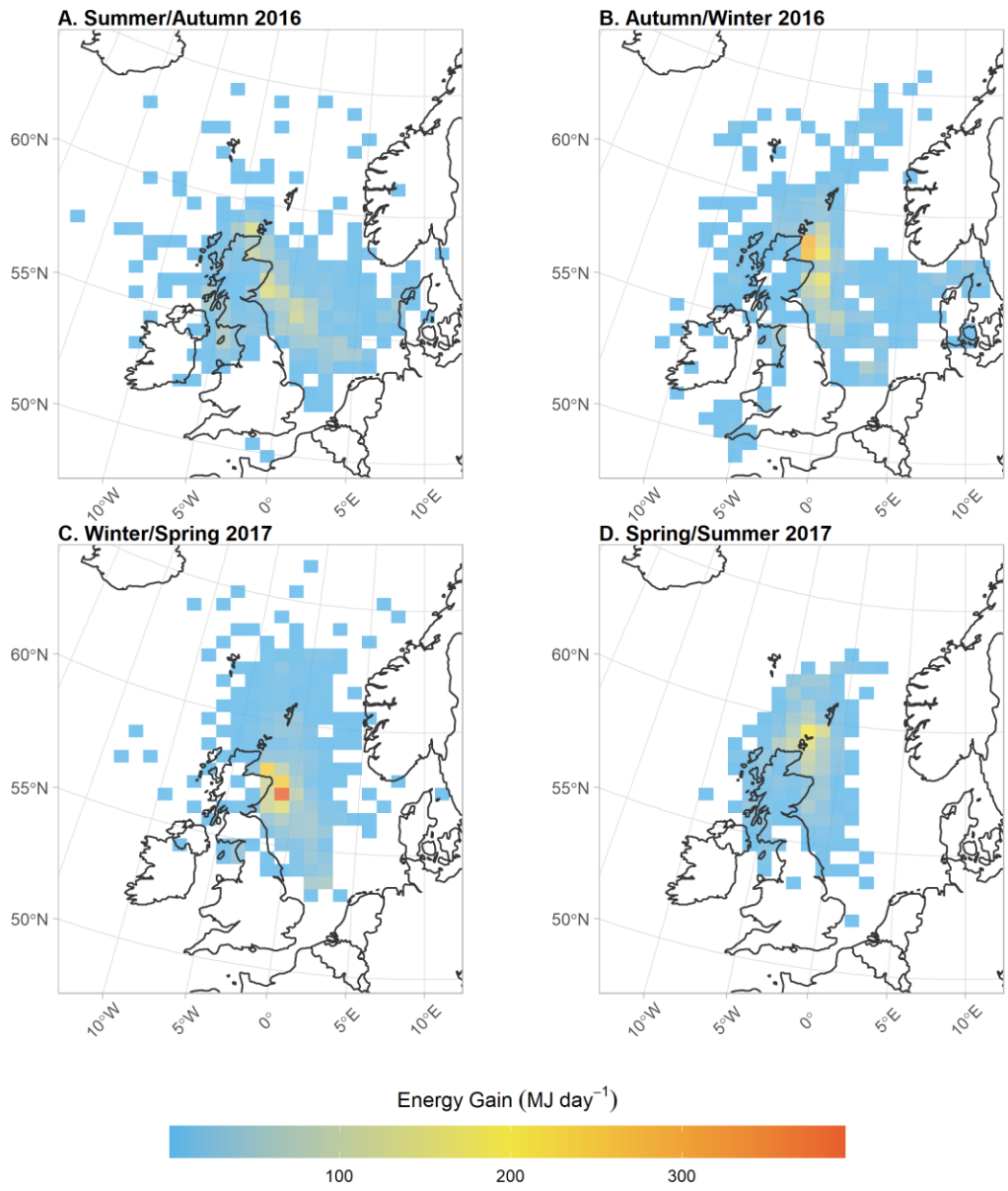


Figure 5.4. Where did common guillemots gain energy? Spatial distribution (100 km resolution) of estimates of total energy gained from the environment (MJ day^{-1}) by 17 guillemots in A. 01/07/2016 – 30/09/2016, B. 1/10/2016 – 31/12/2016, C. 01/01/2017 – 31/03/2017 and D. 01/04/2017 – 07/06/2017.

Of the five covariates investigated within our models, model selection indicated that sea surface temperature, the number of daylight hours and distance from the coast had an effect on energy gain, whereas longitude and latitude did not (Supplementary material Table A5.5). The Bayesian credible intervals (CRIs) of the posterior distributions of sea surface temperature and day length suggested that there was a small but consistent positive effect of these covariates on guillemot energetic gain, whereas

distance from the coast had a consistent negative effect. For example, for an increase of 1°C in sea surface temperature, energy acquisition per hour spent foraging increased by 3% from 171 kJ (CRI = 168-173 kJ) to 176 kJ (CRI = 163-178 kJ). Similarly, energetic gain was expected to increase by 12 kJ (CRI = 10-15 kJ) per hour foraging for each additional hour of daylight. In contrast, being 1 km further from the coastline would produce a decrease of 7 kJ (CRI = 5-9 kJ) per hour foraging. Thus, guillemots tended to gain more energy in relatively warmer waters, on longer days and whilst closer to the coast.

Discussion

We set out to understand where and when a mobile, wild animal experienced mortality risk and energetic rewards over a full annual cycle. Whilst directly collecting data on the year-round energetics and mortality risk of such animals is challenging, here we illustrate the potential to use routinely collected biologging data to initially estimate energy expenditure and subsequently use these data to reconstruct hidden time series of body mass and energy gain over a full annual cycle. We created these reconstructions using a hierarchical Bayesian state-space model, thereby incorporating several items of expert knowledge in the form of Bayesian priors, whilst also increasing the inferential strength of the model by allowing it to be fitted to multiple individuals simultaneously. This approach allowed us to quantify how energetic gain and body mass varied over time and space, and in the case of guillemots, enabled us to highlight times and locations of both unfavourable (critical mass declines associated with increased mortality risk) and favourable (high energy gain) conditions. The identification of key areas, both those of high importance as well as those of high risk, is a fundamental prerequisite for understanding year-round ecophysiology, as well as for informing conservation and management. We have therefore proposed a method that can be used to address both pure and applied scientific questions.

For many species, we currently know very little about where, when and how individuals experience mortality over the annual cycle. In our case study of guillemots, results from the model indicated that all surviving individuals experienced at least one, and in many cases, multiple, critical mass declines during the year (Fig. 5.1). In many cases, the locations where critical mass declines occurred overlapped with high energy gain areas (50% of critical mass decline areas overlapped with top quartile energy gain areas), while in other cases they were distributed more widely across the North Sea as well as near the Baltic Sea (Fig. 5.2). Approximately half of the birds experienced critical mass

declines in at the end of the breeding season, when body mass and fat reserves are known to be at a minimum (Harris et al., 2000). Critical mass declines were also common during August and September when guillemots undergo a costly primary feather moult (Guillemette et al., 2007). They were again frequent in March, when Isle of May guillemots spend an increasing amount of time at the colony, necessitating costly commuting flights between the foraging grounds and the breeding site and therefore high levels of energy expenditure (Dunn et al., 2020). Ultimately, both the periods and places that we highlight as being potentially risky for guillemots are supported either by ringing recovery data within this region (Wernham et al., 2002) or by prior knowledge regarding the Isle of May guillemot system. This gives us confidence that this approach successfully identifies realistic times and locations where wild animals might experience increased risk of mortality, without the need for year-round observations (Lohr et al., 2011; Mann and Watson-Capps, 2005).

Understanding when and where wild animals die is particularly timely due to global environmental change and the detrimental impacts that this can have on individual survival and population demography (Jenouvrier et al., 2005). Animals are also exposed to numerous additional risks across their annual cycles including mortality from hunting and poaching (Frair et al., 2007), potential disruption from roads and shipping lanes (Lamb et al., 2017; Mendel et al., 2019), terrestrial and marine windfarm developments (Carrete et al., 2012; Dierschke et al., 2016) and competition from fisheries (Karpouzi et al., 2007). In seabirds, large-scale mortality events outside the breeding season are often associated with severe and prolonged storms which prevent birds from feeding, leading to a negative energy balance, loss of body mass and, ultimately, death (Harris and Wanless, 1996). The critical mass declines that we estimated were typically relatively short in duration and may have been associated with reduced foraging efficiency in response to stormy conditions (Finney et al., 1999),

irrespective of the potential for energetic gain that an area might have offered. The adult survival rate estimated for the Isle of May population for 2016-17 (0.87 ± 0.21 standard deviation) was lower than that during the preceding 5-year period (0.93 ± 0.07 standard deviation; C. Horswill pers. comm.) suggesting that conditions were unfavourable. Although by definition all the birds in our study survived the annual cycle, it is plausible that in individuals which did not survive, mass loss occurred over longer durations, impairing body function and ultimately resulting in death. Understanding how wild animals, such as guillemots, cope with potential environmental bottlenecks is critical, particularly when storms are predicted to become increasingly severe and frequent under global climate change scenarios (Rahmstorf and Coumou, 2011). Identifying times and location of vulnerability for these high trophic level consumers is important with regards to informing subsequent conservation and management decisions, particularly due to the cascading influence that top predators can exert on marine systems (Estes et al., 2011; Hazen et al., 2019). Furthermore, seabirds are not unique in their exposure to seasonal climatic threats; South American sea lions *Otaria byronia* also experience mortality events in association with stormy conditions (Sepúlveda et al., 2020), severe winter weather impedes white-tailed deer *Odocoileus virginianus* survival (Kautz et al., 2020), and thermal stress and starvation lead to high levels of temperate fish mortality during winter (Hurst, 2007). By expanding our approach, it might therefore become possible to model inter-annual variability in the timing and duration of critical mass declines of species from other trophic levels and taxonomic groups, thereby allowing the formation of mechanistic links between extrinsic covariates and inter-annual variability in animal survival.

In addition to demonstrating the ability to identify times and locations of vulnerability to mortality, we have also illustrated that we can identify individual and seasonal variability in the energetic budgets of wild animals, including otherwise hidden states

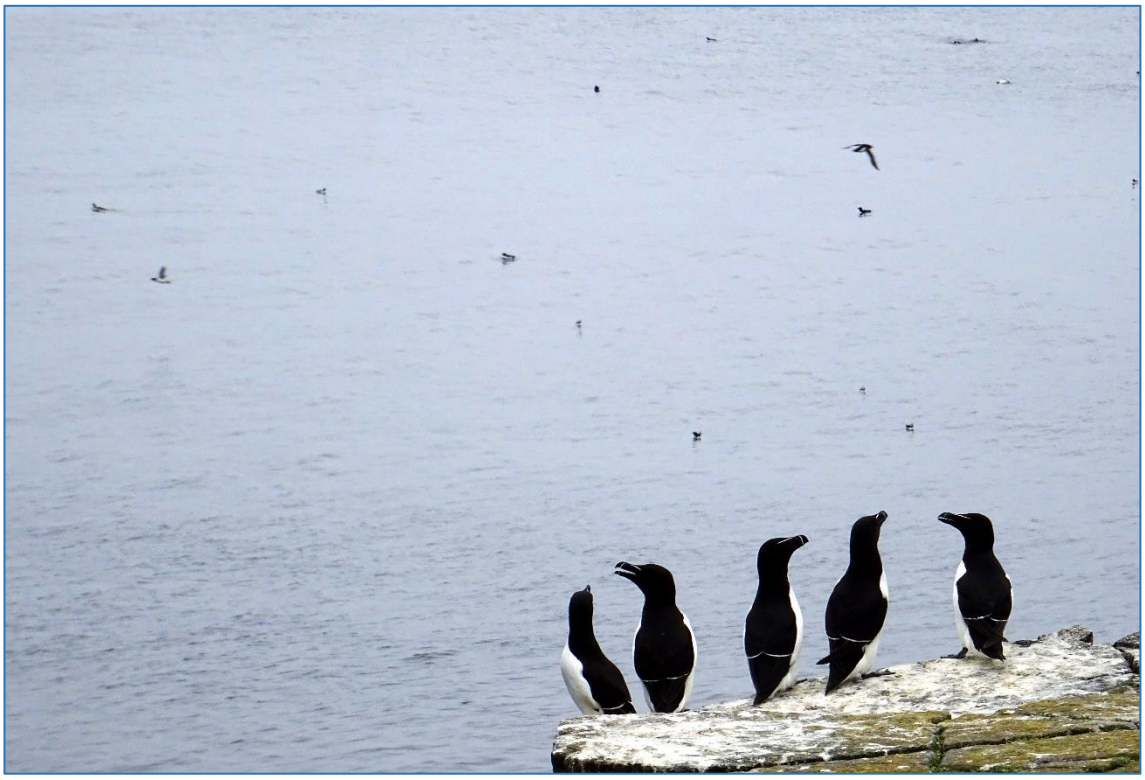
such as energy gain. Our model was able to account for seasonal differences in life-history priorities as well as ecological variation, such as temperature-related changes in thermoregulatory costs and the impacts of sea surface temperature and daylight hours on the ecology of lower trophic levels, which are ultimately likely to have driven year-round temporal variation in guillemot energetic gain (Fig. 5.3). Additionally, our model was sensitive enough to detect biologically interpretable areas of high energy gain. For example, high energy gain areas off the coast of eastern Scotland and north-east of England (Fig. 5.4) overlapped with the Northeast UK sandeel fishery closure area (Daunt et al., 2008), emphasising the year-round importance of this area for this population of guillemots. Investigating the spatial distribution of food consumption of seabirds, and other marine top predators, throughout their annual cycles is important with regards to the conservation and management of marine resources worldwide (Brooke, 2004; Sherley et al, 2020). By applying our methodology to populations of other mobile, wild animals, it will become increasingly possible to generate temporally-specific energy gain surfaces at a regional level. Producing energy gain surfaces (like those in Fig. 5.4) not only has benefits with regards to the management of both terrestrial and marine resources (Cury et al., 2011; Wood et al., 2019), but also has ecological significance due to the dynamic inter- and intra-specific competition pressures that occur as species and populations mix throughout their annual cycles (Block et al., 2011; Frederiksen et al., 2012; González-Solís et al., 2007).

