Using behavioural and energetic insights to assess the impacts of displacement from offshore wind farms on red-throated divers (*Gavia stellata*)

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Thesis Abstract

There is a large-scale need to rapidly construct renewable energy infrastructure to mitigate against the climate crisis. This has applied new anthropogenic pressures to many previously less disturbed species, which must legally be considered during the planning and delivery of construction projects. Observing the behavioural responses of individuals to these pressures marks an important cornerstone in identifying the mechanism of response to anthropogenic stressors. However, understanding the consequences of these behavioural responses is needed to accurately quantify any negative impacts. One key area where we lack an understanding of the consequences of anthropogenic activity, is in the environmental impacts of offshore windfarms (OWF). Specifically, it is important to understand the impact of displacement and barrier effects on the behaviour of individuals. Subsequently, linking these behavioural changes to energetic budgets is vital to accurately quantify the consequences of developments on the demographic rates of populations.

Red-throated divers (*Gavia stellata*, RTDs) have been shown to be a species with one of the highest levels of displacement from OWFs. Therefore, identifying the consequences of displacement for RTDs has become a key research question. Primarily, the effects of disturbance on demographic rates are key to quantifying the stress imposed on a population. Addressing this research question first requires building a more complete understanding of the ecology of RTDs through their annual cycle, as much of their behaviour and ecology is unknown. This is especially true during the non-breeding season, where they are difficult to study, due to their inaccessibility.

To address these questions, I used a combination of biologging, stable isotope analysis and modelling techniques, to build an understanding of RTD behaviour and foraging through the annual cycle. In this thesis, the study populations are comprised of individuals breeding in Scotland, Iceland and Finland, representing three populations on the southern edge of the breeding distribution of this species. I used the newfound ecological understanding of behaviour budgets to explore the energetic costs associated with survival strategies across populations. Finally, synthesising this information, I created an individual based model to simulate the effects of displacement from OWFs on populations and individuals. In many cases, this work provided the first descriptions of key aspects of RTD ecology.

I successfully created the first population-level summaries of diving behaviour for RTDs across the annual cycle and found that RTDs generally dived to shallow depths less than 10 metres. They also showed a mix of benthic and pelagic foraging strategies, with variation both within and between populations. During the non-breeding season, I found that the three separate populations have different behaviour budgets, migration strategies and vulnerability to anthropogenic threats. These behaviour budgets were translated into the first RTD energy budgets, using a novel approach to parametrise an energetics model with allometric scaling equations. The results showed differing costs associated with each of the non-breeding season survival strategies. When simulating the most exposed population to low levels of anthropogenic threats, I found that mortality rates were no higher than those of natural populations. However, when simulating the removal of 45% of foraging habitat, there was a large increase in mortality. Current levels of expected development in most areas of the range of the RTD are unlikely to reach this level.

The work presented in this thesis provides a novel insight into the ecology of RTDs. I also revealed spatial and temporal variation in many survival strategies and quantified the costs of the differing non-breeding season survival strategies. Additionally, these results are contextualised and applied to address a key issue in policy and planning for future offshore wind farm projects.

Chapter 1 General introduction

Anthropogenic pressures and the importance of ecology

It has previously been proposed that high tropic level marine predators can act as indicators of the health of a marine ecosystem (Cairns 1987, Furness and Camphuysen 1997). These species prey on lower trophic levels, therefore in cases where lower trophic levels are experiencing decline and the system is under ‘bottom-up’ control, the higher trophic level predators should also experience changes in their population (Cairns 1987, Hazen et al. 2019). In principle, this means monitoring only the top-level marine predators provides insight into the whole ecosystem. However, in practice there are still significant challenges to monitoring the health of populations of top predators, such as marine birds (Cook et al. 2014). The marine environment is challenging to monitor, due to the effort required to obtain relevant data on individuals and populations, often requiring expensive technology or time-intensive survey methods (Certain and Bretagnolle 2008, Booth et al. 2020). Recently, there have been many advancements in these regards though, from small remote sensing technologies to molecular techniques aimed at increasing our ability to study and monitor marine species in a more cost-effective manner (Haywood et al. 2019, Yoda 2019). However, measurement alone is often not enough to understand complex systems and their interactions with external pressures. Instead, it is essential that insights gained are integrated into predictive frameworks which allow us to predict the consequences of marine threats (Lewison et al. 2012).

Monitoring and assessing the impacts of stressors on species, populations and individuals is perhaps the most important obstacle in protecting the natural world (Smith et al. 2019, Kühl et al. 2020). Climate change, habitat loss and ocean acidification are all very serious threats which are widely predicted to cause large scale species and population loss (Croxall et al. 2012, Shackelford et al. 2018, Mazaris et al. 2019). However, there is much uncertainty around what the exact consequences of the global threats and how wide-reaching the effects will be in reality (Shen et al. 2018, Williams and Newbold 2020). Attempting to understand the consequences of environmental change generally requires a good understanding of the underlying ecology of a species, before predictions on the impacts of stress can be generated (Lewison et al. 2012, Catalán et al. 2019, Rhodes et al. 2022). For example, climate change has caused the timings of some key spawning events in marine fish to change, which could have profound effects on the diet of species that rely on these as a prey source (Asch et al. 2019, Rogers and Dougherty 2019). However, these effects could be offset by predators also shifting annual events to coincide with prey availability (Descamps et al. 2019). This example demonstrates that ecological systems are highly connected and complicated and generally have some degree of adaptability to stress. Therefore, studies examining the effects of a changing environment, or anthropogenic activity, must assess both the effects and the resilience of a species or population to those effects (Travis et al. 2013). In combination, these provide profound applications to conservation, as they inform what effects are likely to require mitigation measures.

The impacts that populations face from anthropogenic threats may not always be lethal, therefore any modelling attempts must integrate metrics which allow for non-lethal effects to be assessed (Drewitt and Langston 2006, Abadi et al. 2017). In this regard, modelling and simulating individuals and populations from an energetics perspective allows both body condition and mortality outputs to be generated (Tomlinson et al. 2014). Generally, these approaches require species-specific data to effectively assess how both the behaviour and environment influence energy gain and usage (Fort et al. 2011). Acquiring this data requires studies involving lab-based experiments to assess the basal metabolic rates (BMR), thermal conductivity, behaviour specific metabolic rates and many other species traits (Fort et al. 2011). These studies can be extremely time intensive and difficult due to the challenges of keeping wild animals in lab conditions, with the associated welfare and ethical issues. Alternatively, carrying out these studies in the real world means a lack of control over experimental conditions. To some degree, these values can be determined from allometric scaling equations (Fort et al. 2011, Dunn et al. 2018). These allow for rates to be derived for species based on the scaling body size relationships of many physiological and morphometric parameters that exist across species (Ellis and Gabrielsen 2002, Porter and Kearney 2009). For many species, this will pose the only avenue to begin exploring problems from an energetic context, where empirical data are not available. However, behaviour budgets specifically require empirical knowledge, as these can change widely across spatial and temporal scales (Bost et al. 2015, Dunn et al. 2020). Therefore, in cases where there is a large spatial distribution of populations experiencing different environmental conditions, then population specific budgets will be needed.

Annual cycles

Many species experience a change in environmental conditions through the annual cycle and subsequently adapt their behaviour. For example, in many species of mammals, individuals will go into hibernation to deal with periods of lower food availability (Humphries et al. 2003). Likewise, many species undertake large-scale migrations in order to exploit seasonal changes in food availability (Alerstam et al. 2003). These behavioural adaptations can also improve survivability through other mechanisms, such as by reducing competition (Lamb et al. 2017) and enabling an individual to have easier maintenance of body condition (Zuberogoitia et al. 2018). However, some survival strategies, such as shifts in behaviour budgets through time, may be more subtle and difficult to detect. In these cases, recording and understanding the mechanisms and drivers behind these survival strategies could provide insight into capability to adapt to additional stress, by looking at the flexibility of populations in their available responses (Bardsen et al. 2018, Gatt et al. 2021). For example, periods in the annual cycle where individuals use energetically intensive survival strategies, could indicate a period of particular vulnerability to additional stress. These may be termed energetic bottlenecks, when individuals struggle to balance energy intake against expenditure (Piersma 2002). Therefore, improving our knowledge on the ecology of a species through the whole annual cycle, can generate an understanding of links between seasonal behaviour changes and vulnerability.

In many marine bird species, annual migrations separate the two broadly defined periods of the annual cycle, the breeding and non-breeding season (Desprez et al. 2018). These large-scale movements can represent a huge change in the environmental conditions a population occupies (Gómez et al. 2018, Pollet et al. 2019). These movements are largely driven by temporal changes to productivity, with populations exploiting seasonal availability of prey at higher latitudes to support breeding attempts (Alerstam et al. 2003, Hunt et al. 2016). Therefore, the pressures that individuals experience during these two seasons can also fluctuate massively. During the breeding season, many individuals expend energy on both producing young and surviving and are under central-place constraints (Boyd et al. 2017, Bolton et al. 2019). However, during the non-breeding season, the pressures of raising offspring are largely removed and birds are also freer to move where and when they want. This disparity in energy demands and food availability/accessibility through the annual cycle (Daunt et al. 2006), raises questions on how populations adapt their behaviour to the changing conditions. Understanding the annual patterns and interactions between seasons, could provide insight into how effects in one season could impact another, through carry-over effects (Norris 2005, Harrison et al. 2011). By understanding the periods of the highest stress in the context of carry-over effects, the year-round effects of stress can be quantified. This is vital, as the effects of stress may not be constrained to the period in which they occur. Instead, they may manifest in latter stages of the annual cycle (Fayet et al. 2016), which could be difficult to assess due to inaccessible breeding locations, like the arctic tundra.

Study organism and context

The red-throated diver (*Gavia stellata*) is a piscivorous bird, foraging on a wide range of prey species of a narrow size category (Kleinschmidt et al. 2019). During the breeding season RTDs are largely constrained to freshwater lakes as central place foragers while breeding attempts occur (Groves et al.

1996, Rizzolo et al. 2014). During the non-breeding season, they generally move into the marine environment and remain there until the start of their subsequent breeding attempt, in a pattern shown by most marine birds (McCloskey et al. 2018, Carboneras et al. 2020). Across Europe, they are known to occupy large areas of coastal habitats (Okill 1994, O'Brien et al. 2010, Black et al. 2015, Irwin et al. 2019), with the size of the UK non-breeding season population estimated to be approximately 21,000 individuals (Frost et al. 2019). Currently, the species globally is regarded as Least Concern by the Birdlife international classification of species vulnerability status (BirdLife International 2023). However, the RTDs in Europe is listed as rare or vulnerable on Annex I of the EC Birds Directive and thus is subject to special conservation measures including the classification of Special Protection Areas (SPAs) (Black et al. 2015). Therefore, the species is provided additional protection beyond the Wildlife and Countryside Act (1981), including protection of populations within SPAs. Therefore, important considerations must be made for any disturbances and/or stressors which could impact a SPA population.

Red-throated divers and their interaction with offshore wind farms, and the associated ship traffic, have been the subject of intensive study (Black et al. 2015, Skov et al. 2016, Irwin et al. 2019, Heinänen et al. 2020). At first, broad investigative studies, like the review out by Dierschke et al. (2017), highlighted evidence from general surveys and species-level traits that suggested strong evidence for avoidance of offshore wind farms by this species. These findings were further corroborated with tag deployment (Dorsch et al. 2019) and surveys (Natural England 2010, Heinänen et al. 2020) specifically looking for displacement of divers from offshore windfarms. In combination, these studies supported evidence from post consent monitoring by developers at their OWFs and demonstrated the displacement of red-throated divers from windfarms occurred at distances of up to 20km, but with the strongest displacement effects occurring within 5km (Heinänen et al. 2020). It is also worth noting that this severity of this displacement effect varies widely across spatial and temporal scales (Natural England 2010, Black et al. 2015, Skov et al. 2016, Dorsch et al. 2019, Irwin et al. 2019, Heinänen et al. 2020).Biologging can offer useful approaches for understanding the behaviour and movements of individuals. However, RTDs are difficult to capture compared with most other marine bird species and there was also strong evidence that even the act of visiting a breeding pair can have a negative effect on breeding success (Uher-Koch et al. 2015). This makes RTDs a tricky species to study, which has subsequently led to a dearth in available information on many areas of their ecology (Dierschke et al. 2017).

However, while the displacement of RTDs from offshore windfarms is now well documented (Heinänen et al. 2020, Stenhouse et al. 2020), there has to date been a pressing need for an assessment of the consequences of displacement on RTD populations. For other anthropogenic impacts caused by wind farms, such as mortality from colliding with a wind turbine, there are well informed and parameterized models, specifically constructed to estimate mortality rates. One such case is the model generated by a study from Band et al. (2007), termed the Band Model. This has seen widespread use in estimating the likelihood of an individual bird failing to avoid a wind turbine and hence the collision mortality a population will experience. Further work extending this model to simulated populations and foraging trips, has allowed predictions based on changes to individual behaviours in the breeding season (Warwick-Evans et al. 2018). Specifically designing models to be implemented in the planning stages of a wind farm, can reduce uncertainty over the ecological consequences of new developments (Geary et al. 2020). This approach maximises the applicability of models to evaluating risk and increases the potential userbase of the model. Currently, there is no widely accepted predictive simulation-based model specifically designed to assess the consequences of displacement from offshore windfarms for birds during the non-breeding season. Displacement costs will likely occur as a smaller chronic effect, which manifests itself over a long period of time, rather than a discrete and lethal effect, such as collision (Masden et al. 2009). This poses a much more nuanced challenge compared to mortality from collisions, as these effects can be difficult to quantify (Fox et al. 2006). Further adding to this uncertainty, the effects are likely to be somewhat different in the non-breeding season compared to the breeding season, where central-place foraging constraints may make the barrier effects more pronounced (Masden et al. 2010, Warwick-Evans et al. 2018). In this thesis, the specific question on the consequences of displacement from windfarms plays a core role (Dierschke et al. 2017).

Ecological understanding

This thesis presents some of the first detailed remote sensing data available on RTD ecology and distributions throughout the annual cycle. There have been previous studies on RTDs during the breeding season, with information on traits like foraging habitat (Eriksson and Sundberg 1991), breeding success (Rizzolo et al. 2014, Waldenström 2016) and egg morphology (Rizzolo and Schmutz 2007), to name a few. However, the difficulty in capturing and tagging individuals has meant that much of the behaviour has been assessed through direct observation of individuals. Specifically, insight into diving and foraging behaviour is lacking, especially when compared to other species thought to be vulnerable to displacement by offshore windfarm development, e.g. common guillemot (*Uria aalge*), razorbill (*Alca torda*), Atlantic puffin (*Fratercula arctica)* (Furness et al. 2013, Christensen-Dalsgaard et al. 2018, Bolton et al. 2019, Pereira et al. 2020). Most understanding of foraging behaviour has come from molecular diet analysis (Guse et al. 2009, Kleinschmidt et al. 2019) rather than investigation or description of diving behaviour. Understanding this species' ecology will play a role in understanding potential impacts of anthropogenic activity on populations. However, for RTD the insight gathered during the breeding season is less pressing in this context. Specifically, this is due to the reduced interaction with anthropogenic pressures during this timeframe and the lack of large breeding colonies in RTDs, which means one development is less likely to affect large numbers of individuals. Therefore, analysis and description of ecology of the RTD during the breeding season is presented as separate chapters (Chapters 2 & 3) in this thesis and the focus is somewhat shifted away from the effects of anthropogenic activity. In these chapters, the focus is on describing the behaviour from a purely ecological standpoint, rather than within the context of anthropogenic pressure. However, these results may provide context on anthropogenic activity in the future, if development begins to encroach on areas of importance in the breeding season, or new pressures begin to apply to this species at this time.

In general, the ecology of a species must first be understood before work on the energetics of a species can be studied (Fort et al. 2011). Specifically, an understanding of how individuals apportion their time across their behaviours is required (Fort et al. 2011, Chimienti et al. 2020). Across the field of ecology, the behaviours of animals can be monitored and categorised through a wide array of methods (Tremblay et al. 2009, Pettorelli et al. 2014). Some studies rely on observations of individuals and populations to describe behaviour and budgets of time to defined behaviour (Paruk 2008, Polak and Ciach 2007). While these methods provided easily verifiable results, they suffered from requiring a large investment of time from the observer and generally limiting studies to periods where the animals were directly observable. Over time, technologies have developed that allow for remote sensing of animals (Tremblay et al. 2009, Booth et al. 2020). The benefits of these technologies are two-fold. Firstly, the time investment per individual is much reduced, such that for each individual observed only the time to deploy and retrieve the device is required (Rishworth et al. 2014). Furthermore, in cases where the logger transmits data, then even retrieval of the device may be unnecessary (Rishworth et al. 2014). This generally means a higher number of individuals can be sampled. Secondly, remote technologies allow for unobservable behaviours and/or time periods to be studied. For example, diving behaviour of many seabird species had been obscured to researchers outside of laboratory environments, until the deployments of depth recording devices (Tremblay et al. 2003). It is the development and widespread deployment of these technologies that has enabled the quantification of energy budgets through time for species which are largely unobservable on a scale suitable to make population-level quantifications (Dunn et al. 2022). These data and insights then are able to form the foundation of energetics approaches to understanding species (Fort et al. 2011, Cooke et al. 2013, Tomlinson et al. 2014).

Thesis methods and technologies

In this project, I used two types of archival tags to record behaviour and location. In each of the individual data chapters, I discuss the relevant methods to deploy, retrieve and analyse the data which is relevant to the aims of that chapter. In this thesis, all data recorders used are archival, so devices must be recovered following deployment. Here, this means deployment in one breeding season and then recovery in a subsequent year.

Briefly, these two devices were time-depth recorder (TDR) tags and light-based geolocator (GLS) tags. GLS tags primarily provide data on locations based on light levels. This method works by relying on the differences in day length and the timing of both midday and midnight across latitude and longitude, respectively (Wilson et al. 1998). While these tags are unable to generate fine-scale movement and location data, they are very small and light. For these reasons, they proved to be an ideal tag to deploy on a species which could be vulnerable to tag effects if inappropriately large tags were used. For this reason, I also used small TDR tags, to record the pressure, as a proxy for depth, across time. This data provides insight into the diving profiles of individuals, as pressure increases with the increasing depth of waters. In addition to these primary functions, the GLS tag also records water immersion and the TDR tag also records temperature. However, both of these additional functions are at a much lower temporal resolution then their primary data recording capabilities. Along with this thesis and the associated publications, additional information on the success and challenges of field seasons has been published through a number of reports written by the JNCC (O'Brien et al. 2018, Duckworth et al. 2020, O'Brien et al. 2020). These reports further discuss the effort and expertise of the fieldworkers in this project. Together, they demonstrated creativity and flexibility in the field in overcoming many trials and tribulations involved. The teams involved managed the sites independently, but worked in parallel, sharing knowledge and insights.

I also used stable isotope analysis for some of the chapters in this thesis. These methods are described in more detail in the relevant chapters. Briefly, this analysis involved sampling the distal end of different feather types and quantifying the relative abundance of the most common isotopes. Isotopes tend to vary in predictable fashion across many scales (Inger and Bearhop 2008, St John Glew et al. 2018). Therefore, using knowledge of these relationships, I attempted to link these values to ecological traits. The two primary elements of analysis in this thesis focus on the link between isotope values with diet and location. Ultimately, such methods could potentially lead to novel methods to assign individuals of unknown origin to moulting grounds and foraging strategies.

Overall, this thesis forms the groundwork for both building an understanding of the year-round RTD ecology and forming predictions on how future construction of windfarms could impact their survival in the non-breeding period (Dierschke et al. 2017). I achieve this using a range of remote sensing technology, modelling, statistics and lab-based techniques. In the following six data chapters, I present what I learned of RTD behaviour and ecology in Chapters 2 through 6, before presenting an IBM in Chapter 7, which draws on empirical data generated during the earlier chapters. Finally, Chapter 8 summarises the key conclusions and discusses how the findings of this thesis fit into the wider literature and addresses knowledge gaps.

Data chapter overview and aims

Chapter 2: First biologging record of a foraging red-throated loon Gavia stellata shows shallow and efficient diving in freshwater environments

A short paper discussing an early tag retrieval during the PhD project which was completed while waiting for the field season and subsequent tag retrievals. The paper documents the first ever diving records of a RTD and primarily demonstrates a lack of marine foraging. This is a short chapter, written predominantly for the purpose of forming an early output of the project and exposing the analytical procedures to peer review early.

Published in: Marine Ornithology, 2020

Chapter 3: Spatial and temporal variation in foraging of breeding red-throated divers

An exploration of the summer foraging behaviour of RTDs across a breeding season. Here, I demonstrate a switch from benthic to pelagic foraging as the breeding season proceeds and how each population demonstrates a proportion of benthic and pelagic dives overall. I also found that foraging time across the summer period varies little, demonstrating a change in the type of foraging effort, rather than a change in time committed. The work in this chapter links to the themes of foraging behaviour and site-level differences explored in other chapters.

Published in: Journal of Avian Biology, 2021

Chapter 4: Winter locations of red-throated divers from geolocation and feather isotope signature

Using remote sensing technology, I show the core distributions of RTDs from their moulting site to their core winter distributions. I also demonstrate the differing strategies across three populations, with examples of resident, migratory and partial migratory strategies. I then link these location differences to differences in isotope values from feather samples. This paper provides the groundwork for a method to apportion individuals to a population based solely on a feather sample, which is a theme shared with other later chapters.

Published in: Ecology & Evolution, 2022

Chapter 5: Linking foraging behaviour to isotope signatures in a diving bird

Following on from the previous chapter, I link changes in isotope signatures to individual benthic and pelagic diving strategies across the three study populations. This chapter attempts to form the groundwork for a future method to determine individual foraging habitat and thus prey based solely on feather samples. This and the previous chapter are heavily linked in both their subject matter and approach to develop methods.

Submitted to: Royal Society Proceedings B, 2023

Chapter 6: Variation in non-breeding season strategy drives differences in behaviour and energy expenditure of red-throated diver

This paper draws on the all the data and insights gathered during the previous chapters to explore the behaviour budgets of RTDs during the non-breeding season. Additionally, I use a mixture of allometric scaling equations and equations from the wider ornithological literature to translate these behaviour budgets into energetic expenditures. I explore both behaviour and energetic changes through the season and link these to environmental changes experienced both spatially and temporally. These are finally linked to the context of constraint and the capability of populations to adapt to additional stress.

Submitted to: Oecologia, 2023

Chapter 7: Development of an Individual based model to explore energetic and behaviour consequences of displacement: with specific application to red-throated divers (*Gavia stellata*)

This chapter presents the framework for an individual based model that simulates energetic expenditure and demographic rates for any marine bird species. The chapter explores how the changes such as those that offshore windfarm development might induce can cause displacement and subsequently apply stress to populations. The impacts of varying the levels of disruption to the overwinter survival rates, body mass and energetic stress for individuals are explored. The model is presented in a broad fashion, to increase wider applicability, but the results are presented specifically for RTDs.

Not submitted for publication

Additional outputs during the PhD:

- Distribution and foraging efficiency limit occupancy of breeding sites in the non-breeding season in a colonial seabird. S. Bennett, F. Daunt, K. R. Searle, M. P. Harris, L. Buckingham, J. Duckworth, R. E. Dunn, S. Wanless, M. A. Newell, J. A. Green. **Submitted to Animal behaviour. 2023.**

- Revisiting fuel tax concessions (FTCs): The economic implications of fuel subsidies for the commercial fishing fleet of the United Kingdom. D. Vaughn, D. Skerritt, J. Duckworth, M. Duffy. Submitted to Marine Policy. 2022.

- Red-Throated Diver Energetics Project: Final Report. 2023. D. L. Thompson, J. Duckworth, L. Ruffino, L. Johnson, P. Lehikoinen, D. Okill, A. Petersen, I.K. Petersen, R. Väisänen, J. Williams, S. William, J. Green, F. Daunt, & S. O'Brien, JNCC Report. JNCC. Peterborough.

- Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. 2023. L. Buckingham, F. Daunt, M. I. Bogdanova, R. W. Furness, S. Bennett, J. Duckworth, R. E. Dunn, S. Wanless, M. P. Harris, D. C. Jardine, M. A. Newell, R. M. Ward, E. D. Weston & J. A. Green. Journal of Avian Biology. 1-2. e03018.

- Red-throated Diver Energetics Project: Preliminary Results from 2018/19. 2020. J. Duckworth, J. A. Green, F. Daunt, L. Johnson, P. Lehikoinen, D. Okill, A. Petersen, I. K. Petersen, R. Väisänen, J. Williams, S. William, S. O'Brien, JNCC Report. JNCC. Peterborough.

The reference and format style of each chapter are kept in the format of the journal they were published in or submitted to for the purpose of consistency across versions. Where the chapter was not submitted to a journal, standard formatting according to the University of Liverpool thesis submission guidelines are used instead.

Chapter 2 First biologging record of a foraging red-throated loon *Gavia stellata* shows shallow and efficient diving in freshwater environments

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Declaration of authorship

JG, SO, FD, IP and JD conceived the ideas and designed methodology; PL and RV collected the data; JD analysed the data and created visualisations; SO, JG, AP and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Key words: Red-throated Loon, Finland, foraging, time depth recorder, Geolocator

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Abstract

Recently, Red-throated Loons *Gavia stellata* (RTL) have been the subject of increased interest due to their negative interactions with shipping, offshore wind farms, and other marine industry activities. This has driven a desire to quantify the behaviour and ecology of this understudied species, particularly during the non-breeding season. To achieve this, Time Depth Recorder (TDR) and Global Location Sensor (GLS) tags were deployed on individuals from several European locations. Due to an incidental mortality, one set of tags was retrieved early. The single set of tags recorded activity from June to August 2018. The TDR collected records for 14 d, providing the first ever biologging data on RTL foraging in Europe. The bird was tagged 90 km from the coast; therefore, it only used freshwater lakes and was never recorded entering saltwater. The individual mostly undertook shallow dives, with maximum and mean depths of 20 m and 5.4 m, respectively. Foraging constituted 22.9 % of total activity during the sampling period. The RTL had diel foraging patterns, with dives being shallower and more frequent at times of “twilight” compared to “daylight.” These results provide novel information on an RTL’s diurnal patterns of water depth usage and foraging effort during the summer, demonstrating the potential of data loggers to provide key insights into the foraging ecology of this species.

Introduction

In recent years, Red-throated Loons *Gavia stellata* (RTL) have received increased attention because of their vulnerability to habitat loss from construction of offshore renewable energy structures and shipping (Garthe et al. 2004, Schwemmer et al. 2011, Mendel et al. 2019). Previous studies have provided insight into many important aspects of RTL ecology, including diet (Reimchen et al. 1984, Guse et al. 2009), foraging (Eriksson et al. 1991, Skov et al. 2001), and behaviour (Polak et al. 2007). As a result of research on diet, RTLs are known to be generalist piscivorous foragers (Eriksson 1985, Morkūnė et al. 2016, Kleinschmidt et al. 2019), with prey that vary by geographic area (Guse et al. 2009). RTLs breed on freshwater ponds and lakes of different sizes during the summer, feeding on either freshwater (Eriksson et al. 1990, Eriksson et al. 1991) or marine prey (Reimchen et al. 1984, Rizzolo et al. 2015), with proximity to the coast being the likely driver of habitats used.

Recent advances in biologging techniques have facilitated a greatly improved understanding of aquatic top predator ecology and behaviour, especially winter behaviour and migrations (Rutz et al. 2009). Much of our current knowledge of RTL ecology is derived from observations at a distance to collect empirical data (Eriksson et al. 1990, Eriksson et al. 1991, Rizzolo et al. 2015, Uher-Koch et al. 2018). However, RTLs breed at low densities (Solovyeva et al. 2017) and are highly sensitive to disturbance both at sea (Mendel et al. 2019) and at their breeding lakes (Rizzolo et al. 2014), limiting our ability to gain a full understanding of their ecology. Biologging techniques, which require few visits to an individual and relatively little disturbance, provide an ideal approach to answer specific questions about RTL foraging, water depth usage, and energetic budgets over long periods. However, this must be measured against the substantial difficulty of recapturing a RTL. Regardless, for a relatively under-studied species such as the RTL, even single biologging records can provide proof of concept for this approach (Sequeira et al. 2019).

During a larger project looking at breeding and non-breeding season energetics and foraging behaviour (O'Brien et al. 2018), a single Time Depth Recorder (TDR) and light-based Global Location Sensor (GLS) were recovered from a bird drowned in a gill net at the end of summer, three months after deployment. The data downloaded from these loggers provided the first biologging record of a foraging RTLD in Europe, allowing estimates of diel patterns of depth usage and foraging behaviour. Here we: (1) determine whether this individual remained in freshwater habitats during the breeding season; (2) describe water depth usage and diving strategy; and (3) quantify diel patterns of diving.

Methods

Study area

The bird was tagged at its nest site on a lake in Mäntyharju, southern Finland, on 04 June 2018, 90 km from the coast.

Deployment of loggers

In southern Finland, most RTLs in the study area nest on artificial rafts on small lakes (Nummi et al. 2013). Nests of RTLs were approached, causing the incubating diver to flush from the nest, following which a nest trap was laid to capture the bird on its return to the nest. Trapping was not attempted during the early stages of egg laying, nor when chicks were less than five days old (O'Brien et al. 2018). The single diver in this study was tagged on 04 June 2018 and found dead on 14 August 2018. After trapping, the pair continued incubation until 07 June, but on 08 June the nest had been abandoned. The pair laid a second clutch to a new nest by 25 June. This clutch failed by 25 July, when no divers were present at the breeding lake.

A Time Depth Recorder (TDR; Cefas G5 Standard TDR, dimensions: 8 mm x 31 mm, weight: 2.7 g) was attached to one 1.5 mm thickness plastic ring using cable ties and epoxy resin glue; the ring was then placed onto the leg of the RTL. A light-based Global Location Sensor (Biotrack MK4083 Geolocator, dimensions: 17 mm x 10 mm x 6.5 mm, weight: 1.8 g) was attached to a plastic ring using the same methods as for the TDR tag and was fitted on the diver's other leg (for full methodology, see O'Brien et al. (2018)).

TDRs were programmed to sample barometric pressure, as a proxy for depth, every 6 s for 24 h, with a 4 d gap between sampling days. These sampling intervals were chosen to allow samples of dive behaviour to be gathered across the year, without impacting the ability to detect individual diving events. TDRs recorded dives with an accuracy of 0.1 m. GLS tags were set to record maximum light levels and saltwater immersion every 10 min (each 10-min record contained a number between 0 and 200, where 200 represents the tag being constantly immersed), for every day of deployment. The RTL was classified as being in saltwater when the GLS tag recorded any number greater than three (Fayet et al. 2016).

Data analysis

The baseline surface reading of a TDR can change over an extended study period (Elliott et al. 2009). A custom script was created, which shifted the dive profiles to set the barometric readings such that the surface was set to 0 m. The minimum value for the detection of a dive at each recording interval was

0.5 m, and only dives where the maximum depth exceeded 1 m were considered for analyses. These limits helped exclude any non-foraging dives or residual error from the shifting baseline (Falk et al. 2000).

The dives were analysed using a custom script in R, and the following values were estimated for each dive: dive duration (duration of the dive event from first to last recording > 0.5 m), maximum dive depth (lowest depth reached in dive) and surface time (time spent on the surface, between the end of the dive and start of the next dive). The bottom time (the duration of time spent at depths deeper than 75 % of the maximum dive depth (Tremblay et al. 2003) was also calculated for dives longer than 18 s. Dives shorter than 18 s would only have one or two data points due to the tag sampling frequency; therefore, the results would always have bottom times greater than half of the total dive length. Due to the resolution of dives, classification of dive shape was not possible.

To further define diving strategy, dives were classified into bouts, defined as a series of dives where the maximum surface time between each dive was less than 60 s. A 60 s cut-off was chosen based on the decreased frequency of surface times above 60 s (Figure 2.1). Bouts with greater than four dives were defined as foraging bouts (Mehlum et al. 2001). Dive depth consistency (difference in maximum dive depth between the current and previous dive) was calculated for all dives within a foraging bout to determine whether dives within a foraging bout had similar depths.

To estimate the proportion of time spent foraging in relation to the time of day, we classified dives as occurring during “daylight” or “twilight”. For each dive, sun elevation angles were generated with the R package ‘oce’ (Kelley et al. 2019) for the location of capture. Location of capture was used to derive the sun elevation angle; because the bird was captured and recovered during the breeding season in the same part of Finland, it was assumed not to have left the area between initial tagging and being found dead. “Daylight” was defined as any sun angle above 0, and “twilight” was defined as a sun angle between 0 and -12 (Regular et al. 2011). Due to the high latitude of the study site and the time of year, < 1 % of the records on the TDR and < 1 % of recorded dives were at sun elevation angles below -12. Therefore, “night” was excluded, and all analyses of diel patterns include only “daylight” and “twilight” dives and timings.

The ratio of variances between maximum dive depths at “twilight” and “daylight” was high (F = 3.007, P < 0.001). Therefore, a Wilcox signed rank test was used to explore differences in maximum foraging depths reached during “daylight” and “twilight”. A Chi-squared test was used to test whether dives occurred uniformly across “daylight” and “twilight”, using expected values calculated from the proportion of “twilight” and “daylight” experienced by the bird. All data analyses and statistics were performed in R version 3.5.1 (R Development Core Team 2018). All means are given as ±1 standard deviation.

Results

Data were gathered from 07 June 2018 to 11 August 2018, for a total of 14 and 66 d of TDR (Figure 2.2) and GLS recordings, respectively. The GLS tag revealed that the saltwater immersion sensor had no positive readings for the duration of the study. This suggests that the bird never entered the marine environment and spent the entire deployment period on land and in freshwater habitats.

There were 5947 dives (Figure 2.1A) and 687 dive bouts throughout the duration of the study; of these 235 bouts were classified as foraging and included 88 % of all dives; 22.9% of time when the TDR was recording data was spent in a foraging bout. The RTL undertook an average of 425 ± 98 dives and 17 ± 6 foraging bouts per day with an average maximum dive depth of 5.4 ± 4.3 m (Figure 2.3) and an overall maximum dive depth of 20 m. Foraging dive bouts comprised a highly variable number of dives, with an average of 22 ± 35 dives, but with 119 bouts containing < 10 dives. The longest bout had 339 dives and lasted 212 min. The mean surface time between dives within a foraging bout was 21.3 ± 10.5 s (Figure 2.1B). Subsequent dives within a foraging bout differed in their maximum dive depth by 0.7 ± 1.4 m. The proportion of time at the bottom depths of the dive across dives longer than 18 s was 0.61 ± 0.18.

Mean maximum dive depth during “daylight” (6.2 ± 5.1 m) was greater than during “twilight” hours (4.4 ± 2.9 m) ($W = 3957800$, $P < 0.001$). Dive frequency changed based on light levels ($X2 = 1868.8$, $df = 1$, $P < 0.001$; Figure 2.3), with the proportion of dives occurring at twilight being greater than would be expected by chance. “Daylight” was recorded for 76 % of the study and had 52 % of the dives; “twilight” was recorded for 24 % of the study and had 48 % of the dives (Figure 2.3).

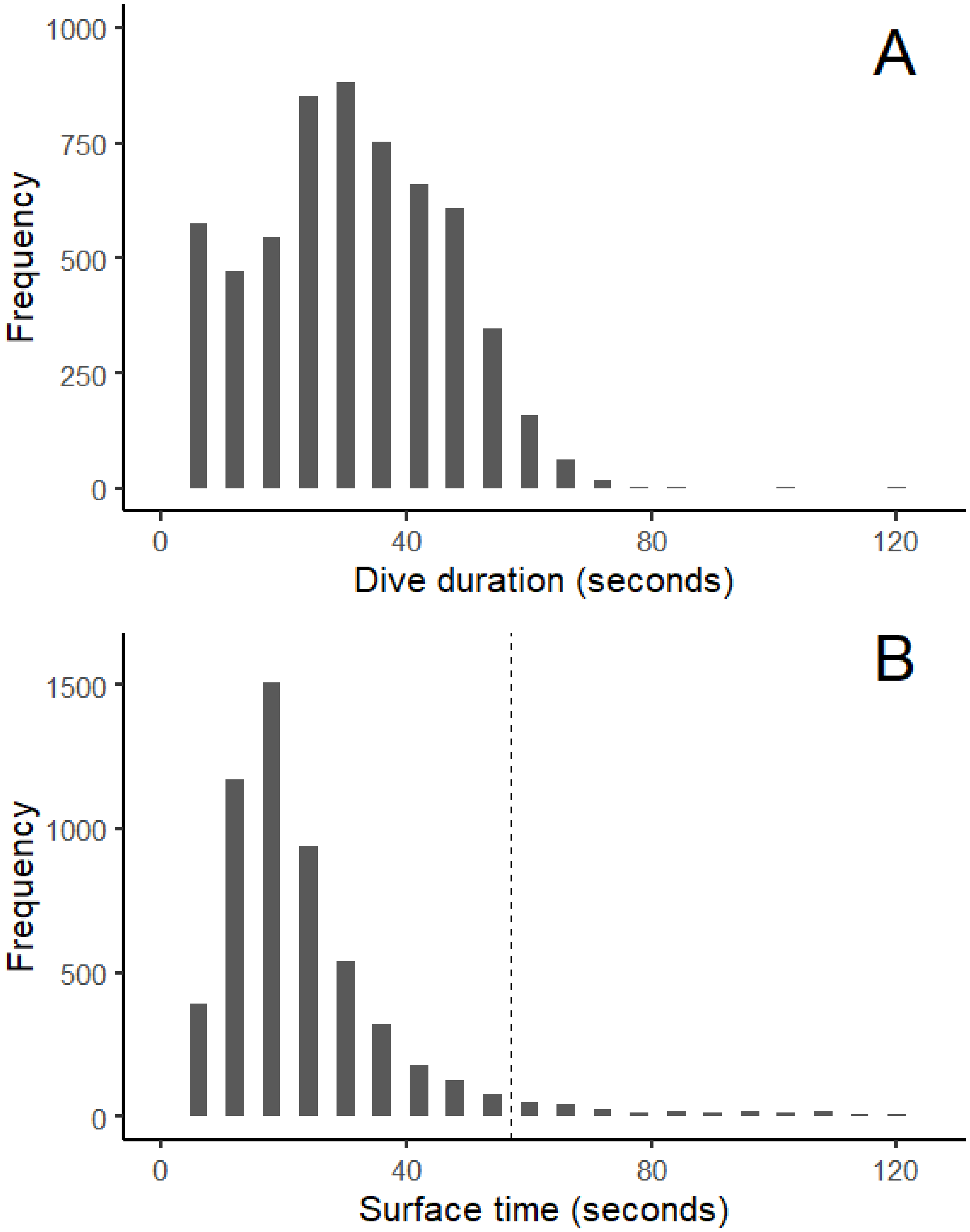

Figure 2.1 Frequency distribution of dive and surface time durations

(A) Frequency of dive durations across the study. The longest confirmed dive was 90 s. Each bar represents a 6-s interval. (B) Frequency of surface times between dives. The vertical dashed line shows the cut-off value, where dives with surface times below 60 s were considered to be within the same dive bout. No surface time above 120 s had a frequency greater than 20. Each bar represents a 6-s interval.