Conclusions

The annual cycles of many highly mobile animals are difficult to observe and so our knowledge of year-round threats to their survival and their energy budgets remain limited, despite their importance for population demography, especially in the face of global environmental change. By using biologging data within a hierarchical Bayesian state-space model we were able to estimate energy budgets, mass changes and

consequent susceptibility to mortality throughout a full annual cycle, using guillemots as a model system. Gaining insights into year-round animal energy budgets allows a far more detailed understanding of when and where individuals, and therefore populations, might both exert and come under pressure. The use of biologging data within energetics-based state-space models offers major opportunities to provide novel insights into the energy balances and mortality risk of other wild, mobile animals.

Chapter 6: General discussion



Key findings

Understanding how animals time, optimise and survive the critical events of their annual cycles is increasingly viewed as a fundamental goal for ecologists (Marra et al., 2015). Animal reproduction, year-round behaviour, energetics and ultimately survival are driven by seasonally-varying combinations of intrinsic and extrinsic drivers. Gaining insights into how these different drivers, particularly those relating to the environment, influence animal behaviour and energetics is especially timely in the face of large-scale environmental change; such insights are integral to our understanding of how species will respond to threats (Culp et al., 2017). Across the globe, between 10 and 50% of well-studied higher taxomonic groups are currently threatened with extinction (Schipper et al., 2008), with nearly half of seabird species experiencing population declines (Croxall et al., 2012). Therefore addressing the influences of environmental change on seabirds is particularly vital, due to their vulnerability to such threats and the consequent substantial declines that many populations have exhibited worldwide (Dias et al., 2019; Lewison et al., 2012). Due to their highly mobile nature, it has previously been challenging to gain insights into aspects of seabird ecology that might occur far from land, in some of the most remote parts of the globe. Instead, until recently, our knowledge of seabird ecology and conservation has been biased towards the breeding season. By studying seabirds throughout the annual cycle we can therefore now attempt to discover novel, mechanistic links between seabird behaviour, energetics and environmental conditions.

In this thesis I present results from a range of approaches investigating how the intrinsic and extrinsic drivers of seabird behaviour and energetics vary across multiple temporal scales. In **Chapter 2** I used a global, multi-species approach to identify differences in seabird energetics across the temporal scale of the breeding season. I also created an app through which to generate estimates of energy expenditure for any

population of breeding seabird. This analysis revealed that seabird energy expenditure was positively influenced by the intrinsic driver of body mass, as well as extrinsic factors associated with higher breeding colony latitudes. In **Chapter 3** I used bird-borne loggers, deployed on three species of auk from a major North Sea seabird colony, to identify temporal changes in behaviour across the months following the breeding season until mid-winter. Auks are a major component of North Atlantic seabird communities (Grandgeorge et al., 2008) and have high wing loading as an adaptation for wing-propelled pursuit diving, but as a consequence incur high flight costs (Elliott et al., 2013). The three auk species differed in body mass and post-breeding strategy, and we therefore observed interspecific differences in their behaviour as well as temporal changes, likely driven by seasonal variability in environmental factors such as changes in light levels and prey distributions. Finally, in **Chapters 4 and 5** I used empirical data and statistical modelling to expand my focus to the full annual cycle for one of the auk species: the common guillemot *Uria aalge*. Firstly, in **Chapter 4**, I used generalised additive mixed models (GAMMs) to infer the patterns linking temporal changes in environmental conditions with behaviour and energy expenditure. Values of energy expenditure were highest prior to and during the breeding season, largely driven by an increase in flight activity associated with guillemots having undertaken a return migration from around the North Sea, back to the breeding colony. Secondly, in **Chapter 5**, I used a Bayesian state-space model to investigate year-round fluctuations in guillemot body mass and energy gain. I then mapped the variation of energy gain and body mass in both space and time, identifying times and locations where guillemots suffered increased susceptibility to mortality as well as when and where they gained energy. By using a variety of analytical approaches and techniques to research key periods of the seabird annual cycle, as well as yearly cycles within their entirety,

this thesis has improved our mechanistic understanding of the links between seabird ecophysiology and its intrinsic and extrinsic drivers.

Implications

Whilst our understanding of seabird behaviour and energetics during the breeding season is increasing (for example, Chapter 2 features data from 64 different studies of energetics across 47 species of seabird), the work presented in this thesis illustrates the variability that both intrinsic and extrinsic drivers can exert at different stages of the annual cycle. Indeed, I found that outside the well-studied chick-rearing period of the breeding season, common guillemots, Atlantic puffins and razorbills showed elevated diving effort compared to the breeding season (Chapter 3). Additionally, post-breeding season diving in all three species was shallower than during the preceding breeding season (Chapter 3), with Isle of May guillemots and razorbills also diving more shallowly than those from Kitsissut Avalliit, Southwest Greenland during the post-breeding period (Linnebjerg et al., 2013). Additionally, whilst the breeding season has previously been hypothesised as a time of particular energetic constraint among seabirds (Drent and Daan, 1980), I found that for guillemots, the period immediately prior to the breeding season was also associated with elevated energetic costs (Chapter 4). Finally, using a Bayesian modelling approach I found that rates of guillemot energy expenditure were estimated to be intrinsically linked to changes in their modelled body mass, such that birds might be particularly susceptible to critical mass declines and potentially mortality at particular times and locations throughout their annual cycles (Chapter 5). This thesis therefore provides novel insights that were only made possible firstly through the study of seabird energetics and secondly through behavioural research that extends outside the seabird breeding season.

Despite the innate importance of single-season studies to offer vital insights into specific life-history events, it is increasingly acknowledged that population responses to environmental change should not be inferred from such studies alone (Ådahl et al., 2006). Instead, by investigating full annual cycles, we are increasingly able to consider key aspects of the ecology of migratory species, particularly the links between different periods and the influence of carry-over effects from one season to another (Small-Lorenz et al., 2013). Furthermore, whilst to date non-breeding season seabird research has largely concentrated on identifying migration routes and important foraging areas, there has been less of a focus on behaviour and an even smaller emphasis on energetics. However, new analytical and technological tools, such as Bayesian state-space modelling (Chapter 5) and miniaturised biologging devices (Chapters 3-5), now enable us to track not only the spatial location of migratory animals, but also how they behave and expend energy across the annual cycle. Therefore, by harnessing these methods to research how seabirds respond to year-round spatial and temporal variation within and between environments, we are increasingly able to contribute towards filling important knowledge gaps and research priorities. Indeed, such advances will revolutionise our understanding of fundamental biology as well as how we can better manage and conserve animal populations at a time of great environmental change. I outline potential future directions of research within both of these realms below.

Future directions

Fundamental biology

Whilst throughout this thesis I have focused on the interplay between temporal variation in environmental conditions and seabird energetics, by doing so I have also uncovered additional interesting behavioural aspects that warrant further study. For example, in guillemots and razorbills I found greater foraging effort and deeper dive

depths in male parents as opposed to females during the period of male-only at-sea chick provisioning when birds had migrated from the breeding colony (Chapter 3). These species have an unusual parental care strategy in which the male parent takes the chick to sea when it is only 20-30% of adult body mass and unable to fly. This distinctive strategy is driven by the higher energetic rewards available whilst living at sea as opposed to delivering single prey items to the chick at the colony (Elliott et al., 2017). However, whilst we identified changes in diving behaviour during the at-sea male-only care period, we were not able to relate these to potential sex-specific differences in the birds' geographic locations or energy budgets, possibly because sample sizes are still quite small. The synchronous deployment of both time depth recorder (TDR) and global location sensing (GLS) devices (similar to that within Chapter 4) would allow estimations of daily energy expenditure to be made for both of these species, something that has not been done previously for razorbills. We might expect sex-specific differences in both energy expenditure and location during the post-fledging period, as has been seen in populations of common guillemots (Burke et al., 2015). Such differences in turn might have implications for the birds' body condition and foraging capabilities, with carry-over effects into the following phases of the annual cycle impacting one sex more than the other (Elliott and Gaston, 2014). Additionally, post-fledgling survival of guillemot chicks is highly variable between years (Harris et al., 2007) and mortality occurs mainly during the autumn and early winter months (Birkhead, 1974); investigating the energetics of not only adult birds, but also their chicks, during this period might therefore help to provide vital insights into the links between environmental variability and chick survival.

The period of male-only parental care in guillemots and razorbills coincides with the annual primary feather moult period during which birds become flightless as they lose and replace their flight feathers. Puffins also experience a flightless moult period,

although the timing of this is more variable (Harris et al., 2014). Again, by equipping guillemots, razorbills and puffins with GLS loggers, that test for saltwater immersion, alongside behavioural classification procedures (similar to those used in Chapters 4 and 5), it might be possible to identify the timing of moult, discernible by a lack of flight activity, at the individual level (Grecian et al., 2016). Identifying the timing and location of the moult period is important as the birds' inability to fly at this time means that they are unable to move to new feeding areas if conditions deteriorate. Auks may therefore be particularly susceptible to starvation if they fail to locate high quality foraging areas or track prey patches effectively (Burke et al., 2015). Flightlessness also makes auks vulnerable to threats such as oil spills, predation and hunting, with limited means through which to escape (Harris et al., 2014; Mosbech et al., 2012). Extracting the precise timings and locations of moult, not only for auks but for seabirds in general, is therefore important and warrants further attention.

Whilst all auks are extremely efficient divers, well adapted for pursuing their forage fish prey meters below the ocean surface, the nocturnal behaviour of guillemots is particularly interesting with regards to the development of future research questions. Within this thesis I discovered that Isle of May guillemots were diving across the 24-hour period (Chapter 3) and also that this nocturnal foraging behaviour appeared to be an active choice, as opposed to the result of daylight constraints (Chapter 4). Whilst seabird foraging behaviour is largely thought to be guided by visual cues, nocturnal diving has previously been recorded in guillemots (Regular et al., 2011) as well as in other seabirds: Arctic great cormorants *Phalacrocorax carbo* dive during the polar night (Grémillet et al., 2005) and Scopoli's Shearwaters *Calonectris diomedea* dive at higher intensities according to moonlight availability (Rubolini et al., 2015). Guillemots are one of the deepest diving birds that can also fly (deepest dive recorded for this species = 250 m; Chimienti et al., 2017) and therefore their ability to forage in low light level

conditions, similar to those that they will experience at depth, is not entirely surprising. Additionally, foraging conditions may themselves be enhanced by non-natural light sources, such as those emitted from fisheries and oil and gas platforms; these artificial light sources can attract prey species to surface waters where it can be more easily captured and exploited by feeding seabirds (Ostaszewska et al., 2017). This being said, the ability of guillemots to forage under starlight conditions, when virtually no light is available within the water column, suggests that they may also use non-visual cues (Regular et al., 2011). It may be that guillemots use their memory of where they dived during the day to relocate and track predictable patches of prey (Hedd et al., 2009; Regular et al., 2010). Furthermore, there is increasing evidence that seabirds might use acoustic cues in order to communicate, navigate, avoid predators and locate prey species (Larsen et al., 2020). For example, great cormorants have high underwater hearing sensitivity and are able to detect the low frequency sounds that their small fish prey, such as sculpin *Cottus paulus,* emit (Hansen et al., 2017). Guillemots also demonstrate a behavioural response when exposed to underwater noise (Anderson Hansen et al., 2020), therefore opening up the possibility that they use acoustic cues in order to successfully forage nocturnally. Indeed, whilst around 820 avian species live on or near water and depend on it to obtain food (Dooling and Therrien, 2012), there remains relatively little information regarding the mechanisms that many of these species deploy in order to capture prey, particularly under reduced light levels.

Throughout this thesis I assumed that activity-specific metabolic rates derived during the breeding season were also representative of those throughout the entire annual cycle (Chapters 4 and 5). In reality, it is likely that seasonal variation in both intrinsic and extrinsic factors led to temporal variation within these values of metabolic rate (Pettersen et al., 2018). Whilst I remain confident that I have estimated daily energy expenditure with the most current information available, following protocols of other

recent literature and accounting for seasonal variation in thermoregulatory costs (Burke and Montevecchi, 2018), this highlights a gap in our knowledge regarding seabird physiology outside the breeding season. Indeed, over the breeding season, from incubation to chick-rearing, guillemots demonstrate a reduction in the size of their metabolically-expensive organs, such as the liver and bladder, buoyant body components, such as lipids, and also reduced energetic costs whilst diving and flying (Elliott et al., 2008; Elliott and Gaston, 2005). Whilst in Chapter 5 I provide novel insights into modelled year-round fluctuations in guillemot body mass, I am currently unable to relate this to potential changes in their body composition and the consequential physiological effects of such changes. Researching the seasonal influence of physiological variation on auk energetics would therefore further enhance our understanding of year-round seabird ecophysiology, potentially providing insights into how seasonal changes in body composition influence seabird diving behaviour and energetics.

Conservation ecology

The creation of marine protected areas (MPAs) is a tool used by governments and conservation bodies to conserve threatened species and ecosystems and it is acknowledged that seabirds should be a focal taxa within their identification and designation (Ronconi et al., 2012). Currently, when seabirds are considered, the emphasis is usually on seeking to protect the locations of key breeding colonies and the important foraging habitat within their vicinity (Cleasby et al., 2020; Critchley et al., 2018). Whilst these breeding and foraging habitats are vital, periods of the annual cycle when seabirds are not constrained to the colony, should also be considered within conservation and management decisions (Dias et al., 2019; Oppel et al., 2018). Indeed Krüger et al. (2017) illustrates the importance of accounting for multiple species, their extinction risk, and also seasonal changes in their locations within the identification of

protected areas. My findings on year-round changes in seabird energetics further emphasise the need to incorporate seasonal variation in seabird space use within conservation efforts. In particular, I demonstrated a method through which to identify key areas with regards to seabird energy gain and also mortality risk throughout the full annual cycle (Chapter 5). For highly mobile species, it is impossible to encompass full species distributions within MPAs (Game et al., 2009). Instead, we should seek to build on current protected area designations (Figure 6.1) by implementing a well-connected network of numerous MPAs. The boundaries of such MPAs should surround key areas of year-round seabird activity and energy extraction, thereby incorporating the seasonal movements of marine top predators and accounting for the complexity of marine systems within our efforts to conserve it (Lascelles et al., 2012).

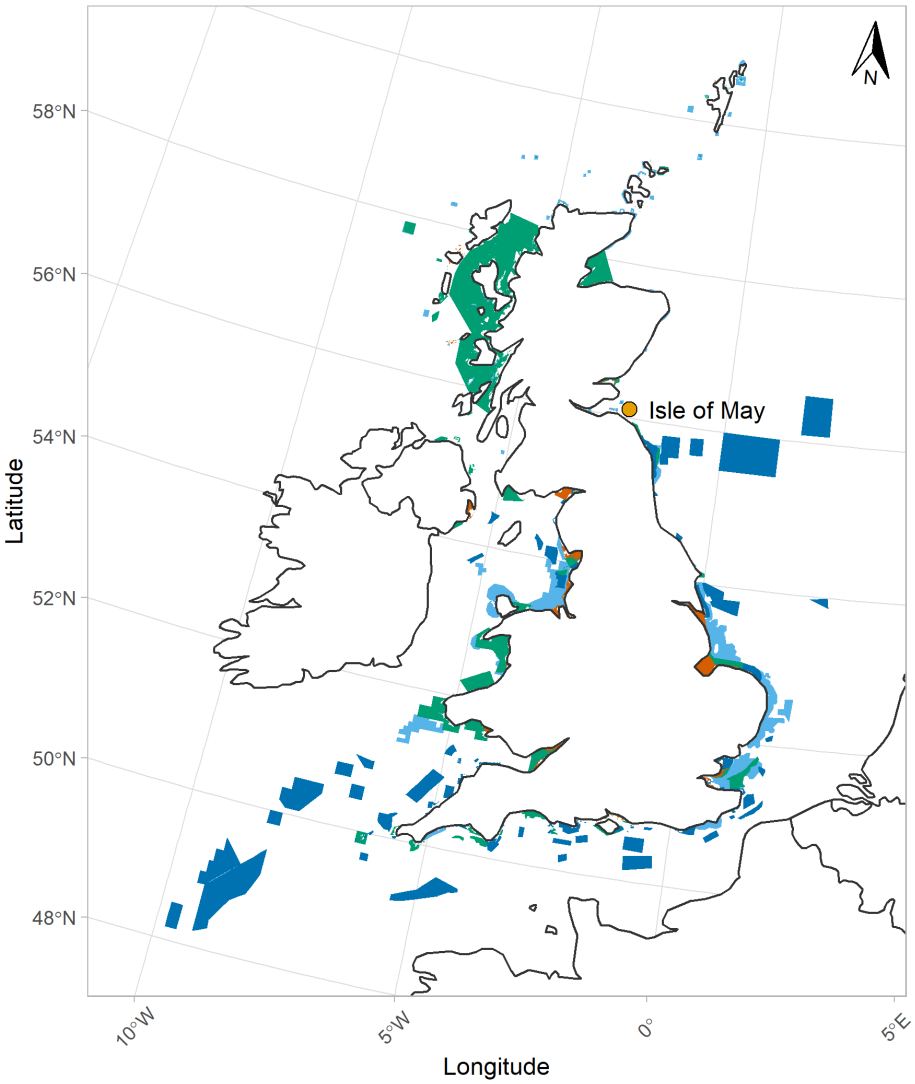


Figure 6.1. Map of designated UK marine protected areas: Special Areas of Conservation (SACs; light blue), Special Protection Areas (SPAs; green), Ramsar sites (orange) and Marine Conservation Zones (MCZs; dark blue). SACs designated under the Conservation of Habitats and Species Regulations 2017 to protect a network of important high-quality conservation sites; SPAs designated under the European Union Directive on the Conservation of Wild Birds to protect the habitats of migratory birds; Ramsar sites designated under the Ramsar Convention and are wetlands of international importance; MCZs designated under the Marine and Coastal Access Act (2009) to protect nationally important marine wildlife, habitats, geology and geomorphology. The Isle of May is illustrated by a yellow circle. Shapefiles sourced from JNCC (https://jncc.gov.uk/our-work/uk-protected-area-datasets-for-download/) and Natural England (https://naturalengland-defra.opendata.arcgis.com/datasets).

In addition to the conservation benefits of MPA designation, the focus of which is often on improving the management of fisheries, auks are also susceptible to further anthropogenic threats such as oil spills (Le Rest et al., 2016) and potential habitat loss via offshore renewable energy developments (Peschko et al., 2020). Multi-colony tracking of North Atlantic Brünnich's guillemots *Uria lomvia* revealed that birds from different breeding populations often mix extensively outside the breeding season,

becoming highly concentrated during particular times (Frederiksen et al., 2016); potential renewable energy developments, oil exploration and future shipping routes within auk non-breeding areas should therefore be carefully considered and managed. In addition to these anthropogenic impacts, climate change is predicted to lead to increases in the frequency of severe weather events, particularly at high latitudes (Young et al., 2011). Seabird mass mortality or 'wreck' events, during which auks often die in particularly large numbers, many of them appearing to be starved, can often be attributed to prolonged exposure to stormy conditions (Louzao et al., 2019). Working towards being able to quantify the critical length of exposure to such conditions would be beneficial in terms of helping to identify extreme weather events that might have population consequences. For example, European shags *Phalacrocorax aristotelis* are another species that are suceptible to winter wreck events (Harris and Wanless, 1996), with adults from the Isle of May having substantially reduced survival rates following Februaries of high rainfall and strong winds (Frederiksen et al., 2008). Although such events can have large impacts on seabird demography, particularly when they act in combination with other anthropogenic impacts or more large-scale climatic conditions (Votier et al., 2005), quantifying levels of mortality during these events is often difficult (Morley et al., 2016). By developing the analysis within Chapter 5, via modelling the links between multi-year individual-level auk energetics and body mass as well as population-level over-winter survival, it would be possible to link individual ecophysiology to population demography. Additionally, by developing our knowledge of how environmental conditions influence auk energetics over a multi-year temporal period, it might also become possible to predict future auk mortality under Intergovernmental Panel on Climate Change (IPCC) climate change scenarios.

An additional way to apply the study of auk behaviour and energetics to conservation ecology is by studying birds from colonies across the range of their breeding

distributions (Ferguson et al., 2020). In this way it may be possible to identify responses to the contrasting environmental conditions that auks from different colonies experience outside their breeding seasons. The breeding range of the Alcidae family is largely concentrated in the high and low Arctic, with some breeding sites extending into northern temperate waters; common guillemots breed across latitudes that range from 40° N (in Portugal) to 75° N (in Svalbard and Novaya Zemlya) in the West Atlantic, with razorbill breeding distributions broadly overlapping with this range (Gaston and Jones, 1998). Elliott and Gaston (2014) identified high levels of daily energy expenditure in a male Brünnich's guillemot from Coat's Island, in the Canadian Arctic during the period that it spent rearing its chick at sea; a similar pattern was not evident within our study of more-temperate Isle of May common guillemots (Chapter 4). Auks from Coat's Island breed over 700 km further north than those from the Isle of May, in a bay that is covered in sea ice during the winter, with pack ice remaining throughout the annual cycle (Gaston et al., 2011); the environments that the two populations experience are drastically different. Auks that inhabit higher latitudes within the western North Atlantic ocean experience sea surface temperatures that are consistently near freezing, with drastic consequences for their thermoregulatory costs and energetic budgets (Burke and Montevecchi, 2018). In contrast, by increasingly investigating the year-round energetic budgets of auks from more temperate eastern locations, such as those from the Isle of May, we might be able to provide insights into how these species will cope in the face of warming ocean temperatures across their breeding ranges. Indeed, as behavioural traits are often at the forefront of evolutionary change (Duckworth, 2009), investigating differences in the behaviour of populations of auks that breed at either temperate or polar latitudes might also broaden our understanding as to the ecological adaptations that these birds might be able to make in response to environmental change (Linnebjerg et al., 2013).

Focusing on the non-breeding ecology of North Atlantic auks provides insights which may help to better conserve them during critical and potentially dangerous periods of the annual cycle. Additionally, adopting a global, multi-species outlook might also have conservation benefits. When studying the ecophysiology of seabirds, a multi-species approach is often particularly necessary due to the broad range of distinctive characteristics that different species of seabird exhibit, thereby mitigating the ability to make generalisations between auk species and seabirds in general. For example whilst we identify patterns in the year-round energetics of guillemots (Chapter 4), this species has exceptionally high flight costs compared to most other seabird species, such as albatrosses and petrels that engage in energetically efficient wind-powered soaring (Pennycuick, 2002). Additionally, whilst guillemots can accumulate fat outside their breeding seasons (Chapter 5), other seabirds, such as great cormorants, are unable to carry energy reserves in this way (Grémillet et al., 2003). Therefore, instead of extrapolating from the species-specific patterns identified throughout this thesis, we should seek to combine our increasing knowledge of seabird time-activity budgets outside the breeding season with species- and activity-specific energetic costs (see Chapters 4 and 5). In this way, the prospect of mapping the food requirements of the world's seabirds in time and space is increasingly tangible. Indeed outputs from the 'Seabird FMR Calculator' (Chapter 2) have recently been used in order to estimate annual seabird food consumption within the North Sea (Sherley et al., 2020). Expanding this approach in order to produce temporally-specific estimates across multiple species for the whole annual cycle would have conservation implications with regards to fisheries management (Brooke, 2004; Cury et al., 2011).