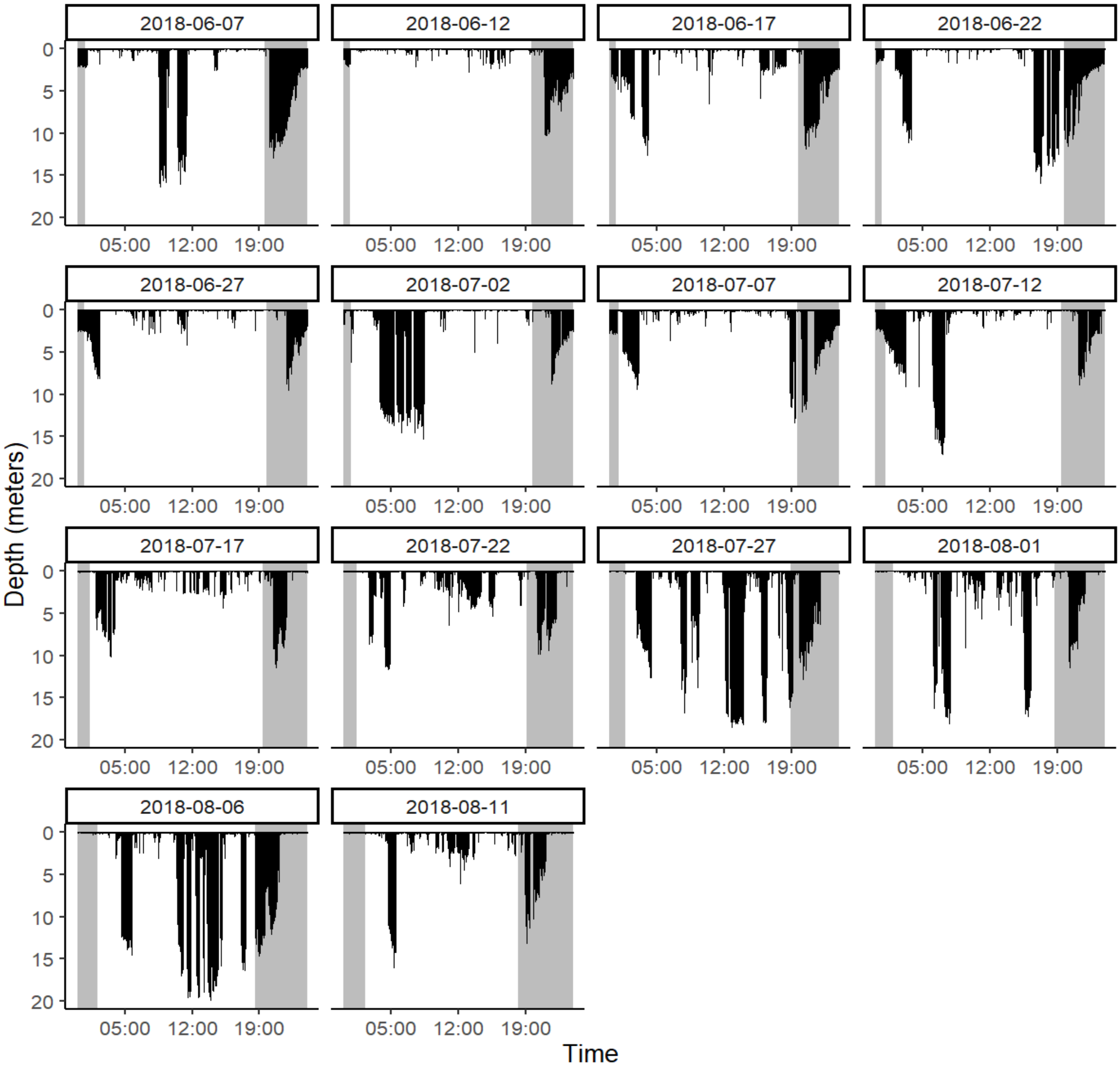

FIGURE 2.2 DIVE PROFILES ACROSS TIME AND LIGHT REGIMES

Dive profiles of the RTL for the 14 d the TDR was active. These lines represent the depth of the RTL at a given time. Shaded areas show times when the sun elevation angle was below 0.

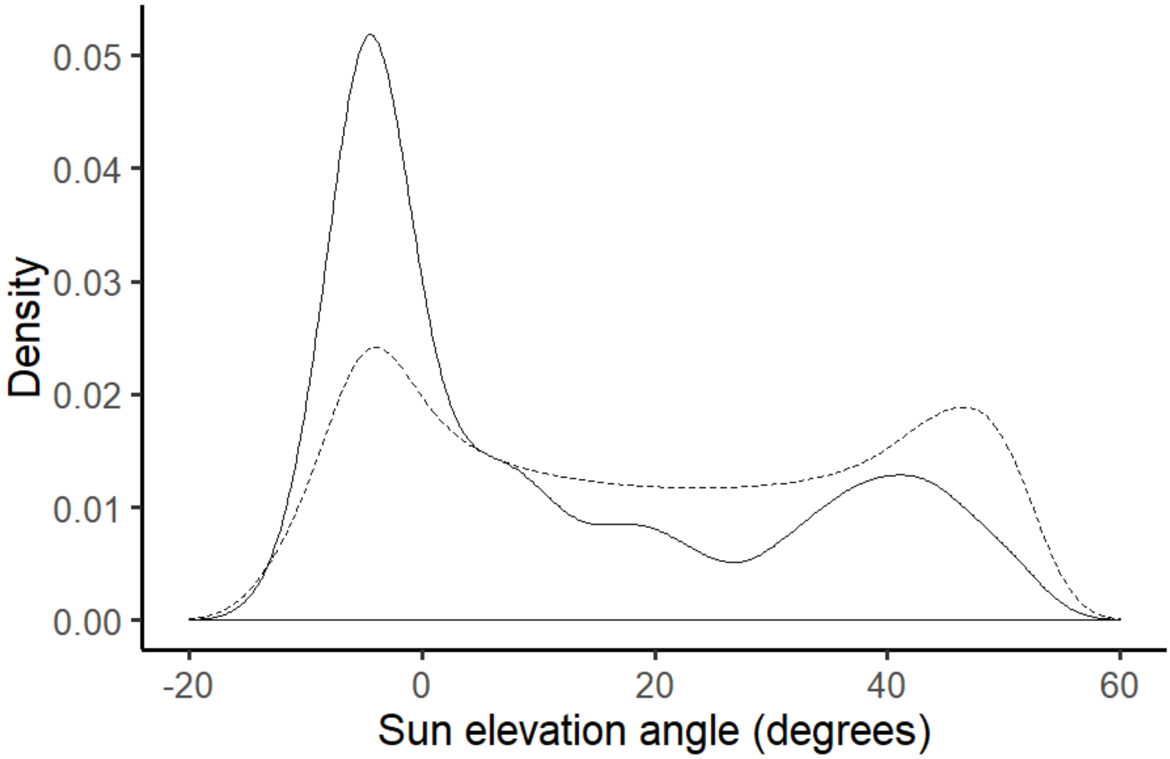

FIGURE 2.3 DENSITY GRAPH OF DIVE DISTRIBUTION AND LIGHT LEVELS EXPERIENCED

Density graph showing timings of RTL dives relative to sun elevation angles, where the solid line represents the density of dives recorded from the recovered TDR at observed sun elevation angles through the deployment period, and the dashed line represents the density of time spent by the RTL at a sun elevation angle across the study period. Smoothing parameter: h = 3 for both densities.

Discussion

This study used biologging technology to provide the first empirical data on RTL foraging depth and behaviour. In the bird studied, we found that dives were always < 20 m deep and varied according to light conditions, with dives tending to be shallower and more frequent during lower light levels. The RTL was capable of undertaking extended bouts of diving, lasting over three hours. Additionally, this study provided empirical evidence of a RTL foraging solely in freshwater environments. Together, these data generate an interesting hypothesis regarding the foraging behaviour of Red-throated Loons.

A previous study found that bouts where the maximum dive depths were within 10 % of the preceding maximum dive depth could be classified as benthic (Tremblay et al. 2000). Here, the average difference between subsequent maximum dive depths was slightly > 10 % of the average maximum dive depth for all dives, which was 5.4 m. This suggests that, although there was some consistency in the depths to which the RTL dived, it is unlikely that the RTL was using a solely benthic foraging strategy. Moreover, the loon was found in a lake with a maximum depth of 29 m, which exceeds the maximum dive depth recorded across the study period. This implies that the dives were likely pelagic and/or that any benthic dives were in the shallower areas of the water.

Our results are consistent with data on RTLs from TDRs recovered by D. Rizzolo (pers. comm.), who recorded shallow dives (median 2.49 m, range 1.1–10.8 m) and a slightly deeper maximum dive depth of 26.9 m. Winter observations of RTLs have revealed high densities of these birds at inshore marine areas with water depths < 20 m (Petersen et al. 2010). Together, these results indicate that the lack of deeper dives is likely due to physiological diving constraints or prey preference, rather than being limited by water column depth. However, analysis of more RTL diving profiles is needed to fully characterize the diving behaviour of this species in various habitats (Sequeira et al. 2019).

The reason for the observed increased rate of foraging during the twilight hours is unknown. One hypothesis is that there was an increased presence of prey in the shallower, more accessible areas of the lake, due to either lower oxygen levels at deeper depths (Kersten et al. 1991) or more favourable light conditions closer to the surface. An increased number of fish in the shallower areas could also provide an explanation for shallower dives at twilight. Additional research could explore whether dive shapes change over the different light levels of the day. This could be determined using a higher-frequency TDR setting to gain more recordings per dive (Schreer et al. 2001).

Other than laying a second clutch (Okill 1994), little is known about the activities of RTLs following a failed breeding attempt. Here, we demonstrate that a Finnish RTL can use an entirely freshwater habitat for foraging during the breeding season, plus continue to remain in freshwater following two failed clutches. This behaviour is likely a consequence of the large distance of the breeding site from the coast. Other studies have shown that, during the non-breeding season, RTLs are entirely dependent on the marine environment (Guse et al. 2009, Morkūnė et al. 2016); therefore, seeing one on freshwater during the winter is exceptional. This seasonal pattern suggests that RTLs are exposed to different stressors during different periods of the annual cycle, which dictates where they reside (Eriksson et al. 1990, Rizzolo et al. 2015). For this reason, with a better understanding of their year-round ecology and movements, RTLs could become a good multisystem indicator of habitat health (Cairns 1987).

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References

CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5: 261–271.

ELLIOTT, K.H. & GASTON, A.J. 2009. Accuracy of depth recorders. Waterbirds 32: 183-191.

ERIKSSON, M.O.G. 1985. Prey detectability for fish-eating birds in relation to fish density and water transparency. Scandinavian Journal of Ornithology 16: 1–7.

ERIKSSON, M.O.G., BLOMQVIST, D., HAKE, M. & JOHANSSON, O.C. 1990. Parental feeding in the Red-throated Diver *Gavia stellata*. Ibis 132: 1–13.

ERIKSSON, M.O.G. & SUNDBERG, P. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. Bird Study 38: 135–144.

FALK, K., BENVENUTI, S., DALL'ANTONIA, L., KAMPP, K. & RIBOLINI, A. 2000. Time allocation and foraging behaviour of chick-rearing Brünnich's Guillemots *Uria lomvia* in high-arctic Greenland. Ibis 142: 82–92.

FAYET, A.L., FREEMAN, R., SHOJI, A. ET AL. 2016. Drivers and fitness consequences of dispersive migration in a pelagic seabird. Behavioral Ecology 27: 1061–1072.

GARTHE, S. & HÜPPOP, O. 2004. Scaling possible adverse effects of marine wind farms on seabirds: developing and applying a vulnerability index. Journal of Applied Ecology 41: 724–734.

GUSE, N., GARTHE, S. & SCHIRMEISTER, B. 2009. Diet of red-throated divers *Gavia stellata* reflects the seasonal availability of Atlantic herring Clupea harengus in the southwestern Baltic Sea. Journal of Sea Research 62: 268–275.

KELLEY, D., RICHARDS, C. & CHANTELLE, L. 2019. 'oce': R Package version 1.1-1 [Available online at: https://CRAN.R-project.org/package=oce. Accessed 20 June 2019].

KERSTEN, M., BRITTON, R.H., DUGAN, P.J. & HAFNER, H. 1991. Flock feeding and food intake in Little Egrets: the effects of prey distribution and behaviour. Journal of Animal Ecology 60: 241–252.

KLEINSCHMIDT, B., BURGER, C., DORSCH, M. ET AL. 2019. The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. Marine Biology 166: 77.

MEHLUM, F., WATANUKI, Y. & TAKAHASHI, A. 2001. Diving behaviour and foraging habitats of Brünnich's guillemots (*Uria lomvia*) breeding in the high-arctic. Journal of Zoology 255: 413–423.

MENDEL, B., SCHWEMMER, P., PESCHKO, V., ET AL. 2019. Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). Journal of Environmental Management 231: 429–438.

MORKŪNĖ, R., LESUTIENĖ, J., BARISEVIČIŪTĖ, R., MORKŪNAS, J. & GASIŪNAITĖ, Z.R. 2016. Food sources of wintering piscivorous waterbirds in coastal waters: a triple stable isotope approach for the southeastern Baltic Sea. Estuarine, Coastal and Shelf Science 171: 41–50.

NUMMI, P., VÄÄNÄNEN, V., PAKARINEN, R. & PIENMUNNE, E. 2013. The Red-throated Diver (*Gavia stellata*) in human-disturbed habitats - building up a local population with the aid of artificial rafts. Ornis Fennica 90: 16–22.

O'BRIEN, S., RUFFINO, L., LEHIKOINEN, P. ET AL. 2018. Red-Throated Diver Energetics Project - 2018 Field Season Report. JNCC Report No. 627. Peterborough, Canada: Joint Nature Conservation Committee.

OKILL, J.D. 1994. Ringing recoveries of red-throated divers *Gavia stellata* in Britain and Ireland. Ringing & Migration 15: 107–118.

PETERSEN, I.K., NIELSEN, R.D., PIHL S., ET AL. 2010. LANDSDÆKKENDE OPTÆLLING AF VANDFUGLE I DANMARK, VINTEREN 2007/2008. Working Report from DMU, Aarhus University. Frederiksborgvej, Denmark: The Danish Environmental Research Institute.

POLAK, M. & CIACH, M. 2007. Behaviour of black-throated diver Gavia arctica and red-throated diver *Gavia stellata* during autumn migration stopover. Ornis Svecica 17: 90–94.

R DEVELOPMENT CORE TEAM. 2018. R: A language and environment for statistical computing. Vienna, Austria. R Foundation for Statistical Computing. [Available online at https://www.R-project.org/].

REGULAR, P.M., HEDD, A. & MONTEVECCHI, W.A. 2011. Fishing in the dark: a pursuit-diving seabird modifies foraging behaviour in response to nocturnal light levels. PLoS One 6: e26763.

REIMCHEN, T.E. & SHEILA, D. 1984. Feeding schedule and daily food consumption in Red-throated Loons (*Gavia stellata*) over the prefledging period. The Auk 101: 593–599.

RIZZOLO, D.J., SCHMUTZ, J., A., MCCLOSKEY, S.E. & FONDELL, T.F. 2014. Factors influencing nest survival and productivity of Red-throated Loons (*Gavia stellata*) in Alaska. The Condor: 574–587.

RIZZOLO, D.J., SCHMUTZ, J.A. & SPEAKMAN, J.R. 2015. Fast and efficient: postnatal growth and energy expenditure in an Arctic-breeding waterbird, the Red-throated Loon (*Gavia stellata*). The Auk 132: 657–670.

RUTZ, C. & HAYS, G.C. 2009. New frontiers in biologging science. Biology Letters 5: 289–292.

SCHREER, J.F., KIT, M.K. & HARA HINES, R.J.O. 2001. Comparative Diving Patterns of Pinnipeds and Seabirds. Ecological Monographs 71: 137.

SCHWEMMER, P., MENDEL, B., SONNTAG, N., DIERSCHKE, V. & GARTHE, S. 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. Ecological Applications 21: 1851–1860.

SEQUEIRA, A.M.M., HEUPEL, M.R., LEA, M.A. ET AL. 2019. The importance of sample size in marine megafauna tagging studies. Ecological Applications 29: e01947.

SKOV, H. & PRINS, E. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. Marine Ecology-Progress Series 214: 279–287.

SOLOVYEVA, D., PARUK, J., TASH, J., ET AL. 2017. Post-breeding densities, population sizes and lake size partitioning of loon species in western Chukotka, Russia. Contemporary Problems of Ecology 10: 621–631.

TREMBLAY, Y. & CHEREL, Y. 2000. Benthic and pelagic dives: a new foraging behaviour in rockhopper penguins. Marine Ecology Progress Series 204: 257–267.

TREMBLAY, Y., CHEREL, Y., OREMUS, M., TVERAA, T. & CHASTEL, O. 2003. Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. Journal of Experimental Biology 206: 1929–1940.

UHER-KOCH, B.D., KOCH, J.C., WRIGHT, K.G. & SCHMUTZ, J.A. 2018. Comparative nest survival of three sympatric loon species breeding in the Arctic. Journal of Avian Biology 49: e01671.

Chapter 3 Spatial and temporal variation in foraging of breeding red-throated divers

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JG, SO, FD, IP and JD conceived the ideas and designed methodology; JG, SO, FD, IKP, JD, AP, GB, LJ, PL, DO, RV, JW and SW collected the data; JD analysed the data and created visualisations; SO, JG, AP and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

Differing environmental conditions can have profound effects on many behaviours in animals, especially where species have large geographic ranges. Seasonal changes or progression through life history stages impose differential constraints, leading to changes in behaviours. Furthermore, species which show flexibility in behaviours, may have a higher capacity to adapt to anthropogenic-induced changes to their environment. The red-throated diver (RTD) is an aquatic bird, that is able to forage in both freshwater and marine environments, though little else is known about its behaviours and its capacity to adapt to different environmental conditions. Here, we use time-depth recorders and saltwater immersion loggers to examine the foraging behaviour of RTDs from three regions across northwest Europe. We found that in the breeding season, birds from two regions (Iceland and Scotland) foraged in the marine environment, while birds from Finland, foraged predominantly in freshwater. Most of the differences in diving characteristics were at least partly explained by differences in foraging habitat. Additionally, while time spent foraging did not change through the breeding season, dives generally became more pelagic and less benthic over the season, suggesting RTDs either switched prey or followed vertical prey movements, rather than increasing foraging effort. There was a preference for foraging in daylight over crepuscular hours, with a stronger effect at two of the three sites. Overall, we provide the first investigation of RTD foraging and diving behaviour from multiple geographic regions and demonstrate variation in foraging strategies in this generalist aquatic predator, most likely due to differences in their local environment.

Introduction

Many species and animal populations are dealing with reduced fecundity and survival from a plethora of anthropogenic pressures, such as marine debris (Horn et al. 2020), pollution (Erikstad et al. 2013, Amelineau et al. 2019) and habitat loss (Harper et al. 2008). These threats can vary widely across geographic landscapes, leading to differential pressures affecting populations (Plumpton and Andersen 1998, Hovick et al. 2014). Additionally, the pressures experienced by populations vary temporally; across annual cycles and between years (Salamolard and Weimerskirch 1993, Shaffer et al. 2001). For example, during the breeding season, some animals must provide parental care and be geographically constrained as central place foragers, which contrasts with non-breeding periods such as migration. Even within a period, demands over time and pressures experienced may not be constant. For example, the behavioural budgets of an individual can change with demands of the growing offspring (Tulp et al. 2009) which might alter their exposure to anthropogenic pressures and/or exacerbate any constraints that they may impose (Thaxter et al. 2015). Understanding the fundamental biology of species and changes in their behaviour and ecology over temporal and spatial gradients is thus key to making informed management decisions to minimise current and future threats (Grémillet and Boulinier 2009).

Foraging behaviour is closely linked to demographic rates, as energy intake plays a vital role in both survival and reproduction (Boggs 1992). Therefore, changes to foraging characteristics that affect energy intake, such as distance to foraging site (Bost et al. 2015), foraging success (Crocker et al. 2006) and prey selection (Peckham et al. 2011) can be linked to changes in population demographic rates. For species which have some flexibility in how and where they forage, then the nature of the environment and ecosystems that they inhabit can have a major influence on foraging behaviour (Maynard and Davoren 2020). Furthermore, for species foraging in areas influenced by humans, anthropogenic activity has the potential to affect foraging characteristics (Senzaki et al. 2016, Scrafford et al. 2017, Millon et al. 2018). This makes the acquisition of knowledge on the foraging behaviour of species vital to understand, in order to know whether conservation efforts or interventions are required (Grémillet and Boulinier 2009).

Red-throated divers (RTDs; *Gavia stellata*) are a northerly distributed species of aquatic bird, generally occupying latitudes above 50°N (Carboneras et al. 2020). This species faces many of the threats previously mentioned (Schmutz et al. 2009, Burger et al. 2019) and is known to be vulnerable to anthropogenic presence (Schwemmer et al. 2011, Nummi et al. 2013, Uher-Koch et al. 2015) and structures (Furness et al. 2013, Mendel et al. 2019, Heinänen et al. 2020). This aversion to anthropogenic presence could be detrimental to demographic rates, through displacement effects

(Drewitt and Langston 2006), but these effects are hard to observe and measure directly, as the birds are often in inaccessible locations. Some information exists on aspects of the behaviour and ecology of this species at the nest during the breeding season, such as descriptions of chick rearing and nesting success (Eriksson et al. 1990, Rizzolo et al. 2015, Uher-Koch et al. 2018). However, there is a lack of information on foraging behaviour and water depth usage compared to other, better studied species (Grémillet et al. 1998, Linnebjerg et al. 2014, Amelineau et al. 2019, Poupart et al. 2019).

To build on this limited body of knowledge, we used biologging technology to examine the breeding season foraging behaviour of RTDs from three geographically distinct regions in northern Europe: Scotland, Finland and Iceland. By looking across multiple sites, we were able to both describe the foraging behaviour of the sampled individuals and examine how local environment may drive foraging behaviour differences between regions. The limited information available on RTD foraging allowed us to generate broad predictions on how foraging behaviour could differ between regions. Surveys of non-breeding season distribution show RTDs tend to favour habitats with water depths less than 20 m (Petersen et al. 2010, O'Brien et al. 2012), but can also be found in deeper waters (Heinänen et al. 2020). Biologging data from a single RTD in the breeding season provided some evidence to support this shallow depth usage, with the individual showing few dives reaching depths deeper than 20 m (Duckworth et al. 2020b).

RTDs in Finland breed at a much greater distance from the coast than the majority of those breeding in Scotland and Iceland, and previous evidence from populations breeding in similar environments further from the coast show RTDs to be likely to forage in freshwater habitats (Eriksson et al. 1990, Eriksson and Sundberg 1991, Duckworth et al. 2020b). In contrast, birds breeding close to the coast, tend to forage in marine environments (Reimchen and Douglas 1984, Black et al. 2015, Rizzolo et al. 2015). Therefore, we predicted that the recorded foraging metrics of birds from Scotland and Iceland, which were all breeding close to the coasts, should be the most similar, while birds breeding inland in Finland should be less so. Overall, we expect RTDs across all regions to be diving to shallow depths, < 20 m and demonstrate a mixture of benthic and pelagic foraging strategies (Kleinschmidt et al. 2019). We also predict that foraging effort would increase as the breeding season progresses, due to the increasing energetic demands of breeding over time (Dunn et al. 2018). The proportion of benthic dives was predicted to decrease over the breeding season, as previous study has shown adults sometimes provide small benthic prey when chicks are young and a wider array of larger benthic and pelagic prey as the chicks grows (Reimchen and Douglas 1984). This was based on the single-prey loading constraint on divers and therefore a need to maximise the energy that can be delivered per foraging trip, while not exceeding the maximum swallowing capacity of a chick at a given age. Among aquatic prey, benthic invertebrates can form a large part of chick diet, due to the small prey size required by young divers during their first days of growth (Jackson 2003). Spatial and temporal drivers may also interact with each other since divers are opportunistic foragers (Kleinschmidt et al. 2019) and have demonstrated an ability to forage in different aquatic habitats. Thus, temporal effects during the breeding season may vary between locations, most likely driven by local prey accessibility. Previous evidence has also suggested RTDs may forage based on light conditions, with crepuscular foraging patterns (Duckworth et al. 2020a).

Our overall goal was to provide the first detailed information on breeding season foraging behaviour from multiple individual RTDs and begin to quantify spatial and temporal variation in this behaviour. To achieve this, we addressed three specific objectives: 1) Describe the foraging and diving behaviour of RTDs from three geographically distinct regions. 2) Investigate variation in foraging behaviour and strategies across these three regions. 3) Look at variation in foraging ecology over long (breeding season) and short (daily light levels) time scales.

Methods

Sampling birds

From May 2018 to July 2018, 74 RTDs were caught at nesting sites across three distinct geographical regions in southern Finland (n=31), north-eastern Iceland (n=12) and the Scottish archipelagos of Orkney and Shetland (n=31) (Figure 3.1). Birds were caught using nest traps, mist nets or walk-in traps (O'Brien et al. 2018). Assessment of the sex of each bird through molecular assessment was not done, due to logistical issues. Both time-depth recorders (TDR; Cefas G5 Standard TDR, dimensions: 8 × 31 mm, weight: 2.7 g) and light-based geolocators (GLS; Biotrack MK4083 Geolocator, dimensions: 17 × 10 × 6.5 mm, weight: 1.8 g) were attached to the legs of each captured RTD. In total 27 birds were recaptured in 2019, using the same capture methods. We recovered 8, 8 and 7 functioning TDRs and 7.7 and 5 functioning GLS tags from Finland, Iceland and Scotland, respectively (Supporting information). Due to the inaccessibility of nests and to avoid undue disturbance to breeding RTDs, it was not possible to observe the fate of breeding attempts or breeding chronology of each of the sampled birds in terms of nest initiation, laying, hatching, fledging and departure for migration.

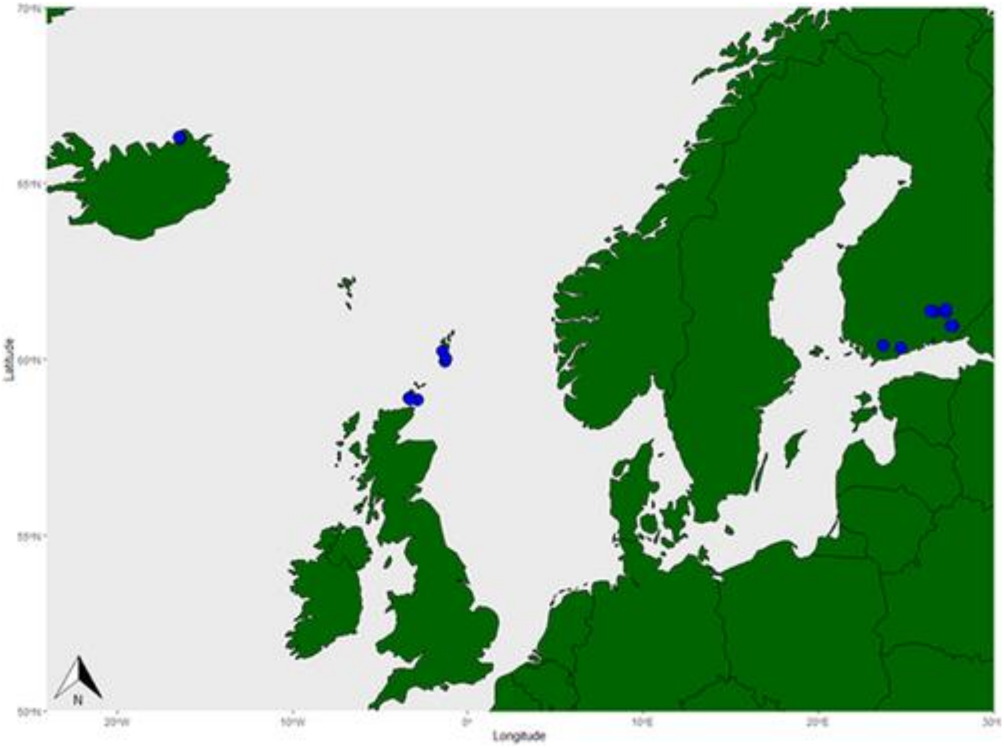

FIGURE 3.1 MAP OF THE BREEDING LOCATIONS ACROSS EUROPE

Capture locations for the studied Gavia stellata across northern Europe. Blue points represent capture and recovery locations, with a small amount of error added to preserve anonymity.

Logger regimes

TDRs recorded pressure, as a proxy for water depth, at six second intervals and temperature every ten minutes. The TDR measured with a precision of 0.03 m and 0.03°C for depth and temperature, respectively. To preserve battery life, the TDRs only recorded data every fifth day. GLS tags recorded maximum light levels for each five-minute period, every day. Additionally, the GLS tags had a salt-water immersion switch, which recorded immersion every three seconds and stored the information as a proportion of each ten-minute period that the tag was immersed in saltwater.

Defining dives and foraging bouts

TDRs are subject to shifts in surface water baseline changes in pressure, due to varying environmental conditions experienced throughout the annual cycle (Hays et al. 2007, Luque and Fried 2011) and extreme temperature changes (Bagniewska et al. 2013). A modified script from Duckworth et al. (2020) was used to correct the shifting baseline of the TDRs. Broadly, this script detects prolonged periods (180 s in this study) of time at values greater or less than 0 m, indicative of surface behaviour, and returns them and subsequent data to 0 m, to ensure all dives start and end at the water surface, while maintaining the integrity of the dive shape. Dives were then defined as any corrected TDR record of depth greater than 1 m. This excluded any noise leftover from the shifting baseline or small depth changes due to swimming on the surface of the water. Visual inspection of the data was then used to remove any remaining erroneous dive records.

Dives were defined using a slightly modified version of the approach from Duckworth et al. (2020b). For all dives, maximum dive depth, duration, bottom time and post-dive interval were recorded. The six second sampling regime used in this study was higher than 10% of the median dive duration (30 s across all dives recorded in this study), which slightly limits our ability to classify bottom time and dive efficiency (Wilson et al. 1995). Therefore, dive shapes were restricted to classification of either U or non-U, where U shaped dives were defined as having at least one recording of bottom time, between two depth records. The bottom time of a dive was defined by two conditions: 1) rate of depth change below 0.2 m s-^{s} ; 2) deeper than 85% of the maximum dive depth within the dive (Rodary et al. 2000, Zimmer et al. 2010). This calculation could not be carried out reliably on dives with a length of 12 s or less due to only having two or fewer records of depth, therefore these dives are always classified as non-U and are not included in any analysis of dive shape. The proportion of U-shaped dives was calculated for each day of data collection.

Groups of dives with post-dive interval less than 66 s (determined using the log-likelihood method from Sibly et al. 1990) were classified into foraging bouts and the duration and number of dives in each of these bouts was recorded (Supporting information). We defined bouts with more than two dives as foraging bouts (Halsey et al. 2007, Foo et al. 2016). Time spent in these foraging bouts was summed over a day to generate a metric of daily time spent foraging. Dives not within these bouts were excluded from further analysis. This enabled the exclusion of isolated dives, which were commonly very shallow, and other miscellaneous events associated with sudden pressure or temperature changes, e.g. landing on water, preening, leg-tucking. Dives within foraging bouts accounted for 94% of all dives. To quantify benthic foraging, the proportion of inter depth zone (IDZ) dives (Tremblay and Cherel 2000, Halsey et al. 2007) was calculated per day as the number of dives where the maximum depth was within 10% of the previous dive's maximum dive depth, within a bout, divided by the total number of dives within a bout minus one. A higher proportion of IDZ dives is indicative of a benthic foraging strategy, since a bird exploiting a benthic environment will serially dive to a similar depth (Tremblay and Cherel 2000, Quillfeldt et al. 2011, Knox et al. 2018).

This process generated seven foraging and diving metrics for further analysis: 1) bout length, 2) number of dives per bout, 3) maximum dive depth, 4) proportion of U-shaped dives, 5) dive duration, 6) proportion of IDZ dives, 7) daily time spent foraging. The saltwater immersion data was used to describe use of salt and freshwater habitats across the three regions.

Analysis

Only data from the second recording day (to remove any immediate effects that catching and handling the bird might have on diving behaviour) until the median departure date were analysed in this study. Since the focus of this study was the RTD breeding season, data were truncated to include only this period. Once RTDs from these regions leave their breeding grounds, they no longer commonly use freshwater habitats (Duckworth et al. 2020a). Therefore, in the absence of observation data, date of departure was determined using the saltwater immersion data to detect extended use of saltwater habitats, characteristic of the overwinter period for all three sites. The end of the breeding season was defined as the first day of 5 consecutive days that had at least 45% of records showing saltwater immersion (values calculated by inspection of known winter data; Supporting information). To account for not all birds having both a functional TDR and GLS (Supporting information), a single date of departure was derived for each region, based on the median departure date across all individuals with functioning tags from within that region.

We used generalised linear mixed effects models and linear mixed effect models, with each of the foraging metrics as response variables in separate models, to look at site level differences. We fitted random effects for bird ID and fixed effect for the three regions using the lme4 package (Bates et al. 2015). The model was compared to a null model, with only the random effects for individual ID included. Models were visually inspected for deviations from assumptions and as a result log transformation of the response variable was carried out on the models for bout duration and maximum dive depth within a dive (Supporting information). We included dive duration as a fixed effect since it was only recorded every six seconds, plus an interaction between site and dive duration, when looking at the proportion of U-shaped dives and only included dives with over 2 data points in analysis of U-shaped dives. This accounted for longer dives having a higher probability of being detected as U-shaped dives, due to having a higher number of data points within the dive. For the two metrics (daily time spent foraging and proportion of IDZ dives) we predicted would have a temporal change, we included three more candidate models, one which included date and time and one with only time (as a continuous variable for the days until breeding site departure) and finally a model with both date, time and an interaction term between date and site (Supporting information). ΔAICc was used to determine the best performing model of the candidate models for all analyses, where the selected model was the most parsimonious model within 2 AICc units of the best model (Arnold 2010). Where the best performing model contained site as a fixed effect, site level differences were determined using pairwise Tukey tests in the R package 'emmeans' (Russell 2020). Details on error distributions used for each model can be found in Supporting information.

We calculated the proportion of time a bird spent in daylight and twilight by classifying each day in six minute intervals, based on light conditions at each nest location. Twilight was defined as a sun elevation angle between 0 and −12 (nautical sunset/sunrise), while 'day' was defined as a sun elevation angle greater than or equal to 0 (Regular et al. 2011). Foraging dives were then classified in the same way as either occurring during the day or twilight (Duckworth et al. 2020b). For all foraging dives, both the proportion of available time which would be classified as night (sun elevation below −12 degrees) and the proportion of foraging dives which occurred at night were less than 0.5% of the total, so were therefore removed from any analysis. To determine whether foraging behaviour was biased towards crepuscular hours, we used Chi-squared tests to compare the combined number of foraging dives in each light category (daylight and twilight) from all birds to the combined proportion of time each light category was available to all individuals. Separate tests were conducted for each site.

All statistical analysis and data processing was carried out in R version 3.5.1 (R Development Core Team 2018). All means are shown with standard deviations, unless stated otherwise.

Results

The median nest departure dates for Scotland (n=5), Finland (n=7) and Iceland (n=7) were 15 August, 31 August and 10 August, respectively (Supporting information). Only one Finnish RTD, breeding ~15 km from the coast, had records of saltwater immersion between deployment and nest departure. This bird recorded between 3 and 11 h in saltwater on ten consecutive days of 102 days of the breeding season. Otherwise, saltwater immersion before the estimated date of departure from the breeding site was not detected for any Finnish birds, indicating that birds from this geographic region foraged nearly exclusively in freshwater. In contrast the Scottish and Icelandic RTDs recorded 8.1 (± 4.8) and 7.7 (± 3.5) hours a day immersed in saltwater, respectively.

The maximum dive depth observed across all sites was 29.3 m, which was performed by a bird in Iceland. In Scotland and Finland maximum depth recordings were 24.6 m and 27.4 m, respectively (Figure 3.2). However, dives were typically shallow in nature with 94% of all foraging dives recorded being less than 15 m depth (Figure 3.2). The longest dive recorded was 84 s, but 98% of all foraging dives were less than 60 s (Figure 3.2). The longest foraging bout recorded overall was 215 min in Finland, while in Iceland and Scotland the maximum duration was 170 and 103 min, respectively. Foraging bouts of RTDs in Finland and Iceland were longer, on average, than those in Scotland (Table 3-1). Longer bouts were achieved by more dives within bouts (Table 3-1) although dive duration was significantly longer in Finland than Iceland and Scotland (Table 3-1). Maximum dive depth and dive duration were both greater, on average, in Finland than in Scotland and Iceland (Table 3-1). The proportion of U-shaped dives was high across all sites and both dive duration and the interaction between site and dive duration were included in the best model for the proportion of U-shaped dives. This showed that as dive duration increased the likelihood of detecting a U-shaped dive increased with a slightly steeper increase in Iceland (Supporting information). In addition to these effects, Iceland showed a higher proportion of U-shaped dives than Scotland and Finland, which were similar (Table 3-1). Results for all model fits and AIC values used for model selection can be found in the Supporting information.

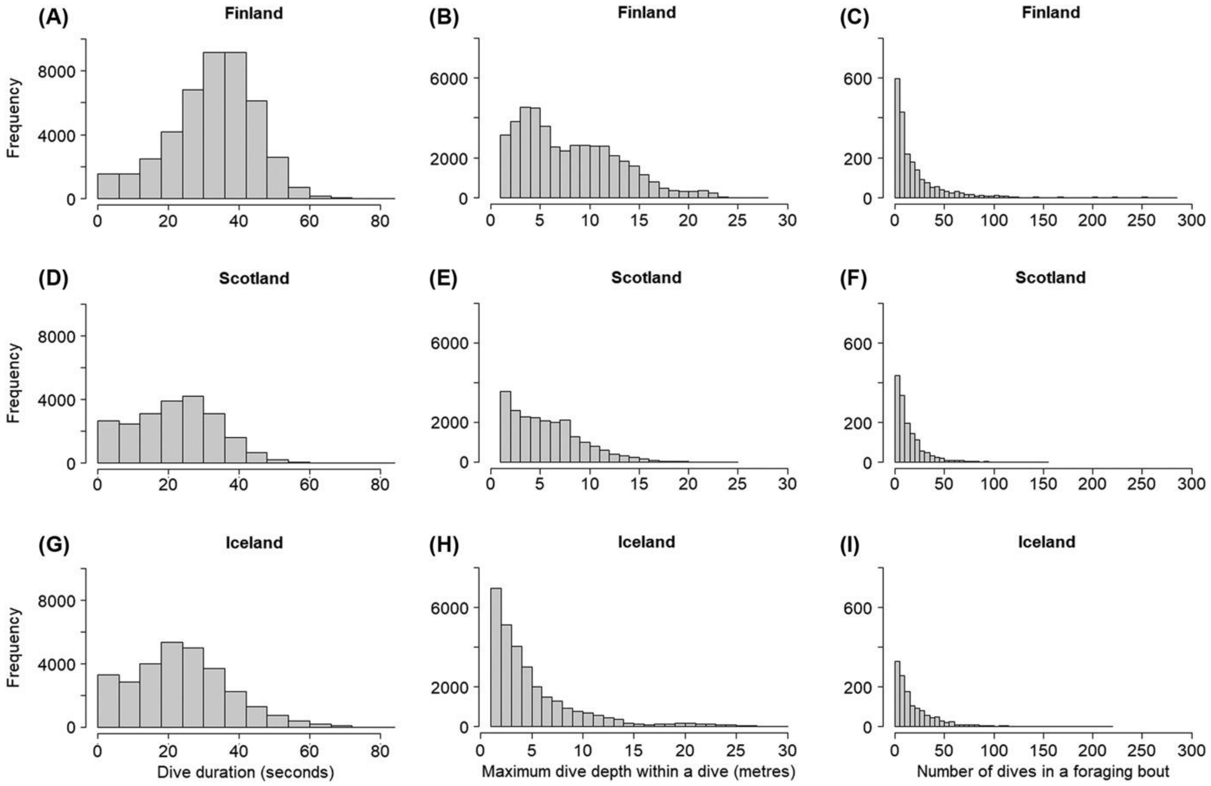

FIGURE 3.2 DISTRIBUTION OF THREE DIVE METRICS ACROSS THREE POPULATIONS OF RTD

Histograms showing the dive duration (panel A, D and G), maximum dive depth within a dive (B, E and H) and number of dives within a foraging bout (C, F and I) at three sites: Finland (A, B and C), Scotland (D, E and F) and Iceland (G, H and I).

The best performing model for daily time spent foraging contained only site as a fixed effect. Finnish birds were shown to spend longer foraging than Scottish birds, with Icelandic birds being intermediate and not different from birds at either of the other two sites (Figure 3.3). The Akaike weight of this model was low ($wi=0.36$), however the model with only time did not outperform the null model (Supporting information), while the three other models did. We therefore decided against model averaging, to avoid over representing the important of time, and instead discuss only the top preforming model and the effects of site level differences.

The best performing model for the proportion of IDZ dives included time, site and an interaction term between site and time. The model showed the proportion of IDZ dives decreased through the season, with the steepest decline in IDZ dives observed in the birds in Scotland (Figure 3.4). Birds breeding in Scotland showed the lowest overall proportion of IDZ dives, while birds from Finland showed the highest and Iceland was intermediate, with all pairwise differences being significant ($p < 0.05$ in all cases; Figure 3.4).

At each site, dives were not distributed evenly between the two light regimes. In Finland, birds showed a bias towards diving during daylight (available daylight: 71%, dives during daylight: 85%) ($p < 0.001$, $df=1$, $\chi2=3720$). In Scotland, dives were biased towards daylight (available daylight: 72%, dives during daylight: 87%; $p < 0.001$, $df=1$, $\chi2=2355$). In Iceland, birds also showed a slight bias towards diving in the daylight (available daylight: 86%, dives during daylight: 88%) ($p < 0.001$, $df=1$, $\chi2=54$). However, the effect size of light regime of foraging effort was lesser in Iceland compared to the other two sites.

TABLE 3-1 SUMMARIES OF DIVING METRICS AND THEIR DIFFERENCES ACROSS THE THREE BREEDING POPULATIONS

*Foraging bout and diving characteristics and tag samples sizes of red-throated divers from three breeding locations. Breeding sites sharing a superscripted letter were not significantly different from each other. Values given are the predicted mean, with ranges in brackets denoting 95% confidence intervals generated by GLMMs. *Adjusted for the effect of dive duration*

	Scotland	Finland	Iceland
Number of individuals with TDRs	8	8	7
Number of individuals with viable GLSs	5	7	7
Bout length (minutes)	7.2^a (6.1–8.5)	10.8^b (9.1–12.8)	10.2^b (8.5–12.2)
Number of dives in a bout	15^a (13–17)	21^b (18–25)	22^b (18–25)
Mean maximum dive depth within a dive (Metres)	4.5^a (3.8–5.3)	6.4^b (5.4–7.6)	3.8^a (3.2–4.6)
Proportion of U-shaped dives*	0.90^a (0.87–0.92)	0.91^a (0.88–0.93)	0.97^b (0.96–0.98)
Dive duration (seconds)	25^a (22–27)	36^b (33–38)	26^a (23–29)

FIGURE 3.3 DAILY TIME SPENT FORAGING FOR THE THREE BREEDING RTD POPULATIONS

The predicted mean time spent foraging per day generated from the best fitting model for Gavia stellata. Breeding sites sharing a letter were not significantly different from each other. Error bars show the 95% upper and lower confidence intervals.

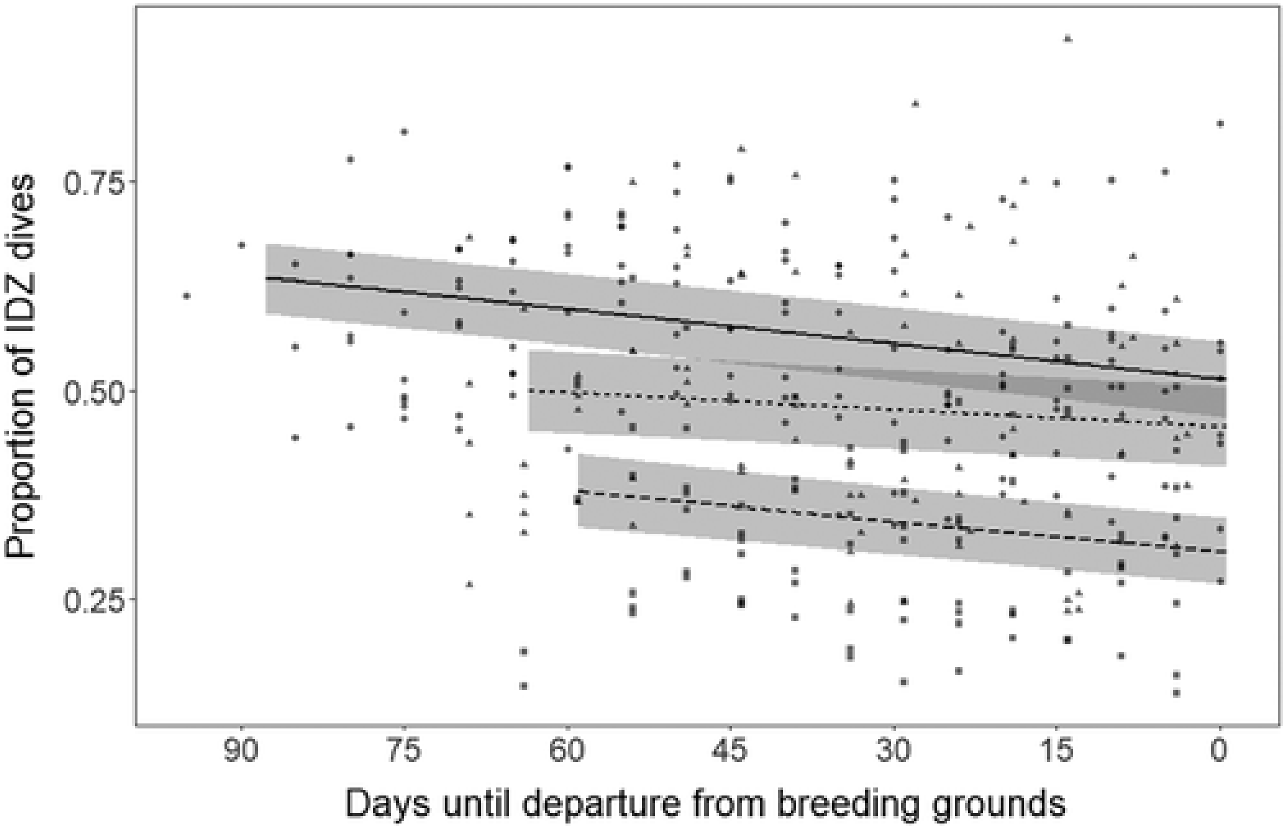

FIGURE 3.4 CHANGE IN FORAGING BEHAVIOUR OF RTD THROUGH THE BREEDING SEASON

The proportion of RTD inter-depth zone (IDZ) dives per day across RTDs breeding in Finland (solid line), Iceland (dotted line) and Scotland (dashed line). Lines show the predicted values from the model, with 95% confidence intervals (grey shading). Black symbols represent the observed proportions of IDZ dives for each individual on each day sampling occurred with circles, triangles and squares representing Finland, Iceland and Scotland, respectively.

Discussion

Our study provides the first description of foraging behaviour of RTDs across three geographically distinct regions in northern Europe. We found RTDs predominantly engaged in short, shallow dives of less than 10 m, in foraging bouts ranging from a few minutes to hours. Among the three regions examined here, there were differences between at least two of them in all of the metrics we tested. In the case of diving metrics, differences were largely between freshwater and marine foraging habitats. With RTDs in Finland undertaking longer deeper dives during longer bouts comprising more dives, compared with birds breeding in Iceland and Scotland. Furthermore, we analysed two of these traits, proportion of IDZ dives and daily time spent foraging, for temporal patterns and found that while the time spent foraging varied between sites, it did not change over time. In contrast, the proportion of benthic dives undertaken decreased as the breeding season progressed. These findings suggest a capability for both spatial and temporal variation in RTD foraging in response to environmental differences. This could indicate RTDs have a high degree of foraging flexibility, which may act as a buffer to anthropogenic change in the breeding grounds for individuals where alternate habitat is available.

Unusually for a diving bird that overwinters in marine environments, RTDs have been shown to forage in both freshwater (Eriksson et al. 1990, Eriksson and Sundberg 1991, Duckworth et al. 2020) and marine environments during the breeding season (Reimchen and Douglas 1984, Black et al. 2015, Rizzolo et al. 2015). As predicted, all diving metrics (dive depth and dive duration) differed between Finland and at least one of the other two sites (Table 3-1). This is likely due to differences in foraging habitat, with Finnish birds foraging almost exclusively in freshwater habitats, while birds breeding at the other two sites regularly used marine habitat. The distance of the nests from the coast was greater at all nests in Finland (> 10 km) than for birds at the other two sites (always < 10 km). Distance from the coast was likely driving these differences in diving metrics, as the energetic cost of flying to the marine environment was presumably not worth the energetic payoff in terms of prey items gained (Lihoreau et al. 2011). At nest sites in Scotland, many of the local acidic lochans were devoid of prey, so marine prey was the only option. RTDs in Finland instead foraged in local lakes, where freshwater prey species provided a much more spatially convenient option. However, one Finnish RTD that bred ~15 km from the coast did forage in the marine environment for several days at the start of the study period, before returning to entirely freshwater habitat for the remainder of the breeding season. Unfortunately, the exact conditions that led to this change in habitat use are unknown, but this observation suggests that RTDs may be able to buffer against poor foraging success in local freshwater habitats.

Large-scale differences in foraging habitats are clearly not the only driver of foraging behaviour in this species. Unexpectedly, number of dives within a bout and bout length, the two foraging metrics that represented how bouts were organised (Table 3-1), differed between Scotland and the other two sites. Specifically, foraging bouts in Scotland were shorter and had fewer dives. This difference could be related to foraging success and food availability, as fewer dives and a shorter time in each foraging bout suggests the time required to meet the energy demand of each foraging bout is lower. This is also partly demonstrated in other aquatic birds, such as kittiwakes (*Rissa tridactyla)* (Chivers et al. 2012) and guillemots (*Uria aalge*) (Davoren and Montevecchi 2003), through birds increasing the duration of foraging bouts in years where food availability is lower. This suggests foraging success could have been higher at Scotland than the other two sites, which is supported by the lower daily time spent foraging (Figure 3.3). However, this did not appear to affect breeding success, with only 38% of monitored RTD pairs in Scotland producing at least one chick in 2018, compared with 62% of monitored RTD pairs in Finland (O'Brien et al. 2018).

Animals foraging during a breeding season have to adapt their foraging effort temporally in order to accommodate the demands of growing young (Tulp et al. 2009, Sotillo et al. 2019). However, at all three sites, the foraging effort for RTDs did not change through the season as we expected. Instead it appears that the tracked divers may have adapted their foraging strategy via prey selection, rather than increasing foraging intensity through time. This is suggested by earlier observations of RTDs from Sweden, where it was found that the number of foraging trips did not change as the breeding season progressed, but instead the size of the prey brought back by the parents changed (Eriksson et al. 1990). This effect was particularly noticeable when the chicks were very young (Reimchen and Douglas 1984). The proportion of IDZ (benthic) dives decreased during the breeding season across all sites. Such changes have previously been linked to differences in prey selection in diving predators, where higher resolution data on location and bathymetry has been available (Kuhn et al. 2010). RTDs are single prey loaders, therefore they may maximise the energy gain per foraging trip by ensuring they bring back food items close to the maximum swallowing capacity of the chick, providing maximum energy returns. This would be more efficient than increasing foraging effort and delivering the same prey items throughout the season. This strategy will avoid the costs of an increased number of flights, which would be exacerbated by the high wing loading of RTDs (Lovvorn and Jones 1994).

The RTDs at the three sites also displayed some evidence of flexibility between regions in how they altered their foraging behaviour as the season progressed. Though the progressive decrease in the proportion of IDZ (benthic) dives was common across sites, the degree of change in the proportion of IDZ dives was not the same, with Iceland showing little biologically meaningful change (a change of 4% over the 65 days) in foraging strategy through the season (Figure 3.4). Diet changes within a breeding season are common for several aquatic bird species in the northern Japanese sea, as the influx of warm water changes the prey availability (Watanuki et al. 2009, Watanuki and Ito 2012). Similar events could affect RTDs in Iceland foraging consistently in the same habitat through the season, but targeting different prey as the season progressed. On the other hand, RTDs in Finland and Scotland showed a more notable decrease in proportion of IDZ dives. This could relate to following vertical prey movement, foraging in different habitat or switching to prey occupying a different area of the water column (Sotillo et al. 2019), to fulfil the food size demand of the chicks (Reimchen and Douglas 1984). The latter could especially be true in Finland, as evidence suggests black-throated divers *Gavia arctica* foraging in freshwater can provision benthic invertebrates to chicks in the early stages of rearing (Jackson 2003). Furthermore, the closed nature of lake systems makes it unlikely that there will be temporal changes in prey availability. This use of invertebrate prey may also explain why RTDs in Finland had the highest proportion of IDZ dives and therefore the most benthic dives, especially early in the season. Conversely, RTDs in Scotland showed a low proportion of IDZ dives overall. Tremblay and Cherel (2000) visually classified groups of dives as either pelagic or benthic and found that groups of pelagic dives had less than 40.3% of IDZ dives within these groups. In our study, the model showed birds from Scotland generally had a proportion of IDZ dives below this threshold. Therefore, it is likely that RTDs in Scotland are mostly foraging pelagically in the marine environment. While this does not preclude the occurrence of benthic dives, it strongly suggests pelagic foraging is more important in Scotland than in Finland and Iceland. These results have demonstrated that local environment has an effect on the foraging behaviour of RTDs, but in order to confirm the prey switching hypothesis, further analysis is required to create a direct link between diet and foraging behaviour, perhaps through the use of stable isotope analysis (Hobson and Clark 1992, Gómez et al. 2018).

Many pursuit divers are dependent on high light levels to target and catch their prey, though nocturnal activity can be observed in some cases (Wilson et al. 1993, Cannell and Cullen 2008, Dunn et al. 2019). Preliminary evidence suggested that RTDs are crepuscular when foraging (Duckworth et al. 2020), but data collection from this study does not support that suggestion. Birds breeding at Scotland and Finland showed differences in the proportion of dives across light conditions, with a preference for foraging in daylight. However, while the same was found in Iceland, the difference in foraging effort between the two light conditions was much smaller. Overall, this preference for diving in daylight would be expected for pursuit diving, visually orientated birds, as high light conditions provide the perfect conditions to track and capture prey (Wilson et al. 1993). However, these findings could be a product of high individual difference and a low sample size. Therefore, further investigation into RTD behaviour is required to determine whether there is a capacity for nocturnal foraging.

This paper provides the first multi-individual descriptions of RTD diving, from three distinct regions and thus form the current best understanding of summer foraging behaviour of this species. We considered temporal change, however, RTDs are not synchronous breeders and can relay clutches, with many breeding pairs at different breeding stages at any given point during the breeding season. Therefore, using days since egg laying or hatching would give a better picture of how the activity budgets differ at each of the breeding stages. Due to the remote locations of many of the nests and the extreme sensitivity of the species to disturbance, we were not able to regularly monitor RTD nests across all sites, both to minimise the effect our attendance had on behaviour and minimise ethical concerns arising from disturbance. Future study could deploy remote camera traps to maximise information on nest attendance while minimising human presence (Edney and Wood 2020). In addition, the lack of precise foraging locations of birds meant we were unable to link foraging to local environmental conditions, so could not relate foraging behaviour to environmental influences such as tidal cycles and hydrographic features (Skov and Prins 2001). To explore this link, we suggest future studies should try to also track birds with GPS, if this can be achieved without additional disturbance. Additionally, the TDR pressure sampling frequency was relatively low, prohibiting more detailed analysis of dive characteristics such as bottom activity, ascent rate and descent rate. As the logger resolution is < 10% of the median dive duration, it is likely that some of the parameters may be imperfect estimations (Wilson et al. 1995). However, this resolution of data allows for valid comparisons between our geographically distinct groups and will still provide accurate values for the proportion of time spent foraging and estimates for other parameters are unlikely to have a substantial error at our resolution (Dunn et al. 2019). We also acknowledge the small sample size of this study limits our ability to make true large-scale comparisons across sites. Instead, our study focusses on description of foraging behaviours and highlights differences between regions. As technology and methodologies develop it may be possible to increase our understanding of this important species, up to the level of better understood aquatic birds (Soanes et al. 2014) but our study is an important first step in this process.

Having demonstrated some degree of spatial and temporal variation in foraging behaviour, our study suggests RTDs have some flexibility in foraging strategies. This could further suggest breeding RTDs have some capacity to resist anthropogenic effects, as the species as a whole is capable of exploiting a range of niches (Devictor et al. 2008, Wilson et al. 2008). However, the two commonalities across all RTDs is their necessity to build nests by freshwater lakes (Rizzolo et al. 2014) and their migration to mostly marine habitats (Polak and Ciach 2007, McCloskey et al. 2018). Therefore, while foraging can vary both within and between individuals, these two fundamental aspects of RTD ecology remain constraints in their annual cycle. Therefore, work must also be done to improve the understanding of the potential effects of climate change on nesting habitat suitability and RTD foraging behaviour during the winter.

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References

AMELINEAU, F., GREMILLET, D., HARDING, A. M. A., WALKUSZ, W., CHOQUET, R. and FORT, J. 2019. Arctic climate change and pollution impact little auk foraging and fitness across a decade. - *Scientific Reports,* **9**: 15.

ARNOLD, T. W. 2010. Uninformative Parameters and Model Selection Using Akaike's Information Criterion. -*The Journal of Wildlife Management,* **74**: 1175-1178.

BAGNIEWSKA, J. M., HART, T., HARRINGTON, L. A. and MACDONALD, D. W. 2013. Hidden Markov analysis describes dive patterns in semiaquatic animals. -*Behavioral Ecology,* **24**: 659-667.

BATES, D., MÄCHLER, M., BOLKER, B. and WALKER, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. -*Journal of Statistical Software; Vol 1, Issue 1 (2015)*.

BLACK, J., DEAN, B. J., WEBB, A., LEWIS, M., OKILL, D. and REID, J. B. 2015. Identification of important marine areas in the UK for red-throated divers (*Gavia stellata*) during the breeding season. JNCC, Peterborough.

BOGGS, C. L. 1992. Resource Allocation: Exploring Connections between Foraging and Life History. - *Functional Ecology,* **6**: 508-518.

BOST, C. A., COTTÉ, C., TERRAY, P., BARBRAUD, C., BON, C., DELORD, K., GIMENEZ, O., HANDRICH, Y., NAITO, Y., GUINET, C. and WEIMERSKIRCH, H. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. -*Nature Communications,* **6**: 8220.

BURGER, C., SCHUBERT, A., HEINÄNEN, S., DORSCH, M., KLEINSCHMIDT, B., ŽYDELIS, R., MORKŪNAS, J., QUILLFELDT, P. and NEHLS, G. 2019. A novel approach for assessing effects of ship traffic on distributions and movements of seabirds. -*Journal of Environmental Management,* **251**: 109511.

CANNELL, B. and CULLEN, J. 2008. The foraging behaviour of Little Penguins Eudyptula minor at different light levels. -*Ibis,* **140**: 467-471.

CARBONERAS, C., CHRISTIE, D. A. and GARCIA, E. F. J. 2020. Red-throated Loon (*Gavia stellata*). In: HOYO, J., ELLIOTT, A., SARGATAL, J., CHRISTIE, D. A. and DE JUANA, E. (eds.) *Handbook of the Birds of the World Alive.* Lynx Edicions, Barcelona.

CHIVERS, L. S., LUNDY, M. G., COLHOUN, K., NEWTON, S. F., HOUGHTON, J. D. R. and REID, N. 2012. Foraging trip time-activity budgets and reproductive success in the black-legged kittiwake. -*Marine Ecology Progress Series,* **456**: 269-277.

CROCKER, D. E., COSTA, D. P., LE BOEUF, B., J. , WEBB, P. M. and HOUSER, D. S. 2006. Impact of El Niño on the foraging behavior of female northern elephant seals. -*Marine Ecology Progress Series,* **309**: 1-10.

DAVOREN, G. K. and MONTEVECCHI, W. A. 2003. Consequences of Foraging Trip Duration on Provisioning Behaviour and Fledging Condition of Common Murres *Uria aalge*. -*Journal of Avian Biology,* **34**: 44-53.

DEVICTOR, V., JULLIARD, R., CLAVEL, J., JIGUET, F., LEE, A. and COUVET, D. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. -*Global Ecology and Biogeography,* **17**: 252-261.

DREWITT, A. L. and LANGSTON, R. H. W. 2006. Assessing the impacts of wind farms on birds. -*Ibis,* **148**: 29-42.

DUCKWORTH, J., O'BRIEN, S., VÄISÄNEN, R., LEHIKOINEN, P., PETERSEN, I. K., DAUNT, F. and GREEN, J. A. 2020. First biologging record of a foraging Red-Throated Loon *Gavia stellata* shows shallow and efficient diving in freshwater environments. -*Marine Ornithology,* **48**: 17-22.

DUNN, R. E., WANLESS, S., GREEN, J. A., HARRIS, M. P. and 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**.

DUNN, R. E., WHITE, C. R. and GREEN, J. A. 2018. A model to estimate seabird field metabolic rates. -*Biology Letters,* **14**: 20180190.

ERIKSSON, M. O. G., BLOMQVIST, D., HAKE, M. and JOHANSSON, O. C. 1990. Parental feeding in the Red-throated Diver *Gavia stellata*. -*Ibis,* **132**: 1-13.

ERIKSSON, M. O. G. and SUNDBERG, P. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. -*Bird Study,* **38**: 135-144.

ERIKSTAD, K. E., SANDVIK, H., REIERTSEN, T. K., BUSTNES, J. O. and STROM, H. 2013. Persistent organic pollution in a high-Arctic top predator: sex-dependent thresholds in adult survival. -*Proceedings of the Royal Society B-Biological Sciences,* **280**: 7.

FOO, D., SEMMENS, J. M., ARNOULD, J. P. Y., DORVILLE, N., HOSKINS, A. J., ABERNATHY, K., MARSHALL, G. J. and HINDELL, M. A. 2016. Testing optimal foraging theory models on benthic divers. -*Animal Behaviour,* **112**: 127-138.

FURNESS, R. W., WADE, H. M. and MASDEN, E. A. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. -*Journal of Environmental Management,* **119**: 56-66.

GÓMEZ, C., LARSEN, T., POPP, B., HOBSON, K. A. and CADENA, C. D. 2018. Assessing seasonal changes in animal diets with stable-isotope analysis of amino acids: a migratory boreal songbird switches diet over its annual cycle. -*Oecologia,* **187**: 1-13.

GRÉMILLET, D. and BOULINIER, T. 2009. Spatial ecology and conservation of seabirds facing global climate change: a review. -*Marine Ecology Progress Series,* **391**: 121-137.

HALSEY, L. G., BOST, C. A. and HANDRICH, Y. 2007. A thorough and quantified method for classifying seabird diving behaviour. -*Polar Biology,* **30**: 991-1004.

HARPER, E. B., RITTENHOUSE, T. A. G. and SEMLITSCH, R. D. 2008. Demographic Consequences of Terrestrial Habitat Loss for Pool-Breeding Amphibians: Predicting Extinction Risks Associated with Inadequate Size of Buffer Zones. -*Conservation Biology,* **22**: 1205-1215.

HAYS, G. C., FORMAN, D. W., HARRINGTON, L. A., ANDREW, L. H., MACDONALD, D. W. and RIGHTON, D. 2007. Recording the Free-Living Behaviour of Small-Bodied, Shallow-Diving Animals with Data Loggers. -*Journal of Animal Ecology,* **76**: 183-190.

HEINÄNEN, S., ŽYDELIS, R., KLEINSCHMIDT, B., DORSCH, M., BURGER, C., MORKŪNAS, J., QUILLFELDT, P. and NEHLS, G. 2020. Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. -*Marine Environmental Research*: 104989.

HOBSON, K. A. and CLARK, R. G. 1992. Assessing Avian Diets Using Stable Isotopes I: Turnover of 13C in Tissues. -*The Condor,* **94**: 181-188.

HORN, D. A., GRANEK, E. F. and STEELE, C. L. 2020. Effects of environmentally relevant concentrations of microplastic fibers on Pacific mole crab (*Emerita analoga*) mortality and reproduction. -*Limnology and Oceanography Letters,* **5**: 74-83.

HOVICK, T. J., ELMORE, R. D., DAHLGREN, D. K., FUHLENDORF, S. D. and ENGLE, D. M. 2014. REVIEW: Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. -*Journal of Applied Ecology,* **51**: 1680-1689.

JACKSON, D. B. 2003. Between-lake differences in the diet and provisioning behaviour of Black-throated Divers *Gavia arctica* breeding in Scotland. -*Ibis,* **145**: 30-44.

KLEINSCHMIDT, B., BURGER, C., DORSCH, M., NEHLS, G., HEINÄNEN, S., MORKŪNAS, J., ŽYDELIS, R., MOORHOUSE-GANN, R. J., HIPPERSON, H., SYMONDSON, W. O. C. and QUILLFELDT, P. 2019. The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. -*Marine Biology,* **166**: 77.

KNOX, T. C., BAYLIS, A. M. M. and ARNOULD, J. P. Y. 2018. Foraging site fidelity in male Australian fur seals. -*Marine Biology,* **165**: 108.

KUHN, C. E., TREMBLAY, Y., REAM, R. R. and GELATT, T. S. 2010. Coupling GPS tracking with dive behavior to examine the relationship between foraging strategy and fine-scale movements of northern fur seals. -*Endangered Species Research,* **12**: 125-139.

LIHOREAU, M., CHITTKA, L., RAINE, N. E. and KUDO, G. 2011. Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. -*Functional ecology,* **25**: 1284-1292.

LINNEBJERG, J. F., HUFFELDT, N. P., FALK, K., MERKEL, F. R., MOSBECH, A. and FREDERIKSEN, M. 2014. Inferring seabird activity budgets from leg-mounted time-depth recorders. -*Journal of Ornithology,* **155**: 301-306.

LOVVORN, J. R. and JONES, D. R. 1994. Biomechanical conflicts between adaptations for diving and aerial flight in estuarine birds. -*Estuaries,* **17**: 62-75.

LUQUE, S. P. and FRIED, R. 2011. Recursive Filtering for Zero Offset Correction of Diving Depth Time Series with GNU R Package diveMove. -*PLOS ONE,* **6**: e15850.

MAYNARD, L. and DAVOREN, G. 2020. Inter-colony and interspecific differences in the isotopic niche of two sympatric gull species in Newfoundland. -*Marine Ornithology,* **48**: 103-109.

MCCLOSKEY, S. E., UHER-KOCH, B. D., SCHMUTZ, J. A. and FONDELL, T. F. 2018. International migration patterns of Red-throated Loons (*Gavia stellata*) from four breeding populations in Alaska. -*PLoS ONE,* **13**: 1-15.

MENDEL, B., SCHWEMMER, P., PESCHKO, V., MÜLLER, S., SCHWEMMER, H., GARTHE, S. and MERCKER, M. 2019. Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). -*Journal of Environmental Management,* **231**: 429-438.

MILLON, L., COLIN, C., BRESCIA, F. and KERBIRIOU, C. 2018. Wind turbines impact bat activity, leading to high losses of habitat use in a biodiversity hotspot. -*Ecological Engineering,* **112**: 51-54.

NUMMI, P., VÄÄNÄNEN, V., PAKARINEN, R. and PIENMUNNE, E. 2013. The Red-throated Diver (*Gavia stellata*) in human-disturbed habitats - building up a local population with the aid of artificial rafts. -*Ornis Fennica,* **90**: 16-22.

O'BRIEN, S., RUFFINO, L., LEHIKOINEN, P., JOHNSON, L., LEWIS, M., PETERSEN, A., PETERSEN, I. K., OKILL, D., VÄISÄNEN, R., WILLIAMS, J. and WILLIAMS, S. 2018. Red-Throated Diver Energetics Project - 2018 Field Season Report. *JNCC Report No. 627.* JNCC, JNCC, Peterborough.

O'BRIEN, S. H., WEBB, A., BREWER, M. J. and REID, J. B. 2012. Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. -*Biological Conservation,* **156**: 15-21.

PECKHAM, S. H., MALDONADO DIAZ, D., TREMBLAY, Y., OCHOA, R., POLOVINA, J., BALAZS, G., DUTTON, P. H. and NICHOLS, W. J. 2011. Demographic implications of alternative foraging strategies in juvenile loggerhead turtles *Caretta caretta* of the North Pacific Ocean. -*Marine Ecology Progress Series,* **425**: 269-280.

PETERSEN, I. K., NIELSEN, R. D., PIHL, S., CLAUSEN, P., THERKILDSEN, O., CHRISTENSEN, T. K., KAHLERT, J. and HOUNISEN, J. P. 2010. LANDSDÆKKENDE OPTÆLLING AF VANDFUGLE I DANMARK, VINTEREN 2007/2008. *Working Report from DMU.* The Danish Environmental Research Institute, Aarhus University.

PLUMPTON, D. L. and ANDERSEN, D. E. 1998. Anthropogenic Effects on Winter Behavior of Ferruginous Hawks. -*The Journal of Wildlife Management,* **62**: 340-346.

POLAK, M. and CIACH, M. 2007. Behaviour of black-throated diver *Gavia arctica* and red-throated diver *Gavia stellata* during autumn migration stopover. -*Ornis Svecica,* **17**: 90-94.

POUPART, T. A., WAUGH, S. M., BOST, C. A., KATO, A., MISKELLY, C. M., ROGERS, K. M. and ARNOULD, J. P. Y. 2019. Foraging ecology of a winter breeder, the Fiordland penguin. -*Marine Ecology Progress Series,* **614**: 183-197.

QUILLFELDT, P., SCHROFF, S., VAN NOORDWIJK, H. J., MICHALIK, A., LUDYNIA, K. and MASELLO, J. F. 2011. Flexible foraging behaviour of a sexually dimorphic seabird: large males do not always dive deep. -*Marine Ecology Progress Series,* **428**: 271-287.

R DEVELOPMENT CORE TEAM. 2018. R: A language and environment for statistical computing. R Foundatin for Statistical Computing, Vienna, Austria.

REGULAR, P. M., HEDD, A. and MONTEVECCHI, W. A. 2011. Fishing in the Dark: A Pursuit-Diving Seabird Modifies Foraging Behaviour in Response to Nocturnal Light Levels. -*PLOS ONE,* 6: e26763.

REIMCHEN, T. E. and DOUGLAS, S. 1984. Feeding Schedule and Daily Food Consumption in Red-Throated Loons (*Gavia stellata*) over the Prefledging Period. -*The Auk,* 101: 593-599.

RIZZOLO, D. J., SCHMUTZ, J., A., MCCLOSKEY, S. E. and FONDELL, T. F. 2014. Factors influencing nest survival and productivity of Red-throated Loons (*Gavia stellata*) in Alaska. -*The Condor*: 574-587.

RIZZOLO, D. J., SCHMUTZ, J. A. and SPEAKMAN, J. R. 2015. Fast and efficient : Postnatal growth and energy expenditure in an Arctic-breeding waterbird, the Red-throated Loon (*Gavia stellata*). -*The Auk,* 132: 657-670.

RODARY, D., WIENECKE, B. C. and BOST, C. A. 2000. Diving behaviour of Adélie penguins (*Pygoscelis adeliae*) at Dumont D'Urville, Antarctica: nocturnal patterns of diving and rapid adaptations to changes in sea-ice condition. -*Polar Biology,* 23: 113-120.

RUSSELL, L. 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means.

SALAMOLARD, M. and WEIMERSKIRCH, H. 1993. Relationship Between Foraging Effort and Energy Requirement Throughout the Breeding Season in the Wandering Albatross. -*Functional Ecology,* 7: 643-652.

SCHMUTZ, J. A., TRUST, K. A. and MATZ, A. C. 2009. Red-throated loons (*Gavia stellata*) breeding in Alaska, USA, are exposed to PCBs while on their Asian wintering grounds. -*Environmental Pollution,* 157: 2386-2393.

SCHWEMMER, P., MENDEL, B., SONNTAG, N., DIERSCHKE, V. and GARTHE, S. 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. -*Ecological Applications,* 21: 1851-1860.

SCRAFFORD, M. A., AVGAR, T., ABERCROMBIE, B., TIGNER, J. and BOYCE, M. S. 2017. Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. -*Forest Ecology and Management,* 395: 27-36.

SENZAKI, M., YAMAURA, Y., FRANCIS, C. D. and NAKAMURA, F. 2016. Traffic noise reduces foraging efficiency in wild owls. -*Scientific Reports,* 6: 30602.

SHAFFER, S. A., COSTA, D. P. and WEIMERSKIRCH, H. 2001. Behavioural factors affecting foraging effort of breeding wandering albatrosses. -*Journal of Animal Ecology,* 70: 864-874.

SIBLY, R. M., NOTT, H. M. R. and FLETCHER, D. J. 1990. Splitting behaviour into bouts. -*Animal Behaviour,* 39: 63-69.

SKOV, H. and PRINS, E. 2001. Impact of estuarine fronts on the dispersal of piscivorous birds in the German Bight. -*Marine Ecology Progress Series,* **214**: 279-287.

SOTILLO, A., BAERT, J. M., MÜLLER, W., STIENEN, E. W. M., SOARES, A. M. V. M. and LENS, L. 2019. Time and energy costs of different foraging choices in an avian generalist species. -*Movement Ecology,* **7**: 41.

THAXTER, C. B., ROSS-SMITH, V. H., BOUTEN, W., CLARK, N. A., CONWAY, G. J., REHFISCH, M. M. and BURTON, N. H. K. 2015. Seabird–wind farm interactions during the breeding season vary within and between years: A case study of lesser black-backed gull *Larus fuscus* in the UK. -*Biological Conservation,* **186**: 347-358.

TREMBLAY, Y. and CHEREL, Y. 2000. Benthic and pelagic dives : a new foraging behaviour in rockhopper penguins. -*Marine Ecology Progress Series,* **204**: 257-267.

TULP, I., SCHEKKERMAN, H., BRUINZEEL, L. W., JUKEMA, J., VISSER, G. H. and PIERSMA, T. 2009. Energetic Demands During Incubation and Chick Rearing in a Uniparental and a Biparental Shorebird Breeding in the High Arctic. -*The Auk,* **126**: 155-164.

UHER-KOCH, B. D., KOCH, J. C., WRIGHT, K. G. and SCHMUTZ, J. A. 2018. Comparative nest survival of three sympatric loon species breeding in the Arctic. -*Journal of Avian Biology,* **49**: e01671.

UHER-KOCH, B. D., SCHMUTZ, J. A. and WRIGHT, K. G. 2015. Nest visits and capture events affect breeding success of Yellow-billed and Pacific loons. -*Condor,* **117**: 121-129.

WATANUKI, Y. and ITO, M. 2012. Climatic effects on breeding seabirds of the northern Japan Sea. -*Marine Ecology Progress Series,* **454**: 183-196.

WATANUKI, Y., ITO, M., DEGUCHI, T. and MINOBE, S. 2009. Climate-forced seasonal mismatch between the hatching of rhinoceros auklets and the availability of anchovy. -*Marine Ecology Progress Series,* **393**.

WILSON, R., PÜTZ, K., BOST, C., CULIK, B., BANNASCH, R., REINS, T. and ADELUNG, D. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: Whose dinner by candlelight? -*Marine Ecology Progress Series,* **94**: 101-104.

WILSON, R. P., PÜTZ, K., CHARRASSIN, J.-B. and LAGE, J. 1995. Artifacts arising from sampling interval in dive depth studies of marine endotherms. -*Polar Biology,* **15**: 575-581.

WILSON, S. K., BURGESS, S. C., CHEAL, A. J., EMSLIE, M., FISHER, R., MILLER, I., POLUNIN, N. V. and SWEATMAN, H. P. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. -*J Anim Ecol,* **77**: 220-8.

ZIMMER, I., WILSON, R. P., BEAULIEU, M., ROPERT-COUDERT, Y., KATO, A., ANCEL, A. and PLOETZ, J. 2010. Dive efficiency versus depth in foraging emperor penguins. -*Aquatic Biology,* **8**: 269-277.

Chapter 4 Winter locations of red-throated divers from geolocation and feather isotope signatures

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JG, SO, FD, IP and JD conceived the ideas and designed methodology; JG, SO, FD, IKP, JD, AP, GB, LJ, PL, DO, RV, JW and SW collected the data; JD analysed the data and created visualisations; SO, JG, AP and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

Migratory species have geographically separate distributions during their annual cycle, and these areas can vary between populations and individuals. This can lead to differential stress levels being experienced across a species range. Gathering information on the areas used during the annual cycle of red-throated divers (RTDs; *Gavia stellata*) has become an increasingly pressing issue, as they are a species of concern when considering the effects of disturbance from offshore wind farms and the associated ship traffic. Here, we use light-based geolocator tags, deployed during the summer breeding season, to determine the non-breeding winter location of RTDs from breeding locations in Scotland, Finland and Iceland. We also use $\delta^{15}N$ and $\delta^{13}C$ isotope signatures, from feather samples, to link population-level differences in areas used in the moult period to population-level differences in isotope signatures. We found from geolocator data that RTDs from the three different breeding locations did not overlap in their winter distributions. Differences in isotope signatures suggested this spatial separation was also evident in the moulting period, when geolocation data was unavailable. We also found that of the three populations, RTDs breeding in Iceland moved the shortest distance from their breeding grounds to their wintering grounds. In contrast, RTDs breeding in Finland moved the furthest, with a westward migration from the Baltic into the southern North Sea. Overall, these results suggest that RTDs breeding in Finland are likely to encounter anthropogenic activity during the winter period, where they currently overlap with areas of future planned developments. Icelandic and Scottish birds are less likely to be affected, due to less ship activity and few or no offshore wind farms in their wintering distributions. We also demonstrate that separating the three populations isotopically is possible and suggest further work to allocate breeding individuals to wintering areas based solely on feather samples.

Introduction

Identifying the migratory strategy and wintering locations of populations and connecting them to the relevant breeding grounds allows for more effective strategies of management and if necessary, conservation (Strøm et al. 2021). Furthermore, the migratory strategy adopted by a population will dictate the geographic area occupied; and therefore, influence the environmental conditions it must withstand during the non-breeding period. As a result, conditions faced by different populations across a species' range can be vastly different, which can, in turn, lead to variation in demographic rates both during the season in question and in the subsequent season through carry-over effects (Frederiksen et al. 2012). For example, carry-over effects from the non-breeding season may cause reduced breeding success due to stress in wintering ground habitat quality (Fayet et al. 2016). However, investigating these processes is challenging during the non-breeding period, particularly for populations that become largely inaccessible due to them solely using marine habitats. Therefore, studies which overcome this difficulty provide a valuable and unique insight into a poorly known period of the annual cycle. This knowledge is all the more pressing in species where negative interactions with future anthropogenic stresses, such as offshore wind farms, are predicted (Dierschke et al. 2016).

For some species of bird, many of the detrimental effects from windfarm developments likely occur specifically during the moult and winter period (Heinänen et al. 2020, Dierschke et al. 2017). Some diving birds, including divers (or "loons"; *Gavia* spp), undergo a synchronous moult of their flight feathers, rendering them flightless for a few weeks (HiDEF 2016, Kjellén 1994). During moult, a combination of a reduced ability to relocate and the high energetic costs of moult, make them particularly vulnerable to anthropogenic effects (Buckingham et al. 2022). Therefore, linking the moulting and winter distributions to the associated breeding population is essential in quantifying the potentially deleterious effects of offshore wind farm interactions on demographic rates, such as survival or breeding success. Red-throated divers (RTDs; *Gavia stellata*) are one such species and have recently been the focus of much interest due to their avoidance of offshore windfarms and associated activity (Heinänen et al. 2020, Furness et al. 2013). One of the most pressing knowledge gaps currently is understanding the moulting and winter distributions used by different populations. This knowledge will enable subsequent research and monitoring to ensure effects of perturbations in the key periods of moult and midwinter can be attributed to the correct breeding populations, to quantify both influences during the non-breeding season and carry-over effects into the breeding period (Harrison et al. 2011).

Studies in North America have shown RTDs moving between continents, with movements up to 8000 km from breeding grounds in Alaska to wintering areas in Asia and along the Pacific (McCloskey et al. 2018). In Europe, birds from many populations can make large migratory flights, while some are thought to fly short distances or remain resident (Duckworth et al. 2020, Dorsch et al. 2019). Furthermore, year-round variation in habitat use can differ between individuals and populations, with RTDs switching from a marine to a wholly freshwater distribution from the non-breeding to the breeding season, respectively (Duckworth et al. 2021). However, in Europe, we currently lack a comprehensive understanding of the year-round distributions of all populations. Therefore, to understand the environmental pressures individuals and populations face, we must first identify the areas that different breeding populations occupy in the non-breeding period. Historically, bird band recoveries have been used to gather information that links breeding and non-breeding season locations of RTDs, e.g., birds breeding in Scotland have been recovered in the Southern North Sea and around Scotland, suggesting a partial migration strategy (Okill 1994). However, these methods generally only provide information on birds which have perished and may be biased towards revealing unsuccessful strategies (Bairlein 2001). Currently, the best methods to determine migratory movements of seabirds is through the deployment of biologging devices (Laurenson et al. 2021), of which leg-mounted light-based geolocators are often the smallest and least intrusive device (Bodey et al. 2018).

While biologging has revolutionised our understanding of avian migration (Fudickar et al. 2021), where possible, attempts should be made to develop methods to determine the distributions of birds of an unknown origin, without the need for any potentially invasive deployments. This is particularly relevant to divers which are vulnerable to disturbance and stress by human interventions (O'Brien et al. 2020, Rizzolo et al. 2014). Isotope analysis has the ability to provide a wide range of insight into the diet (Hobson et al. 1994, Weiss et al. 2009), behaviour (Votier et al. 2011) and movement (St John Glew et al. 2018) of many marine species. Working to build an understanding of the isotopic differences within and between populations of a species has the potential to inform methods for less invasive identification of migratory behaviours (Jaeger et al. 2010). For example, previous work by St John Glew et al. (2018) to understand the locations of wintering guillemots using feathers grown during their annual moult. This work has allowed for the broad determination of moult location in the North Sea from a combination of $\delta^{15}N$ and $\delta^{13}C$, isotope signatures in feather samples using an isoscape. The full development of such methodologies requires calibration using data on environment and location of the population along with a suitable habitat-based isoscape covering the relevant area (Carpenter-Kling et al. 2020). The principal metric required for this work is an enrichment factor, representing the difference in isotope values between the study organism and organism the isoscape was built with, driven by differences in both the prey and trophic level the organisms consume. While such information is not currently available for RTDs, beginning to link distribution to isotope values in RTDs will undoubtedly have a role in developing future methodologies for movement patterns in this species. Furthermore, isotope data retrieved from feathers will provide information over the time period they were grown, which in RTDs is during the autumn equinox. During the equinox periods, GLS data are less reliable, as the differences in day length, the metric used to determine latitude, across latitudes becomes near uniform globally. Therefore, isotope approaches can be used to provide information on distribution when GLS data is potentially unviable due to the equinox (Lisovski et al. 2012).

In this study, we aim to present the first biologging and isotope data on locations used by RTDs from three populations in NW Europe during the winter non-breeding season and describe the migration strategies of each of the populations. To achieve this, we deployed light-based geolocators to show the distribution of the birds during the winter. We also plucked feathers from RTDs during recapture events. These feathers were used to reveal the differences in isotope signatures between the three populations during the moult period, through stable isotope analysis. Through combining these two data streams, we firstly provide results on the distribution of the populations during the non-breeding period. Secondly, we explore whether future work could identify non-breeding distributions of individuals using only feather isotopes.