Conclusion

Marine predators are key components of coastal and oceanic ecosystems, having cascading ecological effects throughout the lower trophic levels of these systems (Block

et al., 2011). For example, it has been estimated that seabirds consume 70 million tonnes of prey each year globally (Brooke, 2004). Outside their breeding seasons, many seabird species are wide-ranging; they inhabit the marine environment and are often out of sight from land-based observers (Egevang et al., 2010). During the non-breeding period, seabirds also often experience harsh environmental conditions, with the extremity of these conditions predicted to intensify as a result of climate change and increased human exploitation of the world's oceans (Croxall et al., 2012). Although currently many seabird populations are in decline (Dias et al., 2019), there is a lack of information regarding how energetic processes drive seabird population dynamics. In this thesis I therefore explored the links between seabird behaviour, energetics and environmental conditions, using North Atlantic auks as a model system. This thesis therefore offers new insights into the links between seabird behaviour and energetics, demonstrating that these vary temporally due to a variety of intrinsic and extrinsic drivers. The results illustrate the potential of expanding our knowledge of seabird ecology outside the breeding season as well as the importance of doing so in order to better understand and conserve these vital species

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Supplementary Materials

Supplementary Materials for Chapter 2: A model to estimate seabird field metabolic rates

Appendix 2.1

The 346 seabird species, as defined by Croxall et al. (2012), were initially selected for inclusion within the phylogenetically-controlled analyses. Species within the Anatidae (n = 18), Gaviidae (n = 5), Podicipediformes (n = 4) and Scolopacidae (n = 2) families were then removed since the life-history strategies of these species are different to those typical of the other seabird families. In addition, 4 extinct seabird species (Olson's petrel, *Bulweria bifax*; Guadalupe storm petrel, *Oceanodroma macrodactyla*; Great auk, *Pinguinus impennis* and Saint Helena petrel, *Pterodroma rupinarum*) were also removed.

Appendix 2.2

When jackknife estimates were plotted against the original values upon which the model was built, a linear relationship was detected, with no evidence of systematic bias (Fig. A2.2).

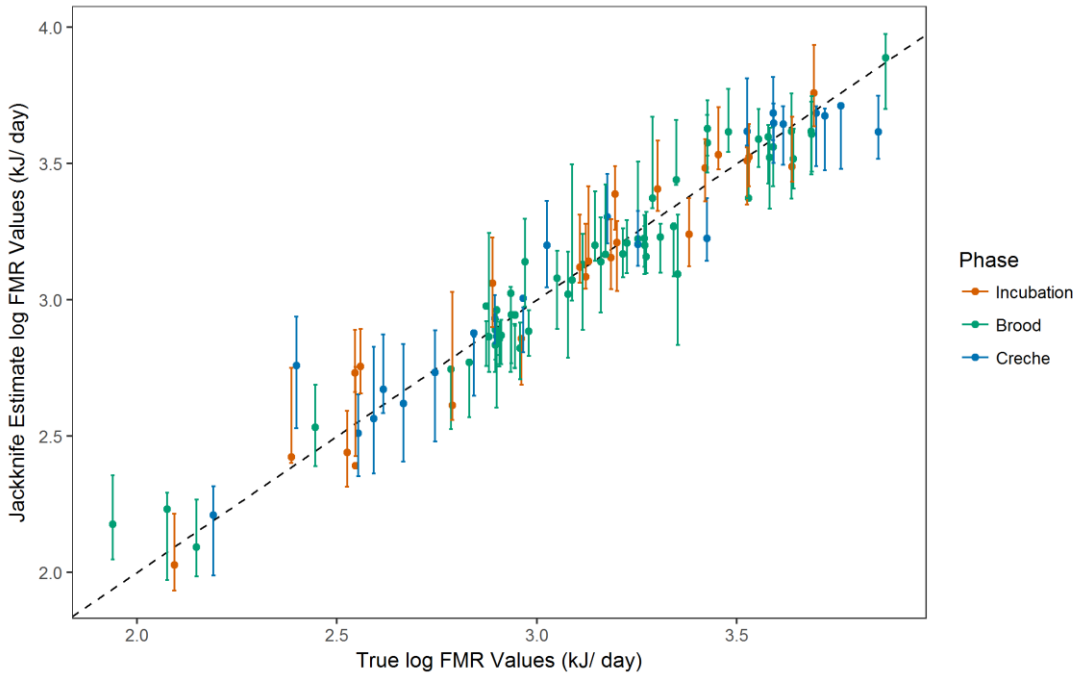

Figure A2.2. Values of FMR extracted from the literature and posterior estimates of FMR produced by jackknife analyses. Error bars represent lower and upper 95% credible intervals.

Appendix 2.3

Table A2.3. Deviance information criterion (DIC) values, variance components (species, colony, phylogeny and residual) and phylogenetic heritability (H^2; mean ± standard deviation) for 4 models comparing the key drivers of field metabolic rate (FMR) in breeding seabirds. Asterixis indicate pMCMC < 0.005. The optimum model is highlighted in bold.

Fixed effects	DIC	Variance components				H^2
		Species	Colony	Phylogeny	Residual	
Mass*; latitude*; breeding stage*; brood size; pairs × mass$^{2/3}$	-217.80	0.0025	0.0034	0.00032	0.0039	0.034 ± 0.017
Mass*; latitude*; breeding stage*; pairs × mass$^{2/3}$	-218.65	0.0025	0.0035	0.00033	0.0039	0.035 ± 0.018
Mass*; latitude*; breeding stage*; brood size	-218.42	0.0025	0.0033	0.00032	0.0040	0.034 ± 0.020
Mass*; latitude*; breeding stage*	**-219.50**	**0.0025**	**0.0035**	**0.00033**	**0.0039**	**0.035 ± 0.019**

Supplementary Materials for Chapter 3: Effects of body size, sex, parental care and moult strategies on auk diving behaviour outside the breeding season

Appendix 3.1

TDRs were deployed on guillemots, razorbills and puffins on the Isle of May National Nature Reserve during the breeding season (Table A3.1). Two sampling rates were used for each species (guillemots: 16 s every 30 days or 32 s every 15 days; razorbills and puffins: 3 s every 10 days or 30 s every day) in order to balance resolution with number of days of data, due to the limited memory size of the loggers. Guillemot data were curtailed within the analysis because of data termination for the other two species.

Table A3.1. Details of TDRs retrieved from common guillemots, razorbills and Atlantic puffins breeding on the Isle of May. Loggers recorded time and depth at a sampling rate of either 16 or 32 s at 30 or 15 day intervals (guillemots), or at a sampling rate of either 3 or 30 s at 10 or 1 day intervals (razorbills and puffins). The sampling period was defined as the species-specific population-level fledging date until the TDR stopped functioning or the last sampling date in January. Sex was not determined for two individual birds (Na).

Species	Sampling rate (s)	Sampling interval (days)	Bird ID	Sampling Period		N_{Days}	Sex
Guillemot	16	30	A13193	05/08/05	12/01/06	6	M
			A13195	05/08/05	12/01/06	6	F
			A13196	05/08/05	12/01/06	8	F
			A13199	05/08/05	12/01/06	6	M
			A13200	05/08/05	12/01/06	8	M
			A13202	05/08/05	12/01/06	6	Na
			A13211	05/08/05	12/01/06	6	F
			A13228	05/08/05	12/01/06	8	F
			A13233	05/08/05	12/01/06	5	F
	32	15	A13237	05/08/05	28/01/06	13	M
			A13275	20/07/05	28/01/06	15	F
			A13197	20/07/05	28/01/06	15	M
			A13226	05/08/05	28/01/06	12	F
Razorbill	3	10	A01926	06/07/08	02/01/09	19	M
			A01929	06/07/08	23/11/08	15	F
			A01930	06/07/08	02/01/09	19	F
			A01941	06/07/08	15/08/08	4	M

			A01943	06/07/08	22/01/09	21	F
			A01946	06/07/08	02/01/09	19	F
			A01947	06/07/08	05/08/08	4	M
	30	1	A01935	01/07/08	25/01/09	207	Na
			A01936	01/07/08	13/08/08	44	M
			A01938	01/07/08	09/10/08	100	F
			A01948	01/07/08	03/09/08	65	F
			A01950	01/07/08	11/11/08	141	F
			A01952	01/07/08	06/12/08	159	M
Puffin	3	10	A01959	26/07/08	06/12/08	11	M
			A01976	26/07/08	04/09/08	5	F
			A01977	26/07/08	04/09/08	4	F
			A01980	26/07/08	03/12/08	14	M
			A01991	26/07/08	16/07/08	1	M
			A01993	26/07/08	15/08/08	3	M
	30	1	A01967	19/07/08	22/09/08	66	M
			A01971	19/07/08	21/07/08	4	M
			A01984	19/07/08	24/07/08	7	F
			A01985	19/07/08	13/07/08	4	F
			A01986	19/07/08	04/08/08	18	M
			A01996	19/07/08	02/10/08	76	F

Appendix 3.2

The mean population fledging dates of Isle of May guillemots, razorbills and puffins in the years of TDR deployment were 10 July 2005, 30 June 2008 and 18 July 2008, respectively. Dive data recorded prior to these dates were therefore assumed to reflect diving behaviour during the breeding season.

During the breeding season, the mean MDD of razorbills and puffins were 3.5 ± 0.1 and 3.8 ± 0.1 m respectively (Fig. A3.2.1). The density distributions of guillemot dive depth were bimodal (Fig. A3.2.1). Shallow dives (< 30 m) had a mean depth of 4.0 ± 0.1 m and deep dives (> 30 m) had a mean depth of 50.5 ± 0.3 m. MDD was similar between the sexes of all species during the breeding season, and dives were generally deeper during this time, compared to those that occurred outside the breeding season.

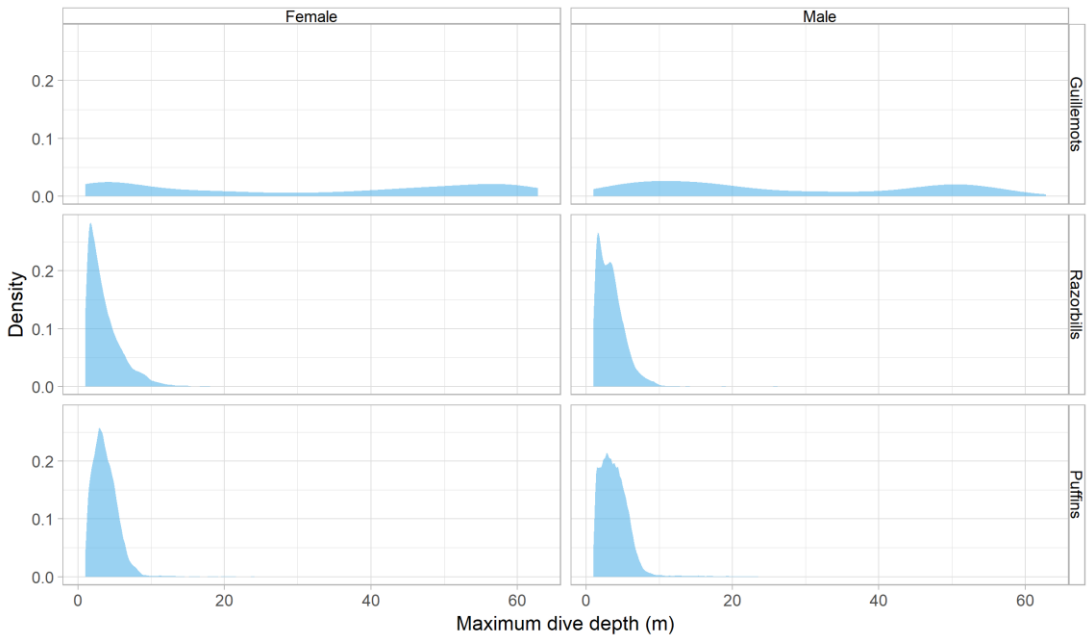

Figure A3.2.1. Density plots of maximum dive depths (MDD) of male and female common guillemots (Nbirds = 11, N dives = 1,766), razorbills (Nbirds = 12, N dives = 5,204) and Atlantic puffins (Nbirds = 12, N dives = 23,524) during the breeding period, prior to the mean population fledging dates.

Guillemots, razorbills and puffins spent 3.45 ± 0.46, 2.38 ± 0.19 and 4.69 ± 0.21 h submerged respectively per day during the breeding season (Fig. A3.2.2). DTS was similar across the sexes (razorbills males: 2.80 ± 0.28 h; razorbill females: 2. 60 ± 0.22

h; puffin males: 4.92 ± 0.29 h; puffin females: 4.28 ± 0.29 h), although female guillemots (3.95 ± 0.66 h) had greater DTS than male guillemots (2.56 ± 0.20 h). This result may be reflective of female guillemots feeding their chicks more frequently than males (Thaxter et al., 2009; Wanless and Harris, 1986). Breeding season DTS was lower than that recorded outside the breeding season.

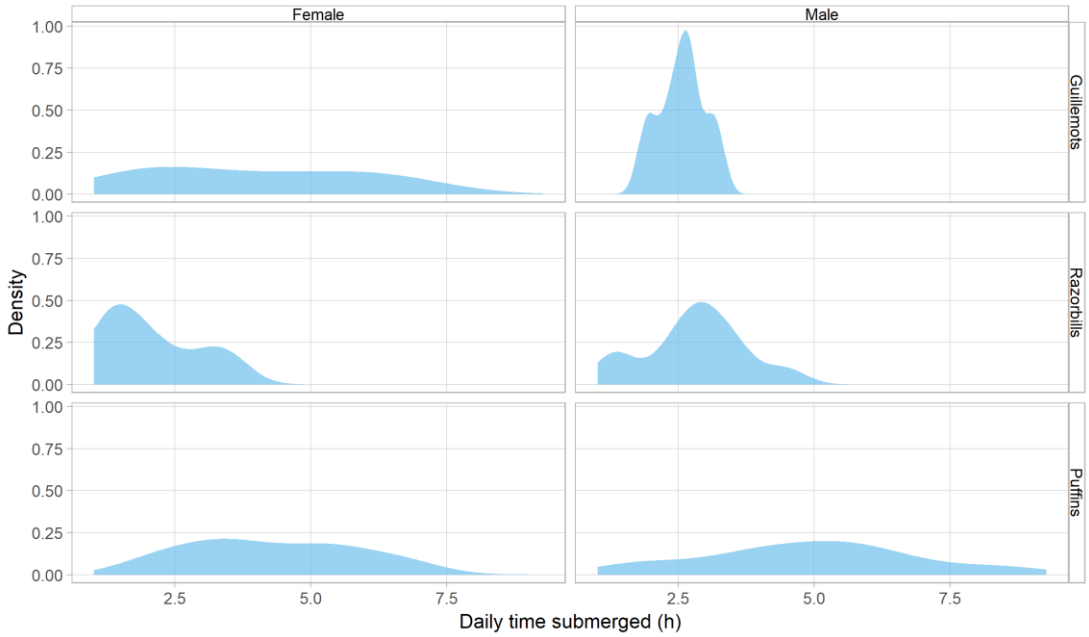

Figure A3.2.2. Density plots displaying the distribution of daily time submerged (DTS) by male and female common guillemots (Nbirds = 10, Ndays = 14), razorbills (Nbirds = 11, Ndays = 25) and Atlantic puffins (Nbirds = 11, Ndays = 74) during the breeding period, prior to the mean population fledging dates.

Appendix 3.3

In order to identify bimodality in guillemot dive depth, as previously described during the breeding season (Thaxter et al., 2010), we fitted finite mixture models to each month of guillemot maximum dive depth (MDD) data using the Expectation-Maximisation algorithm in the *cutoff* package (Choisy, 2015). Whilst these models force bimodality into the distributions, only the model that was fitted for the July data accurately represented the distribution of the data (Fig. A3.3.1). For the remaining months covering the non-breeding period (August – January), distributions of MDD seemed more likely to be multimodal with high densities of shallow dives, precluding simple classifications into shallow and deep dives (Fig. A3.3.1).

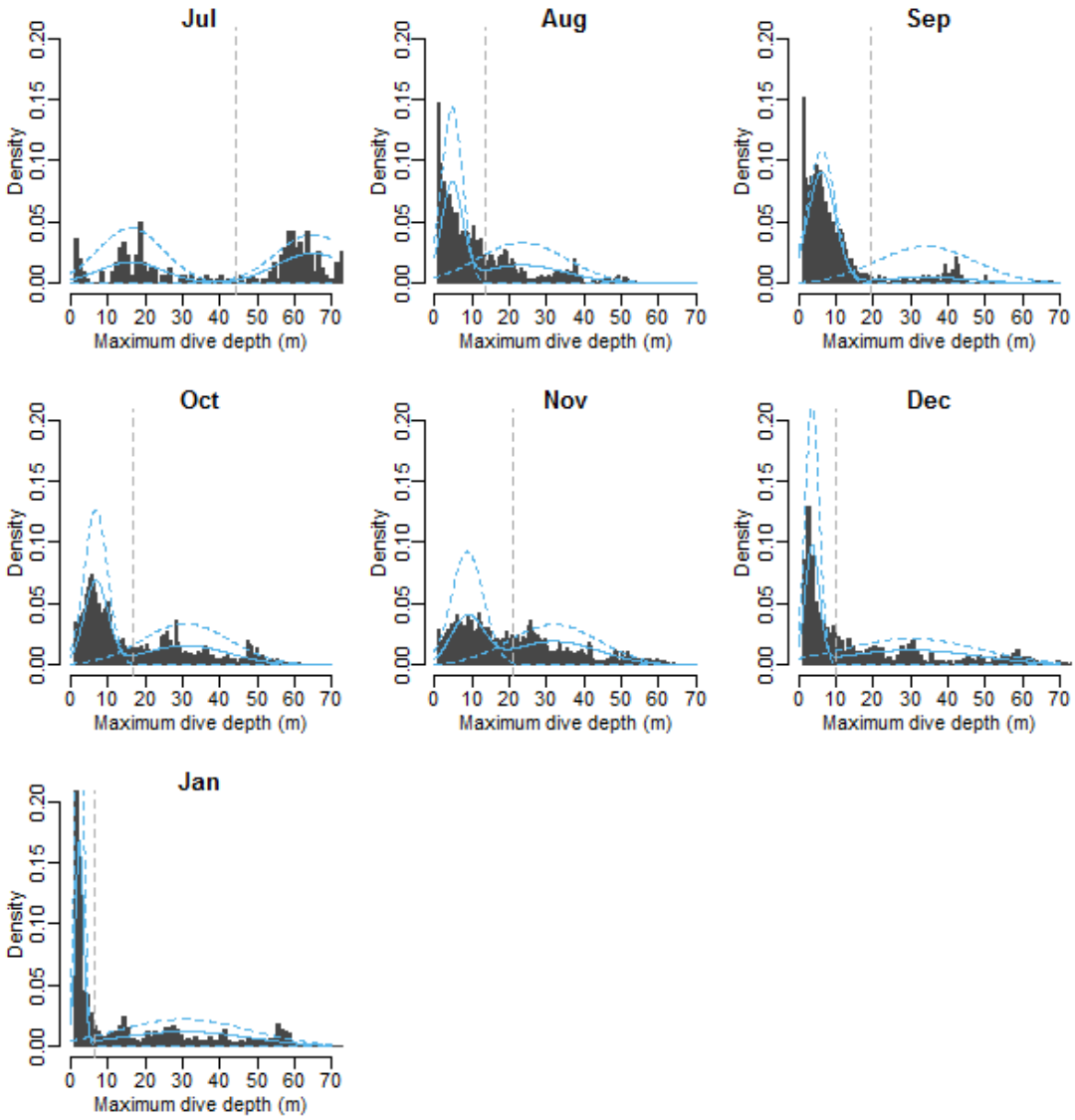

Figure A3.3.1. Density histograms of the maximum dive depths (MDD) recorded by TDRs attached to common guillemots (n = 13) from the Isle of May over the 2005/06 winter. Grey dashed lines illustrate a cut-off value generated by finite mixture models to identify two peaks within bimodal data. Blue lines illustrate the confidence intervals of the mixture parameter.

Appendix 3.4

Across all three species, TDRs recorded time and depth at one of two different sampling frequencies: 16 s every 30 days (high frequency) or 32 s every 15 days (low frequency) for guillemots; 3 s every 10 days (high frequency) or 30 s every day (low frequency) for razorbills and puffins. Neither maximum dive depth (MDD) nor daily time submerged (DTS) differed between the two sampling rates for any of the three species (Fig. A3.4.1).

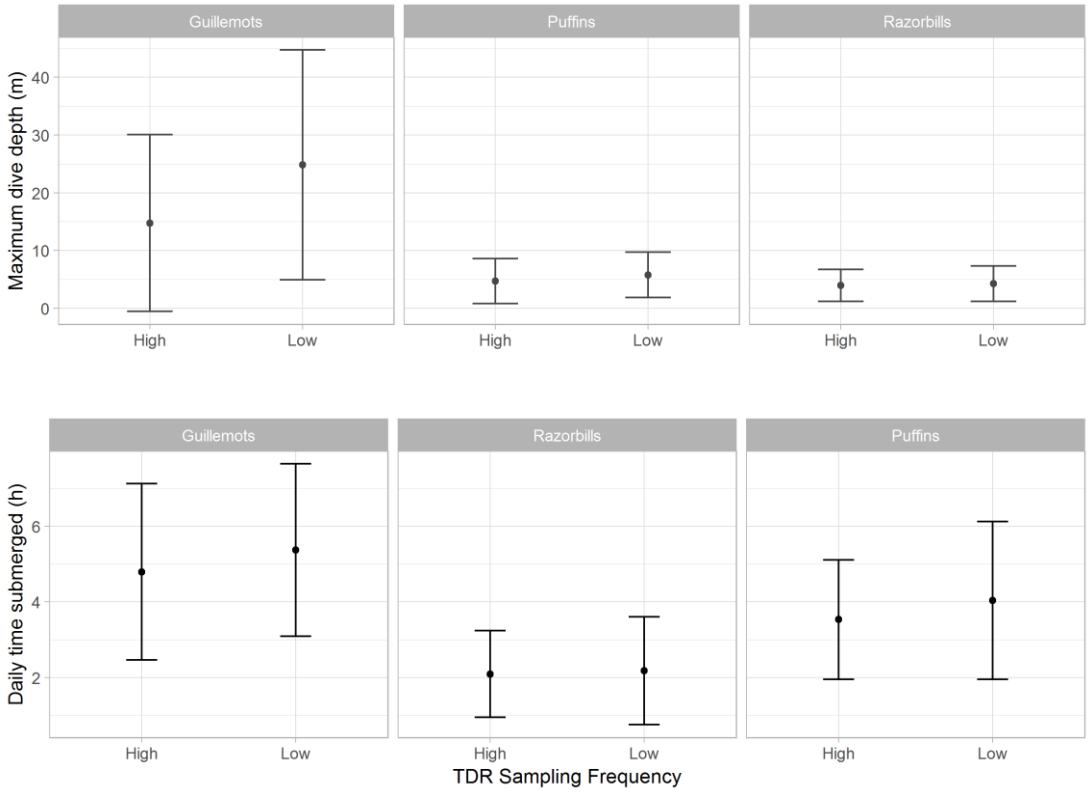

Figure A3.4.1. Mean maximum dive depth (MDD) and mean daily time submerged (DTS) estimated from TDRs sampling at high and low frequencies during the non-breeding period. Common guillemot (high frequency 16 s, n = 9 birds; low frequency 32 s, n = 4 birds); razorbill (high frequency 3 s, n = 6 birds; low frequency 30 s, n = 6 birds) and Atlantic puffin (high frequency 3 s, n = 7 birds; low frequency 30 s, n = 6 birds). Values are means ± SD.

The relatively low sampling frequency of some data loggers precluded us from presenting data on dive duration with confidence, since low sampling rates will not detect short dives and may overestimate the duration of individual dives (Wilson et al., 1995). We felt confident that our calculated quantity of daily time submerged (DTS) would not be affected by sampling frequency (Takahashi et al., 2018), but conducted a

simulation exercise to establish whether this was indeed the case. We randomly generated 100 versions of a four hour period. Birds were modelled as being at the surface at the beginning of this period and then had a 95% likelihood of staying in the same "at-surface" state and a 5% likelihood of switching into a "dive" state. This method allowed us to generate an alternative sequence of surface intervals and dives with realistic durations. To simulate the effect of the different sampling frequencies, we sampled each of the 100 iterations every 1, 2, 4, 8, 16 and 32 s. We then extracted the number of dives recorded, mean dive duration, and daily time submerged for each of the sampling frequencies.