Methods

From May to July in 2018-2019, 89 (Finland n=32; Scotland n=38; North-eastern Iceland n=19) RTDs were captured using a combination of nest traps and extended mist nets (O'Brien et al. 2020) and equipped with GLS tags (Biotrack/Lotek MK4083 Geolocator) on a plastic leg ring. Fifty-four of the deployed tags were recovered and removed 1-3 years after deployment, each with 1-2 years of data (Thompson et al. 2022). All birds were handled for less than ten minutes and if any sign of skin damage was observed, the bird was not retagged. In total, sufficient data on the wintering periods (defined as where the GLS functioned until at least December) were obtained for 8, 8 and 11 individuals (from 11, 8 and 13 retrieved functioning GLS tags) from Finland, Scotland and Iceland, respectively, including individuals where tags were deployed twice. Seventy-six Secondary flight and 64 secondary covert feather samples were taken for isotopic analysis from birds in the 2019 and 2020 field seasons. These samples corresponded to the moult period from September and October (Dorsch et al. 2019) in 2018 and 2019. GLS tags were also deployed from 2007-2012 in Scotland and Western Iceland in earlier studies, using the same methods as above, with six and five functioning GLS tags recovered in subsequent field seasons from Scotland (Shetland only) and Western Iceland, respectively. No feathers were taken during this earlier study period. Here, we present all data from the non-breeding period obtained by GLS tags.

Two locations per day were generated from the GLS data using the BASTrack collection of software packages. Following initial observations of light levels during twilight events and values suggested by the software instructions, a light threshold value of 15 was used to determine sunset and sunrise. Across individuals this light threshold value related to a mean sun elevation angle of -5. No other post-processing or landmask was used to generate locations. Population level estimates of core distributions used were estimated from the 50% kernel density contour, which has been shown to provide the best estimate for location estimates of populations when considering GLS errors (Buckingham et al. 2023). These were generated using the adehabitatHR R package (Calenge 2006), with the "href" function used to generate the smoothing parameter, with the grid size set to 1000 and an extent of 1. All available locations from all individuals within the stated timeframes are used to generate estimates. RTDs from our study populations completed their breeding attempts by mid-late August (Duckworth et al. 2021), but locations shown are from the early winter period (22nd October – 31st December) and late winter period (1st January – 20th February) to exclude periods where there is still a noticeable impact on locations from the equinox periods. To further exclude any clearly anomalous data points, any points above 75° North were excluded, as often locations extracted when the GLS logger is heavily shaded are pushed to the northernmost degrees of latitude. To ensure kernel distributions for populations were not biased towards individuals with more years of data, an average location for each calendar date was taken for those individuals across the study period. This meant each individual had equal weighting in the final population kernel. This averaging is justified by the high repeatability of movements of individuals between years seen within our study and others on divers (Dorsch et al. 2019, Paruk et al. 2015).

Feathers were stored in paper envelopes at room temperature for four months prior to isotope analysis, which was carried out by Elemtex Ltd (Cornwall, UK). Samples were washed 3 times in a solution of 2:1 chloroform:methanol (v/v) and rinsed in distilled water, before being oven-dried at 60°C. Subsequently, the samples were run on an ANCA/2020 isotope ratio mass spectrometer, which was set to run in continuous flow mode. Finally, data were normalised to Vienna PeeDee Belemnite for δ^{13}C and Air for δ^{15}N using USGS40, USGS41A and USG42 as reference materials (Qi et al. 2016), with typical precisions being better than 0.3‰. Isotope values are expressed as δ^{15}N‰ and δ^{13}C‰, which represent the relative difference, in parts per thousand, of the ^{15}N and ^{13}C isotopes, relative to their respective standard.

To determine whether isotope values and hence locations used during moult were distinct across the three sampled locations, linear discriminant analysis (LDA) was applied to the $\delta^{15}N$ and $\delta^{13}C$ signatures of all feathers (regardless of whether GLS tags were retrieved from birds caught during the 2019 and 2020 field season). A model was generated with LDA separately for isotope signatures from the secondary covert and secondary flight feathers to determine whether either of the feathers are better able to separate the populations. If a successful LDA model could be created with either secondary flight or covert feathers, it would mean only covert feathers would need to be sampled for future isotope work, which is thought to be less disruptive to the birds. Training of the LDA models was carried out with a subset of 80% of the available data, and testing was carried out with the remaining 20% to verify the classifications.

Results

RTDs from Finland migrated westwards from their breeding grounds in mainland Finland through to the western Baltic in the early winter (Figure 4.1a) and southern North Sea by late winter (Figure 4.1b). Birds from Scotland in both study periods showed a varied pattern of movement (Figure 4.2a & 4.2c), with some birds remaining around the northern Scottish isles. In contrast, others migrated a short distance to other coastlines around northern mainland Britain and Northern Ireland. In the later winter period for Scotland RTDs (Figure 4.2b & 4.2d), the 50% kernel indicated much of the core area is on land in Scotland. This may be the result of some individuals making movements southwards along either the East or West coasts of the British Isles, as well as some of the GLS tags failing before the late winter period. These results suggest RTDs from the Scotland population on Orkney and Shetland can be thought of as partial migrants, with some individuals remaining resident and others migrating for at least some of the period. Birds from both East Iceland (Figure 4.3a & 4.3b) and West Iceland (Figure 4.3c & 4.3d) were resident year-round, largely remaining around the northern coast of Iceland throughout the winter, only moving distances over 200 km from their breeding season locations in a few cases (Figure 4.3). These small movements were largely longitudinal; therefore, we can conclude this was likely due to movement rather than GLS errors. While our sample size was not sufficient to formally investigate inter-annual consistency in wintering grounds, all individuals sampled across multiple years showed consistency in sites used in the winter.

LDA models created with the isotope data were both able to separate the populations based on the isotope signatures. The models had an accuracy of 91% and 86% for secondary flight feathers and secondary covert feathers, respectively, when applied to the testing datasets (Table 4-1). The outputs of the two LDA models are visualised in Figure 4.4 to show boundaries of the classification regions.

Table 4-2 shows that in terms of population average, the differences between the two feather types are small. In the case of both feather types, linear discriminant (LD) 1 is strongly associated with $\delta^{13}C$ and LD 1 subsequently contributes greater than 90% of the trace in both models, suggesting $\delta^{13}C$ is the more important isotope when looking at spatial separation (Table 4-1). Figure 4.4 demonstrates this importance with the majority of variation being shown across the $\delta^{13}C$ axis and variation in $\delta^{15}N$ mostly occurring within sites, especially in Finland.

TABLE 4-1 OUTPUT OF THE FINAL MODEL FROM LINEAR DISCRIMINANT ANALYSIS FOR FEATHER ISOTOPES

Results of the linear discriminant analysis showing the loadings of $\delta^{15}N$ *and* $\delta^{13}C$ *onto the linear discriminant axes for models generated from the secondary covert and secondary flight feathers. Model accuracy gives the proportion of correctly identified country of origins of the test data predicted by the model built from the training data.*

Feather	Model accuracy	Coefficients of linear discriminant 1		Coefficients of linear discriminant 2		Proportion of trace for linear discriminants	
		$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	1	2
Flight	0.909	0.009	1.05	0.810	-0.131	0.902	0.098
Covert	0.857	-0.265	1.258	0.768	-0.107	0.9137	0.0863

TABLE 4-2 SUMMARY OF ISOTOPE VALUES FOR EACH POPULATION ACROSS FEATHER TYPES

Group means and standard deviations from the secondary flight and secondary covert LDA models for their $\delta^{13}C$ *and* $\delta^{15}N$ *signatures.*

Feather	Finland		Iceland		Scotland	
	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$
Flight	15.6 (2.0)	-20.9 (1.4)	14.7 (0.6)	-18.3 (0.8)	16.4 (0.9)	-17.2 (0.6)
Covert	15.4 (2.3)	-21.0 (1.3)	14.8 (0.6)	-18.5 (0.7)	16.4 (1.0)	-17.6 (0.6)

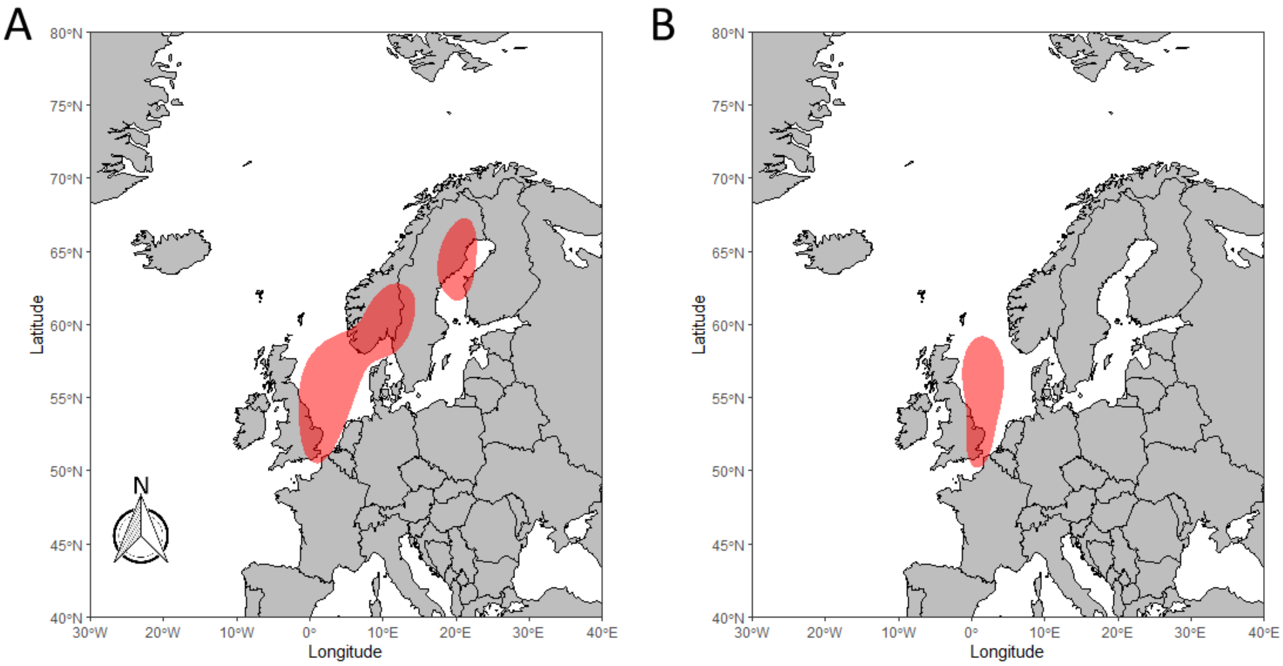

FIGURE 4.1 LOCATIONS OF RTD FROM FINLAND ACROSS THE NON-BREEDING SEASON

50% kernel density distribution of the locations of RTDs sampled in Finland during the early (A) and late (B) winter period. Both panels show the 2017-2021 study period.

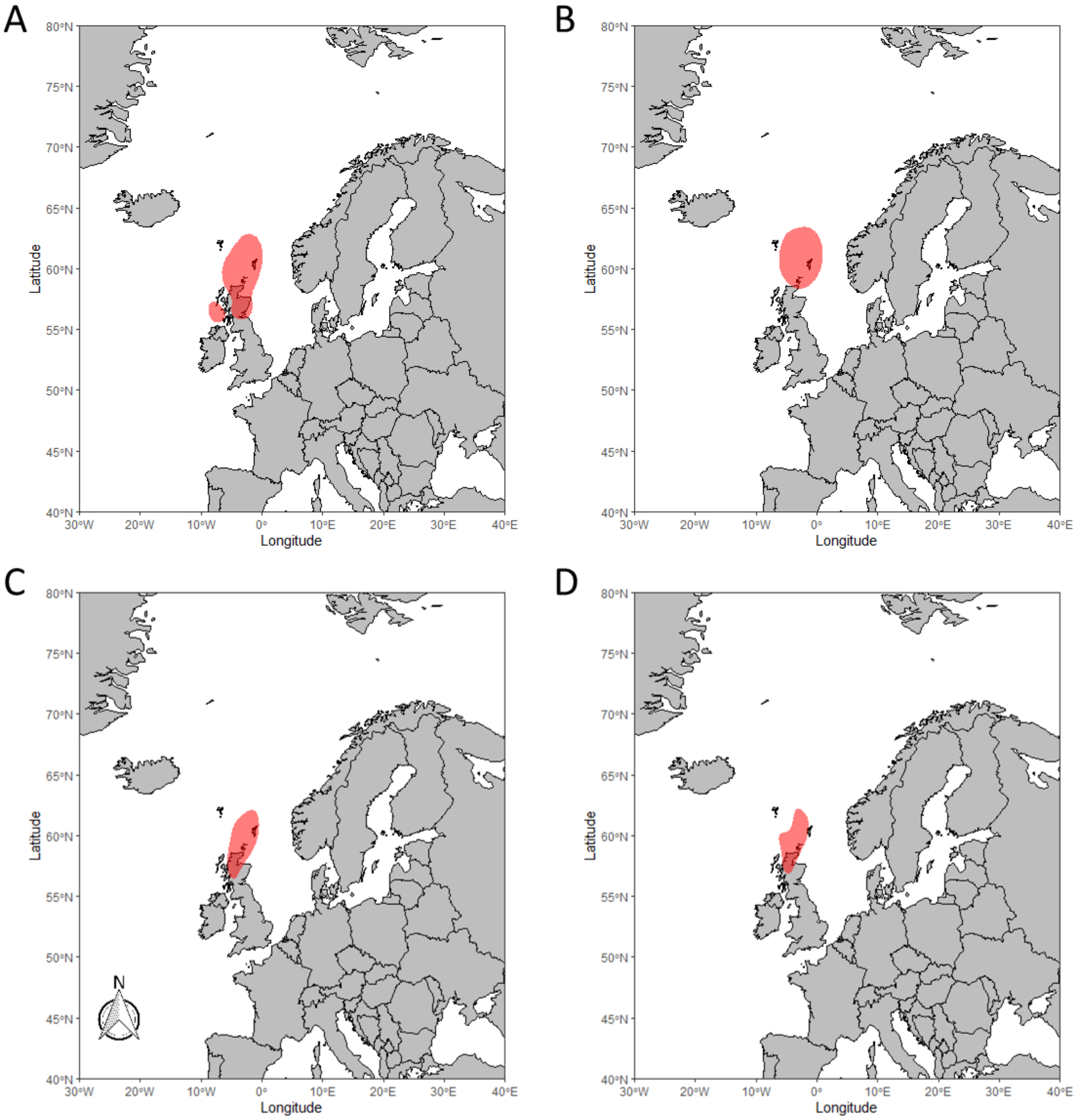

FIGURE 4.2 LOCATIONS OF RTD FROM SCOTLAND ACROSS THE NON-BREEDING SEASON

50% kernel density distribution of the locations of RTDs sampled in Scotland during the early (A & C) and late (B & D) winter period. Panels A and B show the 2017 to-2021 study period, while C and D show the 2007-2010 study period.

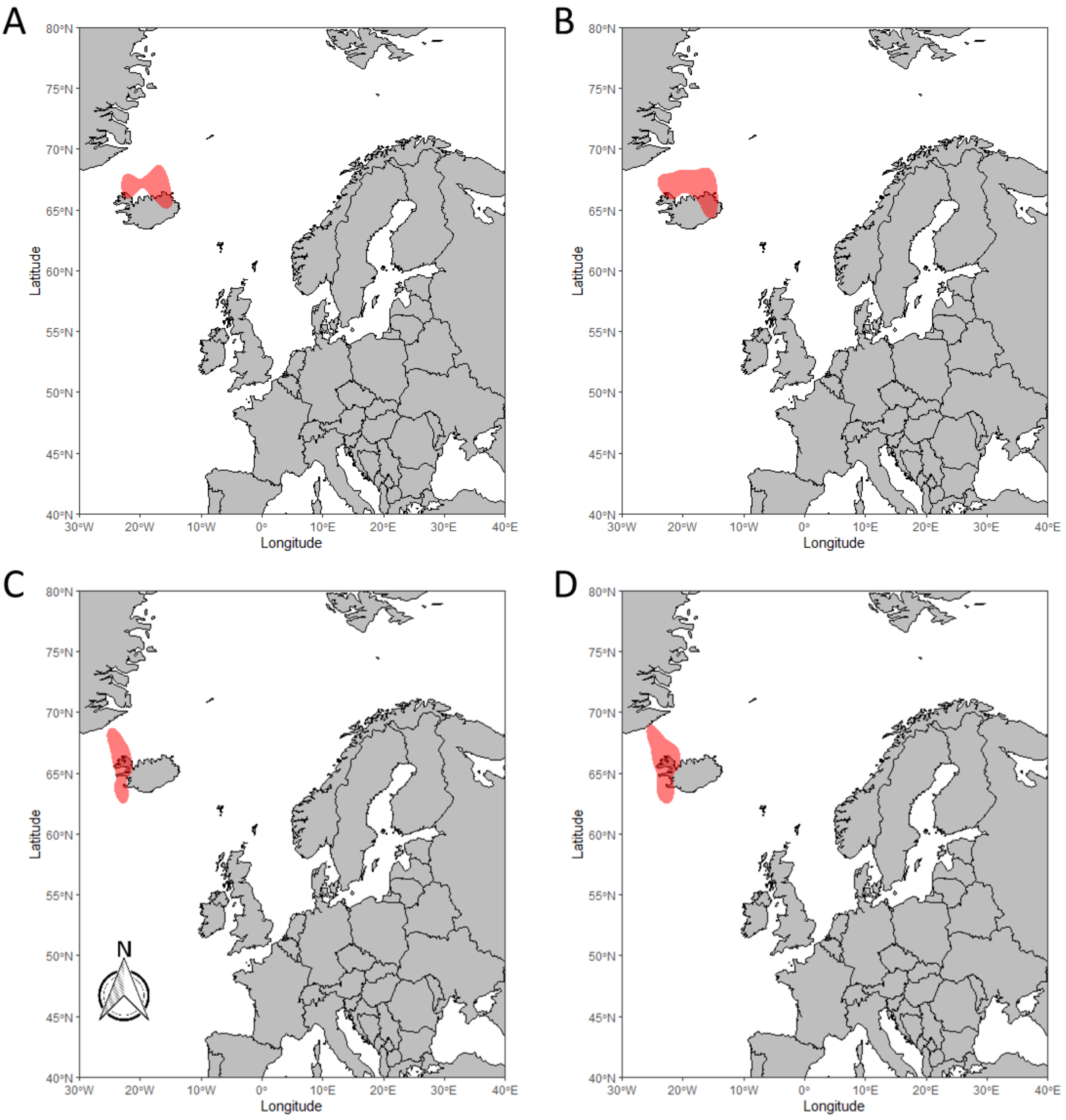

Figure 4.3 Locations of RTD from Iceland across the non-breeding season

50% kernel density distribution of the locations of RTDs sampled in Iceland during the early (A & C) and late (B & D) winter period. Panels A and B show the 2017-2021 study period in East Iceland, while C and D show the 2007-2010 study period in West Iceland.

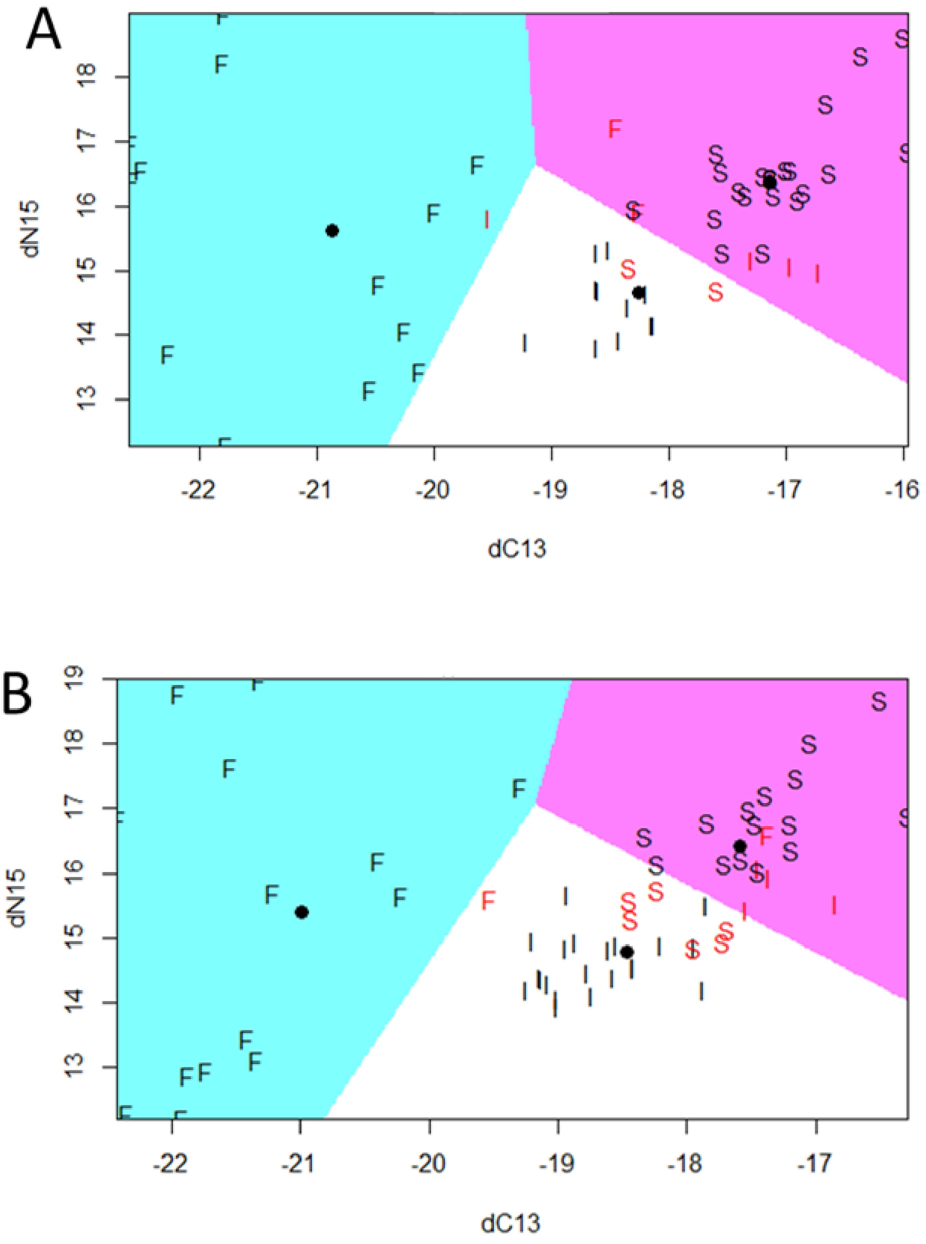

FIGURE 4.4 VISUALISATION OF THE ISOTOPE SPACE OCCUPIED BY THE THREE RTD POPULATIONS

*Outputs of the linear discriminant analysis. Data shown here are from the training partition of the overall dataset. Letters represent the population an individual data point was sampled from. Letters in red represent points from the training dataset that were misclassified. Shaded areas represent the population within which a point would be classified as originating from Finland, Iceland or Scotland as blue, white or pink, respectively. (**A**) shows the model for the secondary flight feather and (**B**) shows the model for secondary covert feathers.*

Discussion

Both the GLS and isotope data lend support to the three populations of RTDs spending the non-breeding season in spatially separated locations and demonstrating three different migratory strategies. The results from GLS devices suggest the RTDs from Iceland remain resident around Iceland, with only movements around the coasts of Iceland being observed. RTDs from Scotland (Shetland and Orkney) are shown to either remain resident, move to the coastal waters of the Western Isles or make movements south to the coasts of mainland Scotland and Northern Ireland. However, during the late winter period, we no longer see the separate distributions for the migrants and residents with only the resident distribution remaining. This is likely due to logger failure within the population. Previous studies have demonstrated that individuals from Scotland have migrated and likely remained in these areas beyond the early winter (Okill 1994). Therefore, this evidence suggests RTDs from Scotland are partial migrants. RTDs from Finland have the longest migration distance of the three populations, and the population kernel was shown to move westward as the season progressed (Figure 4.1), indicative of a fully migratory strategy. This population was shown to move from the eastern Baltic Sea, likely moulting in this area, through to the western Baltic, southern North Sea and east coast of England. Our isotope results corroborate these findings of geographic separation, as the three populations have distinct isotopic signatures derived from the moult period (assumed to occur in September-October). The differences in $\delta^{15}N$ and $\delta^{13}C$ values across the three populations indicating use of different locations at this time. However, there is likely only a small temporal overlap in our GLS locations and isotope results, as the equinox precludes the inclusion of GLS data during part of the moult period. Therefore, the results in tandem provide evidence of complete segregation of populations from the start of moult, through to the end of the wintering period.

The limited amount of movement observed in the Icelandic birds likely means moult is occurring in similar locations to the rest of the non-breeding period locations. This population does still experience some seasonal change though, as they cease spending time in freshwater environments during the non-breeding season (Duckworth et al. 2021). Our maps showed a westward movement for some birds during the study period (Figure 4.3a & 4.3b), from the north-east to north-west coast of Iceland. This suggests there may be short movements for some individuals. In contrast, others, including those from the earlier deployments (Figure 4.3C & 4.3D), remain at locations indistinguishable by GLS tags from their breeding season locations in most scenarios. Scottish RTDs which do not leave the waters surrounding Shetland and Orkney will likely moult in the location they over-winter in. However, it is unclear whether the Scottish RTDs that are migratory, moving to the coasts around either mainland Great Britain or Ireland, moult before or after departure from their breeding grounds.

This study used stable isotope data to demonstrate the separation of three populations during the moult period and suggests further work could apportion breeding individuals to moulting locations based solely on feather samples. We found the $\delta^{13}C$ signatures of the three populations separate into distinct clusters, along with $\delta^{15}N$ to a lesser degree (Figure 4.4 & Table 4-1). These results suggest that a method to identify the moulting grounds of individual birds based on feather samples and isotope analysis is possible, like those created in other study systems (Cruz-Flores et al. 2018, Jaeger et al. 2010). Further refinement of the methodology requires additional research to identify a wider range of moulting areas from feather isotopes to establish the most commonly used moulting locations by RTDs in Europe and their associated isotopic signature. Additionally, in its current form, these results allow for identification of individuals carrying out novel migration movements. This could be observed through individuals which deviate from the population-specific mean isotope signature detected in this study. In this regard, a better understanding of a wider array of locations used during moult in NW Europe could help identify movements across the metapopulation range.

The mean observed $\delta^{15}N$ and $\delta^{13}C$ value from the Finnish RTDs aligned with isotope signatures found by Dorsch et al. (2019) among RTDs moulting in the Eastern Baltic (Figure 4.4). The locations we estimate our Finland RTD population to be in during the end of the moulting period (mid-late October) also lines up with their locations for birds from other breeding populations, like Siberia, identified to moult in the Baltic Sea (Dorsch et al. 2019) (Figure 4.1). This provides us with a degree of confidence that any RTDs moulting in the Baltic Sea will lie within the "Isotopic area" identified by our LDA. However, it is not possible to determine with a high degree of accuracy where exactly RTDs were moulting within the Baltic Sea with the current isotope and location data. The cluster of individuals with a $\delta^{13}C$ of -22‰, could be moving further North in the Baltic, as this area is known to produce more negative $\delta^{13}C$ than the Southern areas of the Baltic Sea (Magozzi et al. 2017). Movement data with a high accuracy, like GPS, along with feather samples grown during the tracked period, would allow for investigation into whether a higher temporal resolution of isotope location differentiation is possible (Votier et al. 2011).

The accuracy of the two LDA models suggests using secondary flight feathers is preferable to secondary covert feathers when trying to separate the three populations (Table 4-1 & Figure 4.4). The two feather types performed differently could be due to the specific timing and duration of the moult on the feather type. In terms of impact, it is worth noting that the impact of removal of part of a secondary flight feather is likely to be greater on aerodynamics and effort required for flight, compared to a covert feather. However, other studies have sampled primary flight feathers (Yerkes et al. 2008, White and Dawson 2021), so our approach of using a small section of secondary flight feathers over primaries should be seen as cautious. We believe future effort should be invested into further developing feather isotope maps with secondary flight feathers, as the slight increase in accuracy may be enough to help distinguish sites with smaller spatial differences, for a small trade-off in disturbance. Additionally, RTDs are large birds, and only a small section of a secondary flight feather is needed to assess isotopic signatures, meaning the effects of removing this small section are likely to be minimal.

Another observation in this study is within-population variation of isotope signatures was greater for RTDs from Finland than the other two populations, with Finland demonstrating a much higher range of $\delta^{15}N$ values (Figure 4.4). This high variability is unlikely to be driven by location and movements alone, as RTD $\delta^{15}N$ does not vary as much spatially as $\delta^{13}C$ and RTD are constrained in their movements at their moulting areas, due to their inability to fly (Gómez et al. 2018, Ceia et al. 2018). The variation could be driven by variation in diet, habitat use or an isotopically diverse local environment (Dorsch et al. 2019, Duckworth et al. 2020). This could be a product of individual RTD selecting for different prey species within the same area, leading to the patterns we observed in $\delta^{15}N$ signatures being driven by either benthic/pelagic or trophic level differences of prey. RTDs are generalist foragers (Kleinschmidt et al. 2019); therefore, a wide range of $\delta^{15}N$ signatures is expected as RTDs distribute their foraging efforts across a wider range of prey species. Cementing this relationship would require future work to link foraging behaviour metrics on dive depth and behaviour to $\delta^{15}N$ isotope signatures.

Through the processing of GLS tags in our work, this study also flags the difficulties of using GLS tags with RTDs. Primarily, the interference to light levels experienced through various resting behaviours, such as leg tucking while resting, is a significant disadvantage. Such shading will affect the reliability of latitudinal estimates, tending to drag locations of these northern hemisphere birds towards the north. However, if tucking occurs at both the sunset and sunrise equally it is unlikely to affect estimates of longitude. Other studies have noted the effects of sensor shading on the accuracy of light-based geolocation and deployed methods to remedy the issue (Bindoff et al. 2018, Merkel et al. 2016). However, shading of the sensors was so pronounced that even these methods failed to produce realistic estimates of locations and movements. For this reason, we used a simple method that applies no post-processing adjustments or landmasks to generate locations. The locations presented here are much in-line with recent work by Halpin et al. (2021), who suggest the location errors of 186 and 202 km for GLS are not uniform across species. We therefore strongly recommend that future studies aimed at exploring detailed locations of RTDs avoid the use of GLS. However, for research questions focussed on establishing the type and scale of migration or only requiring data from the immersion sensor, GLS is a valid tool. This is compounded by the relatively low recovery rates of GLS loggers from the RTDs in our study, which was driven by a combination of inaccessible field sites, aversion of birds to human presence and Covid-19 restrictions. Despite the errors in our individual location fixes, our overall population-based location estimates give a good indication of the areas used during the non-breeding season. Hence the results provide reliable insights into the migration strategy of RTDs from three NW European populations. Furthermore, the areas shown here overlap with the current understanding of distributions of RTDs during winter (Heinänen et al. 2020, Kleinschmidt et al. 2019, O'Brien et al. 2012) providing reassurance that the distributions presented here are reliable. Subsequent work should build on these results by continuing to link isotopes to locations, as the importance of developing a robust and low impact method for apportioning individuals to moulting locations cannot be overstated.

Our results have shed light on moult and winter distributions of RTDs and demonstrated the different migration strategies across populations. Isotope signatures shown here have demonstrated differences between the three populations and hinted that future methods, such as the use of isoscapes, to determine moult locations of an individual of an unknown origin might be possible. This study has also helped emphasise that future work is needed to address the spatial and temporal extent to which different populations of RTDs might come into contact with anthropogenic activity. Importantly, our work suggests that populations from Iceland and Scotland may be less affected by offshore wind farm developments. This was due to less overlap of movements with current areas of development in the Scotland and Iceland populations. Conversely, RTDs from the Finland population are shown to move into areas of current and future development, specifically in the south North Sea.

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References

Bairlein, F. (2001). Results of bird ringing in the study of migration routes. Ardea, 89, 7-19.

Bindoff, A. D., Wotherspoon, S. J., Guinet, C., & Hindell, M. A. (2018). Twilight-free geolocation from noisy light data. Methods in Ecology and Evolution, 9(5), 1190-1198

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & Bearhop, S. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. Methods in Ecology and Evolution, 9(4), 946-955.

Buckingham, L., Bogdanova, M. I., Green, J. A., Dunn, R. E., Wanless, S., Bennett, S., . . . Daunt, F. (2022). Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. Marine Ecology Progress Series, 684, 181-197.

Buckingham, L., Daunt, F., Bogdanova, M. I., Furness, R. W., Bennett, S., Duckworth, J., . . . Green, J. A. (2023). Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. Journal of Avian Biology, 1-2, e03018.

Calenge, C. (2006). The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling, 197, 516-519.

Carpenter-Kling, T., Pistorius, P., Reisinger, R., Cherel, Y., & Connan, M. (2020). A critical assessment of marine predator isoscapes within the southern Indian Ocean. Movement Ecology, 8(1), 29.

Ceia, F. R., Cherel, Y., Paiva, V. H., & Ramos, J. A. (2018). Stable isotope dynamics (δ13C and δ15N) in neritic and oceanic waters of the North Atlantic inferred From GPS-tracked Cory's shearwaters. Frontiers in Marine Science, 5.

Cruz-Flores, M., Militão, T., Ramos, R., & González-Solís, J. (2018). Using marine isoscapes to infer movements of oceanic migrants: The case of Bulwer's petrel, *Bulweria bulwerii*, in the Atlantic Ocean. PLoS ONE, 13(6), e0198667.

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

Dierschke, V., Furness, R. W., Gray, C. E., Petersen, I. K., Schmutz, J., Zydelis, R., & Daunt, F. (2017). Possible behavioural, energetic and demographic effects of displacement of red-throated divers. JNCC Report, 605.

Dorsch, M., Burger, C., Heinänen, S., Kleinschmidt, B., Morkūnas, J., Nehls, G., . . . R., Ž. (2019). German tracking study of seabirds in areas of planned offshore wind farms at the example of divers. Final report on the joint project DIVER, FKZ 0325747A/B, funded by the Federal Ministry of Economics and Energy (BMWi) on the basis of a decision by the German Bundestag.

Duckworth, J., Green, J., Daunt, F., Johnson, L., Lehikoinen, P., Okill, D., . . . O’Brien, S. (2020). Red-throated diver energetics project: preliminary results from 2018/19. JNCC Report, 638.

Duckworth, J., O'Brien, S., Petersen, I. K., Petersen, A., Benediktsson, G., Johnson, L., . . . Green, J. A. (2021). Spatial and temporal variation in foraging of breeding red-throated divers. Journal of Avian Biology, 52(6).

Fayet, A. L., Freeman, R., Shoji, A., Kirk, H. L., Padget, O., Perrins, C. M., & Guilford, T. (2016). Carry-over effects on the annual cycle of a migratory seabird: An experimental study. Journal of Animal Ecology, 85(6), 1516-1527.

Frederiksen, M., Moe, B., Daunt, F., Phillips, R. A., Barrett, R. T., Bogdanova, M. I., . . . Anker-Nilssen, T. (2012). Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. Diversity and Distributions, 18(6), 530-542.

Fudickar, A., Jahn, A., & Ketterson, E. (2021). Animal migration: An overview of one of nature's great spectacles. Annual Review of Ecology, Evolution, and Systematics, 52, 479-497.

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

Gómez, C., Larsen, T., Popp, B., Hobson, K. A., & Cadena, C. D. (2018). Assessing seasonal changes in animal diets with stable-isotope analysis of amino acids: A migratory boreal songbird switches diet over its annual cycle. Oecologia, 187(1), 1-13.

Halpin, L. R., Ross, J. D., Ramos, R., Mott, R., Carlile, N., Golding, N., . . . Clarke, R. H. (2021). Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. Methods in Ecology and Evolution, 12(11), 2243-2255.

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

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

HiDEF. (2016). Sensitivity of offshore seabird concentrations to oil pollution around the United Kingdom: Report to Oil & Gas UK. Retrieved from https://hub.jncc.gov.uk/assets/4253a571-146c-48bf-bf06-6fb29b8f59b1

Hobson, K. A., Piatt, J. F., & Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology, 63(4), 786-798.

Jaeger, A., Lecomte, V., Weimerskirch, H., Richard, P., & Cherel, Y. (2010). Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. Rapid communications in mass spectrometry, 24, 3456-3460.

Kjellén, N. (1994). Moult in relation to migration in birds—a review. Ornis Svecica, 4(1), 1-24.

Kleinschmidt, B., Burger, C., Dorsch, M., Nehls, G., Heinänen, S., Morkūnas, J., . . . Quillfeldt, P. (2019). The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. Marine Biology, 166(6), 77.

Laurenson, K., Atkins, K., Clark, B., Morgan, G., Morgan, L., & Votier, S. (2021). Gannet Morus Bassanus ring recoveries suggest shorter migrations than geolocator tracking, but indicate no long-term change in migration distances. Bird Study, 68(1), 1-8.

Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W., & Hahn, S. (2012). Geolocation by light: Accuracy and precision affected by environmental factors. Methods in Ecology and Evolution, 3(3), 603-612.

Magozzi, S., Yool, A., Vander Zanden, H. B., Wunder, M. B., & Trueman, C. N. (2017). Using ocean models to predict spatial and temporal variation in marine carbon isotopes. Ecosphere, 8(5), e01763.

McCloskey, S. E., Uher-Koch, B. D., Schmutz, J. A., & Fondell, T. F. (2018). International migration patterns of red-throated loons (*Gavia stellata*) from four breeding populations in Alaska. PLoS ONE, 13(1), 1-15.

Merkel, B., Phillips, R. A., Descamps, S., Yoccoz, N. G., Moe, B., & Strøm, H. (2016). A probabilistic algorithm to process geolocation data. Movement Ecology, 4(1), 26.

O'Brien, S., Ruffino, L., Johnson, L., Lehikoinen, P., Okill, D., Petersen, A., . . . Williams, S. (2020). Red-throated diver energetics project: 2019 field season report. JNCC Report, 637.

O’Brien, S. H., Webb, A., Brewer, M. J., & Reid, J. B. (2012). Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. Biological Conservation, 156, 15-21.

Okill, J. D. (1994). Ringing recoveries of red-throated divers *Gavia stellata* in Britain and Ireland. Ringing & Migration, 15(2), 107-118.

Paruk, J. D., Chickering, M. D., Long, D., IV, Uher-Koch, H., East, A., Poleschook, D., . . . Evers, D. C. (2015). Winter site fidelity and winter movements in Common Loons (*Gavia* immer) across North America. The Condor, 117(4), 485-493.

Qi, H., Coplen, T. B., Mroczkowski, S. J., Brand, W. A., Brandes, L., Geilmann, H., & Schimmelmann, A. (2016). A new organic reference material, l-glutamic acid, USGS41a, for δ13C and δ15N measurements − a replacement for USGS41. Rapid Communications in Mass Spectrometry, 30(7), 859-866.

Rizzolo, D. J., Schmutz, J., A., McCloskey, S. E., & Fondell, T. F. (2014). Factors influencing nest survival and productivity of red-throated Loons (*Gavia stellata*) in Alaska. The Condor(4), 574-587.

St John Glew, K., Wanless, S., Harris, M. P., Daunt, F., Erikstad, K. E., Strøm, H., & Trueman, C. N. (2018). Moult location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. Marine Ecology Progress Series, 599, 239-251.

Strøm, H., Descamps, S., Ekker, M., Fauchald, P., & Moe, B. (2021). Tracking the movements of North Atlantic seabirds: Steps towards a better understanding of population dynamics and marine ecosystem conservation. Marine Ecology Progress Series, 676, 97-116.

Thompson, D. L., Johnson, L., Williams, J., & Lehikoinen, P. (2022). Red-throated diver energetics project: 2021 field season report. Retrieved from JNCC Peterborough:

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

Weiss, F., Furness, R. W., McGill, R. A. R., Strange, I. J., Masello, J. F., & Quillfeldt, P. (2009). Trophic segregation of Falkland Islands seabirds: Insights from stable isotope analysis. Polar Biology, 32(12), 1753-1763.

White, A. F., & Dawson, R. D. (2021). Can diet composition estimates using stable isotope analysis of feathers predict growth and condition in nestling mountain bluebirds (Sialia currucoides)? Ecology and Evolution, 11(21), 15273-15288.

Yerkes, T., Hobson, K. A., Wassenaar, L. I., Macleod, R., & Coluccy, J. M. (2008). Stable isotopes (δD, δ13C, δ15N) reveal associations among geographic location and condition of alaskan northern pintails. The Journal of Wildlife Management, 72(3), 715-725.