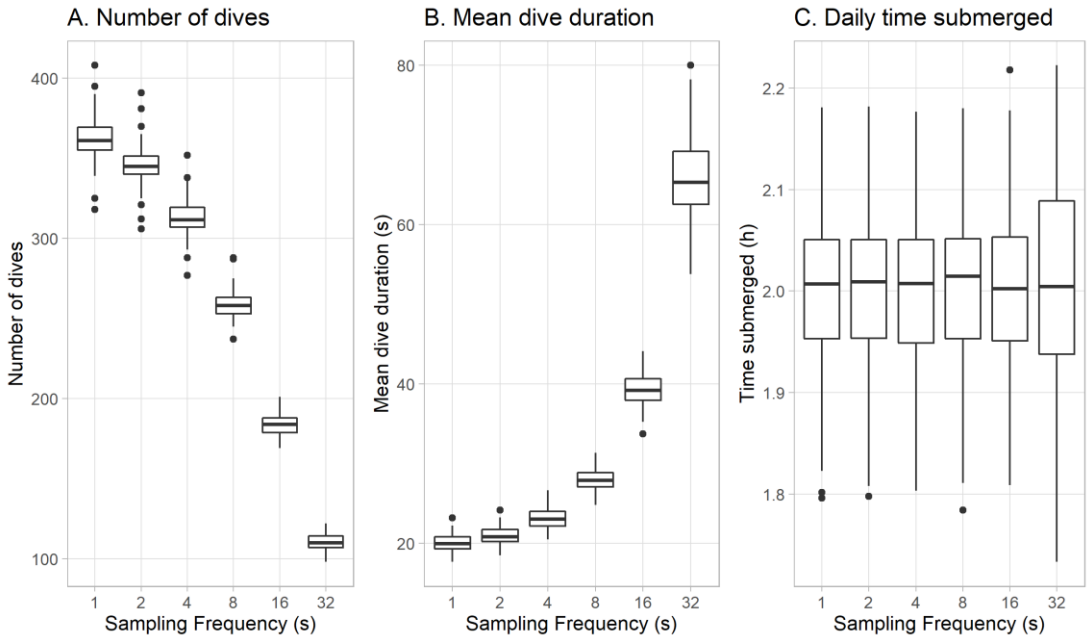

Figure A3.4.2. Boxplots of A. the number of dives, B. mean dive duration and C. daily time submerged (DTS) generated from 100 random iterations of 24 hour periods comprised of 70% diving and 30% non-diving activity and extracted at sampling rates of 1 s, 3 s, 16 s, 30 s and 32 s.

Whilst an outcome of the low sampling frequencies (32 and 30 s) was that some dives were missed, resulting in a lower number of recorded dives (Fig. A3.4.2 A), this sampling frequency also led to an overestimation of dive duration (Fig. A3.4.2 B). The combination of this underestimation of dive number and overestimation of dive duration meant that when the dive durations were summed to calculate daily time

submerged (DTS), DTS was consistent between the different sampling frequencies (Fig. A3.4.2 C). Unfortunately it was not possible to simulate the effect of sampling rate on MDD in the same way since we did not have the required information on the shape and nature of auk winter dive profiles at an adequately high temporal resolution.

Supplementary Materials for Chapter 4: A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle

Appendix 4.1

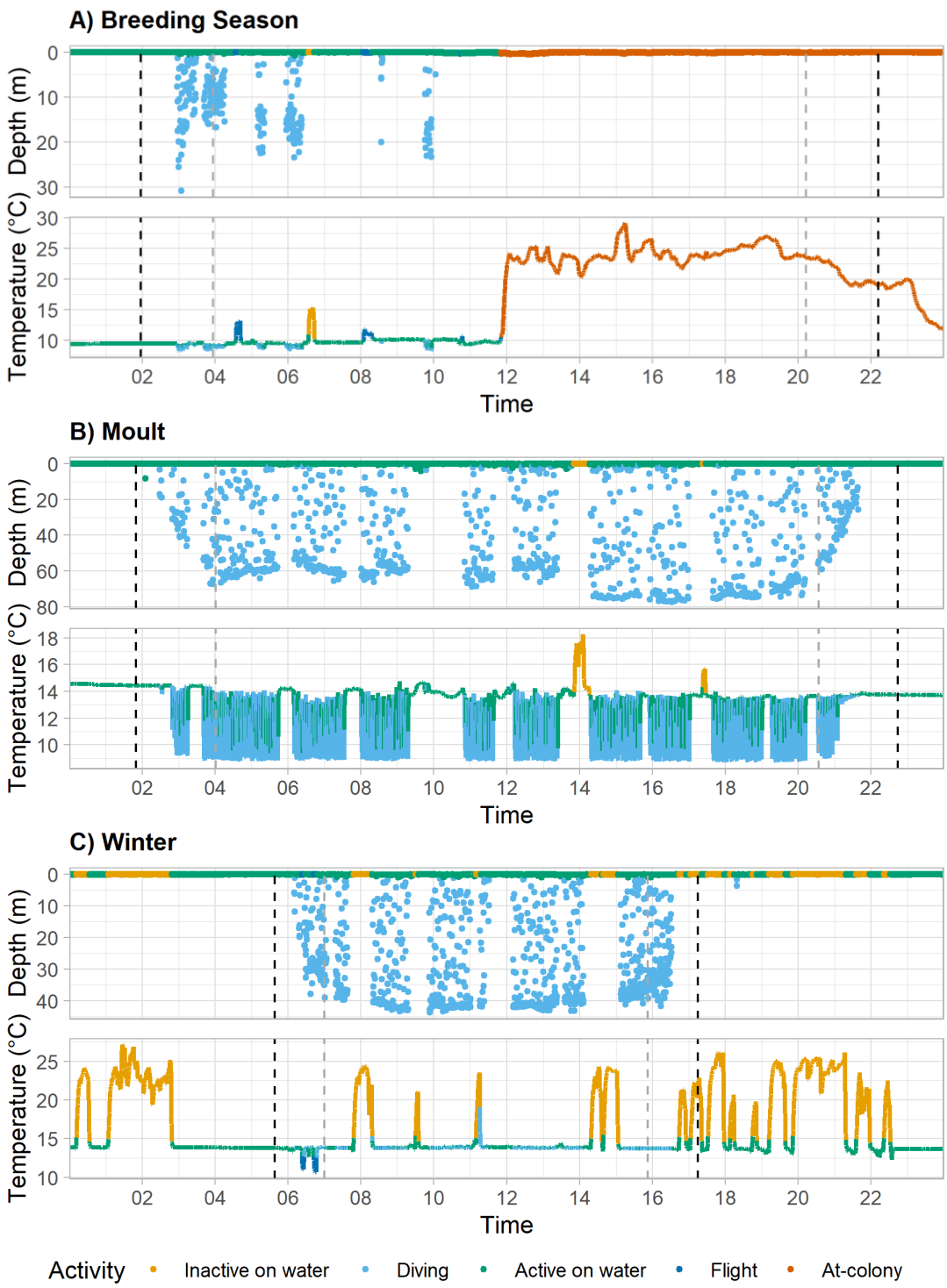

Figure A4.1. Examples of results of the classification of guillemot activity from depth and temperature profiles across three 24 h periods from key periods of the annual cycle. Grey dashed vertical lines indicate the start of day and dusk respectively; Black dashed vertical lines indicate the start of dawn and night respectively.

Appendix 4.2

We assessed the classification of logger temperature data into flight behaviour (T_f) and inactive on water (T_i) by fitting a mixed model using the lmer function in the *lme4* package (Bates et al., 2015). The interaction between log-transformed time-in-activity (a continuous variable) and behavioural classification (a two-level categorical variable) was fitted as a predictor of log-transformed maximum temperature. Individual bird ID was included as a random factor to account for potential non-independence.

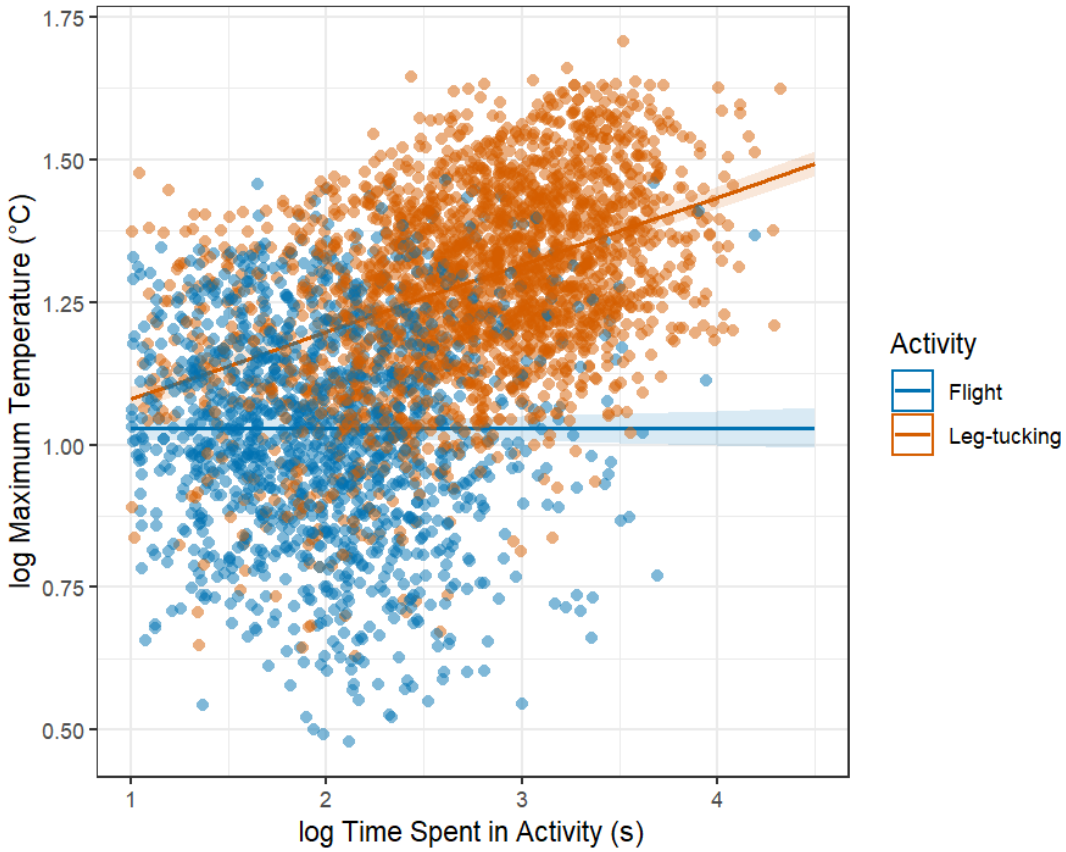

Figure A4.2. The log of the relationship between the amount of time spent in activity (s) and behavioural classification on maximum temperature (°C) for common guillemots throughout the annual cycle.

There was a significant interaction between behaviour and bout duration (ANOVA F = 238.97, P < 0.01; Fig. A4.2), confirming that the nature of the relationship and hence the time taken to reach maximum temperature differed between leg-tucking and flight behaviour. For leg-tucking (T_i), longer times incurred higher temperatures but with an

asymptote due to temperature approaching body surface temperature. For flight (T_f), there was no clear relationship because air temperature, and hence ΔT, varied substantially between flights, independent of their duration.

Appendix 4.3

Table A4.3. Results of generalised additive mixed models (GAMMs). Significant P-values are highlighted in bold.

Response	Model term	*df*	*F*	*P-value*
DEE	s(dDay)	6.64	14.87	**<0.001**
	Sex	2	0.22	0.81
SST	s(dDay)	8.06	311.5	**<0.001**
Time spent diving	s(dDay)	6.92	6.00	**<0.001**
	Sex	2	0.62	0.54
Time spent flying	s(dDay)	7.54	18.39	**<0.001**
	Sex	2	0.75	0.48
Energetic cost of diving	s(dDay)	2.12	3.07	**0.04**
	Sex	2	0.18	0.83
Energetic cost of flying	s(dDay)	7.54	18.39	**<0.001**
	Sex	2	0.75	0.48
Response	**Model term**	***df***	**χ^2**	***P-value***
Diving activity occurring during daylight	s(dDay)	8.99	223521	**<0.001**
	Sex	2	6.57	0.06
Diving activity occurring during twilight	s(dDay)	8.99	56996	**<0.001**
	Sex	2	5.20	0.07
Diving activity occurring during night	s(dDay)	8.99	197079	**<0.001**
	Sex	2	1.81	0.40

Supplementary Materials for Chapter 5: Modelling and mapping the mortality risk and energetic reward of a wild, mobile animal over its full annual cycle

Appendix 5.1

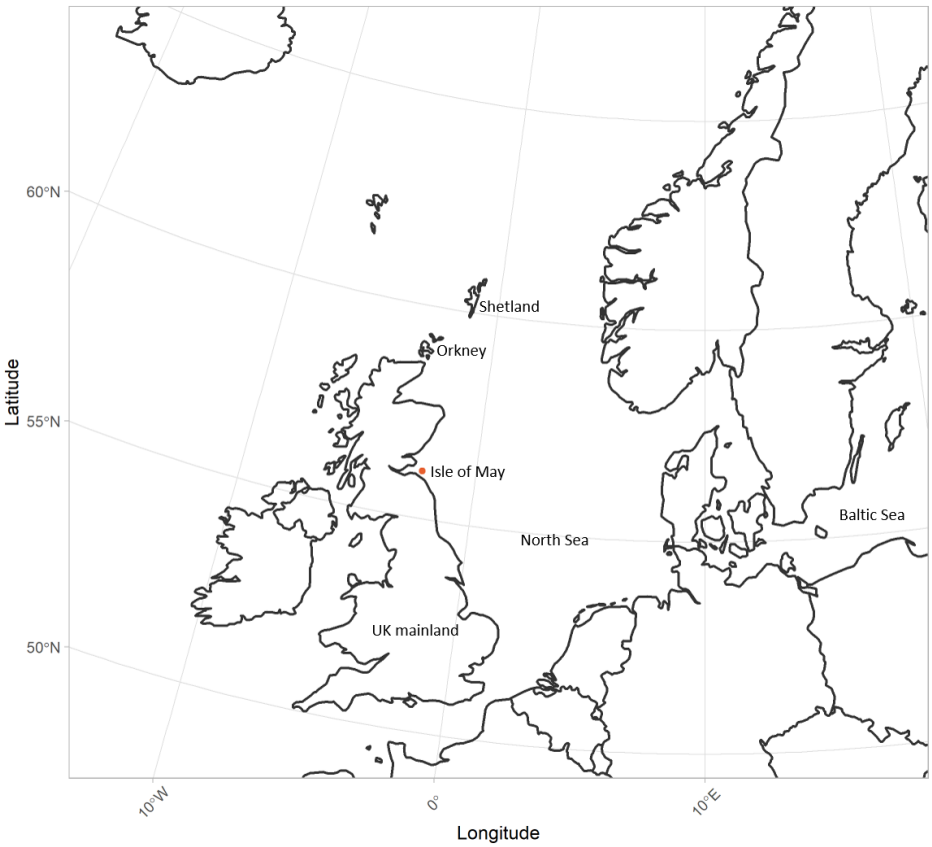

Figure A5.1. Location of the Isle of May study site (shown in orange) as well as other key locations, mentioned within the results.