Chapter 5 Linking foraging behaviour to isotope signatures in a diving bird

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JG, SO, FD, IP and JD conceived the ideas and designed methodology; JG, SO, FD, IKP, JD, AP, GB, LJ, PL, DO, RV, JW and SW collected the data; JD analysed the data and created visualisations; SO, JG, AP and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

Understanding the habitat use of individuals can facilitate methods to measure the degree to which populations will be affected by stressors. This insight can help with predicting how populations will deal with changing conditions, helping planning, policy and conservation. Here, we quantify the link between diet and foraging behaviour, which reflect habitat use, in a marine generalist forager, the red-throated diver (RTD, *Gavia stellata*). Specifically, we quantify the relationship between feather isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) and diving behaviour, within and between populations. We found a strong positive relationship between the use of benthic diving strategies and higher $\delta^{15}N$‰ values. This scaling relationship was consistent across three populations, but the actual values for $\delta^{15}N$ varied slightly across sites. $\delta^{13}C$ varied across the three populations and showed a weak relationship with foraging strategy. These results provide an insight into the range of foraging habitats used in terms of strategies demonstrated by RTDs and the degree of variability within and between populations. Additionally, we demonstrate that stable isotope analysis of feather samples is a simple indicator of individual foraging strategies and hence habitat use of RTDs and could potentially be applied to other generalist foragers. This approach has the potential to quickly quantify foraging strategies within and between populations with a known isotopic value and therefore assess responses to environmental change and the relative importance of habitats to a population.

Introduction

Linking different habitat use to environmental properties can provide new insights into the ecology of a species and facilitate new methods for monitoring and conservation [1, 2]. Specifically, in cases where behaviours are strongly associated with habitats, discovering indicators of habitat use can allow methodological developments to quantify the relative importance of habitat types within and between populations [3, 4]. In the context of foraging, the connection between an individual and its environment can be expressed through the prey consumed [5, 6]. In this relationship, the materials of the prey are integrated into the consumer tissue, therefore changes in foraging behaviour and prey type associated with different habitats lead to changes in the chemical composition of the consumer tissue [6, 7]. For example, in a study on brown bears (*Ursus actos*) by Ben-David [4], individuals were found to either forage in close proximity to rivers and feed on salmon, or distribute more distantly from rivers and feed on berries. Through differences in the isotope composition of individuals, the strategy of an individual could be determined through a tissue sample. Understanding these strategies could have applications for predicting the impacts of climate change, anthropogenic activity and other threats [8, 9]. The main mechanism of this would be through apportioning the population to the stressor, based individuals having different isotope signatures due to different habitats, life histories or behaviours based on exposure to the stressor. Gaining this information through a tissue sample potentially mitigates the need for time and cost intensive deployments of remote sensing devices. In the case of the brown bear, knowledge of foraging strategies, which could be drawn from isotope values, allowed for predictions on cub mortality due to the lower quality diet of individuals foraging on berries [4]. This demonstrates the practical benefit of understanding links between behaviour and isotope values.

Stable isotope analysis (SIA) has demonstrated an ability to provide insight into a wide range of aspects including diet [10] and behaviour [11]. For example, studies have previously linked variation in specific nitrogen isotopes ($\delta^{15}N$) to the trophic level an organism consumes [12, 13]. Generally, higher values of $\delta^{15}N$ are linked to higher trophic levels [8], however many other factors can influence this relationship. However, this variation is well-established across many environments [14-16]. However, linking individual stable isotope values to foraging behaviour, and indirectly habitat use, is less well studied, despite its potential to better understand this individual-level behaviour. Most studies in this area focus on the explicit link between diet and isotope signatures [6, 16, 17]. Instead, quantifying the link between the foraging behaviour and stable isotope composition of individuals will reveal associations between foraging strategies and diet, yielding further insight into habitat use. This could prove useful when quantifying differences in a range of foraging and associated metrics between [3, 4] or within populations [18]. Such information could aid conservation efforts, where understanding resource use across a population can more explicitly link individuals to threats [19]. This could be especially applicable to species where individuals become inaccessible and difficult to study (e.g. during the non-breeding period of marine bird species).

Assessing the capabilities of SIA to explain foraging behaviours and diet is most applicable for species that use a range of habitats and show a range of foraging behaviours. Therefore, application of this concept is best tested on a species which exhibits a generalist foraging behaviour. Red throated divers (*Gavia stellata*, RTDs) are a generalist marine forager switching between freshwater and marine ecosystems and benthic and pelagic habitats [20]. Further, this species is vulnerable to displacement from marine anthropogenic activities such as shipping [21] and offshore wind farms [21, 22]. This concern has caused an increased demand for knowledge on their non-breeding season habitat use and behaviour, when the species is thought to be the most exposed to these activities [23]. Previously, a multi species study inferred RTD diet with isotope signatures, suggesting a largely pelagic diet (~50% of prey) during the winter [16]. However, there has not been any work linking isotope signatures to foraging metrics in this species. An established way to measure foraging behaviour in diving birds is by looking at intra-dive zone (IDZ) dives. These indicate whether an individual is targeting benthic (and demersal) or pelagic habitats and prey [24]. In cases where a threat may impact individuals prioritising one foraging strategy and hence habitat over another, it provides an ideal context for this present study.

In this study, we use biologging technology to determine the diving behaviour of RTDs during the moult period of their annual cycle. Simultaneously, the isotope signatures of these same individuals are determined with bulk stable isotope analysis of feathers grown during the moult period. This gives us a discrete timeframe to quantify the links between foraging behaviour and isotope signatures during a phase of the annual cycle that is otherwise hard to study. We aim to quantify the relationship between the isotope values and an important foraging metric, as well as assess the impact of feather type and population-level differences on these relationships. This study will provide the first quantification of the differences in foraging strategies across RTD populations, as well as explore the strength of the relationship with isotope signatures. This approach will also provide evidence for whether individual feather samples are able to provide information on foraging behaviour and habitat use. Additionally, exploring the effects of feather type will ensure that future studies can sample the lowest impact feathers while being confident in the relationship of the isotope signatures with diet.

Materials and methods

Birds were caught at their breeding sites in Finland, Iceland and Scotland, using a mixture of suspended mist nets and nest traps (n=32, 19, 38 individual birds caught, respectively) during the 2018 and 2019 breeding seasons [25]. Time-depth recorders (TDR) and light-based geolocators were deployed on each captured bird (combined weight of loggers was <1% body mass, in all cases). Location results are presented in Duckworth, O'Brien [20, 22, 26]. Upon recovery of the archival tags in 2019 and 2020, secondary flight feather and secondary covert feather clippings were taken of the distal 2 cm of the feather. Of the 26 individuals that were recaptured 11, 9 and 6 individuals from Finland, Iceland and Scotland, respectively, had both a functional TDR and at least one successfully analysed feather sample [25]. TDRs were programmed to record data on every fifth day of deployment, to conserve battery. Our period of interest to examine the relationship between foraging behaviour and isotope signatures was September 10th to October 10th and only data from this period were considered. This is broadly defined here as the moult period [26] and is predicted to be the time that the feather growth occurred. These feathers therefore provide a snapshot of the environment and food source a RTD was utilising for feather growth. The time period chosen may not reflect the full moult period [27], as there is currently uncertainty over the exact timings of RTD feather moult across the geographic range of the species. Whilst using a shorter timeframe risks missing individuals that were moulting earlier or later, this ensures that no foraging behaviour outside of the moult period was inadvertently included in analysis and erroneously compared with isotope signatures of feathers grown at a different time.

TDR tags were processed and dive events, defined as any recorded depth below one metre, were extracted [20]. These dives were then clustered into foraging bouts, where each bout was classified as at least three related dives with less than 66 seconds between each dive [20]. The number of intra-depth zone (IDZ) dives was defined as the number of dives where the maximum dive depth fell within 90% of the maximum dive depth of the preceding dive within a foraging bout [24]. This measure gives an estimate of whether a given bout has repeated dives to a similar depth, indicating foraging is more likely to be benthic (foraging on the sea floor) or has repeated dives to varying depths, indicating foraging is pelagic (foraging in the water column), based on a higher or lower proportion of IDZ dives, respectively. The proportion of IDZ dives was calculated as the total number of IDZ dives divided by the sum of the number of dives within a bout minus one [24]. For analysis, an individual's proportion of IDZ dives was calculated as the number of IDZ dives divided by the total number of dives in bouts minus the number of bouts. Feathers were stored in paper envelopes at room temperature for four months prior to isotope analysis, which was carried out by Elemtex Ltd. (Cornwall, UK). Samples were washed 3 times in a solution of 2:1 chloroform methanol (v/v) and rinsed in distilled water, before being oven-dried at 60°C. Subsequently, the samples were run on an ANCA/2020 isotope ratio mass spectrometer, which was set to run in continuous flow mode. Finally, data were normalised to Vienna PeeDee Belemnite for $\delta^{13}C$ and Air for $\delta^{15}N$ using USGS40, USGS41A and USGS42 as reference materials, with typical precisions being better than 0.3‰. Isotope values are expressed as $\delta^{15}N$‰ and $\delta^{13}C$‰, which represents the difference, in parts per thousand, of the ^{15}N and ^{13}C isotopes, relative to their respective standard.

Linear mixed effect regression models were created for two response variables ($\delta^{15}N$ and $\delta^{13}C$) to assess the effect of population, proportion of IDZ dives and feather type. This was to investigate the extent to which average isotopic signatures varied among populations, with pelagic versus benthic foraging (proportion of IDZ dives) and with the feather type from which samples were obtained. The full model included: proportion of IDZ dives, population, feather type, an interaction between feather type and proportion of IDZ dive and an interaction between population and proportion of IDZ dives. All models included the ID of the individual as a random effect to account for some individuals being tagged and sampled in two years. All nested versions of this model were also generated, with all combinations of fixed effects, and ΔAICc values were used to assess the ability of each model to explain the variance within data, compared to the best fitting model. Model averaging was carried out on all models within four ΔAICc units of the best fitting model. The averaged model for each of the response variables is referred to here as the “final model”, with the weight of each candidate model in the final model being based on their AICc value. The importance of each variable and interaction is discussed by considering (1) the associated effect size in the final mode, (2) the prevalence in the top (ΔAICc<4) models and final model and (3) the overall support for the models in which they occur. All analysis was done in R version 4.2.1. [28].

Results

The high number of models within 4 AICc units of the best fitting model (Table 5-1) for $\delta^{15}N$ suggests that the relative difference in explanatory power of the models is small (Table 5-2). However, the proportion of IDZ dives appeared in all candidate models (Table 5-1), suggesting this was an important predictor for $\delta^{15}N$. This was reflected in the final averaged model including a strong positive relationship between the proportion of IDZ dives and $\delta^{15}N$ (Figure 5.1). $\delta^{15}N$ is predicted to change by 6.9‰, 4.5‰ and 3.7‰ across Finland, Iceland and Scotland respectively, when going from an IDZ of zero to one (i.e. from pelagic to benthic). Feather type also appeared in the top ranked $\delta^{15}N$ model, plus several of the other candidate models; however, the effect size in the final averaged model was small (Table 5-2) with a difference of -0.15 and a very weak interaction with the proportion of IDZ dives. For instance, the predicted δ^{15}N values for the flight and covert feathers in Finland for an individual with a predicted 0.84 proportion of IDZ dives in the final model was 18.1‰ and 18.2‰, respectively. Population had a strong effect on δ^{15}N and also appeared in many of the candidate models, along with an interaction with the proportion of IDZ dives. The largest difference presented was between Finland and Scotland, where the gradient of the slope between δ^{15}N and proportion of IDZ dives was 6.9‰ and 3.7‰, respectively.

The final averaged model for δ^{13}C showed a much larger effect of population (Table 5-2 & Figure 5.2), with it being included in all candidate models (Table 5-1). The largest difference in δ^{13}C was between Finland and Scotland, with an estimated difference of δ^{13}C 4.0‰ (SE 0.5) in the final model (Figure 5.2). δ^{13}C was weakly affected by the proportion of IDZ dives, with it appearing in all top models, but having a much weaker effect size than on δ^{15}N (estimated δ^{13}C 3.2‰ change from a value of 0 to 1 for the proportion of IDZ dives). While an interaction between the proportion of IDZ dives and population was in the final model for δ^{13}C (Table 5-1), the effect size was weak, with a maximum difference of 0.7‰ between the slope of the Finland and Scotland populations (Figure 5.2). Only one candidate model included feather type, with an effect size of 0.02‰. This and the results from the final δ^{15}N model led to a conclusion that there was no strong difference between secondary flight and secondary coverts in terms of either δ^{15}N or δ^{13}C when comparing across populations and foraging behaviour.

TABLE 5-1 TOP RANKED MODELS USED IN MODEL AVERAGING FOR THE RELATIONSHIP BETWEEN FORAGING AND ISOTOPE VALUES

Top models ranked by ΔAICc values, where ΔAICc values were less than 4 ΔAICc shows the number of AICc units away from the best fitting model. DF represents the degrees of freedom. W shows the weight of the model in the final averaged model. IDZ represents the proportion of IDZ dives. Feather represents feather type. Interactions are denoted by colons between variables.

$\delta^{15}N$ models			
Model	ΔAICc	DF	W
$\delta^{15}N$ ~ IDZ + feather	0	5	0.202
$\delta^{15}N$ ~ IDZ	0.07	4	0.196
$\delta^{15}N$ ~ IDZ + population	0.78	6	0.137
$\delta^{15}N$ ~ IDZ + population+ population:IDZ	0.87	8	0.131
$\delta^{15}N$ ~ IDZ + population+ feather	0.92	7	0.128
$\delta^{15}N$ ~ IDZ + population+ feather + population:IDZ	1.01	9	0.122
$\delta^{15}N$ ~ IDZ + feather + feather:IDZ	2.61	6	0.055
$\delta^{15}N$ ~ IDZ + population+ feather + feather:IDZ	3.81	8	0.03
$\delta^{13}C$ models			
Model	ΔAICc	df	W
$\delta^{13}C$ ~ population + IDZ	0	6	0.673
$\delta^{13}C$ ~ population + IDZ + feather	2.35	7	0.208
$\delta^{13}C$ ~ population + IDZ + population:IDZ	3.47	8	0.119

TABLE 5-2 PROPERTIES OF THE FINAL AVERAGED MODEL DESCRIBING THE RELATIONSHIP BETWEEN FORAGING AND ISOTOPE VALUES

Final averaged model for Nitrogen and Carbon models. The intercept is set for population = Finland, feather = Covert, IDZ = 0. A tilde (~) indicates no difference from the intercept. Population shows the effect of population on the intercept. Feather shows the effect of feather type on the intercept. IDZ represents the increase in the response variable from the intercept for an increase in IDZ from zero to one, with each population representing the population-specific effect of the proportion of IDZ dives after accounting for an interaction. "IDZ : feather" represents the interactive effect of feather type on the relationship between IDZ and isotope signature, per unit increase of proportion of IDZ dives.

Response variable	Intercept	Population			Feather		IDZ			IDZ : feather	
		Finland	Iceland	Scotland	Covert	Flight	Finland	Iceland	Scotland	Covert	Flight
$\delta^{15}N$	12.45	~	0.41	1.93	~	-0.15	6.86	4.5	3.74	~	0.005
$\delta^{13}C$	-22.68	~	2.73	3.96	~	0.03	3.24	3.08	2.56	~	~

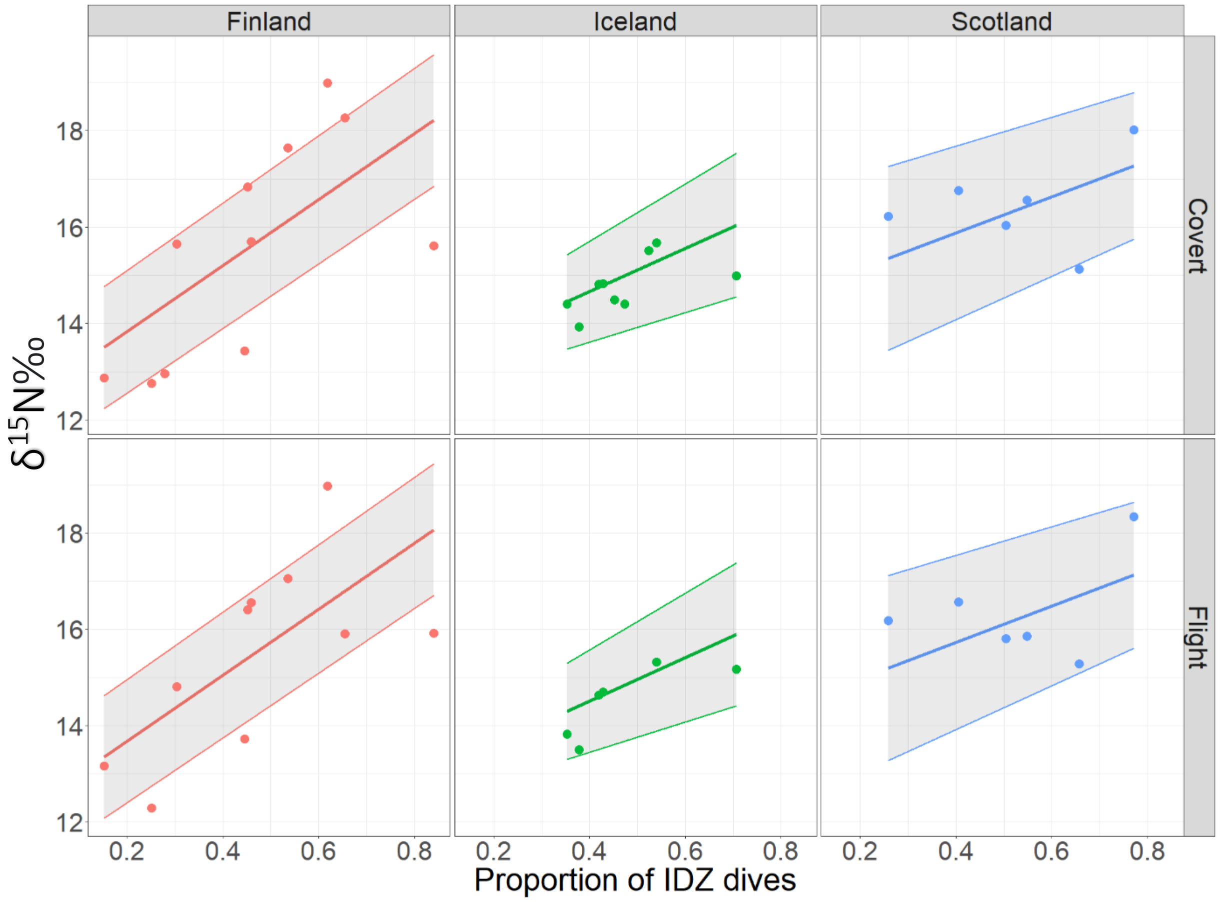

FIGURE 5.1 RELATIONSHIP BETWEEN NITROGEN ISOTOPES AND FORAGING STRATERGY ACROSS POPULATIONS AND FEATHER TYPES

δ^{15}N‰ signatures across the three populations and two feather types sampled in this study against the proportion of IDZ dives taken across the predicted moult period generated by the final model. Populations are represented by red, green and blue for Finland, Iceland and Scotland, respectively. Shaded regions show standard error of the model.

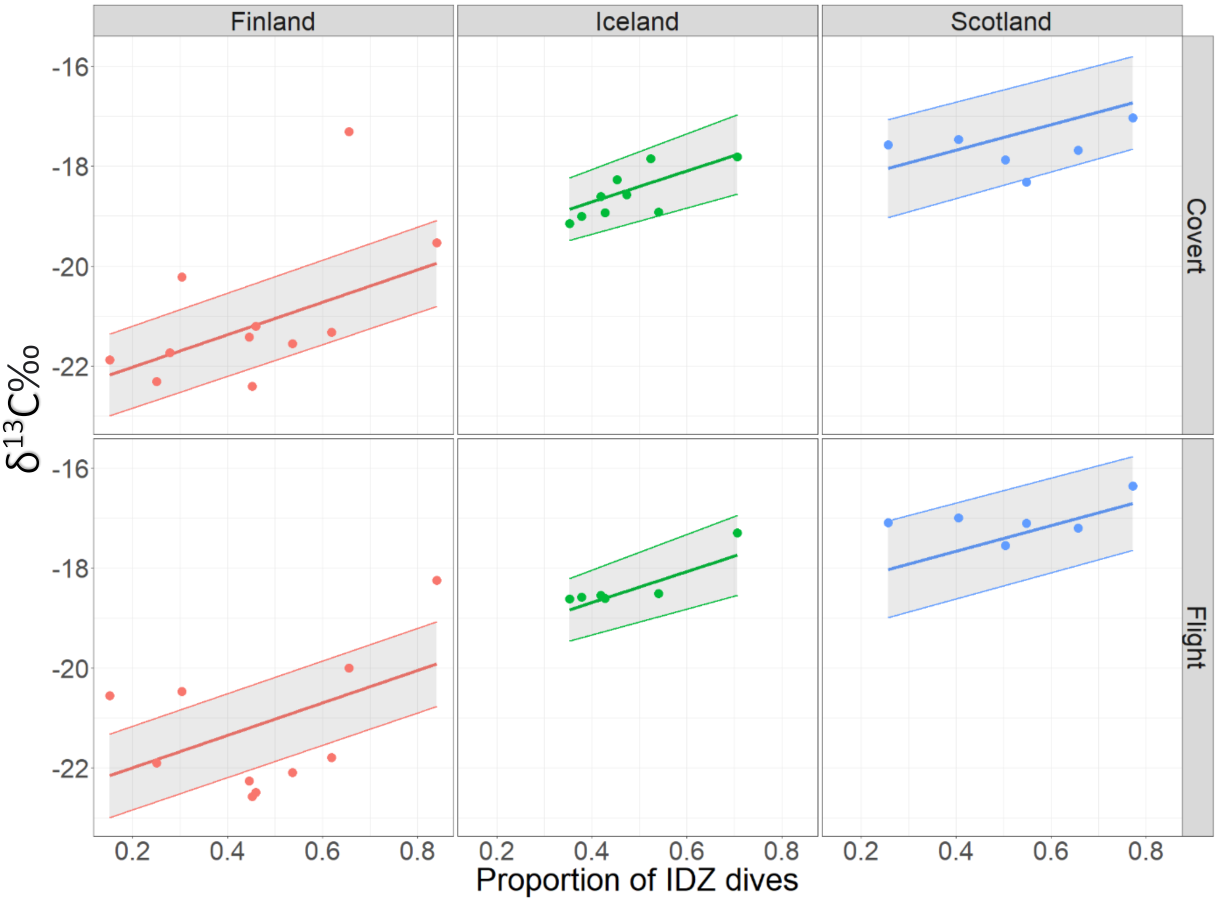

FIGURE 5.2 RELATIONSHIP BETWEEN CARBON ISOTOPES AND FORAGING STRATERGY ACROSS POPULATIONS AND FEATHER TYPES

$\delta^{13}C‰$ signatures across the three populations and two feather types sampled in this study against the proportion of IDZ dives taken across the predicted moult period generated by the final model. Populations are represented by red, green and blue for Finland, Iceland and Scotland, respectively. Shaded regions show standard error of the model.

Discussion

In this study, we have demonstrated a link between individual foraging behaviour and stable isotope signatures, which is consistent across populations of RTDs. Specifically, we have shown that as benthic foraging increases the values of both $\delta^{15}N$ and $\delta^{13}C$ increase, with the slope of this relationship varying between the three study populations. Finally, we found that $\delta^{15}N$ showed a stronger relationship with benthic foraging and therefore has a better capability to reflect individual foraging behaviour than $\delta^{13}C$. There was little evidence that the effects of population and foraging behaviour on isotope values differed across feather types, indicating the two feather types were grown over the same timeframe, whilst the RTD were using the same food resource. These results suggest that among generalist foragers, where individuals vary in their habitat use and exhibit a range of foraging strategies; a single feather sample may be enough to give significant insight on diet and habitat use for both individuals and populations.

The prevalence of the proportion of benthic dives as an explanatory variable in the models for both $\delta^{15}N$ and $\delta^{13}C$, lends strong support for feather samples alone to be able to indicate foraging behaviour in RTDs. This could have applications for conservation and protection of species where threats may vary depending on habitat use, as other studies have demonstrated [3, 4, 19]. Following initial work to understand how $\delta^{15}N$ varies across the range of foraging behaviours, feathers samples alone could be used to understand the wider frequency of these strategies and potential variation in space and time [15, 29]. Such a method could be of use when trying to minimise the need to recapture individuals, and/or when looking at populations at risk of decline, for example, among populations where there is concern that anthropogenic activity may push individuals away from current foraging habitat [22]. Previous similar work on gannets has linked isotope values to the importance of fisheries discards in the diets of individuals, with implications for conservation of the species [3]. In this case, the estimation of the proportion of individuals using different foraging habitats can quantify the detrimental effects on a population if that habitat is removed or degraded.

Previous study of these populations of RTDs suggested that individuals from each population are likely moulting within a specific discrete geographic area [26]. The main areas are the North coast of Iceland, the Baltic Sea and around the northern Scottish Isles, for Iceland, Finland and Scotland, respectively [26, 27]. This suggests the intra-population differences in stable isotope signatures are driven by differences in diet changes within the area they occupy, as individuals within each population essentially share a moulting location [15, 30]. In the case of $\delta^{15}N$, the relationship with benthic dives is reinforced by a study by Cousins et al. [31]. They showed $\delta^{15}N$ of feathers across a range of species was higher in benthic over pelagic environments in the south-east Baltic Sea, which is close to where the Finnish population spent their moulting period [26]. In fact, previous work linking diet to the stable isotope values of RTDs in the Baltic Sea suggests that here the benthic foragers (with a $\delta^{15}N$ of ~17‰) may be foraging on benthopelagic smelt [16]. Conversely, those with a lower $\delta^{15}N$ (12-14‰) may consuming pelagic herring and sprat [16]. These differences in $\delta^{15}N$ values of about ~4‰ from a benthic to pelagic diet align with the highest and lowest predicted values for our Finnish population (Figure 5.1). Thus, while geographic differences in study site led to prospective differences in isotope signatures, our data also lend support to different foraging behaviours being reflective of the importance of benthic and pelagic prey in the diet of an individual.

The populations in this study showed different levels of variation in the proportion of benthic vs pelagic dives, with Finland showing the largest range (Figure 5.1 & 5.2). This is indicative of individuals showing preferences to certain foraging strategies, with IDZ values closer to one and zero showing a strong preference for benthic and pelagic foraging, respectively. Conversely, within the Iceland population, the range was small, with proportions of IDZ dives largely centred on 0.5, suggesting more intra-individual flexibility in foraging strategy within and/or between bouts (Supplementary Figure 5.1). Previous work on RTDs isotope signatures and diet in the Baltic Sea has revealed largely pelagic diets of individuals [16]. Although our work is not able to directly describe the diets of individuals, we are able to suggest that benthic foraging constitutes a significant part of the diet of some individuals during the moult period (Figure 5.1). This suggests individuals can show a preference for either benthic or pelagic foraging where both options are available. Among specialist foraging species, which do not forage on multiple different prey sources or habitats, we would expect less variation of isotopes within populations from a particular foraging location [32, 33]. For these species, it is less likely that individual foraging strategies could be determined from isotope signatures. In this context, the work carried out here could also allow for an understanding of the width of prey diversity a species is eating, based on intra-population differences in stable isotopic signatures [34].

Our results indicate that using either a secondary flight or secondary covert feather for the purpose of linking foraging behaviour to stable isotope values is possible. This corroborates our previous study that showed these two feather types both had relatively even power in predicting the moult location of individuals [26]. This similarity between feather types is likely caused by both feathers being grown simultaneously, so the same food sources are being integrated into both feather types. In this context, future studies should sample only secondary covert feathers, as the loss of these feathers will further reduce any small potential for a fitness cost, as they play a lesser role in flight. This will likely be the case in all marine birds which undergo a seasonal synchronous moult of flight feathers, where secondary coverts and flight feathers are grown near-simultaneously [35, 36].

Bulk isotope analysis does however have limits, as without an understanding of the spatial and temporal baseline isotopic baseline, accurate conclusions on the exact trophic level preyed upon by the consumer cannot be drawn [37]. While looking at the isotope signatures of lower trophic levels at the bottom of the food web is one way to solve this issue, other methods have been developed which do not necessarily require this additional sampling effort. In this regard, compound specific SIA allows for comparison of different amino acids which are integrated at different rates across trophic levels, allowing for more detailed investigation albeit at orders of magnitude greater financial costs, which currently limit their application [38, 39]. Additionally, while the results here show a strong relationship between $\delta^{15}N$ and IDZ dives, changes in isotope signatures can also be linked to many other environmental factors, such as urbanization, agricultural runoff, freshwater inputs and other natural variations [40, 41]. Gathering data to fully identify the links between foraging strategy and habitat, while still using bulk isotope analysis, would require high resolution location data and prey consumption, as in other studies [3, 42].

In conclusion, we identified a relationship between a foraging metric and the stable isotope signatures of individuals. The relationships identified varied both within and between populations. This firstly indicates that intra-population variation in habitat use and foraging strategy can be quantified with isotope signatures, though the relationship and baseline isotope signatures must first be determined for a population. These results indicate future use of stable isotope analysis for quantifying foraging behaviour, in species where the relationship has been calibrated, is possible. This will allow for assessing the importance of habitat types and prey species to specific populations. We also propose this method could be used for other generalist foraging species marine bird, where differing habitat use can be used to apportion the effects of habitat-specific stress to populations for species and times of year that are hard to study.

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Bibliography

1. Bro-Jørgensen J., Franks D.W., Meise K. 2019 Linking behaviour to dynamics of populations and communities: application of novel approaches in behavioural ecology to conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**(1781), 20190008. (doi:10.1098/rstb.2019.0008).
2. Layman C.A., Arrington D.A., Montaña C.G., Post D.M. 2007 Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* **88**(1), 42-48. (doi:https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2).
3. Votier S.C., Bearhop S., Witt M.J., Inger R., Thompson D., Newton J. 2010 Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* **47**(2), 487-497. (doi:https://doi.org/10.1111/j.1365-2664.2010.01790.x).
4. Ben-David M., Titus K., Beier L.R. 2004 Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* **138**(3), 465-474. (doi:10.1007/s00442-003-1442-x).
5. Chiaradia A., Forero M.G., McInnes J.C., Ramírez F. 2014 Searching for the True Diet of Marine Predators: Incorporating Bayesian Priors into Stable Isotope Mixing Models. *PLOS ONE* **9**(3), e92665. (doi:10.1371/journal.pone.0092665).
6. Zapata-Hernández G., Sellanes J., Letourneur Y., Harrod C., Morales N.A., Plaza P., Meerhoff E., Yannicelli B., Carrasco S.A., Hinojosa I., et al. 2021 Tracing trophic pathways through the marine ecosystem of Rapa Nui (Easter Island). *Aquatic Conservation: Marine and Freshwater Ecosystems* **31**(2), 304-323. (doi:https://doi.org/10.1002/aqc.3500).
7. Carbia P.S., Brown C., Park J.M., Gaston T.F., Raoult V., Williamson J.E. 2020 Seasonal and developmental diet shifts in sympatric and allopatric intertidal gobies determined by stomach content and stable isotope analysis. *Journal of Fish Biology* **97**(4), 1051-1062. (doi:https://doi.org/10.1111/jfb.14463).
8. Cabana G., Rasmussen J.B. 1994 Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* **372**(6503), 255-257. (doi:10.1038/372255a0).
9. Haywood J.C., Fuller W.J., Godley B.J., Shutler J.D., Widdicombe S., Broderick A.C. 2019 Global review and inventory: how stable isotopes are helping us understand ecology and inform

conservation of marine turtles. *Marine Ecology Progress Series* **613**, 217-245. (doi:https://doi.org/10.3354/meps12889).

10. White A.F., Dawson R.D. 2021 Can diet composition estimates using stable isotope analysis of feathers predict growth and condition in nestling mountain bluebirds (*Sialia currucoides*)? *Ecology and Evolution* **11**(21), 15273-15288. (doi:https://doi.org/10.1002/ece3.8210).

11. Votier S.C., Grecian W.J., Patrick S., Newton J. 2011 Inter-colony movements, at-sea behaviour and foraging in an immature seabird: Results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology* **158**(2), 355-362. (doi:10.1007/s00227-010-1563-9).

12. Hobson K.A., Piatt J.F., Pitocchelli J. 1994 Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology* **63**(4), 786-798. (doi:10.2307/5256).

13. Weiss F., Furness R.W., McGill R.A.R., Strange I.J., Masello J.F., Quillfeldt P. 2009 Trophic segregation of Falkland Islands seabirds: Insights from stable isotope analysis. *Polar Biology* **32**(12), 1753-1763. (doi:10.1007/s00300-009-0674-6).

14. Magozzi S., Yool A., Vander Zanden H.B., Wunder M.B., Trueman C.N. 2017 Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* **8**(5), e01763. (doi:https://doi.org/10.1002/ecs2.1763).

15. Bond A.L., Jardine T.D., Hobson K.A. 2016 Multi-tissue stable-isotope analyses can identify dietary specialization. *Methods in Ecology and Evolution* **7**(12), 1428-1437. (doi:https://doi.org/10.1111/2041-210X.12620).

16. Morkūnė R., Lesutienė J., Barisevičiūtė R., Morkūnas J., Gasiūnaitė Z.R. 2016 Food sources of wintering piscivorous waterbirds in coastal waters: A triple stable isotope approach for the southeastern Baltic Sea. *Estuarine, Coastal and Shelf Science* **171**, 41-50. (doi:10.1016/j.ecss.2016.01.032).

17. Yerkes T., Hobson K.A., Wassenaar L.I., Macleod R., Coluccy J.M. 2008 Stable isotopes (δD, δ13C, δ15N) reveal associations among geographic location and condition of alaskan northern pintails. *The Journal of Wildlife Management* **72**(3), 715-725. (doi:https://doi.org/10.2193/2007-115).

18. Ito M., Minami H., Tanaka Y., Watanuki Y. 2009 Seasonal and inter-annual oceanographic changes induce diet switching in a piscivorous seabird. *Marine Ecology Progress Series* **393**, 273-284. (doi:https://www.jstor.org/stable/24874211).

19. Lei W., Masero J.A., Dingle C., Liu Y., Chai Z., Zhu B., Peng H., Zhang Z., Piersma T. 2021 The value of coastal saltpans for migratory shorebirds: conservation insights from a stable isotope approach based on feeding guild and body size. *Animal Conservation* **24**(6), 1071-1083. (doi:https://doi.org/10.1111/acv.12717).

20. Duckworth J., O'Brien S., Petersen I.K., Petersen A., Benediktsson G., Johnson L., Lehikoinen P., Okill D., Väisänen R., Williams J., et al. 2021 Spatial and temporal variation in foraging of breeding red-throated divers. *Journal of Avian Biology* **52**(6). (doi:https://doi.org/10.1111/jav.02702).

21. Mendel B., Schwemmer P., Peschko V., Müller S., Schwemmer H., Garthe S., Mercker M. 2019 Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). *Journal of Environmental Management* **231**, 429-438. (doi:10.1016/j.jenvman.2018.10.053).

22. Heinänen S., Žydelis R., Kleinschmidt B., Dorsch M., Burger C., Morkūnas J., Quillfeldt P., Nehls G. 2020 Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. *Marine Environmental Research*, 104989. (doi:https://doi.org/10.1016/j.marenvres.2020.104989).

23. Dierschke V., Furness R.W., Gray C.E., Petersen I.K., Schmutz J., Zydelis R., Daunt F. 2017 Possible behavioural, energetic and demographic effects of displacement of red-throated divers. *JNCC Report* **605**.

24. Tremblay Y., Cherel Y. 2000 Benthic and pelagic dives : a new foraging behaviour in rockhopper penguins. *Marine Ecology Progress Series* **204**, 257-267. (doi:https://www.jstor.org/stable/24863638).

25. Thompson D.L., Johnson L., Williams J., Lehikoinen P. 2022 Red-throated diver energetics project: 2021 field season report. In *JNCC Report* (JNCC Peterborough).

26. Duckworth J., O'Brien S., Petersen I.K., Petersen A., Benediktsson G., Johnson L., Lehikoinen P., Okill D., Väisänen R., Williams J., et al. 2022 Winter locations of red-throated divers from geolocation and feather isotope signatures. *Ecology and Evolution* **12**(8), e9209. (doi:https://doi.org/10.1002/ece3.9209).

27. Kleinschmidt B., Burger C., Bustamante P., Dorsch M., Heinänen S., Morkūnas J., Žydelis R., Nehls G., Quillfeldt P. 2022 Annual movements of a migratory seabird—the NW European red-throated diver (*Gavia stellata*)—reveals high individual repeatability but low migratory connectivity. *Marine Biology* **169**(9), 114. (doi:10.1007/s00227-022-04096-x).

28. R Core Team. 2022 R: A Language and Environment for Statistical Computing. (Vienna, Austria, R Foundation for Statistical Computing.

29. Inger R., Bearhop S. 2008 Applications of stable isotope analyses to avian ecology. *Ibis* **150**(3), 447-461. (doi:https://doi.org/10.1111/j.1474-919X.2008.00839.x).

30. Bearhop S., Phillips R., McGill R., Cherel Y., Dawson D., Croxall J. 2006 Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Marine Ecology Progress Series* **311**, 157-164. (doi:10.3354/meps311157).

31. Nfon E., Cousins I.T., Broman D. 2008 Biomagnification of organic pollutants in benthic and pelagic marine food chains from the Baltic Sea. *Sci Total Environ* **397**(1), 190-204. (doi:https://doi.org/10.1016/j.scitotenv.2008.02.029).

32. Hofman-Kamińska E., Bocherens H., Borowik T., Drucker D.G., Kowalczyk R. 2018 Stable isotope signatures of large herbivore foraging habitats across Europe. *PLOS ONE* **13**(1), e0190723. (doi:10.1371/journal.pone.0190723).

33. Vander Zanden H.B., Bjorndal K.A., Reich K.J., Bolten A.B. 2010 Individual specialists in a generalist population: results from a long-term stable isotope series. *Biology Letters* **6**(5), 711-714. (doi:doi:10.1098/rsbl.2010.0124).

34. Denton M.J., Demopoulos A.W.J., Baldwin J.D., Smith B.J., Hart K.M. 2019 Stable Isotope Analysis Enhances Our Understanding of Diamondback Terrapin (*Malaclemys terrapin*) Foraging Ecology. *Estuaries and Coasts* **42**(2), 596-611. (doi:10.1007/s12237-018-0476-6).

35. Fox T., Christensen T.K., Bearhop S., Newton J. 2007 Using stable isotope analysis of multiple feather tracts to identify moulting provenance of vagrant birds: a case study of Baikal Teal *Anas formosa* in Denmark. *Ibis* **149**(3), 622-625. (doi:https://doi.org/10.1111/j.1474-919X.2007.00672.x).

36. Rohwer V.G., Rohwer S. 2013 How do Birds Adjust the Time Required to Replace their Flight Feathers? *The Auk* **130**(4), 699-707. (doi:10.1525/auk.2013.13042).

37. Post D.M. 2002 Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**(3), 703-718. (doi:https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).

38. Bradley C.J., Wallsgrove N.J., Choy C.A., Drazen J.C., Hetherington E.D., Hoen D.K., Popp B.N. 2015 Trophic position estimates of marine teleosts using amino acid compound specific isotopic analysis. *Limnology and Oceanography: Methods* **13**(9), 476-493. (doi:https://doi.org/10.1002/lom3.10041).

39. Pollierer M.M., Larsen T., Potapov A., Brückner A., Heethoff M., Dyckmans J., Scheu S. 2019 Compound-specific isotope analysis of amino acids as a new tool to uncover trophic chains in soil food webs. *Ecological Monographs* **89**(4), e01384. (doi:https://doi.org/10.1002/ecm.1384).

40. McClelland J.W., Valiela I., Michener R.H. 1997 Nitrogen-stable isotope signatures in estuarine food webs: A record of increasing urbanization in coastal watersheds. *Limnology and Oceanography* **42**(5), 930-937. (doi:https://doi.org/10.4319/lo.1997.42.5.0930).

41. Careddu G., Costantini M.L., Calizza E., Carlino P., Bentivoglio F., Orlandi L., Rossi L. 2015 Effects of terrestrial input on macrobenthic food webs of coastal sea are detected by stable isotope analysis in Gaeta Gulf. *Estuarine, Coastal and Shelf Science* **154**, 158-168. (doi:https://doi.org/10.1016/j.ecss.2015.01.013).

42. Ceia F.R., Cherel Y., Paiva V.H., Ramos J.A. 2018 Stable isotope dynamics (δ13C and δ15N) in neritic and oceanic waters of the North Atlantic inferred From GPS-tracked Cory's shearwaters. *Frontiers in Marine Science* **5**. (doi:10.3389/fmars.2018.00377).

Chapter 6 Variation in non-breeding season strategy drives differences in behaviour and energy expenditure of red-throated divers

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Declaration of authorship

JG, SO, FD, IP and JD conceived the ideas and designed methodology; JG, SO, FD, IKP, JD, AP, GB, LJ, PL, DO, RV, JW and SW collected the data; JD analysed the data and created visualisations; SO, JG, AP and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

The non-breeding period is the least understood part of the annual cycle for many long lived seasonally reproducing animals. Quantifying the behaviour and energetics of a species during this crucial period allows for a more nuanced understanding of how that species may respond to additional stresses. Specifically, knowledge of how behaviour and energetics vary across spatial and temporal scales can aid in understanding the range of strategies a species can use to adapt. Here, we used archival data loggers to record the behaviour budgets of red-throated divers (*Gavia stellata*, RTD) at the start of the non-breeding season (mid-August to mid-December), when this species is known to be sensitive to offshore wind developments. We then estimated daily energy expenditure (DEE) through time. This was used to explore the consequences of contrasting behaviour and energetic strategies from populations originating from breeding grounds in Finland, Iceland and Scotland, where individuals are migratory, resident and partially migratory, respectively. We found that DEE increased as the non-breeding season progressed for RTDs originating from breeding sites in Finland and Iceland but decreased for birds from Scotland. For RTDs from Iceland, which had the highest DEE, this increase is likely driven by increased costs of thermoregulation. For birds from Finland, the increase was driven by a change in behaviour. Behaviour budgets also varied through time, with birds from Finland showing the most temporal variation. These results begin to reveal divergent survival strategies for geographically separated populations and suggest strategies can change temporally, with links to different migration strategies.