Appendix 5.2

Light intensity data for the entire annual cycle were downloaded from 17 loggers (71%) and were decompressed utilising the BASTrack software suit (British Antarctic Survey, UK). From these data, the timings of dawn and dusk events were determined using the TwGeos (Lisovski et al., 2016) and GeoLight (Lisovski & Hahn, 2013) packages, following established methods (Lisovski et al., 2020). For each day, latitude was estimated from the duration of night and day and longitude was estimated from the timing of local midnight or midday, providing two positions per day. The subsequent locations (Fig. S1) were processed using an iterative forward step selection framework through the probGLS package (Merkel, 2018) as in Dunn et al. (2020). Utilising probGLS we determined the daily sea surface temperature values experienced by each individual. Additionally, we used the timings of dawn and dusk events to calculate the total hours of daylight experienced by individual guillemots for each day. The distance from each guillemot location to the closest point on the coastline (extracted using the ne_countries function in package rnaturalearth; South, 2017) was calculated using the dist2Line function in the geosphere package (Hijmans, 2015).

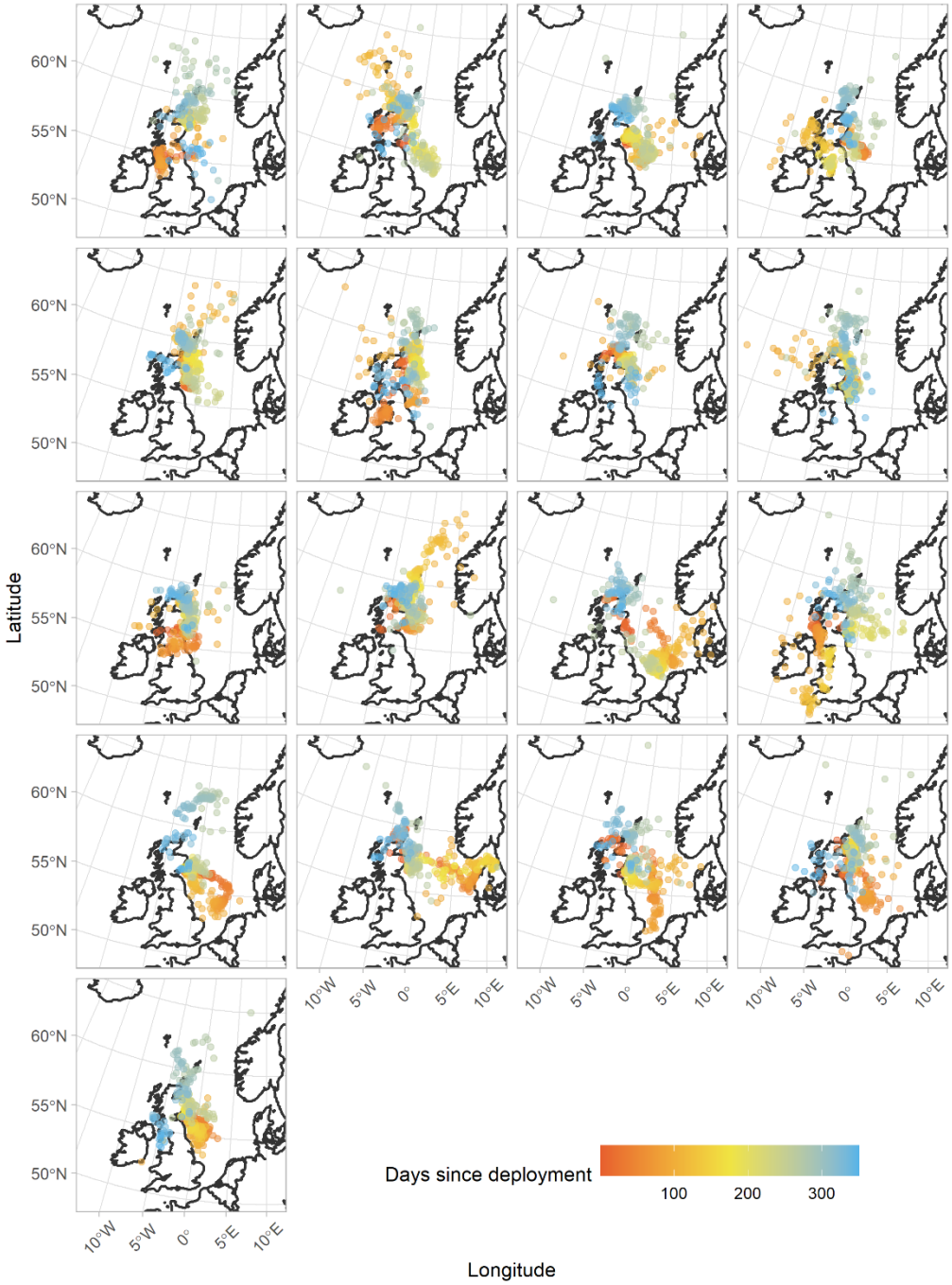

Figure A5.2. Median daily locations of 17 individuals across the 2016-17 annual cycle.

Appendix 5.3

Data loggers tested for saltwater immersion every three seconds and recorded the proportion of time that the logger was immersed in saltwater at ten-minute intervals. Guillemot daily time-activity budgets were estimated from these data based on a number of assumptions regarding guillemot behaviour. Similar classification approaches have been used in previous studies of auk activity budgets (e.g. Dunn et al., 2020; Elliott & Gaston, 2014; Fayet et al., 2017; Linnebjerg et al., 2014). We allocated every ten-minute interval to one of four categories:

- *Daily time in flight:* the amount of time that the logger was mostly (≥98%) dry for periods of up to two hours during daylight. This criterion was selected because guillemots rarely fly at night (Robertson et al., 2012) and are unlikely to be able to fly for more than two hours at a time. This assumption was based on behaviour observed during the breeding season (Thaxter et al., 2010) and the heat dissipation requirements associated with the energetically-costly flapping flight performed by auks (Schraft et al., 2019). Extracted flight durations were consistent with those from Dunn et al. (2020).
- *Daily time resting:* the amount of time during night when the logger was mostly dry (≥98%) and the amount of time during day when the logger was mostly dry (≥98%) for more than two hours. These times represent periods when guillemots either withdrew their leg and foot into their plumage whilst roosting on the surface of the water, or periods when they were at the colony (Robertson et al., 2012).
- *Daily time active on water:* the amount of time that birds spent engaged in behaviours such as swimming, preening and stretching, identified as periods when the logger was between 98% dry and 98% wet (threshold based on Fayet et al., 2017).

- *Daily time foraging*: the amount of time that the logger was mostly wet (≥98%), following field observations which indicate that guillemot legs remain submerged and hence the logger remains continuously wet during bouts of intense foraging. We assumed that all birds spent no less than 1 minute foraging each day.

We combined the resultant daily time-activity budgets (Fig. A5.3.1) with estimates of activity-specific energetic costs to determine the daily energy expenditure (E in kJ) of adult guillemots throughout the annual cycle. To do this we used the following equation based on energy expenditure by the closely related Brünnich's guillemot *Uria lomvia* (Elliott *et al.*, 2013; Elliott and Gaston, 2014; Burke and Montevecchi, 2018):

$$\mathrm{E} = 33.12\ \mathrm{R} + 507.6\ \mathrm{F} + (113 - 2.75\ T)\mathrm{A} + 97.2\ \mathrm{D} \qquad \text{eqn A5.3.1}$$

Here, R represents the hours per day spent resting, F represents the hours per day spent in flight, A represents the hours per day spent active on water, D represents the hours per day spent foraging and T represents sea surface temperature. For simplicity, as is common practice, we assumed that there was no uncertainty within this calculation (Burke and Montevecchi, 2018; Elliott and Gaston, 2014; Fayet et al., 2016). To this value of E, we then added the energy requirements of warming ingested food (65 ± 13 kJ day^{-1}; Thaxter et al., 2013). During the chick-rearing period, we also added the daily energy requirements of a chick (221.71 kJ; Harris and Wanless, 1985; Enstipp *et al.*, 2006) divided by two, due to dual parenting, to the value of E. In 2016, we assumed that logger deployment occurred mid-way through the 24 day chick-rearing period (Harris et al., 2020). In 2017, we estimated the start of the chick-rearing period by adding 32 days (the duration of incubation; Wanless and Harris, 1986) to the commencement of the incubation period and assumed the mean 2017 chick-rearing period length of 22 days (Harris et al., 2020). We identified the commencement of the incubation period for

each individual as the first instance where the data indicated eight consecutive hours of 'resting' across three consecutive nights that occurred after the start of UK spring (20th March 2017). This selection criterion was chosen because Isle of May guillemots attend the colony during the non-breeding period, but do not attend during the night outside the breeding season (Dunn et al., 2020). Individual laying dates were not available for study individuals, but all estimated laying dates fell within the observed range of laying on the Isle of May in 2017 (M.P. Harris pers. comm.). Individual daily energy expenditure estimates are shown in Fig. A.5.3.2.

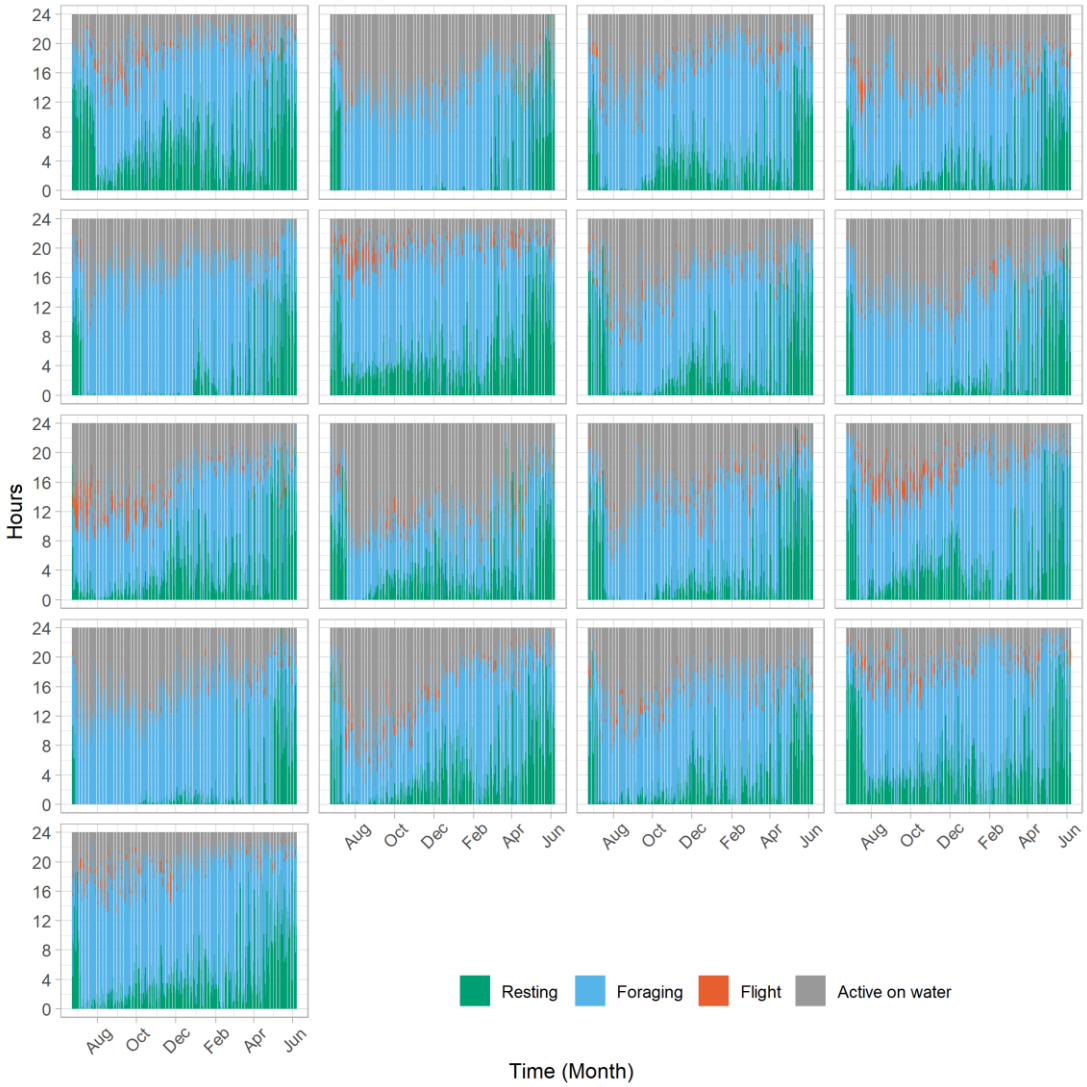

Figure A5.3.1. Daily activity budgets of 17 individuals across the 2016-17 annual cycle.