Introduction

The non-breeding period is the least understood part of the annual cycle for many long lived seasonally reproducing animals (Marra et al. 2015a). During this time, the primary aim of individuals is to survive and optimize their physical condition prior to the next breeding season (Salewski and Bruderer 2007). For those that do survive, there may be carryover effects that impact future breeding success as a result of their experiences during the non-breeding season (Fayet et al. 2016b; Norris 2005). Strategies to deal with the often-challenging conditions of the non-breeding season can vary between species, populations and individuals (Arizaga et al. 2012; Dinkins et al. 2017). One such strategy is to leave the breeding area during the non-breeding season and migrate, defined as the seasonal relocation of an animal which typically occurs at a scale greater than daily movements (Dingle and Drake 2007). Migrations allow animals to move between areas following seasonal changes in the availability and use of food resources (Jessopp et al. 2013; Southwood 1962). Divergent strategies between individuals and populations for migration have been linked to changes in competition (Lamb et al. 2017), age (Péron and Grémillet 2013) and a suite of other factors (Phillips et al. 2017). Regardless of migratory tendency, differing conditions experienced geographically and temporally during the non-breeding period can lead to some individuals or populations experiencing disproportionate amounts of stress (Marra and Holberton 1998). Indeed, while it is acknowledged that there are often fitness differences between resident and migrant populations (Buchan et al. 2020), we lack a mechanistic understanding of why such differences persist. Furthermore, quantifying our understanding of the consequences of variation in migratory strategy within a species also has important implications for predicting how populations and species might respond to environmental stressors (Reid et al. 2018). However, monitoring and assessing the potential costs and benefits of these differences in strategy can be difficult without a quantifiable method of examination.

Physiological energetics is the study of energy gain and loss at an organism level (Brett and Groves 1970). Broadly, this approach examines the energy expenditure and intake of individuals using a mixture of knowledge drawn from the ecology and physiology of a species (Brett and Groves 1970; Cooke et al. 2013; Dunn et al. 2020). This knowledge can then be applied, using the principle of physiological energetics, to effectively quantify the costs of existence, through examination of an energy budget (Anthony et al. 2009; Clausen et al. 2013; Dunn et al. 2018). Approaching problems in this way allows investigators to explore the specific energy costs and benefits (in terms of individual and/or reproductive fitness), temporally and spatially (Fort et al. 2013), which can then be used to assess the impact on demographic rates (Anthony et al. 2009; Czapanskiy et al. 2021; Fitzgerald-Dehoog et al. 2012). Innovations in biotelemetry have made it possible to obtain the necessary information, such as behavioural budgets, for the annual cycle of many avian species, including those species which are otherwise hard to observe (Rutz and Hays 2009; Yoda 2019). Physiological energetics thus has great potential to further our understanding of the costs, benefits and variation of different non-breeding season migratory, behavioural and energetic strategies observed in natural populations. This insight thus far has been limited primarily to single population studies (Kubetzki et al. 2009; White et al. 2013), which have suggested equal benefits of different migration strategies within a population (Pelletier et al. 2020). However, physiological energetics also has the potential to help us understand how variation in migratory strategy among populations might be maintained, though very few studies (Fayet et al. 2017) have attempted to address this.

Red-throated divers (RTDs; *Gavia stellata*) are a northerly distributed bird in the order *Gaviiformes*, which are a family of generalist foragers (Guse et al. 2009; Jackson 2003; Kleinschmidt et al. 2019), highly adapted for aquatic environments (Gayk et al. 2018). During the breeding season RTDs nest next to freshwater lakes and then generally move into the marine environment during the non-breeding season (Duckworth et al. 2020; McCloskey et al. 2018). Knowledge on the behaviour of RTDs during the non-breeding season, beyond locations used (Dorsch et al. 2019; Duckworth et al. 2022; McCloskey et al. 2018; O'Brien et al. 2012), is relatively sparse. However, recent work on the movements of RTDs has revealed individuals breeding in some parts of this species' range remain largely resident, while at other parts of the range all individuals migrate once breeding has finished (Dorsch et al. 2019; Duckworth et al. 2022; McCloskey et al. 2018). There are also sites that exhibit partial migration, with some individuals migrating while others remain in the same area used during the breeding season (Duckworth et al. 2022). This exposes different populations of RTDs to a diverse range of locations and habitats, during the non-breeding season, with consequent diversity of environmental conditions experienced. In particular, water temperature, prey differences and associated thermoregulatory challenges are likely to be important for animals when fully aquatic (Fort et al. 2009). This makes RTDs a useful study species to quantify the consequences of variation between populations in non-breeding season strategies, via the application of physiological energetics to estimate the energy expenditure and/or intake of individuals (Braithwaite et al. 2015; Dunn et al. 2020). Gaining understanding of behaviour and energetics in the non-breeding season is important, as anthropogenic activities have caused some migrating RTDs to experience large-scale redistribution, away from the vicinity of offshore windfarms (Furness et al. 2013; Heinänen et al. 2020; Mendel et al. 2019), although the energetic and demographic consequences of this displacement effect is unknown.

In this study we looked at three populations of RTDs, breeding in Finland, Scotland and Iceland, which are migratory, partially migratory and non-migratory, respectively (Duckworth et al. 2022). Previous work has shown that RTDs from Finland move through the Baltic Sea into the North Sea. RTDs breeding in Scotland either remain resident around Orkney and Shetland or migrate a short distance to north Ireland or the east coast of Scotland and RTDs from Iceland remain resident, off the north coast of Iceland (Duckworth et al. 2022). While this behaviour means that some individuals from these breeding populations may diverge spatially during the non-breeding season, here we will refer to each of the three sites studied by their breeding population location, as this grouping largely reflects different non-breeding season migratory strategies. Our aim was to make one of the first assessments of the energetic costs and benefits of variation in non-breeding season strategies among populations. This was achieved primarily through the creation of a physiological energetics model, using a combination of data obtained from archival data loggers and metabolic scaling equations. This enabled us to determine time and energy expended each day on key behaviours and the daily energetic expenditure (DEE) of individuals through time during the first four months of their non-breeding season. Looking across our three populations with different non-breeding season strategies, our objectives were to examine: (1) Whether the behaviour budgets vary with time and between populations and how these drive DEE, (2) Whether DEE and foraging efficiency changes over time and among the populations, and (3) To what extent the energy expended on thermoregulation drives DEE changes (Moe et al. 2021). We hypothesised that while behaviour and associated costs and benefits in terms of foraging efficiency may vary temporally and between populations, the overall mass specific DEE would be similar across populations, consistent with single-population studies of inter-individual variability (Pelletier et al. 2020).

Methods

Logger deployment

From May to July in 2018 and 2019, RTDs were caught at nesting sites across southern Finland (31 in 2018, 10 in 2019), the Orkney and Shetland archipelagos, in northern Scotland (31 in 2018, 11 in 2019) and north-eastern Iceland (12 in 2018, 12 in 2019). Birds were caught using nest traps, mist nets or walk-in traps (O'Brien et al. 2018). Time-depth recorders (TDR; Cefas G5 Standard TDR, dimensions: 8 mm x 31 mm, weight: 2.7 g) and light-based geolocators (GLS; Biotrack MK4083 Geolocator, dimensions: 17 mm x 10 mm x 6.5 mm, weight: 1.8 g) were attached, one to each leg, of each captured RTD. The combined weight of both tags was <0.5% of the weight of the lightest RTD. In total 42 birds were recaptured (27 in 2019 and 15 in 2020), using the same capture methods mentioned previously. After accounting for tag loss and failures and redeployment of tags, we were left with data from a total of 24 non-breeding periods with functioning GLS and TDR tags (11, 5 and 8 from Finland, Scotland and Iceland, respectively), across 21 individuals (9, 5, and 7 from Finland, Scotland and Iceland, respectively). Using mixed effects models accounting for individual identity, we found no difference in either time spent foraging or diving metrics between the two years in preliminary analyses, so given the relatively small sample sizes we pooled individuals across both years for subsequent formal analyses.

Behaviour classification

TDR tags recorded dive depth every six seconds and temperature every 10 minutes on every fifth day to extend the period of data collection. The GLS tags recorded light data, used to infer location, and conductivity data summarised at 10 minute intervals, giving the proportion of time the tag was submerged in saltwater (given as a range from 0-200, where 200 represented the whole 10-minute period being submerged). TDR and GLS tags were always deployed on different legs, so leg tucking behaviour, indicative of rest periods, could be determined separately for each leg. Data from the TDR and GLS data were processed following the same methodology as Duckworth et al. (2021). Previously published location data (Duckworth et al. 2022) was used to define night and day through the study period for each individual. Body mass and wing length were also measured for each individual on deployment of tags.

The data with the coarsest temporal resolution was temperature and immersion, for which a single reading and a proportion of time immersed every 10 minutes were recorded, respectively. Therefore, behaviour was assessed at a resolution of 10 minutes. Consequently, for each individual every fifth day, we had 144 10-minute recordings of: proportion of time in salt water, TDR temperature and number of dives.

Additionally, we calculated the daily average sea temperature (ST) experienced each day by each bird by extracting any temperature recordings that occurred within one minute of a dive and calculating a daily mean. This allowed us to calculate the relative ($\sqrt{\overline{ST - TDR\ temperature}^{2}}$) and absolute difference ($ST - TDR\ temperature$) between the daily ST and TDR temperature for each 10-minute period. These values are used in subsequent behaviour classification steps to determine whether the TDR tag (leg) was either in or out of the water.

In an initial classification stage, each 10-minute period was defined as either: resting, active on water, swimming or flight using a decision tree (Figure 6.1). Resting behaviour occurred when at least one leg was tucked in the plumage (high TDR temperature or no saltwater immersion), indicating that the bird was not moving or undertaking any other active behaviours. This is detected by the temperature of the TDR tag along with saltwater immersion, with either one of the sensors showing a leg out of the water and the other showing a sensor as in the water. While this may not encapsulate all resting behaviours, it defines the least energy intensive period of resting behaviour. Active on water behaviour was detected when the bird had an intermediate value for the proportion of time spent in water, but was not leg tucking (resting). This means the TDR tag recorded the ST and the GLS tag recorded intermediate saltwater immersion (i.e., a value between 10-190). For example, this type of behaviour and immersion pattern can be observed during preening, when birds turn on their sides and expose one leg while preening body feathers, interacting with conspecifics or foot-waggling (Paruk 2009). Active on water can also be seen as a transition between other behaviours or other various behaviours that can lead to the leg leaving the water. Swimming was defined as a time when the TDR tag recorded a relative temperature within 1°C of the daily ST and the GLS tag was in salt water for the majority of the period (Figure 6.1). This period may also encapsulate some resting periods when individuals are unable to tuck their legs, however, this is likely to be in cases of turbulent sea, when additional support and energy is needed to remain afloat upright. Periods were classified into flight when the GLS tag recorded less than 95% of the period immersed and the TDR tag recorded a relative temperature difference exceeding 1 °C from the ST. Flight was also constrained to only happen during daylight hours, when the sun was greater than -12 degrees above the horizon as previous studies suggest divers do not fly during the night (Paruk 2008). While this definition will be unable to detect flight when air temperatures match ST, this was the only method available to detect flight given the resolution of available data. Definitions and cut-off criteria for metrics defining each behaviour were informed through initial clustering (k-means), visual inspection of histograms and values derived for other species using similar approaches (Christensen-Dalsgaard et al. 2018; McKnight et al. 2011).

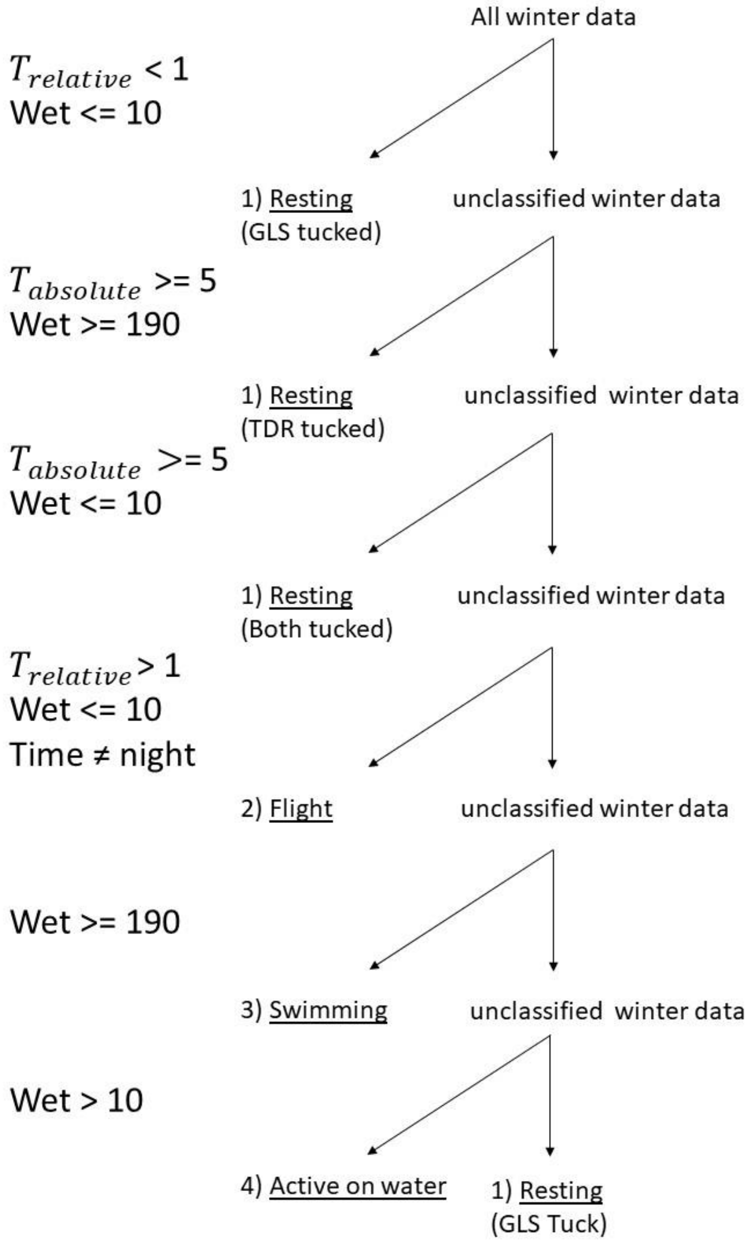

FIGURE 6.1 DECISION TREE FOR BEHAVIOUR CLASSIFICATION OF BEHAVIUOUR IN RTD

Decision tree to classify each 10-minute period of each sample day into one of four behaviours in an initial classification stage. Foraging behaviour was defined at a resolution of 6 seconds independently of this process using data from only the TDR devices. The calculated time spent foraging was subtracted from the estimated time spent swimming and active on water, proportionally, as the large majority of foraging behaviour (81%) was found to occur when swimming or active on water (19%). $T_{absolute}$ *represents the actual difference in temperature observed in the 10-minute period compared to the sea temperature.* $T_{relative}$ *is the square root of the squared difference between the observed temperature and sea temperature. Wet* *is a number ranging from 0-200 representing the amount of time the GLS tag spent submerged in saltwater. Time is a binary operator as either "day" or "night". The category "Both tucked" is unlikely to be when both legs are tucked, but rather a transition between different legs being tucked or resting and another behaviour. Active on water behaviour includes all times where the TDR showed a temperature related to being in water and the GLS showed intermediate time submerged. Intervals are presented by behaviour rather than site in Supplementary Materials 4.*

A further classification was made at a higher resolution to identify foraging and diving behaviour. Diving behaviour was classified as any 6-second interval where the pressure sensor recorded depth greater than one metre. Foraging behaviour was defined as periods where at least 3 dives occurred within 66 seconds of each other, following previous definitions of foraging bouts in RTDs (Duckworth et al. 2021). Therefore, foraging behaviour included diving and dive-pause intervals. Dives outside of these foraging bouts were generally isolated and shallow and are likely associated with other behaviours or initial exploration of a potential foraging area. We found that 90% of foraging behaviour occurred during time defined as swimming behaviour in the initial classification stage while the other 10% occurred during the active on water behaviour. We therefore subtracted 90% and 10% of the daily time spent foraging from the swimming and active on water behaviour classifications, respectively. This ensured the sum of the time spent in all five main behaviours (resting, active on water, swimming, flight, foraging) was 24 hours, despite the difference in classification resolution.

The criteria to determine the end of the breeding season was defined as the GLS detecting at least 45% of the time immersed in saltwater for 5 continuous days (Duckworth et al. 2021). This criterion failed to exclude two days from one individual where recordings suggested an individual was present on freshwater after commencement of the non-breeding period, which were removed manually. In all cases, logger failure occurred before any detectable return to breeding grounds, ranging from 10th September to 15th March (mean duration = 92 days).

Energetic modelling

As empirical data on three key physiological metrics (basal metabolic rate (BMR), thermal conductance (TC) and lower thermal limit (LTL)) were unavailable for RTDs, we estimated these values using allometric scaling equations for physiologically and behaviourally similar groups of species. For all estimates, body mass was taken from the instance that the diver was caught in the summer and is assumed to be constant through the study period. This assumption may be violated if individuals aim to gain or lose mass through the study period, but other energetic models have made broadly similar assumptions (Dunn et al. 2022) . There is also evidence that, at least within a season, RTD mass varies minimally (O'Brien et al. 2020).

BMR was derived from the mean of estimates from two allometric scaling equations for sea ducks (Equation 1a; McKinney and McWilliams (2005)) and seabirds (Equation 1b; Ellis and Gabrielsen (2002)). The mean difference in the estimates from these two equations across all days and individuals was 17 +- 6.2 kJ, which accounts for less than 3% variation in the calculated BMR. Equation 1a was originally given in units ml O_2 h^{-1} and the equation includes the necessary components to convert this to kJ h^{-1}, Equation 1b gave BMR as kJ day^{-1} in the original paper but is presented here as kJ h^{-1}.

$$\text{Equation } 1a. \quad BMR = (((4.05 * Body\ Mass^{0.79})/1000) * 18.8)$$
$$\text{Equation } 1b. \quad BMR = (3.201 * Body\ Mass^{0.719})/24$$

Thermal conductance (TC, kJ h^{-1} kg^{-1} $℃^{-1}$) was estimated from an equation for a diverse range of aquatic avian species, including a RTD (de Vries and van Eerden Mennobart 1995) for three states: fully submerged in water (Equation 2a), partially submerged in water (Equation 2b) and out of water (Equation 2c). Also, the study found that sex and age class did not affect the relationship between body mass and TC, meaning this equation is robust when applied to individuals of unknown sex and/or age.

$$\text{Equation } 2a. \quad TC_{diving} = 3.47 * Body\ Mass^{-0.573}$$

$$\text{Equation } 2b. \quad TC_{water} = 1.532 * Body\ Mass^{-0.546}$$

$$\text{Equation } 2c. \quad TC_{air} = 0.705 * Body\ Mass^{-0.461}$$

Equation 3 shows the lower critical temperature (LCT), which represents the temperature below which there becomes an additional cost of thermoregulation (Kendeigh et al. 1977; McKinney and McWilliams 2005). Equation 3 shows that with increasing body size the LCT decreases.

$$\text{Equation } 3. \quad LCT = 47.2 * Body\ Mass^{-0.18}$$

Work by McKinney and McWilliams (2005) on Buffleheads (*Bucephala albeola*) summarised suitable BMR multipliers for 10 distinct behaviours from a range of studies across several waterfowl species. Here, we used values for the five behaviours classified for RTDs in our study: resting, active on water, swimming, flight, foraging, which can be seen in Equation 4a. We looked across the literature to see whether these BMR multiplier values were consistent with other large or foot-propelled marine diving birds, like cormorants (Enstipp et al. 2006; Gremillet et al. 2003), and found that the values are largely consistent for the chosen behaviours (Heath and Gilchrist 2010). To get a value for the energy an individual expends on a given behaviour per day, we multiplied the time, in hours, spent in that behaviour state with the individual's BMR and the behaviour specific BMR multiplier. This gave us the behaviour-specific energy expenditure in kJ, for each day, the sum for all behaviours then provided us with the daily energy expenditure for behaviours (DEE_B) in kJ (Equation 4a). Equations 1 - 3 are metabolic scaling equations, where fixed values, shown numerically above, represent constants.

To calculate the additional daily energetic expenditure on thermoregulation (DEE_T), we summed the time spent in either fully or partially submerged in water (Equation 4b). The equation was used to calculate heat loss when the RTDs were classed as partially in water, when $T_{behaviour}$ was the sum of time spent: resting, active on water swimming, and inter-dive periods (foraging time minus diving time). Additionally, heat loss when fully submerged was calculated where $T_{behaviour}$ was when individuals showed diving behaviour. This additional expenditure was only calculated when the ST on a given day was lower than the LCT. Outside of the breeding season, divers are only ever out of water when in flight behaviour (Cramp 1977), during which time LCT is unlikely to be relevant, due to the high energy cost and heat production of flight (Guillemette et al. 2016). The sum of values DEE_B and DEE_T (where relevant) gave the daily energy expenditure (DEE).

Using these three metrics and the previous behaviour classifications and BMR multipliers we created Equation 4 to calculate the daily energy expenditure (DEE) for every bird on each day recording occurred. On cases where the sea temperature is below the LCT, then the solution to equation 4b is added to that of 4a, while when this is not the case, equation 4a alone gives the DEE.

$$\text{Equation } 4a.\ DEE_B = \left(T_{Resting} * (BMR * 1.4)\right) + \left(T_{Active\ on\ water} * (BMR * 1.9)\right) + \left(T_{Swimming} * (BMR * 3.5)\right) + \left(T_{Flying} * (BMR * 12.5)\right) + \left(T_{Foraging} * (BMR * 5.1)\right)$$

$$\text{Equation } 4b.\ DEE_T = Body\ Mass * \Delta t * T_{behaviour} * TC$$

To check the robustness of the decision tree to errors in assumptions, we carried out a sensitivity analysis. The two groups with the most uncertain classifications were: flight and resting behaviour, while the other groups are generated using previously established and tested methods. The two parameters that divided these behaviours are the relative and absolute temperature cut-offs. The cut-offs of these two metrics were varied by 50%, 75%, 125%, 150% and 200% and then behaviour classification was carried out again to assess whether this led to vastly different behaviour budgets.

Each parameter was varied in turn. Results of these analysis can be found in Supplementary Materials 1 and suggested that the cut-off values were robust, leading to only small changes in behaviour classification with minimal consequences for DEE that are acceptable for a comparative study such as this one.

Key methodological assumptions

Several key assumptions have been made in order to derive the final behaviour budgets, DEE and DEE_T values. Firstly, BMR, thermal conductance and lower critical temperature are all based on allometric scaling equations, meaning the values do not include any species-specific adaptations, which could lead to small changes in these rates from broader relationships. Secondly, behaviour classifications and the associated cut-offs used here to define behaviours are novel and derived from the data alone rather than validated with observations. While this is a commonplace practice (Buckingham et al. 2022; Dunn et al. 2022), it is important to accept that the true behaviour budget of individuals is not completely described. We have attempted to show the methods are viable using sensitivity analysis and demonstrate that changes in the parameters cause small changes to final classifications. Finally, the BMR multipliers for the costs of behaviours are not species specific, as these values are not known for RTDs. We instead based these rates on a paper exploring the behaviour of ducks confirmed by similar studies of other foot propelled diving birds. We felt these provided the most relevant rates, as like the RTD, the species is a foot-propelled diver that rarely dives to depth over 15 metres and in general, the exact energy requirement of a behaviour is likely influenced by many external and internal factors. For this reason, we strongly encourage work to determine the behaviour specific costs for *Gaviidae* and other species the subject of future similar studies. Overall, we propose that these assumptions form the best available current estimates to explore RTD behaviour and energetics and are appropriate for a comparative study such as this one. This can be further justified by the pressing need for an understanding of avian energetics in the context of offshore anthropogenic activities (Dierschke et al. 2017).

Analysis

We first looked at site level differences in body mass and wing length to both uncover any population level differences and to assess whether differences in DEE could be attributed to variation in morphology across sites. This analysis is detailed in Supplementary Materials 2 and revealed that while RTDs from Finland were larger and heavier than those from Scotland and Iceland, there was no difference in the relationship between wing length and body mass, suggesting that differences in mass were due to differences in structural size of the body. DEE and DEE_T were then analysed as KJ per unit body mass to the power of the average scaling exponent from Equation 1 (Mass$^{0.7545}$) throughout.

To model the changes in DEE and behaviour through time for the RTDs originating from the three breeding sites, we created a set of candidate models. In order to accommodate the non-linear seasonal changes through time we opted to use Generalised Additive Mixed Effect Models (GAMMs) to capture as much of this variation with time as possible, where a smooth function was used on the fixed effect representing time. GAMM smoothers were constrained to four knots to prevent overfitting of the data (Phillips et al. 2021). The full set of covariates can be found in Supplementary Materials 3. Broadly, models included combinations of the covariates of site and time, along with their interactions both with each other and allowing the smoothing factor for time to vary by site. All models included bird ID as a random effect. The same modelling framework and candidate model set were applied for response variables of DEE, DEE$_T$ and time spent: resting, active on water, swimming, flying and foraging. Candidate models for all response variables were ranked using Akaike's information criteria corrected for small sample sizes (AIC$_c$) (Johnson and Omland 2004), where the final model was the most parsimonious model within 2 ΔAIC$_c$ units of the best fitting model (Arnold 2010). Any post hoc tests to find group level differences were carried out using a Tukey post-hoc test.

Finally, foraging efficiency is presented by dividing the DEE (accounting for body mass) by the predicted time spent foraging. In the absence of data on energy store deposition and usage in the form of body mass from free-ranging non-breeding RTDs, this method assumes that on each day, birds will match their energy intake and expenditure (White et al. 2013). Estimates and standard errors for the foraging efficiency are derived from the best fitting DEE and foraging time models. GAMMs were fitted with gamm4 (Wood and Scheipl 2020) and linear mixed effect models were fitted with lme4 (Bates et al. 2015). All analyses were performed with R software (R Core Team 2020).

Results

There were some notable differences in the temporal pattern of time allocation to the five behaviours between sites. All models included some element of time in the best fitting model with a smoothing factor, except flight, for which time was a linear predictor. All behaviours except active on water and resting also included site as a fixed effect and as an interaction between site and time. Figure 6.2 shows the estimated behaviour budget of RTDs from three populations predicted from the best fitting GAMMs and GLMM. The full set of final models for each of these behaviours can be seen in Supplementary Materials 3.

RTDs from Finland increase then decrease their time spent swimming, at the expense of time spent foraging, which first increases then decreases (Figure 6.2). RTDs from Iceland and Scotland show a similar pattern of little change in their time spent swimming and overall are more similar to each other in their behaviour budgets than to Finland. All three populations increased their time allocated to resting through the early winter study period and reduce their time active on water. Flight was rarely detected across the study period, with a maximum of 24 (SE: 0.08) minutes per day in August at the start of the study period in Scotland. This is largely consistent with most other studies of aquatic birds with a high cost of flight (Gremillet et al. 2003). However, it is likely that our fifth day sampling regime has led to us being unable to detect enough migratory flights for them to appear in our final models.

The best fitting model for DEE through the study period, accounting for body mass, contained a fixed effect for time and site as well as an interaction term between these two covariates, but did not include any smoothing factor (Figure 6.3). Predicted DEE for Finland increased through the non-breeding season to a maximum of 1271 KJ/kg^{07545} (SE=43) in late December from a minimum of 1146 KJ/kg^{07545} (SE=39) in mid-August. Meanwhile, birds from Scotland showed a small decrease in DEE as time progressed through the observed period, with the model predicting the highest cost of 1176 KJ/kg^{07545} (SE=53) in August and the lowest value of 1130 KJ/kg^{07545} (SE = 57) in December (Figure 6.3). Iceland RTDs showed the biggest change with an increase in DEE, to a maximum of 1482 KJ/kg^{07545} (SE=42) from a minimum of 1270 KJ/kg^{07545} across the period (SE=44) (Figure 6.3).

Birds from Scotland showed a low level of variation in foraging efficiency, with the mean value ranging from 322 – 344 KJ/kg^{07545} h^{-1} (Figure 6.4). RTDs from Iceland and Finland showed a higher variability, with Finland having a peak foraging efficiency of 563 KJ/kg^{07545} h^{-1} (SE: 104) at the end of September and Iceland having a peak of 347 KJ/kg^{07545} h^{-1} (SE: 63) and 369 KJ/kg^{07545} h^{-1} (SE: 52) at the start and end of the study period, respectively. Iceland and Finland therefore reached peak foraging efficiency at different times during the study period.

The best fitting model for DEE$_T$ included site as a fixed effect along with time with a smoothing factor, where each site had a separate smoothing factor (Supplementary Materials 3 & 4). DEE$_T$ was shown to be much higher in Iceland compared to Scotland and Finland throughout the duration of the study (Figure 6.5). The maximum cost of DEE$_T$ for the Iceland population was 310 KJ/kg^{07545} (SE: 8.1), compared to 101 KJ/kg^{07545} (SE: 8.9) and 80 KJ/kg^{07545} (SE: 11.2) for Finland and Scotland, respectively. The cost also increased through the study period across all sites, but with a much greater increase experienced by the birds from Iceland (Figure 6.5).

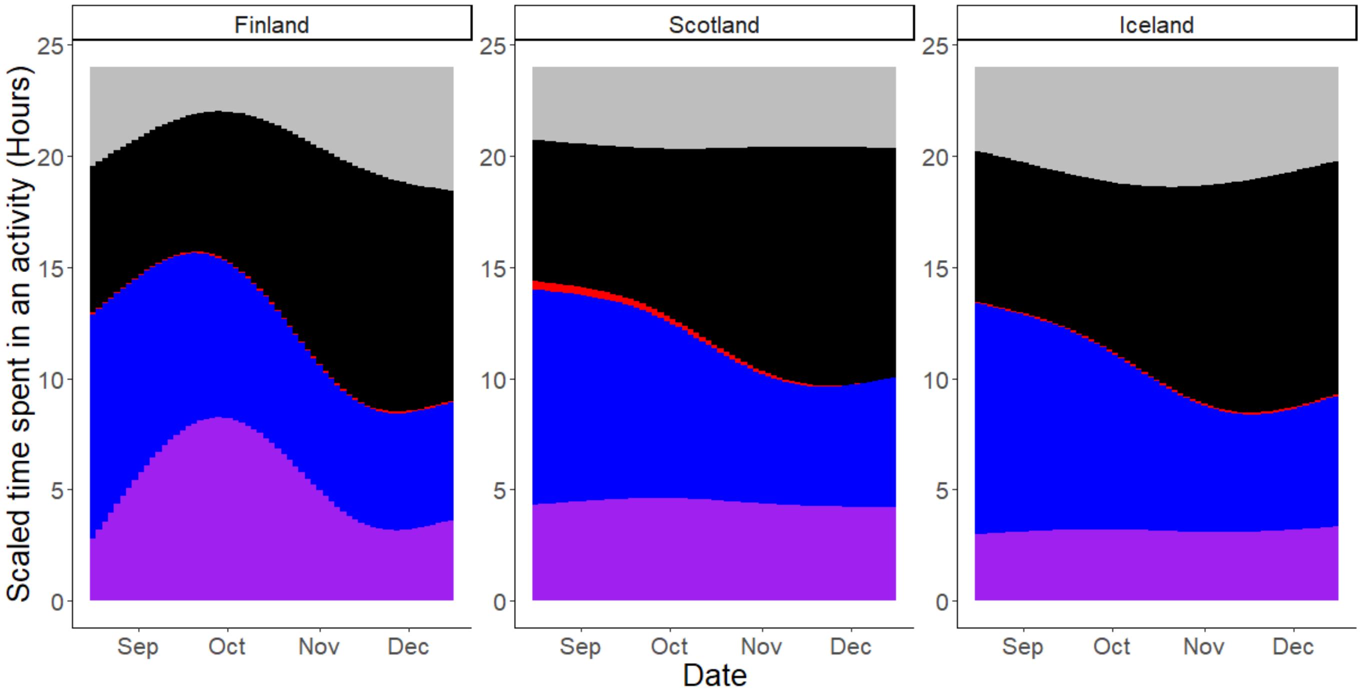

FIGURE 6.2 BEHAVIOUR BUDGETS OF RTD POPULATIONS THROUGH TIME

The amount of time spent in each of the five behaviours classified through the study period. Times in each behaviour are predicted from the best fitting models described in Supplementary Materials 3. The sum of predicted time in each of these behaviours predicted from did not equal 24 hours. Therefore, behaviour budgets are scaled, with the total time predicted across all activities per day, so they show the proportion of the day the RTDs were predicted to allocate to each behaviour. In descending order, the behaviours are: foraging (grey), resting (black), flying (red), active on water (blue) and swimming (purple). Raw data including fitted relationships and confidence

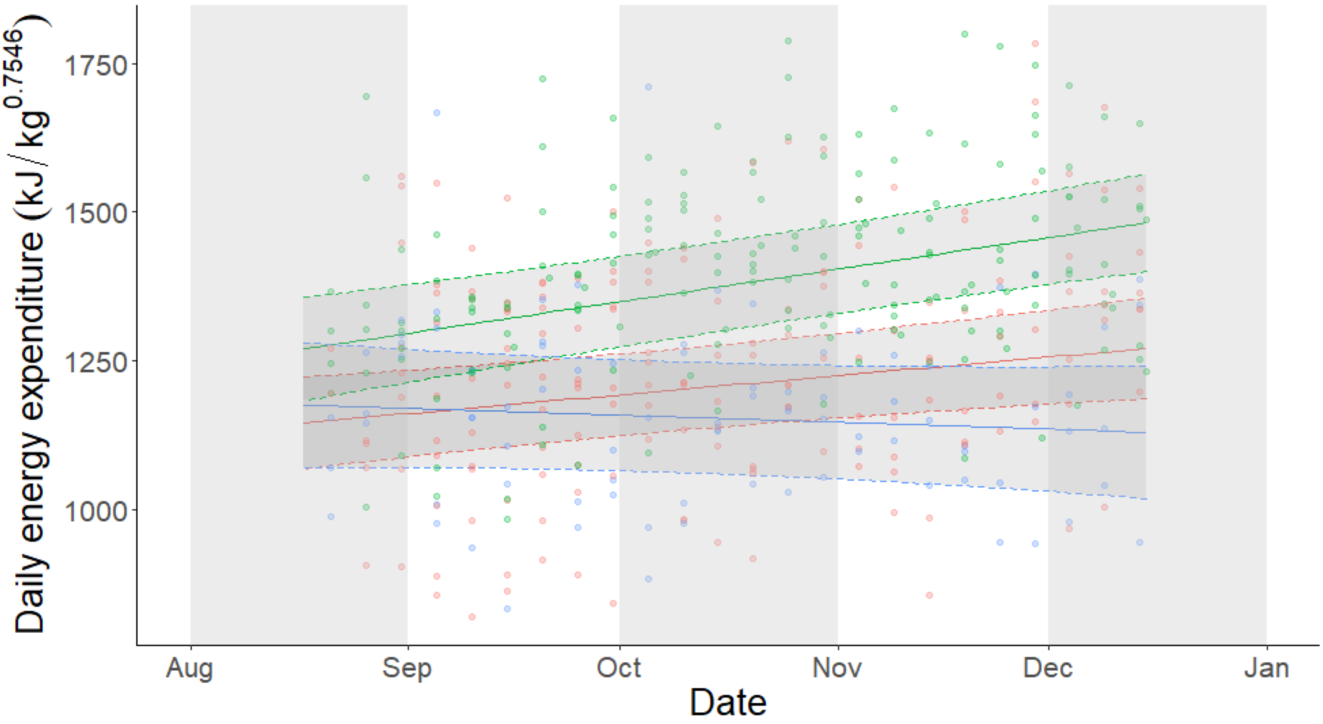

FIGURE 6.3 DAILY ENERGY EXPENDITURE OF RTDS ACROSS THE START OF THE WINTER PERIOD

Output from the best fitting model, showing the DEE for each population of RTDs from the three sampled breeding locations. Finland, Scotland and Iceland, are shown in red, blue and green, respectively. Shaded areas outlined by dashed lines show the 95% confidence intervals. Grey shading and no shading represent changes in the month.

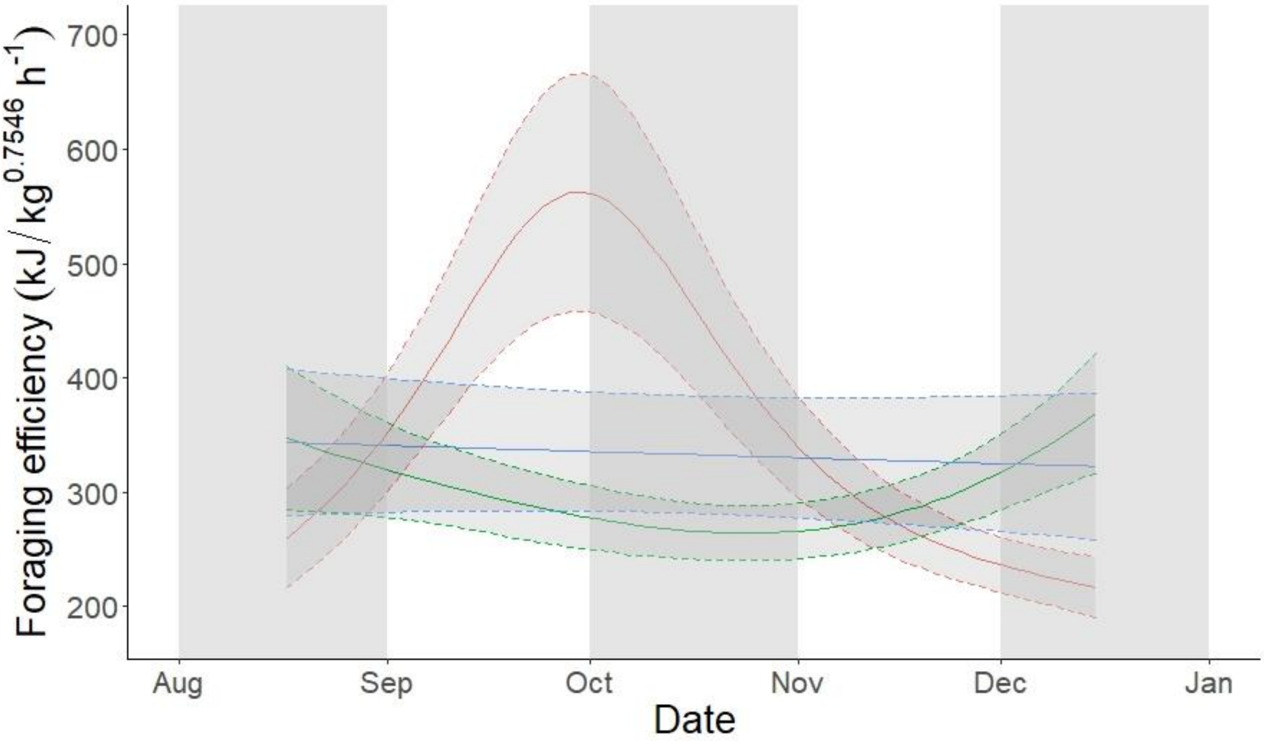

FIGURE 6.4 FORAGING EFFICIENCY OF RTD POPULATIONS THROUGH THE STUDY PERIOD

Foraging efficiency of RTDs from Finland, Scotland & Iceland, shown in red, blue and green respectively. Dashed lines and shaded areas represent the standard error around the mean. Grey shading and no shading represent changes in the month.

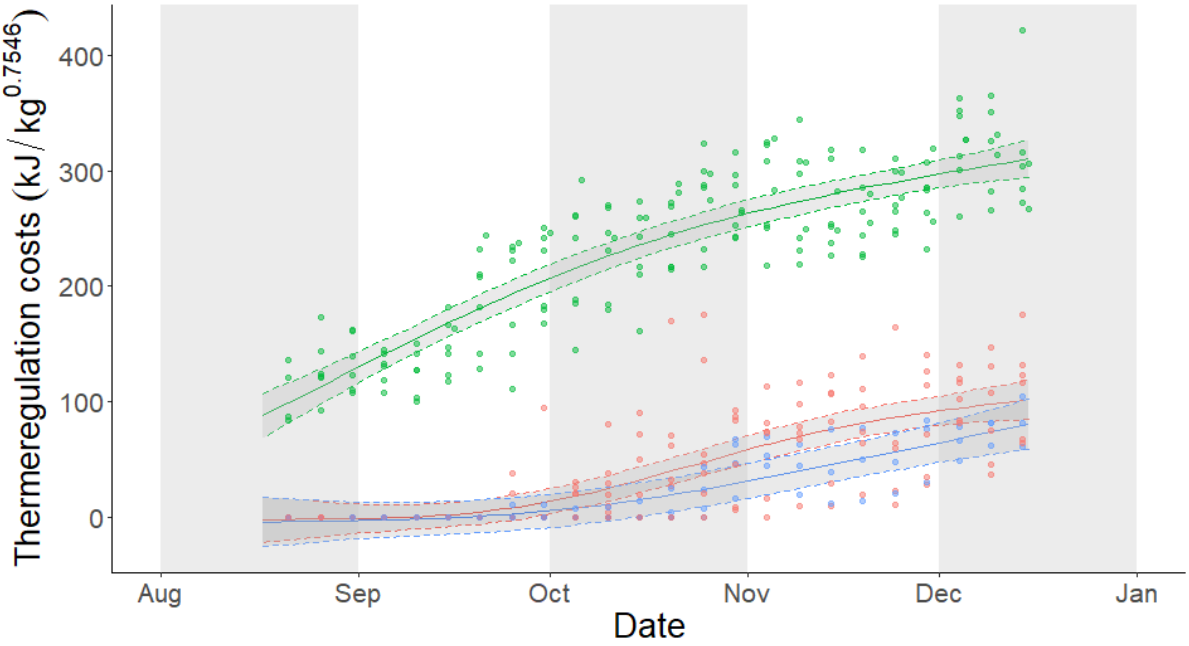

FIGURE 6.5 COST OF THERMOREGULATION FOR RTD POPULATIONS THROUGH THE STUDY PERIOD

Lines show the model output from the best fitting model of the daily energy expended on thermoregulation (DEE$_T$) per gram of adjusted mass for each sampled breeding location. Points show the observed values from the individuals. Finland, Scotland & Iceland shown in red, blue & green, respectively. Grey shading and no shading represent changes in the month.

Discussion

We aimed to establish the consequences of population differences in non-breeding season strategies, through behavioural decisions, and how these affect DEE. Overall, we revealed interacting spatial and temporal variation in DEE and the behaviour budgets of RTDs during the start of the non-breeding period. Birds originating from Iceland (resident) showed the highest DEE through the study period, driven by their high cost of DEE_T. Individuals from Finland and Iceland both exhibited an increase in DEE through the period, demonstrating the opposite trend to Scotland. However, Finland and Scotland had a similar DEE, especially at the start of the period. The most pronounced difference between the three populations was observed at the end of the study period. Across all populations there was some degree of temporal change in behaviour allocation, most likely driven by available daylight and variation in energetic demands. These behaviour changes drove the differences observed in DEE between Finland and Scotland, with the other main DEE cost, DEE_T, remaining low for both through the study. Foraging efficiency also varied across the study period, with Icelandic RTDs showing a marked difference, with the lowest foraging efficiency being in late October, while Finnish birds demonstrated their highest foraging efficiency in late September. These results provide not only the first systematic descriptions of RTD behaviour and energetics during this period, but give novel insight into inter-population variation across these metrics within a species more broadly. In particular, the differences in DEE observed between populations contrast with single-population studies (Kubetzki et al. 2009; White et al. 2013) and suggest that populations may vary in their sensitivity to environmental change acting during the non-breeding season.

The differences in migration strategies across these populations doubtless plays a key role in driving the behaviour and energetic budgets of these populations. Migration decisions are generally driven by factors affecting survivability, like the food availability around the breeding location in the non-breeding period (Chapman et al. 2011; Fayet et al. 2017). This difference in strategies was evidenced by all populations showing differences in either their DEE, DEE_T or behaviour budgets compared to the other two sites (Figure 6.2, 6.3 & 6.5). Similar to studies from single populations (Pelletier et al. 2020), we reveal that more than one strategy is successful at enabling survival through the non-breeding season and these divergent strategies may have evolved in response to differing environmental conditions (Desprez et al. 2018; Pereira et al. 2020). Nevertheless, the DEE of RTDs did vary between strategies and so this diversity might leave some populations more vulnerable to stochastic events (Fort et al. 2013; Marra et al. 2015b). In the short term, it could be possible to offset the costs and compensate for periods of low food availability through the storage of body fat (Biebach 1996; Smith and Moore 2003). However, when the whole non-breeding period is considered, fat storage cannot compensate for the differences in total energy requirements between populations, and hence different amounts of food required. The relative paucity of data available in this study precludes individual-level examination of the drivers of migration. However, there is evidently a high degree of individual variation in migration strategies, especially within the Scotland and Finland populations of RTDs, as these individuals show greater within-group differences in over-wintering movement (Duckworth et al. 2022).

In each of the three populations, there were changes in behaviour budget time allocations across the study period. Birds originating from Finland showed a marked seasonal change in time spent foraging and swimming. These changes aligned with the presumed timings of the post-moult migration (Dorsch et al. 2019; Duckworth et al. 2020; Duckworth et al. 2022), which suggests foraging strategies and energy intake varied between the two areas where they spent most of their time during the first part of the non-breeding season (North Sea and Baltic Sea). Finnish RTDs increased their time swimming during October, when many individuals would presumably have been undergoing moult (Dorsch et al. 2019) in the Baltic Sea, and reduced their time spent swimming in the latter half of the study period. This could suggest that during the moulting period, birds from Finland needed to swim more often between geographically distinct foraging patches. Following migration, the birds then increased the time spent foraging, but swam less, suggesting either the use of fewer and/or less spatially segregated foraging areas on a daily basis (Cowie 1977; Yu et al. 2020), or that patch quality or prey type was different between the two locations (Sutton et al. 2021; Tessier and Bost 2020). The beginning of the non-breeding season for Finnish RTDs also showed the highest increase in foraging efficiency, suggesting prey may be more abundant or accessible during this time (Waggitt et al. 2018). However, what drives further subsequent migration made by the Finnish RTDs away from this apparently prey rich area, in the Baltic Sea, is currently unknown.

Despite their contrasting migration strategy, RTDs originating from Finland and Scotland had the most similar DEE and DEE_T. Clearly, the lower DEE_T will have been the driving factor in keeping the DEE within these populations lower than Iceland. However, there is still a difference in the temporal change in DEE between the Finland and Scotland populations. This difference is driven by divergent behavioural decisions between the populations, such as Scottish RTDs showing little change in the time allocated to foraging, while Finnish RTDs increased their foraging time towards the end of the study period. Largely, this reflects an overall pattern of Scottish RTDs moving into lower energy activities, while Finland does the converse. The most parsimonious explanation for this is the difference in migratory strategies, with Finnish RTDs moving westward, which perhaps necessitates changes in behaviour budgets. Similar to RTDs from Finland, resident birds from Iceland showed an increase in DEE though the non-breeding period. However, this was driven by the increase in energy expended on thermoregulation, which was more than twice as expensive for Icelandic RTDs than for

Finnish or Scottish birds for most of the study period. The smaller body size and body mass of the birds over-wintering in Iceland (Supplementary Materials 2) reduces their resistance to cold conditions and seems counter-intuitive when compared to existing data and theory about latitude and body size distribution (Ashton 2002; Bergmann 1847). Currently, there is no hypothesis as to why this size difference exists, but future study on life history and diet differences between populations could help find an answer.

Temporal constraints on behaviours seemed to play a large role in the behaviour budgets of the RTD. In this study, we found less than 1% of dives occurring during the night. This suggests RTDs are seemingly unable or extremely averse to foraging during night, with the small number of dives we observed being close to the twilight periods. Therefore, a degree of limitation is imposed during the long nights of winter when available time to forage is reduced (Daunt et al. 2006). There was no discernible difference in foraging time at night between the sites, despite Icelandic birds experiencing the greatest amount of night by the end of the study. The increase in time resting is displayed by birds at all sites and was closely correlated with the duration of darkness, i.e. night a population experienced and the consequent reduction in available daylight for foraging and other activities which may be more efficient in the day (Indykiewicz et al. 2021).

The difficulty in detecting flight behaviour in the tagged RTDs illustrates the limitations of our study approach. In our study, we failed to capture any meaningful number of days with extended periods of flight behaviour, characteristic of migration. For the Finland population of RTD, this could potentially constitute a large cost that is missing from our estimates (McCloskey et al. 2018; Vincze et al. 2019). The average cost of flight for a RTD from our study would be 374 kJ h^{-1} and RTDs are estimated to have an average flight speed of around 77.9 km h^{-1} (Davis 1971; Norberg and Ulla Maria 1971). Given the ~1000 km migration distance from the Baltic Sea to the North Sea, the likely cost of this migration is 4800 kJ. The total energy expenditure of an individual from Finland across the study period is approximately 300,000 kJ (multiplying the mean DEE by length of the study period). Therefore, while the short-term costs of migration could be high (depending on the duration of migration), the total cost will have little effect on the total energy expenditure across the season, with the predicted cost of migration made by the RTDs from Finland being only 1.6% of this total energy expenditure. This value could also be subject to further uncertainty in the exact cost of flight, as in many species the cost is difficult to determine. For example, in black-necked grebes, estimates can range from a multiple of 12 to 30 of the BMR (Jehl 1994).

The ability to reliably detect flight during the non-breeding period remains the greatest challenge when attempting to reconstruct behaviour budgets from limited biologging data for birds with high flight costs and consequent brief flight duration (Dunn et al. 2022). The resolution of our data was at 10 minute intervals so excludes any short flights that could occur. Additionally, a study on eider ducks (*Somateria mollissima*) has demonstrated bouts of flight are short (~15 minutes) when flight is expensive, in order to avoid overheating (Pelletier et al. 2008). While this study is unable to detect such flights, using the data we have generated as a baseline, it would be possible to project the energetic consequences of increased number of flights, e.g., due to anthropogenic activity, with the application of individual based models (Murphy et al. 2020).

While our models provide novel insight into the ecology of RTDs, there are limitations which must be considered before interpreting these outputs in a wider context. For example, our foraging efficiency calculation assumes the energy expenditure on any day is roughly equal to the energy intake. However, as suggested, RTDs may be able to store excess energy intake as fat, so this assumption may be violated. The ability to store energy as fat varies between aquatic avian species (Dunn et al. 2019; Green et al. 2009). More sophisticated modelling allows this to be estimated (Dunn et al. 2022), but we currently lack sufficient data on red-throated divers to effectively parameterise such models. Despite this, there will still be some link between energy output and foraging time, as fat stores alone could not be sufficient to last the whole non-breeding season. However, as noted above, all the possible limitations in the current study would influence the different populations of divers in a consistent way, so our main findings on the links between survival strategy and energy expenditure and the differences in these between populations remain robust.

Changes in the demands of wintering individuals and populations exposes them to differential levels of susceptibility to additional stressors. Previous research has shown through changes in individual behaviour how some overwinter strategies lead to lower levels of capacity to deal with such stressors (Buchan et al. 2020; Fayet et al. 2016a). The present study presents important preliminary evidence suggesting the capacity of RTDs to accommodate stressors is unlikely to be equal across populations (Phillips et al. 2017). With their higher DEE and lower number of daylight hours, RTDs in Iceland are potentially most vulnerable, however this population is unlikely to encounter many anthropogenic stressors. Alternatively, those from Finland are more likely to encounter an increasing amount of anthropogenic activity, in the North Sea and Baltic Sea, but seem to have some capacity to alter their behaviour budgets or increase DEE when compared to Iceland, provided sufficient food resources are available. Understanding the current behaviour and energy budgets will be crucial in understanding how future stressors can translate into changes to demographic rates (Czapanskiy et al. 2021) through predictive modelling (Murphy et al. 2020).

In summary, we created a physiological energetics model to derive DEE during the beginning of the winter for three populations of RTDs, with different non-breeding strategies. As well as providing a baseline understanding for the behaviours of RTDs across this period, we have shown how differences in energy budgets can occur based on the strategy used to survive this demanding over-winter period and the environmental conditions subsequently encountered. This has provided evidence to support the idea that winter survival strategies vary beyond just the decision to migrate or not, and have consequences that might also lead to differential susceptibility to environmental change. Tactics likely require daily decisions based on how to budget behaviour based on spatially and temporally varying environmental conditions and foraging opportunities. We have also shown how the cost of thermoregulation may be the most important factor in determining overall DEE. Furthermore, our work has shown that even for a species with relatively little empirical work on physiology, important conclusions on energy expenditure can still be drawn using remote sensing technologies and allometric scaling equations. Further work in this area will explore how environmental changes in their local environment could impact the behavioural budget and thus the DEE of RTDs and how this might be connected to survival, and to breeding success through carryover effects.

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References

Anthony KRN, Hoogenboom MO, Maynard JA, Grottoli AG, Middlebrook R (2009) Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Functional Ecology 23:539-550. doi: https://doi.org/10.1111/j.1365-2435.2008.01531.x

Arizaga J et al. (2012) Wintering survival of insect-eating passerines in southern Europe. Bird Study 59:37-42. doi: 10.1080/00063657.2011.623765

Arnold TW (2010) Uninformative Parameters and Model Selection Using Akaike's Information Criterion. The Journal of Wildlife Management 74:1175-1178. doi: 10.1111/j.1937-2817.2010.tb01236.x

Ashton KG (2002) Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. Global Ecology and Biogeography 11:505-523. doi: https://doi.org/10.1046/j.1466-822X.2002.00313.x

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software; Vol 1, Issue 1 (2015) 67:1-48

Bergmann C (1847) Uber die Verhaltnisse der warmeokonomie der Thiere zu uber Grosso. Gottinger studien 3:595-708

Biebach H (1996) Energetics of Winter and Migratory Fattening. In: Carey C (ed) Avian Energetics and Nutritional Ecology. Springer US, Boston, MA, pp 280-323

Braithwaite JE, Meeuwig JJ, Hipsey MR (2015) Optimal migration energetics of humpback whales and the implications of disturbance. Conservation Physiology 3:5. doi: 10.1093/conphys/cov001

Brett JR, Groves TDD (1970) Physiological energetics. Fish physiology, vol 8. Academic Press

Buchan C, Gilroy JJ, Catry I, Franco AMA (2020) Fitness consequences of different migratory strategies in partially migratory populations: A multi-taxa meta-analysis. Journal of Animal Ecology 89:678-690. doi: https://doi.org/10.1111/1365-2656.13155

Buckingham L et al. (2022) Synchrony in peak non-breeding season energy expenditure for guillemots from four colonies: implications for severity of marine threats. Journal of Avian Biology In Review

Chapman BB, Brönmark C, Nilsson J-Å, Hansson L-A (2011) The ecology and evolution of partial migration. Oikos 120:1764-1775. doi: https://doi.org/10.1111/j.1600-0706.2011.20131.x

Christensen-Dalsgaard S, May R, Lorentsen S-H (2018) Taking a trip to the shelf: Behavioral decisions are mediated by the proximity to foraging habitats in the black-legged kittiwake. Ecology and Evolution 8:866-878. doi: https://doi.org/10.1002/ece3.3700

Clausen KK, Clausen P, Fox AD, Fælled CC, Madsen J (2013) Varying energetic costs of Brent Geese along a continuum from aquatic to agricultural habitats: the importance of habitat-specific energy expenditure. J. Ornithol. 154:155-162. doi: 10.1007/s10336-012-0881-8

Cooke SJ et al. (2013) What is conservation physiology? Perspectives on an increasingly integrated and essential science. Conservation Physiology 1. doi: 10.1093/conphys/cot001

Cowie RJ (1977) Optimal foraging in great tits (*Parus major*). Nature 268:137-139. doi: 10.1038/268137a0

Cramp S (1977) Handbook of the Birds of Europe, the Middle East and North Africa: Birds of the Western Palearctic, Vol. 1, Ostrich to Ducks. In: Cramp S (ed) Handbook of the Birds of Europe, the Middle East and North Africa: Birds of the Western Palearctic, Vol. 1, vol 14, 2009/04/24 edn. Oxford University Press

Czapanskiy MF et al. (2021) Modelling short-term energetic costs of sonar disturbance to cetaceans using high-resolution foraging data. Journal of Applied Ecology 58:1643-1657. doi: https://doi.org/10.1111/1365-2664.13903

Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behavioral Ecology and Sociobiology 59:381-388. doi: 10.1007/s00265-005-0061-4

Davis RA (1971) Flight Speed of Arctic and Red-Throated Loons. The Auk 88:169-169. doi: 10.2307/4083974

de Vries J, van Eerden Mennobart R (1995) Thermal Conductance in Aquatic Birds in Relation to the Degree of Water Contact, Body Mass, and Body Fat: Energetic Implications of Living in a Strong Cooling Environment. Physiological Zoology 68:1143-1163

Desprez M, Jenouvrier S, Barbraud C, Delord K, Weimerskirch H (2018) Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. Functional Ecology 32:2040-2053. doi: https://doi.org/10.1111/1365-2435.13117

Dierschke V et al. (2017) Possible behavioural, energetic and demographic effects of displacement of red-throated divers. JNCC Report 605

Dingle H, Drake VA (2007) What Is Migration? BioScience 57:113-121. doi: 10.1641/b570206

Dinkins JB et al. (2017) Quantifying overlap and fitness consequences of migration strategy with seasonal habitat use and a conservation policy. Ecosphere 8:14. doi: 10.1002/ecs2.1991

Dorsch M et al. (2019) German tracking study of seabirds in areas of planned offshore wind farms at the example of divers. Final report on the joint project DIVER, FKZ 0325747A/B, funded by the

Federal Ministry of Economics and Energy (BMWi) on the basis of a decision by the German Bundestag.

Duckworth J et al. (2020) Red-throated diver energetics project: preliminary results from 2018/19. JNCC Report 638. doi: ISSN 0963-8091

Duckworth J et al. (2021) Spatial and temporal variation in foraging of breeding red-throated divers. Journal of Avian Biology 52. doi: https://doi.org/10.1111/jav.02702

Duckworth J et al. (2022) Winter locations of red-throated divers from geolocation and feather isotope signatures. Ecology and Evolution 12:e9209

Dunn RE et al. (2022) Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle. Functional Ecology 00:1-15. doi: https://doi.org/10.1111/1365-2435.14059

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. Sci Rep 10:5993. doi: 10.1038/s41598-020-62842-x

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. doi: 10.1111/jav.02012

Dunn RE, White CR, Green JA (2018) A model to estimate seabird field metabolic rates. Biology Letters 14:20180190. doi: doi:10.1098/rsbl.2018.0190

Ellis HI, Gabrielsen GW (2002) Energetics of free-ranging seabirds. CRC Press, Boca Raton, FL

Enstipp MR, Grémillet D, Jones DR (2006) The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (Phalacrocorax auritus). J Exp Biol 209:845-859. doi: 10.1242/jeb.02064

Fayet AL et al. (2017) Ocean-wide Drivers of Migration Strategies and Their Influence on Population Breeding Performance in a Declining Seabird. Current Biology 27:3871-3878.e3873. doi: 10.1016/j.cub.2017.11.009

Fayet AL et al. (2016a) Drivers and fitness consequences of dispersive migration in a pelagic seabird. Behavioral Ecology 27:1061-1072. doi: 10.1093/beheco/arw013

Fayet AL et al. (2016b) Carry-over effects on the annual cycle of a migratory seabird: An experimental study. Journal of Animal Ecology 85:1516-1527. doi: https://doi.org/10.1111/1365-2656.12580

Fitzgerald-Dehoog L, Browning J, Allen BJ (2012) Food and Heat Stress in the California Mussel: Evidence for an Energetic Trade-off Between Survival and Growth. The Biological Bulletin 223:205-216. doi: 10.1086/BBLv223n2p205

Fort J, Grémillet D, Porter WP (2009) Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. Journal of Experimental Biology 212:2483-2490. doi: 10.1242/jeb.032300

Fort J et al. (2013) Energetic consequences of contrasting winter migratory strategies in a sympatric Arctic seabird duet. Journal of Avian Biology 44:255-262. doi: https://doi.org/10.1111/j.1600-048X.2012.00128.x

Furness RW, Wade HM, Masden EA (2013) Assessing vulnerability of marine bird populations to offshore wind farms. Journal of Environmental Management 119:56-66. doi: 10.1016/j.jenvman.2013.01.025

Gayk ZG, Le Duc D, Horn J, Lindsay AR (2018) Genomic insights into natural selection in the common loon (*Gavia immer*): evidence for aquatic adaptation. BMC Evolutionary Biology 18:64. doi: 10.1186/s12862-018-1181-6

Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. Journal of Avian Biology 40:529-538. doi: https://doi.org/10.1111/j.1600-048X.2009.04639.x

Gremillet D, Wright G, Lauder A, Carss DN, Wanless S (2003) Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. Journal of Applied Ecology 40:266-277. doi: https://doi.org/10.1046/j.1365-2664.2003.00806.x

Guillemette M et al. (2016) Does hyperthermia constrain flight duration in a short-distance migrant? Philosophical Transactions of the Royal Society B: Biological Sciences 371:20150386. doi: doi:10.1098/rstb.2015.0386

Guse N, Garthe S, Schirmeister B (2009) Diet of red-throated divers *Gavia stellata* reflects the seasonal availability of Atlantic herring *Clupea harengus* in the southwestern Baltic Sea. Journal of Sea Research 62:268-275. doi: 10.1016/j.seares.2009.06.006

Heath JPHP, Gilchrist HG (2010) When foraging becomes unprofitable: energetics of diving in tidal currents by common eiders wintering in the Arctic. Marine Ecology Progress Series 403:279-290

Heinänen S et al. (2020) Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. Marine Environmental Research:104989. doi: https://doi.org/10.1016/j.marenvres.2020.104989

Indykiewicz P, Jakubas D, Gerke J (2021) Gulls of a feather do not sleep whenever—circadian rhythm of activity of black-headed gulls *Chroicocephalus ridibundus* during the incubation period. J. Ornithol. doi: 10.1007/s10336-021-01896-8

Jackson DB (2003) Between-lake differences in the diet and provisioning behaviour of Black-throated Divers *Gavia arctica* breeding in Scotland. Ibis 145:30-44. doi: 10.1046/j.1474-919X.2003.00119.x

Jehl JR (1994) Field Estimates of Energetics in Migrating and Downed Blacknecked Grebes. Journal of Avian Biology 25:63-68. doi: 10.2307/3677295

Jessopp MJ et al. (2013) Transatlantic migration by post-breeding puffins: a strategy to exploit a temporarily abundant food resource? Marine Biology 160:2755-2762. doi: 10.1007/s00227-013-2268-7

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends in Ecology & Evolution 19:101-108. doi: https://doi.org/10.1016/j.tree.2003.10.013

Kendeigh SC, Dol'nik VR, Gavrilov VM (1977) Granivorous birds in ecosystems: their evolution, populations, energetics, adaptations, impact, and control. In: Pinowski J, Kendeigh SC (eds) Avian energetics. Cambridge University Press, New York, pp 127–204

Kleinschmidt B et al. (2019) The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. Marine Biology 166:77. doi: 10.1007/s00227-019-3523-3

Kubetzki U, Garthe S, Fifield D, Mendel B, Furness R (2009) Individual migratory schedules and wintering areas of northern gannets. Marine Ecology Progress Series 391. doi: 10.3354/meps08254

Lamb JS, Satgé YG, Jodice PGR (2017) Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. Ecology and Evolution 7:6469-6481. doi: https://doi.org/10.1002/ece3.3216

Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015a) A call for full annual cycle research in animal ecology. Biology Letters 11:20150552. doi: doi:10.1098/rsbl.2015.0552

Marra PP, Holberton RL (1998) Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. Oecologia 116:284-292. doi: 10.1007/s004420050590

Marra PP, Studds CE, Wilson S, Sillett TS, Sherry TW, Holmes RT (2015b) Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. Proceedings of the Royal Society B: Biological Sciences 282:20150624. doi: doi:10.1098/rspb.2015.0624

McCloskey SE, Uher-Koch BD, Schmutz JA, Fondell TF (2018) International migration patterns of red-throated loons (*Gavia stellata*) from four breeding populations in Alaska. PLoS ONE 13:1-15. doi: 10.1371/journal.pone.0189954

McKinney RA, McWilliams SR (2005) A new model to estimate daily energy expenditure for wintering waterfowl. The Wilson Bulletin 117:44-55, 12

McKnight A, Irons DB, Allyn AJ, Sullivan KM, Suryan RM (2011) Winter dispersal and activity patterns of post-breeding black-legged kittiwakes *Rissa tridactyla* from Prince William Sound, Alaska. Marine Ecology Progress Series 442:241-253

Mendel B et al. (2019) Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). Journal of Environmental Management 231:429-438. doi: 10.1016/j.jenvman.2018.10.053

Moe B et al. (2021) Twilight foraging enables European shags to survive the winter across their latitudinal range. Marine Ecology Progress Series SEA. doi: 10.3354/meps13697

Murphy KJ, Ciuti S, Kane A (2020) An introduction to agent-based models as an accessible surrogate to field-based research and teaching. Ecology and Evolution 10:12482-12498. doi: https://doi.org/10.1002/ece3.6848

Norberg RÅ, Ulla Maria N (1971) Take-Off, Landing, and Flight Speed during Fishing Flights of *Gavia stellata* (Pont.). Ornis Scandinavica (Scandinavian Journal of Ornithology):55. doi: 10.2307/3676239

Norris DR (2005) Carry-over effects and habitat quality in migratory populations. Oikos 109:178-186. doi: 10.1111/j.0030-1299.2005.13671.x

O'Brien S et al. (2020) Red-throated diver energetics project: 2019 field season report. JNCC Report 637

O’Brien S et al. (2018) Red-Throated Diver Energetics Project - 2018 Field Season Report JNCC Report No. 627. JNCC, JNCC, Peterborough

O’Brien SH, Webb A, Brewer MJ, Reid JB (2012) Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. Biological Conservation 156:15-21. doi: 10.1016/j.biocon.2011.12.033

Paruk DJ (2008) Nocturnal Behavior of the Common Loon, *Gavia immer*. Can. Field-Nat. 122. doi: https://doi.org/10.22621/cfn.v122i1.548

Paruk JD (2009) Function of the Common Loon Foot Waggle. The Wilson Journal of Ornithology 121:392-398

Pelletier D, Guillemette M, Grandbois J-M, Butler PJ (2008) To fly or not to fly: high flight costs in a large sea duck do not imply an expensive lifestyle. Proceedings of the Royal Society B: Biological Sciences 275:2117-2124. doi: doi:10.1098/rspb.2008.0422

Pelletier D, Seyer Y, Garthe S, Bonnefoi S, Phillips RA, Guillemette M (2020) So far, so good… Similar fitness consequences and overall energetic costs for short and long-distance migrants in a seabird. PLOS ONE 15:e0230262. doi: 10.1371/journal.pone.0230262

Pereira JM, Paiva VH, Ceia FR, Ramos JA (2020) Facing extremes: Cory's shearwaters adjust their foraging behaviour differently in response to contrasting phases of North Atlantic Oscillation. Regional Environmental Change 20:77. doi: 10.1007/s10113-020-01662-1

Péron C, Grémillet D (2013) Tracking through Life Stages: Adult, Immature and Juvenile Autumn Migration in a Long-Lived Seabird. PLOS ONE 8:e72713. doi: 10.1371/journal.pone.0072713

Phillips JA et al. (2021) Consistent concentrations of critically endangered Balearic shearwaters in UK waters revealed by at-sea surveys. Ecology and Evolution 11:1544-1557. doi: https://doi.org/10.1002/ece3.7059

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

R Core Team (2020) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria

Reid JM, Travis JMJ, Daunt F, Burthe SJ, Wanless S, Dytham C (2018) Population and evolutionary dynamics in spatially structured seasonally varying environments. Biological Reviews 93:1578-1603. doi: https://doi.org/10.1111/brv.12409

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

Salewski V, Bruderer B (2007) The evolution of bird migration—a synthesis. Naturwissenschaften 94:268-279. doi: 10.1007/s00114-006-0186-y

Smith RJ, Moore FR (2003) Arrival fat and reproductive performance in a long-distance passerine migrant. Oecologia 134:325-331. doi: 10.1007/s00442-002-1152-9

Southwood TRE (1962) Migration of terrestrial arthropods in relation to habitat. Biological Reviews 37:171-211. doi: https://doi.org/10.1111/j.1469-185X.1962.tb01609.x

Sutton GJ, Bost CA, Kouzani AZ, Adams SD, Mitchell K, Arnould JPY (2021) Fine-scale foraging effort and efficiency of Macaroni penguins is influenced by prey type, patch density and temporal dynamics. Marine Biology 168:3. doi: 10.1007/s00227-020-03811-w

Tessier E, Bost C-A (2020) Behavioural adjustments during foraging in two diving seabirds: king and macaroni penguins. Marine Biology 167:138. doi: 10.1007/s00227-020-03711-z

Vincze O, Vágási CI, Pap PL, Palmer C, Møller AP (2019) Wing morphology, flight type and migration distance predict accumulated fuel load in birds. Journal of Experimental Biology 222. doi: 10.1242/jeb.183517

Waggitt JJ, Cazenave PW, Howarth LM, Evans PGH, van der Kooij J, Hiddink JG (2018) Combined measurements of prey availability explain habitat selection in foraging seabirds. Biology Letters 14:20180348. doi: doi:10.1098/rsbl.2018.0348

White CR, Green JA, Martin GR, Butler PJ, Grémillet D (2013) Energetic constraints may limit the capacity of visually guided predators to respond to Arctic warming. Journal of Zoology 289:119-126. doi: https://doi.org/10.1111/j.1469-7998.2012.00968.x

Wood S, Scheipl F (2020) gamm4: Generalized Additive Mixed Models using 'mgcv' and 'lme4', 0.2-6 edn, pp Estimate generalized additive mixed models via a version of function gamm() from 'mgcv', using 'lme4' for estimation.

Yoda K (2019) Advances in bio-logging techniques and their application to study navigation in wild seabirds. Advanced Robotics 33:108-117. doi: 10.1080/01691864.2018.1553686

Yu C, Zhou L, Mahtab N, Fan S, Song Y (2020) Microhabitat variables explain patch switching by wintering Bewick’s swans through giving-up net energy intake rates. Environmental Science and Pollution Research 27:18843-18852. doi: 10.1007/s11356-020-08343-w

Chapter 7 An individual based modelling framework to explore demographic, energetic and behavioural consequences of displacement: with specific application to red-throated divers (*Gavia stellata*)

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Declaration of authorship

JG, SO, FD, IP and JD conceived the ideas and designed methodology; JD constructed the IBM, carried out the analysis and created visualisations; SO, JG and JD managed funding acquisition; JD led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Keywords

Individual based model, Human-wildlife interaction, loon, energetics.

Abstract

Assessing the impacts of anthropogenic activity and infrastructure on species and populations requires a robust framework capable of effectively simulating the responses of individuals. Individual based models (IBMs) provide an ideal approach where following parameterisation of individuals, additional stress based on theoretical impacts can be applied to simulated populations. Here, we develop an IBM framework to explore the effects of offshore wind farm construction and operation on survival, energetics and body mass of marine birds, focussing specifically on the non-breeding season when birds are free of central-place constraints. We used migratory red-throated divers (*Gavia stellata*) as a case study. To aid in generality, the two simulated effects of displacement are the loss of foraging habitat (expressed as reduced foraging efficiency) and the displacement behaviour itself, here demonstrated as additional flights. We found the model was able to complete a single simulation of 4000 divers for 120 days in less than 30 minutes on a standard desktop computer. On a cluster with 100 computers, 440 permutations of altered foraging efficiency and flight duration were completed in less than three hours. Foraging stress had the largest effect on survival, with a 50% reduction in foraging efficiency leading to a ~50% reduction of the population size. Values of foraging stress below 40% had little impact on mortality. We also showed effects of disturbance on both the chance of experiencing energetic stress and loss of body mass. Body mass was reduced even at lower levels of foraging stress, demonstrating that even low levels of disturbance could have impacts on demographic rates. The chance of energetic stress only began to increase at intermediate levels of foraging stress, but may impose additional stressors to populations beyond body mass and mortality. Generally, displacement flights had a much smaller effect, especially at lower values of foraging efficiency, as individuals were able to increase foraging time to compensate. This study provides one of the first IBMs to assess the effects of displacement during the non-breeding season of a seabird. We present this framework in the highly pressing case of the RTD, but demonstrate its capability for adaptation to any marine bird species. We also describe how this model can simulate the consequences of a range of threats beyond just displacement.

Introduction

In recent years there have been huge developments in the use of Individual based models (IBM) to answer a wide range of ecological questions (Murphy et al. 2020, Reid et al. 2018). This is in part driven by the increased accessibility of analysis frameworks available to researchers (Grimm and Railsback 2005). The improved understanding of the application and developments of IBM has had the knock-on effect of making these models more accessible to the wider community, as it has led to software packages making development easier (Kazil et al. 2020, Bauer et al. 2017). Additionally, the improved understanding and availability of data on ecological systems has made parameterisation of models easier. This is possible due to a greater range of devices for measuring and/or monitoring previously obscured elements of the natural world, such as migrations (Buckingham et al. 2022) and inaccessible populations (Edney and Wood 2020). Through the application of IBM, we can now gain an understanding of how individuals, populations and species will respond to future stresses and quantify these effects in a plethora of ways (Warwick-Evans et al. 2018). Furthermore, the increasing accessibility of horizontal computing has played a key role in increasing the ability of researchers to deal with complex biological problems (Murphy et al. 2020, Pickles et al. 2021, Zhang et al. 2022). Without a horizontal computing framework, researchers would need to use huge amounts of time to allow their computations to run on isolated machines, which can limit the number of permutations and iterations that can be explored (Warwick-Evans et al. 2018). Additionally, creating models which work in a high throughput scenario can often move scientists out of languages they traditionally work in, such as R or Netlogo, and into other languages, such as Java, C++ or Matlab (Pickles et al. 2021, Zhang et al. 2022). Ultimately, IBMs have demonstrated a capability to provide a robust method to explore the consequences of a wide range of threats across a huge array of scientific fields (Murphy et al. 2020, Reid et al. 2018).

For many species of birds occupying marine habitats, the non-breeding season can expose them to a wide range of evolving threats (Mazaris et al. 2019, Croxall et al. 2012). One of the more pressing issues in the marine environment is quantifying the threats of developments on populations to minimise the potential adverse impacts. Specifically, quantifying the effects of displacement from offshore wind farms for the most vulnerable and protected populations and species (Heinänen et al. 2020, Kelsey et al. 2018, Furness et al. 2013). This evaluation is an important component in facilitating the construction of offshore wind farms to tackle both the ongoing energy crisis and threat of climate change (Berling and Surwillo 2022). Previously, many studies have focussed on quantifying the negative effects of wind farms by applying previously observed effects to future projects (e.g. Cleasby et al. 2015, Shaffer and Buhl 2016, Marques et al. 2021). However, this approach will not account for observed differences in demographic and behaviours across spatial scales (Chapter 6), which will affect their ability to respond to additional pressures (Andersen et al. 2020). In order to integrate the differences in the capability to respond to threats, a robust predictive approach with an inherent ability to be parametrised on a by-individual or by-population basis is required (Piorkowski et al. 2012, Virtanen et al. 2022). To this end, an IBM provides an ideal modelling framework to address this challenge, as well as have the capacity to model a range of other threats (Warwick-Evans et al. 2018, McLane et al. 2011, Searle et al. 2018). For example, through modifying parameters for temperature and food availability, an IBM could concurrently test the effects of both ocean warming and reduced food availability on populations.

Approaching IBMs from an energetics perspective can provide an inclusive and flexible approach for both the quantification of the inputs and the outcomes for individuals (Dierschke et al. 2017, Drewitt and Langston 2006, Searle et al. 2018). In terms of parametrising inputs, assigning energetic costs to behaviours and stresses provides an ideal method to quantify the cost of stresses in terms of changes to behaviour budgets and energy costs (Andersen et al. 2020, Bardsen et al. 2018). For the outputs, an energetics approach allows for body mass and long-term energetic stress to be explored, in addition to direct mortality. An energetics approach to modelling has previously proved successful in a range of other projects looking at disturbance, including in predicting the migrations of whales in the presence of anthropogenic pressure (Braithwaite et al. 2015). Additionally, an IBM has quantified the breeding season demographic consequences of displacement on guillemots, razorbills, puffins and kittiwakes (Searle et al. 2018). One of the more challenging aspects to creating energetics models is correctly parametrising the model and its constituent rates (e.g. Daunt et al. 2020). For many species these rates are well documented through studies explicitly linking behaviour to energetics (Dunn et al. 2018, Ellis and Gabrielsen 2002). In species where such studies are deficient, using broader metabolic scaling equations derived from relationships across broad taxa groups could be used as a substitute (Dunn et al. 2018, Ellis and Gabrielsen 2002, Chapter 6).

One of the species most frequently identified as being at risk of displacement from both offshore wind and shipping are red-throated divers (*Gavia stellata*; 'RTD'), especially during the non-breeding period (Heinänen et al. 2020, Mendel et al. 2019). The extent of displacement in RTDs has been well quantified and studied with displacement occurring at distances of up to 20 km (Heinänen et al. 2020, Furness et al. 2013). This has led to concern over how future developments may impact both the fitness of individuals and whether adverse effects on individual fitness will translate into consequences for the demographic rates of populations (Daunt et al. 2020, Searle et al. 2018). Indeed, this has become a key concern for developers, as consent for construction of windfarms cannot be granted without evidence that the construction will have minimal impact on the environment (Natural England 2010). Perhaps more importantly, the protection of important populations of RTDs must be considered, as both the marine realm (Mazaris et al. 2019) and marine birds continue to come under an increasing number of threats (Croxall et al. 2012). This increase leads to increasing baseline levels of stress that all species must deal with (Andersen et al. 2020, Bardsen et al. 2018). With this in mind, assessing how RTDs will respond to future development scenarios is vital to make data-driven decisions on future development (Dierschke et al. 2017) and ensure legal requirements to avoid affecting SPA populations are met (Black et al. 2015).

Modelling the predicted consequences of disturbance in any species poses a difficult challenge, as often the process can be exceptionally “data intensive” in parameterisation (Robinson et al. 2007). Historically, there has been little information on the distributions and behaviour of marine birds, including RTDs, during the winter period. However, for RTDs, recent work has revealed insights into some of their over-winter behaviours (Duckworth et al. 2022, Kleinschmidt et al. 2022). Furthermore, across seabird species, we are increasing our insights into the behaviour budgets of marine birds during the winter months (Buckingham et al. 2023, Dunn et al. 2020, Patterson et al. 2022). This information provides us context on both the environmental conditions and behaviour strategies deployed by these birds. Using this information, it becomes possible to project future scenarios of development and impose the estimated disturbance costs on individuals and populations. Traditionally, a wide range of other physiology-related parameters would be necessary to produce energetic models for a species. However, by using allometric equations to estimate these parameters, any species can have their daily energy budget estimated, given some knowledge on behaviour (Chapter 6). In this regard, the RTD is an ideal species to test a novel IBM framework as they can demonstrate how energetic modelling is possible, even when many traditionally important parameters are unknown.

Overall, this study aims to create an IBM framework capable of simulating the behavioural and energetic budget of a non-breeding marine bird. The applications of this model are primarily for exploring the consequences of disturbance through additional movement activities and reduced foraging success. Through full open access to the underlying code, the model will be constructed to allow future projects to use or develop the IBM for similarly related questions in other aquatic bird species, where some empirical data on behaviour is available. The secondary aim of the study is to explore the possible impacts of displacement due to offshore windfarms on individual RTDs in terms of survival probability, body mass change and energetic stress. This will demonstrate, across disturbance parameters, what the possible consequences of wind farm development on populations might be.

Methods

Model format and infrastructure

The IBM generated in the study is described here using the overview, design concepts, and details (ODD) protocol suggested by Grimm et al. (2010). Use of this format aims to standardise IBM descriptions across studies and fields. The model described here was built with R 4.2.0 (R Core Team 2022) and parallel computing is carried out with the University of Liverpool Condor cluster (details at: http://condor.liv.ac.uk/).

1. Purpose and patterns

This IBM simulates the daily behaviours of individuals of a marine bird species in a changing environment through their wintering period. The IBM uses these behaviour budgets to calculate energy expenditure, changes to body mass and final body mass each day over the designated study period (Table 7-1). If daily body mass falls below the mass mortality threshold, the birds are considered to have perished. Under scenarios of various levels of disturbance, induced through additional displacement behaviours and reduced foraging efficiency, the effects on the population are quantified.

2. Entities, state variables and scales

Each entity in this simulation is a marine bird capable of determining, with some error, its current body mass and the energy requirements to stay at the ideal (starting) body mass (Table 7-1). Each individual is capable of five different behavioural states: foraging, swimming, flying, resting and active on water (activities like preening and minor movements) which capture the repertoire of behaviours typically undertaken by marine birds (Chapter 6). Foraging time is generated based on prior knowledge of their DEE from the previous day and their current body mass relative to their ideal mass to inform their energy requirements. Flight time is generated on a daily basis per individual from a distribution informed by empirical data. Flight and foraging are only able to occur in daytime. Therefore, the sum of flight time and foraging time can never exceed daylight time. In a case where the amount of foraging time an individual requires exceeds the available daylight, then it is instead calculated as the total available daylight minus the time spent in flight (Table 7-1). The remaining time not occupied by flight or foraging is apportioned to the three remaining behaviours according to the empirical data on behaviour budgets through the period under consideration. This assumes these behaviours will continue in the same proportions observed, regardless of light levels.