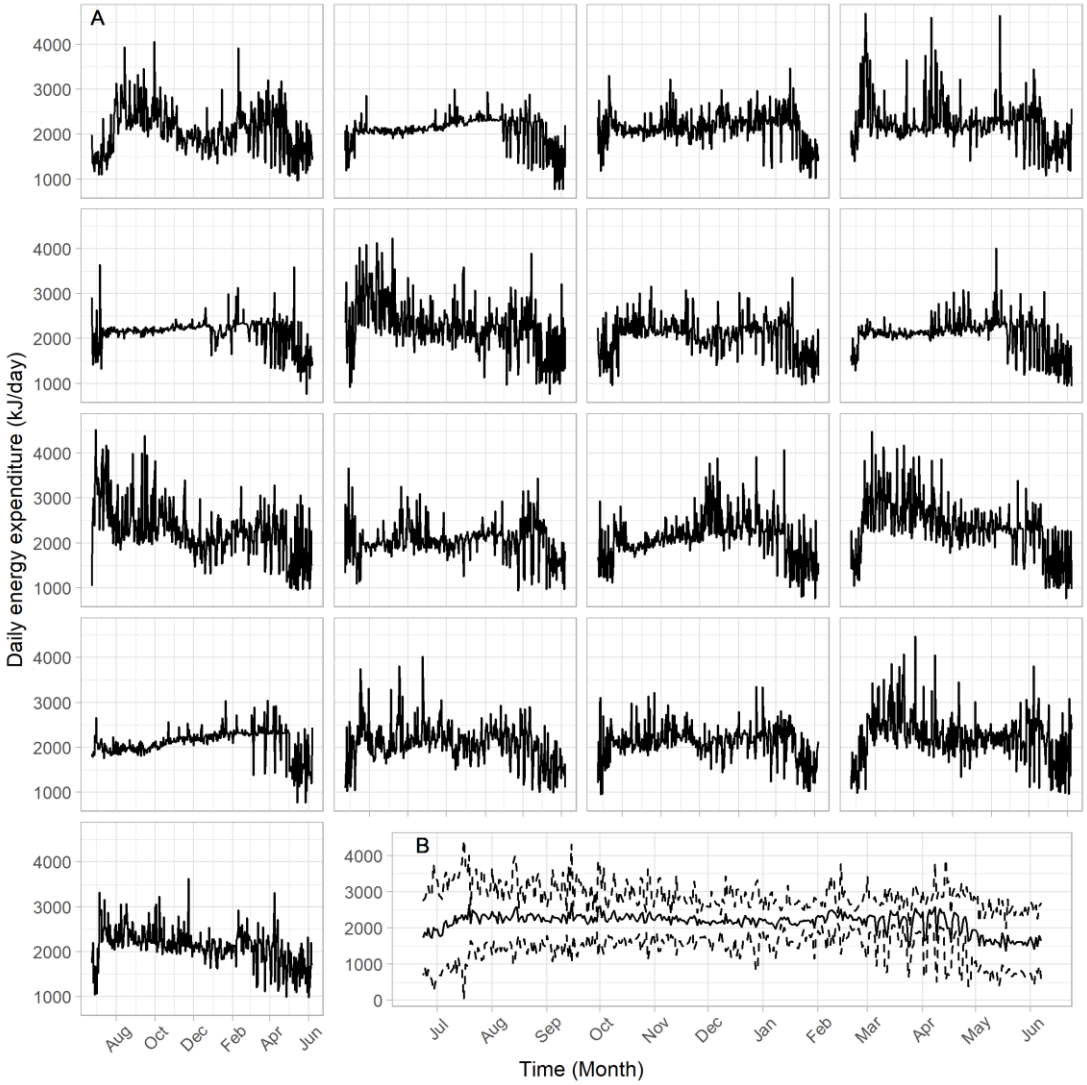

Figure A5.3.2. A: Daily energy expenditure of 17 individuals across the 2016-17 annual cycle. B: The population mean energy expenditure with the standard deviation indicated with dashed lines.

Appendix 5.4

JAGS code:

```
model{
   for(i in 1:nbirds){
   for(t in 1:(days-1)){

     # Linear predictor of energy intake
     Gmu[t,i] <- (D[t,i] + 0.0167) * exp(r0 + r1*T[t,i] + r2*L[t,i] + r3*X[t,i]
                                          + r4*Y[t,i] + r5*C[t,i])
     Gshape[t,i] <- Gmu[t,i]^2/Gsd^2
     Grate[t,i] <- Gmu[t,i]/Gsd^2
     G[t,i] ~ dgamma(Gshape[t,i],Grate[t,i])

     # Standardised residuals
     res[t,i] <- (G[t,i] - Gmu[t,i])/(Td[t,i] + 0.0167)

     # Energy/mass conversion
     mmu[t+1,i] <- M[t,i] - V * E[t,i] + V * G[t,i]
     M[t+1,i] ~ dnorm(mmu[t+1,i], mpr)

     # Mass constraint
     mmid[t+1,i] ~ dnorm(M[t+1, i], mprec)
   }
   }

  # Priors

  r0 ~ dgamma(4.65, 0.94)
  rsd ~ dnorm(500, 0.0001)

  r1 ~ dnorm(0, 0.01)
  r2 ~ dnorm(0, 0.01)
  r3 ~ dnorm(0, 0.01)
  r4 ~ dnorm(0, 0.01)
  r5 ~ dnorm(0, 0.01)

  V ~ dgamma(20793.64, 288400)
  mpr ~ dgamma(2.351, 51.11)

} #end model
```

Appendix 5.5

Table A5.5. Description of the linear predictors $G_{i,t}$ of all fitted models, based on equation 5.4, and resultant Deviance Information Criterion (DIC). The selected model is highlighted in bold.

Linear predictor	DIC
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_3X_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78008
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_3X_{t,i} + r_4Y_{t,i}$	78021
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_3X_{t,i} + r_5C_{t,i}$	78007
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78009
$r_0 + r_1T_{t,i} + r_3X_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78011
$r_0 + r_2L_{t,i} + r_3X_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78024
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_3X_{t,i}$	78031
$r_0 + r_1T_{t,i} + r_2L_{t,i} + r_4Y_{t,i}$	78022
$\boldsymbol{r_0 + r_1T_{t,i} + r_2L_{t,i} + r_5C_{t,i}}$	**78008**
$r_0 + r_1T_{t,i} + r_3X_{t,i} + r_4Y_{t,i}$	78055
$r_0 + r_1T_{t,i} + r_3X_{t,i} + r_5C_{t,i}$	78037
$r_0 + r_1T_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78039
$r_0 + r_2L_{t,i} + r_3X_{t,i} + r_4Y_{t,i}$	78032
$r_0 + r_2L_{t,i} + r_3X_{t,i} + r_5C_{t,i}$	78028
$r_0 + r_2L_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78023
$r_0 + r_2X_{t,i} + r_4Y_{t,i} + r_5C_{t,i}$	78090
$r_0 + r_1T_{t,i} + r_2L_{t,i}$	78031
$r_0 + r_1T_{t,i} + r_5C_{t,i}$	78041
$r_0 + r_2L_{t,i} + r_5C_{t,i}$	78028
$r_0 + r_1T_{t,i}$	78073
$r_0 + r_2L_{t,i}$	78052
$r_0 + r_5C_{t,i}$	78093
r_0	78140

Appendix 5.6

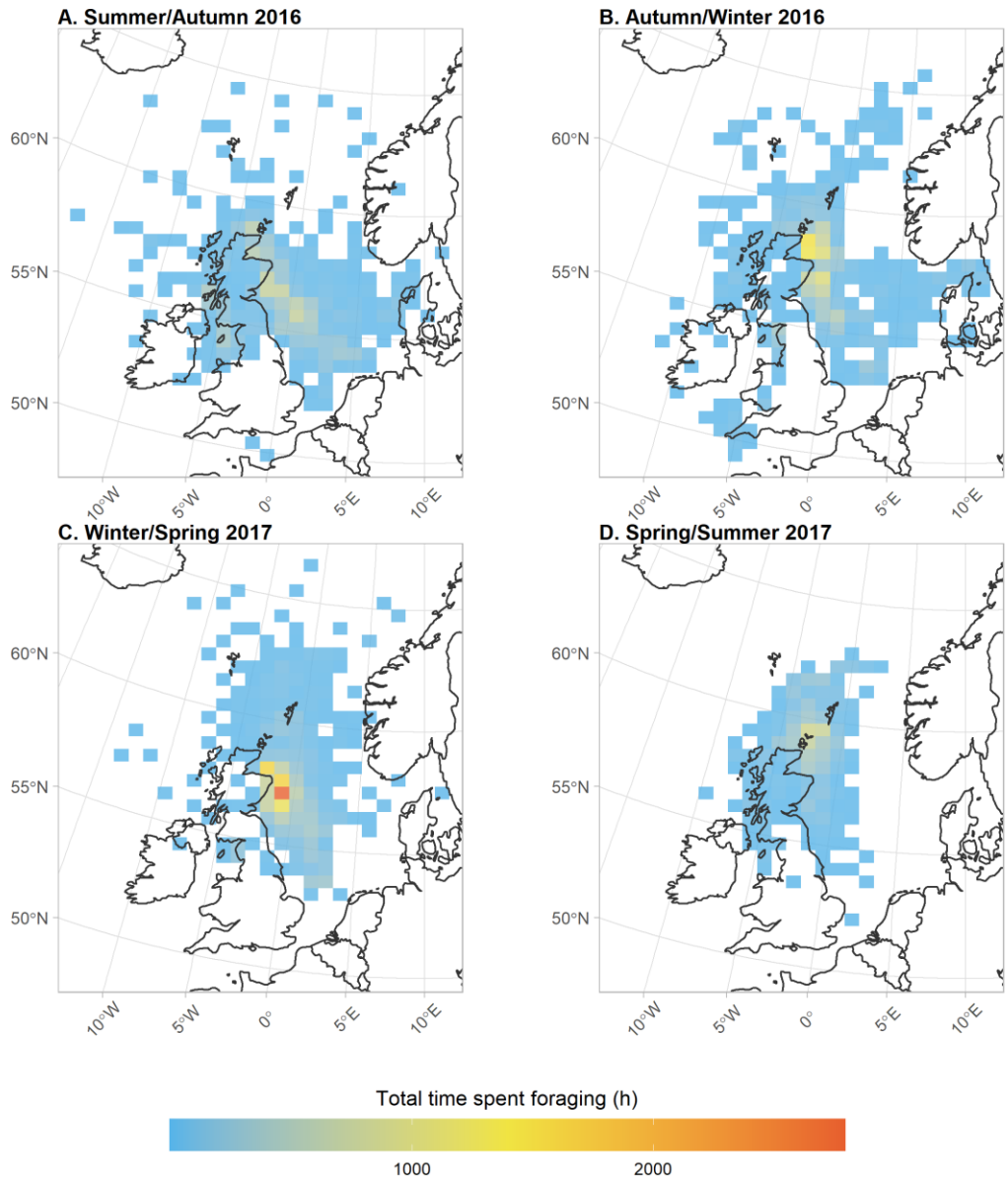

Figure A5.6. Spatial distribution (100 km resolution) of total hours spent foraging by 17 individuals across the 2016-17 annual cycle.

A razorbill chick and its father swim away from the Isle of May.