When applied to RTDs, the IBM functions for 4000 individuals (a population size large enough to calculate small changes in mortality without excessive computation time) across 120 days using empirical data from Chapter 6, representing 16th August to 14th December. This study period is constructed to represent the core wintering period of a population of RTDs from Finland, which migrate into the south North Sea. The study period is constrained in this example due to the availability of empirical data, but can be adapted to run for any number of days, if appropriate data are available.

3. Process overview and scheduling

Firstly, parameters for the day that are shared across all individuals are generated. These include the available daylight and the sea surface temperature (SST) for the population (Table 7-2). These are generated at the beginning of each new day cycle before the simulations of all the individuals within that day have started (Figure 7.1). Future developments could easily incorporate individual level data on daylight and SST, should they be available.

Within each day every living individual is simulated sequentially. First the BMR is calculated based on either the start mass or the mass from the previous day, depending on whether it is the first day of the simulation or any subsequent day. The other daily global parameters for the bird are then calculated based on these metrics, including thermal conductance, lower critical temperature and foraging efficiency (Figure 7.1).

Following this, the behaviour budgets are calculated, with additional displacement behaviour being added at this point in the process. Then, the costs of thermoregulation are calculated based on the thermal conductance, lower critical temperature and behaviour budgets. Finally, these are translated into DEE and then converted into a predicted change to body mass. If the new predicted body mass causes the individual to fall below the body mass threshold for survival, then the individual is said to have died during the simulated day and is not included in any subsequent simulation (Figure 7.1). After each individual has been simulated on that day, the model proceeds to the next day and continues to the end of the study period or until all individuals are dead.

4. Design concepts

The hypothesis this model was designed to test was: are RTDs vulnerable to additional stress, in the form of displacement and loss of habitat from an offshore wind farm. To test this hypothesis the model relies on four key principles and assumptions: (1) each individual can assess their own body condition, with some error, and can change their behaviour budget to remain at their ideal body mass. Individuals are able to gain mass, but will adjust their behaviour budget in an effort to stay at their ideal mass. (2) Individuals are classified as dead when their mass falls below the mass mortality threshold (Table 7-1). (3) Individuals do not directly interact with each other. In the case of RTDs, there is no evidence of social foraging and large aggregations of closely associated individuals in the winter are rare (Irwin et al. 2019). (4) The outcome of an individual's foraging activities on a given day are generated from known values of foraging efficiency and body mass change occurs on a daily scale. Each simulation of the IBM contains a population of individuals, on which a specific hypothesis is tested. For RTDs this population was 4000, representing a population size capable of encapsulating variation across parameters without imposing unnecessarily high computational demands.

While the mass of an individual bird can change throughout its lifetime, the proportions of the body do not change (Chapter 6), as individuals cease growing when they reach maturity and body mass changes become driven by fat reserves. Therefore, through the annual cycle the ideal body mass, given their body and skeleton proportions, remains constant (Martin-Silverstone et al. 2015). The body proportions of an individual are determined by an array of environmental factors during the juvenile and chick period (Liker et al. 2008, Sun et al. 2017). This is important to consider, as the relative change in mass from the original mass, becomes an important indicator of fitness. This model assumes that an individual will attempt to maintain an ideal body mass, given its body size. In cases where survival is challenged, individuals will begin to apportion more time to foraging, both in order to try and attain an ideal body mass, but also to survive. However, there is also evidence for some species that body mass changes within seasons, as energy demands shift (Coulson et al. 1983). While this could be true for RTDs, there are not yet repeated body mass measures on single individuals through the entire annual cycle to quantify this.

From modelled individuals, data is collected on whether they survive, the day they died, body mass, time spent foraging and energy income. The only population level data gathered is on the proportion of individuals surviving at the end of the simulation period. Individuals can experience stochastic events (simulated disturbance) through the study period but are incapable of learning from these events. In a simulation with no added stress, all individuals will survive, as there is assumed to be adequate energy in the system for the population to be sustained. This is consistent with the use of empirical data from data loggers retrieved from birds at the end of a study period who have necessarily survived long enough to return to the breeding colony. There is currently no parameter included which will simulate death by other causes (age, storms, disease or collision etc.) beyond the displacement probability and foraging stress, which impose indirect pressure, though a stochastic mortality term derived from annual survival data could easily be added.

Stress is modelled as probability of displacement behaviour and a reduction in forging efficiency. Both are inputs for each individual simulation. Displacement behaviour is given as the probability of experiencing a given behaviour caused by an interaction with a threat. In this example of the IBM on RTDs, this is the probability of undertaking a 30-minute displacement flight (Table 7-1). The foraging efficiency reduction is modelled as the proportion of foraging habitat lost to a given threat which is directly translated into a reduction in the foraging efficiency of all simulated individuals. Therefore, all individuals feel the effects of displacement through increased competition for resources. Both displacement behaviour and foraging efficiency stressors are parametrised as a static effect across the study period (Table 7-1). However, these could instead be entered as an array, to change the effect through time in other applications of the IBM.

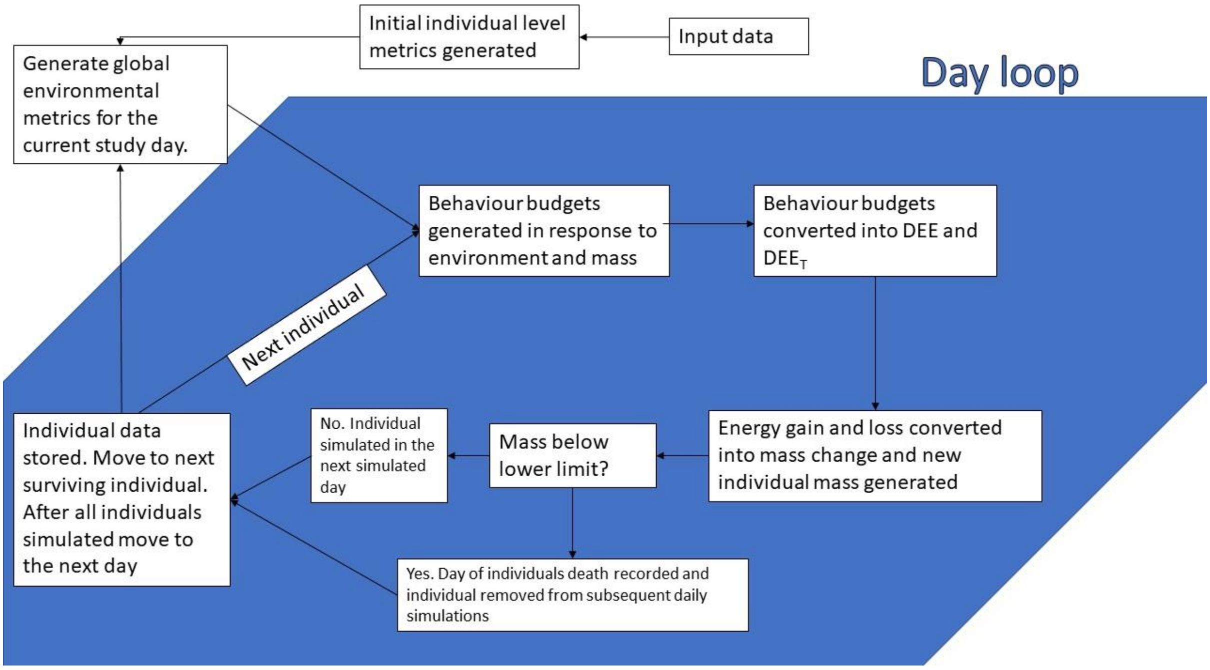

Figure 7.1 Simplified structure of the Individual Based Model in a flow diagram format

The flow of the IBM, from the initial data inputs on individuals and environments into the day specific metrics and the looping through of simulations for each individual on the given day. The blue area represents the daily loop each individual goes through while alive.

5. Initialisation

This model includes no initialisation period. However, the first few days are seen as a “burn in” period where individuals move towards a steady state. As the behaviours of an individual are informed by both the experiences of the previous day and their current body condition, the first day assumes the starting mass is the current mass and that the previous day (day 1) had an energy expenditure of the daily BMR multiplied by a specified amount. This is 2.6 for RTDs based on the mean observed energetic expenditure of empirical birds from a previous study (Chapter 6). This value is likely applicable to many other species, as energy expenditure in the non-breeding season is generally around this value (Dunn et al. 2020, Brown et al. 2023). Generally, unless the stress is at extreme levels individual do not die over the initial days of simulation. However, preventing the death of individuals over the initialisation period would lead to unrealistic behaviours of birds for whom there was not sufficient overall energy in the ecosystem to survive. The model has a capacity to facilitate an initialisation period, where simulations occur over longer time periods and data from the burn in periods are disregarded. The purpose of this period would be to allow individuals to reach a steady state based on simulation rather than initial parameters. This would be useful in simulations which extend over longer periods of time.

Starting masses of individuals drawn from a normal distribution based on empirical data (with the parameters N(2000, 160) for RTDs. These starting masses are generated at the start of each new simulation of the model. All other starting parameters are generated from data used to inform the environmental conditions of the study area.

6. Input data

The IBM includes three sources of external data in generating the environmental context of the study area and behaviour of the agents. For RTDs, the baseline foraging efficiency is drawn from empirical data from Chapter 6, which is calculated by dividing the daily energy expenditure by the time spent foraging and the scaled body mass. This foraging efficiency is affected by linear density dependence (Table 7-1), where a percentage loss in the population size has an equal compensating effect on foraging efficiency. There is currently no empirical data on the density dependence of foraging efficiency in RTDs. Therefore, for this demonstration of the IBM, we chose to include this relationship both to demonstrate the feature and have the most accurate representation of how a population challenged for resources would manage. The time in the non-simulated behaviours (active on water, swimming and rest) are drawn from predicted times individuals spend in these behaviours from

Chapter 6. The temperature of the water is drawn from on board data loggers and/or information on location based on assumptions and/or empirical data. For RTDs these locations were assumed to be off the coast of the North Sea, which aligns with areas the population has previously been apportioned to and with reliable temperature records (Morris et al. 2016). The available daylight for the supplied location(s) is generated using the R package Maptools (Bivand and Lewin-Koh 2022), which is used to calculate the total daytime on each day across the study period. This is generated within the IBM framework and requires no external data.

Simulations and statistical analysis for the RTD example

The IBM was run with different combinations of disturbance metrics, with three simulations of each combination. Disturbance behaviour was set up as a probability with values of zero to one in intervals of 0.05 (i.e. 0, 0.05, 0.1…). Foraging efficiency was simulated in the same way, with values from zero to one in intervals of 0.05. All possible combinations of the values for disturbance metrics were run giving a total of 441 combinations, each of which was simulated three times, giving 1323 total simulations. This allowed us to test the relative importance of the effects of varying disturbance probability and foraging efficiency reductions in our case study, as well as test for interactions. In this example study on RTDs, survival, proportion of body mass lost and the number of days exceeding a DEE over 3.5 * BMR are presented across individuals. Additional outputs can be generated, including behaviour budgets, energetic budgets and all metrics on a daily time scale. However, these are not presented or discussed here.

We created a binomial model mixed effects regression model with a ‘probit’ link function to explore the effects of the parameter changes on survival probability. Survival was modelled as the response variable, with the fate of each individual recorded at the end of the study period as a binary fate of dead or alive, represented as a “0” or “1”, respectively. Each simulation was assigned a random effect, to account for the relationship between individuals within a simulated population. Candidate models were created with full, subset and null models containing the explanatory variables: foraging stress, displacement behaviour and the interaction between them.

To model the body mass of the surviving individuals we used the proportion of starting body mass lost by the end of the study period as the response variable. We used a Gaussian distributed linear mixed effects model to assess the effects of foraging stress, displacement behaviour and their interaction, along with a quadratic effect for foraging stress and displacement probability. This quadratic term allowed for modelling of non-linear relationships when predicting the values which approached the mass mortality threshold. The term was limited to a fourth order polynomial, to avoid overfitting the model to the data. Simulation ID was fitted as a random effect, as described for the mortality model.

Only simulations where the value for foraging stress was below 0.9 were considered in this analysis, due to the low number of surviving individuals at values higher than 0.9.

To model days individuals within a simulation exceeded energy expenditures exceeding BMR*3.5 we treated the data as a Bernoulli process. Therefore, days where energy exceeded 3.5*BMR was a 'success' (1) and days where energy expenditure was below 3.5*BMR was a 'failure' (0). To assess the proportion of days DEE exceeded BMR*3.5 we used a binomial GLM. We used a global model with fixed effects for: displacement probability, foraging efficiency reduction, their interaction and quadratic terms for both displacement probability and foraging efficiency. This analysis is only carried out on individuals that survived the study period, so as to capture the non-lethal stress imposed on surviving individuals. Similar to the previously described model, only simulations where foraging stress was below 0.9 were considered in this analysis.

Given the incredibly large sample size capable of being generated through these simulation methods, the focus of the results is put on effect size rather than the significance of terms. The best fitting model was defined as the simplest model within 2 ΔAIC units of the best fitting model. All analysis was carried out in R version 4.2.0 (R Core Team 2022) with linear models created using the lme4 R package (Bates et al. 2015). Computers on the cluster generally had average specifications of 2.33 GHz Intel Core 2 processers, 2 GB of RAM, each with two potential job slots (each PC can run two simulations simultaneously). All accompanying data (Table 7-2) is sent out to each computer along with the script necessary to run a simulation with defined inputs based on parameterisation.

Results

The model run time for a single simulation (complete model run for 4000 individuals under one scenario of foraging stress and displacement behaviour) was generally 10-30 minutes on a single node of the Condor cluster. Run time varied widely and was strongly associated with the number of surviving individuals within a simulation. With an average computer pool of ~100, the full set of simulations finished in approximately three hours. If the sample size was increased to 8000 individuals and the number of repeats was set to 10, we would expect a run time of approximately 24 hours. However, the value is likely due to be higher, due to the additional time each process would take given the greater volume of calculations and stress on each node.

The most parsimonious model for the survival probability of RTDs included foraging stress (with a second order quadratic effect) and displacement behaviour (Table 7-3). The model showed a very strong effect for foraging stress (Figure 7.2), with foraging stress alone leading to a range of outcomes from all individuals surviving to nearly all individuals dying. However, the models failed to encapsulate the full relationship between mortality and the two stress parameters, due to the extremely non-linear relationship, that even a multi-order quadratic term could not correctly describe (Figure 7.2). Predominantly, this relationship can be explained as having a threshold at a value of 45% habitat loss. At this point, the majority of variation in mortality is explained by the value of displacement behaviour, where a higher probability leads to a lower surviving population. For example, when the value of foraging stress was 0.45; at a displacement behaviour probability of 0 the mortality was 1.75% (Figure 7.3). Conversely, at a displacement behaviour probability of 1, at the same level of foraging stress, the mortality was 44.1%. These results signal that there is a clear break point for the population between a foraging stress value of 0.4 and 0.5, where individuals are no longer able to compensate further stress without significant mortality (Figure 7.3). At this point, any additional stress leads to increased mortality in the population.

The most parsimonious model for change in body mass included displacement behaviour, foraging stress, a fourth-order quadratic effect of foraging stress (to the power of two, three and four) and an interaction between displacement behaviour and foraging stress. The model showed a substantial decrease in the body mass of surviving individuals with increasing levels of foraging stress (Figure 7.4). However, this predicted reduction stopped just before a reduction of 0.3, due to the mass related mortality threshold. Beyond a foraging stress level of 0.6, mass began to increase for surviving individuals, due to the low number of surviving individuals (Figure 7.3). Displacement probability remained in the final model as a fixed effect but had a smaller effect on body mass then foraging stress. The change in the proportion of mass lost was 1.5% when going from a displacement behaviour of zero to one.

The most parsimonious model for the probability of exceeding BMR*3.5 on a given day included foraging stress, displacement behaviour and a fourth-order quadratic effect of foraging stress (foraging stress to the power of two, three and four). This quadratic effect meant there was a non-linear relationship between the probability of DEE exceeding the BMR*3.5 and foraging stress (Figure 7.5). The relationship showed that at lower levels of foraging stress, the likelihood of exceeding BMR*3.5 was 0. However, at values of 0.4 - 0.8 foraging stress, there was an increased probability of exceeding BMR*3.5. The effect of displacement behaviour was also more pronounced at values closer to foraging stress of 0.7. For example, at a foraging stress of 0.65, the effect of displacement behaviour was a 19% increase in probability to exceed the threshold for a change of displacement behaviour from 0 to 1. This same change in displacement behaviour at a foraging stress of 0.45 was a reduction of 6%. This seeming interaction between foraging stress and displacement behaviour, is not driven by an explicit interaction in the model, but instead is a product of the quadratic effect of foraging stress.

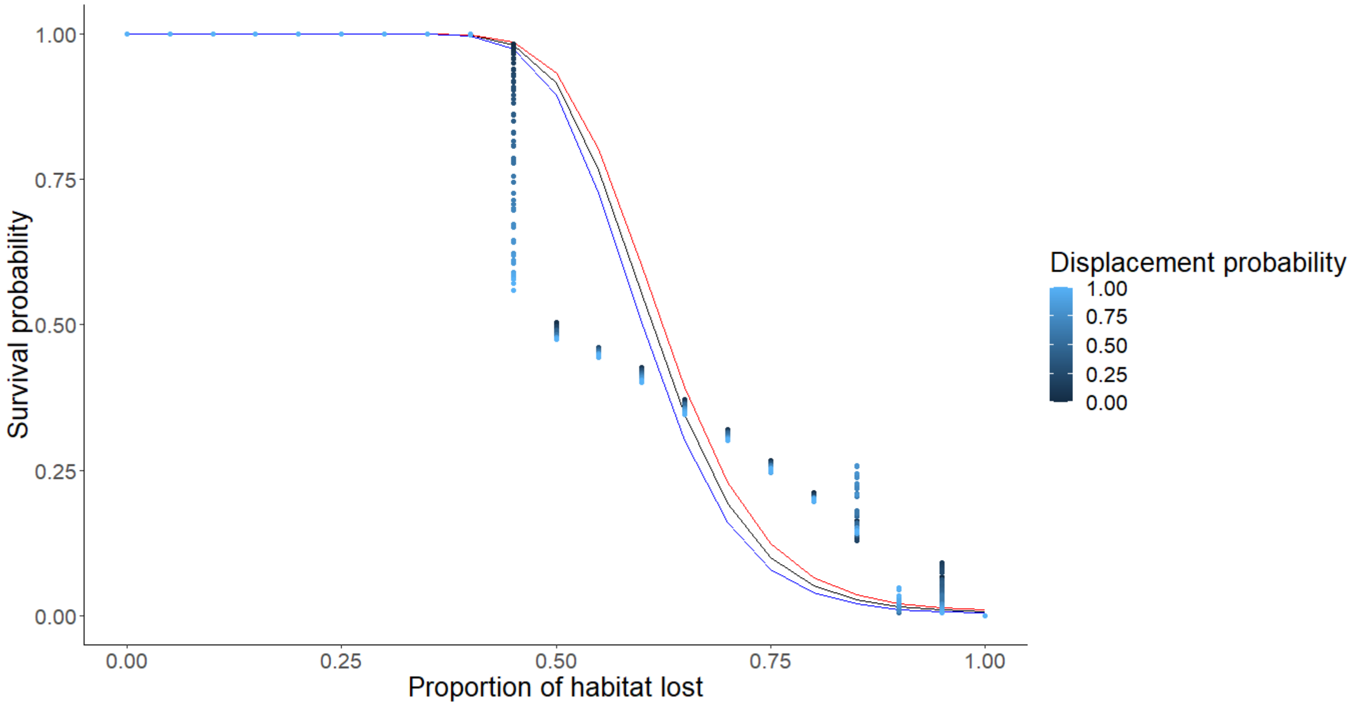

FIGURE 7.2 MORTALITY PREDICTIONS DUE TO DISPLACEMENT ACROSS PARAMETERS FROM THE INDIVIDUAL BASED MODEL

Results from model predictions showing habitat loss has a large effect on population survival probability. Line colour shows predicted proportions at given values of displacement probability. Displacement probability values of 0, 0.5 and 1 are shown in red, black and blue, respectively. This also represents the poor fit of the model to the data and its inability to accurately reflect the break point for survival at values of 0.4 foraging stress. Points show the proportion of surviving individuals across each simulation. Here, the displacement probability is represented as the intensity of the colour of the point ranging from a dark to pale blue, for a value of 0 and 1, respectively.

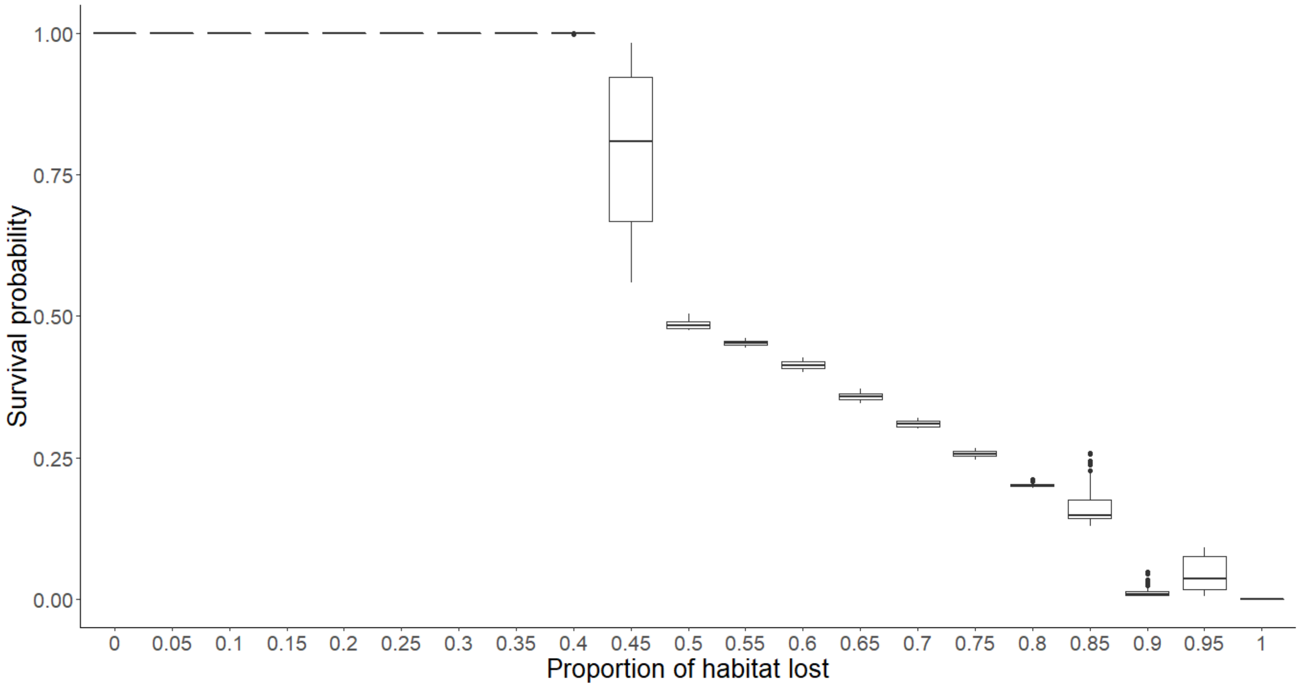

FIGURE 7.3 BOXPLOT SHOWING THE PROPORTION OF SURVIVING INDIVIDUALS IN A POPULATION ACROSS MODEL PARAMETERS

Box plot showing the summarised proportion of surviving individuals across all simulations with different proportions of habitat lost (foraging stress). The majority of the variation in these boxplots is apportioned to the range of displacement behaviour parameters contained within them.

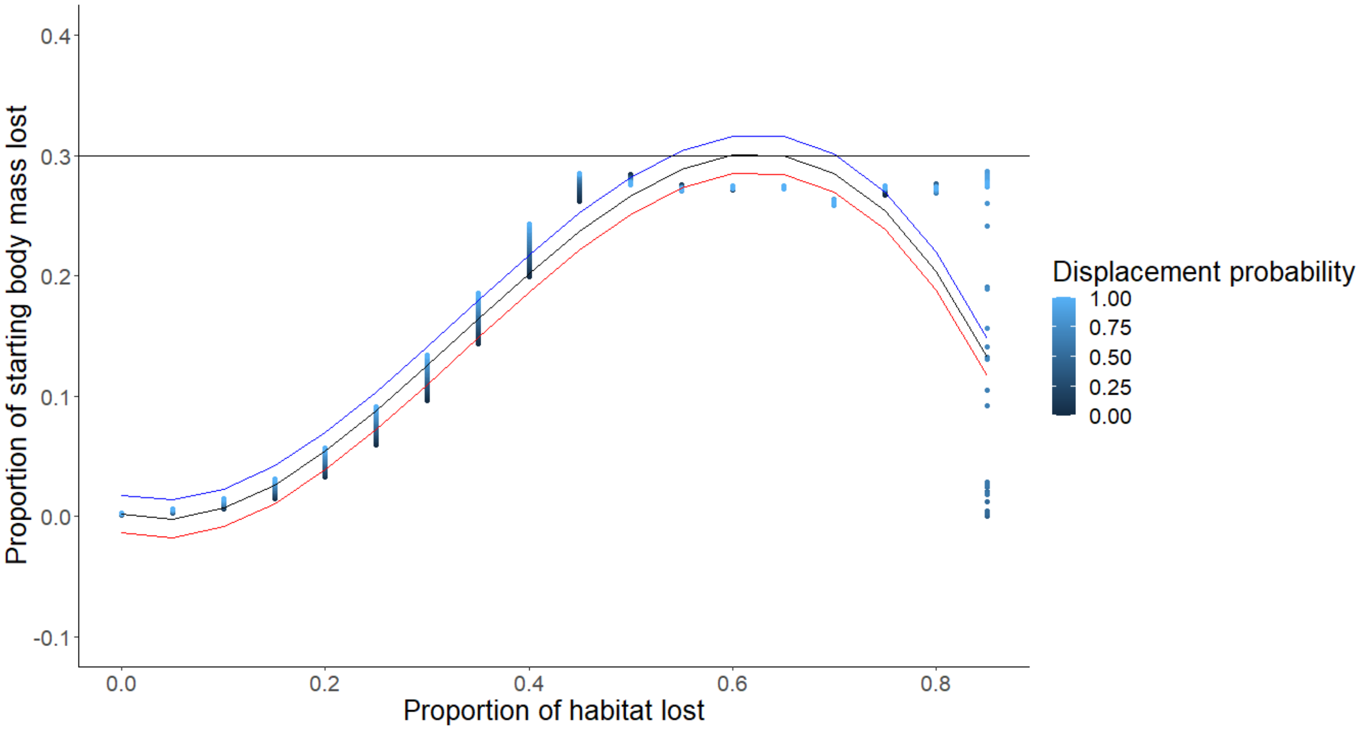

FIGURE 7.4 PREDICTED PROPORTION OF MASS LOST ACROSS MODEL PARAMETERS

Body mass loss at different levels of foraging stress and habitat loss. Line colour shows predicted levels at displacement probability. Red = 0, Blue = 1, Black = 0.5. Solid horizontal line at 0.3 proportion of body mass shows the limit beyond which if an individual loses mass they are considered to have perished. Points show the mean proportion of mass lost across each simulation. Here, the displacement probability is represented as the intensity of the colour of the point ranging from a dark to pale blue, for a value of 0 and 1, respectively.

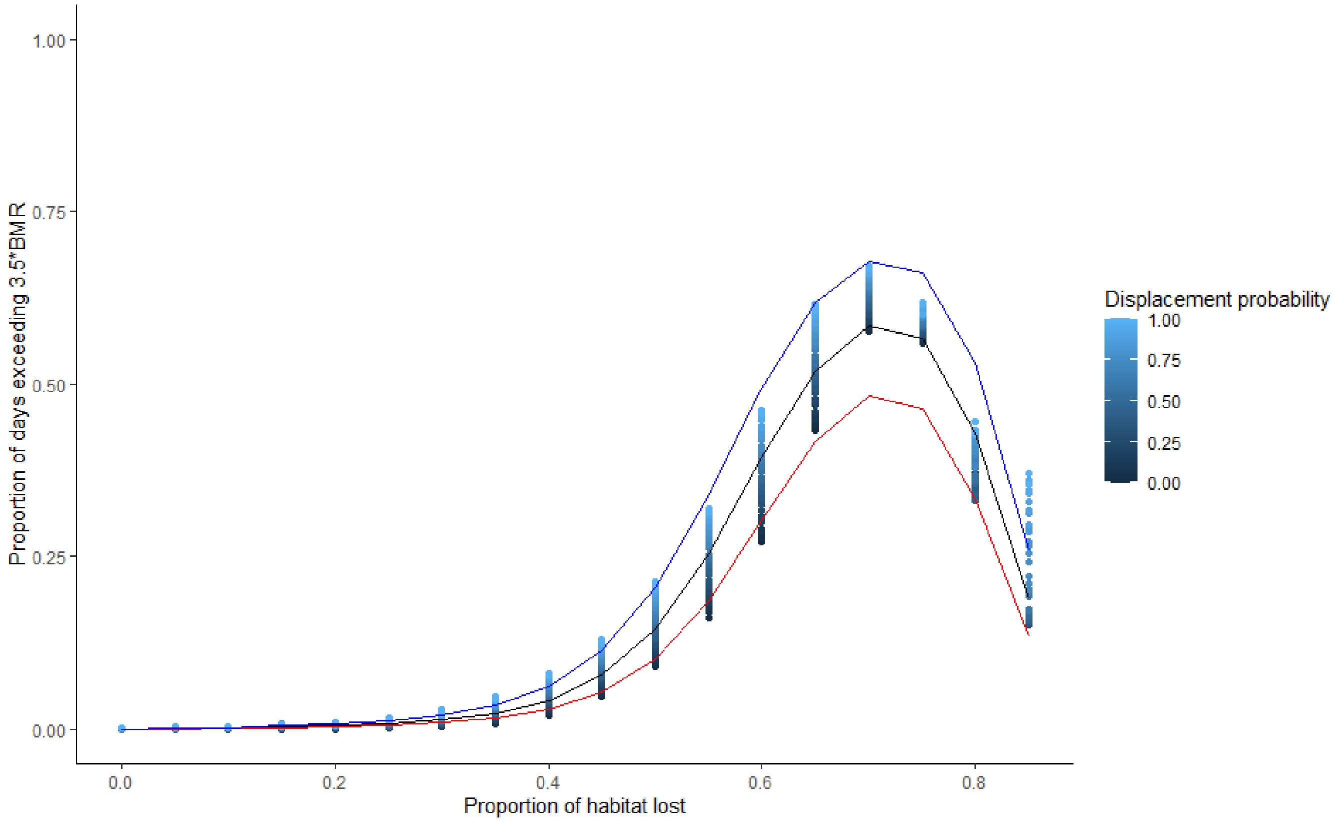

FIGURE 7.5 PREDICTED PROPORTION OF DAYS AN INDIVIDUAL EXPERIENCES ENERGETIC STRESS ACROSS MODEL PARAMETERS

*Proportion of days experienced energetic stress at different levels of foraging stress and displacement probability. Line colour shows predicted proportions at given values of displacement probability. Red = 0, Blue = 1, Black = 0.5. Points show the mean proportion of days where DEE*3.5 was exceeded across each simulation. Here, the displacement probability is represented as the intensity of the colour of the point ranging from a dark to pale blue, for a value of 0 and 1, respectively.*

TABLE 7-1 PROCESSES AND PARAMETERS FOR THE INDIVIDUAL BASED MODEL

Summary of the attributes generated either for the environment or the individual, which describe the processes and environment of each RTD simulated. The table included the name, the process used to generate the value and a short description and reference to where the process was derived from, where applicable.

Metric name	Short description	Process	Parameters chosen for RTD
Starting mass	A normal distribution to draw body mass from to give the starting mass of each individual. Both Mass and SD are manual inputs.	$N(Mass, SD)$	*Mass* = 2000 *SD* = 160
Lower body mass living limit	The mass below which an individual marine bird will perish. Starting mass is drawn from other parameters, but limit is a manual input.	$Starting\ Mass * limit$	*limit* = 0.7
Behaviour stress probability	A Boolean statement where if a randomly generated number between 0 and 1 is below $disP$ (probability of an individual being displaced on a given day) then displacement behaviour is expressed. Stress behaviour here is expressed as flight.	$Unif(0,1) < disP$	*disP* = range from 0 to 1 across simulations
Behaviour stress effect	The amount of additional time spent in the stress response behaviour state.	$N(mean, SD)$	*Mean*=0.25 *SD*=0.02
Foraging efficiency	The reduction to foraging efficiency calculated daily, where FES is the proportion		*FES* = range from 0 to 1 across simulations

	by which foraging efficiency is reduced. $\overline{X_i}$ and s_i gives the mean foraging efficiency and standard deviation, respectively, on day *i*. This function incorporates density dependence by scaling the value of foraging efficiency based on the population remaining on the *i*th day.	$N\left(\overline{X_i}\frac{N_i*(1-FES)}{N_i}, s_i * \frac{N_i*(1-FES)}{N_i}\right)$	
Foraging time	$Mass_{i0}$ represents the starting, ideal, mass. $Mass_i$ represents the current mass. DEE_{i-1} represents the expenditure of the individual on the previous study day. A simplifying assumption is made that each gram of mass is assumed to be equivalent to 38kj both for the intake and expenditure of food (Langton et al. 2014, Gabrielsen 1996).	$N((Mass_{i0} - Mass_i) * 38, SD) + N(DEE_{i-1}, (DEE_{i-1} * 0.05)))$	*SD*=30 Arbitrary value chosen to represent some error in knowledge of current body condition
Date	Current date of the simulation (yyyy/mm/dd)	Commencement date – termination date	2018/08/16 – 2018/12/31
Individual ID	The number assigned to differentiate individuals within the population	From simulation initiation	1 - 4000
Basal metabolic rate (Kj/h)	The basal metabolic rate used is the average of two equations from Ellis and Gabrielsen (2002) and	$((\frac{3.201 * bm^{0.719}}{24}) + (\frac{4.05 * bm^{0.79}}{1000} * 18.8))/2$	

	McKinney and McWilliams (2005). *bm* is body mass		
Lower critical temperature (LCT)	The temperature below which individuals experience the costs of thermoregulation.	$47.2 * Body\ Mass^{-0.18}$	
Thermal conductance (water)	The measure of heat loss through surface when an individual is sat in water (swimming/resting/active on water/inter-dive period)	$1.532 * Body\ Mass^{-0.546}$	
Thermal conductance (diving)	The measure of heat loss through surface when an individual is diving (the diving period of foraging behaviour)	$3.47 * Body\ Mass^{-0.573}$	
Daily energy expenditure on thermoregulation (DEE$_T$)	Calculation of daily energy expenditure on thermoregulation. This is only calculated if the sea surface temperature (SST) is below the LCT.	$\left(TC_{water} * \left(T_{Resting} + T_{Active\ on\ water} + T_{Swimming} + T_{Foraging} - T_{diving}\right) * Body\ Mass * (LCT - SST)\right) + \left(TC_{diving} * T_{diving} * Body\ Mass * (LCT - SST)\right)$	
Daily energy expenditure (DEE)	Sum of the BMR multiplied by the activity specific BMR multiplier and time spent in a behaviour for each behaviour.	$\left(\left(T_{Resting} * (BMR * \mathrm{E.Resting})\right) + \left(T_{Active\ on\ water} * (BMR * \mathrm{E.Active})\right) + \left(T_{Swimming} * (BMR * \mathrm{E.Swimming})\right) + \left(T_{Flying} * (BMR * \mathrm{E.Flying})\right) + \left(T_{Foraging} * (BMR * \mathrm{E.Foraging})\right)\right)$	E.Resting=1.4 E.Active=1.9 E.Swimming=3.5 E.Flying=12.5 E.Foraging=5.1
Weight change	Calculates mass (g) at the next time step by adding the current mass to the	$Mass_{t+1} = Mass_t + \left(\frac{Energy\ gain + DEE}{Enegy\ content\ of\ mass}\right)$	

	sum of the energy expenditure and energy gain, divided by the energy specific content of body mass (kj/g). The energy specific content of body mass here is 38 kj/g (Langton et al. 2014, Gabrielsen 1996), which is calculated for guillemots and assumed to be similar for divers.		

TABLE 7-2 EXTERNAL DATA SOURCES USED FOR THE INDIVIDUAL BASED MODEL

External data and sources used in parameterisation of the model.

External data name	External data description	Suggested/current data source
Foraging efficiency	The amount of energy returned (kJ) per unit of time (hours) spent foraging, with standard errors.	Data can be derived from any empirical studies measuring foraging efficiency. Data here are retrieved from Chapter 6.
Behaviour proportions (resting, active on water and swimming)	The time (hours) an individual from the study population spends in a behaviour, with standard errors. The behaviours of interest are transformed into proportion of time based on a whole day of 24 hours. These behaviour proportions are applied to the remaining time after foraging and flight are accounted for.	Data can be derived from any empirical studies measuring behaviour budgets. Data here are retrieved from Chapter 6.
Sea surface temperature	Data in °C related to the surface temperature of the water close to the study area. This could be gathered from loggers deployed on the birds or from weather monitors.	Data for temperature can be accessed from anywhere as long as it is representative of the study area. Preferably includes some measure of annual/local variation (Morris et al. 2016).

TABLE 7-3 MODELS STRUCTURES AND THEIR RANKINGS FOR THE OUTPUTS OF THE INDIVIDUAL BASED MODEL

*The top three fitting models for predicting the effects of foraging stress ('forstress') and displacement behaviour ('disp') on survival, change in body mass and energetic stress. Table shows the model structure, degrees of freedom, delta AICc and whether the model was selected as the top fitting model. In model infrastructure, ":" represents an interaction between two terms and poly() represents a variable where a polynomial relationship was modelled. The number within the brackets represents the order of the polynomial used. I.e. poly(*forstress*, 3) would represent a linear effects long with forstress*^{2} *and forstress*^{3}*.* (1|sim) represents a random effect for the simulation ID.

Survival	K	Delta AICc	Top model
~ disp + poly(forstress, 2) + disp:forstress + (1|sim)	6	0	
~ disp + poly(forstress, 2) + (1|sim)	5	1.26	++
~ poly(forstress, 2) + (1|sim)	4	5.52	
Body mass change			
~disp + poly(forstress,4) + disp:forstress + (1|sim)	9	0	+ +
~disp + poly(forstress,4) + (1|sim)	8	45.57	
~disp + poly(forstress,3) + (1|sim)	7	45.89	
Days DEE exceeded BMR*3.5			
~ disp + poly(forstress,4)	6	0	+ +
~ disp + poly(forstress,4) + disp:forstress	7	842	
~ poly(forstress,4)	5	10198	

Discussion

We have successfully constructed and demonstrated the capabilities of an IBM framework specifically designed to address the consequences of stress in non-breeding marine birds. In the specific example shown here, we have revealed that RTDs have some capacity to deal with additional levels of stress. They experienced no changes to population survival with reductions to foraging efficiency between 0 and 40%. However, reductions in foraging efficiency at 50% led to reductions of around 40% of the population, varying widely based on levels of displacement behaviour (Figure 7.3). As expected, the foraging efficiency change had a much larger impact than disturbance probability on all outputs. This suggests that the greatest threat to the RTD is the habitat loss caused by windfarms, rather than the cost of avoidance behaviours. However, even at lower levels of stress (~25% habitat loss), we have shown that there are still some effects on the body masses of populations, with surviving individuals losing ~8% of their mass at this stage. Our framework simulates how additional stressors can affect the behaviour and energetic budgets in terms of survival and fitness of a population. Through the use of horizontal computing, we were able to complete a large number of simulations simultaneously, allowing for the full range of the effects of parameter changes to be explored. The script and accompanying horizontal computing deployment capability is freely available for other researchers to develop and apply to their own case studies.

Our results have shown the full spectrum of impacts for an increase in foraging stress, which reduces foraging efficiency from 100% to 0%. This reflects a situation where none of the foraging area and all of the forging area are made inaccessible to individual RTDs, respectively. A reduction in foraging area of 100% is practically impossible for a population, as no planned windfarm projects come close to causing this level of disruption across a large spatial scale (Bloor et al. 2020). The realistic range of disruption in terms of foraging area loss is likely less than 20% (Gusatu et al. 2020). However, it is worth noting that many other areas are still exposed to other anthropogenic activity and that total foraging area lost also depends on the effect range of displacement imposed. In cases where the area lost is low, the effects are much less severe, with anything below 40% having a negligible effect on mortality. However, the effects on adult mortality above this threshold are highly unlikely to be sustainable in population terms for long-lived marine bird species (Miller et al. 2019). Additionally, the effects of displacement behaviour are more pronounced at this breakpoint, whereas at other values of foraging stress the effects are less. This is likely due to individuals being very close to their energetic limit and unable to handle additional stress. Furthermore, the sub-lethal effects of displacement behaviour on body mass and energetic stress are apparent even at lower levels of foraging stress (Figure 4 & 5). These effects occur at lower levels of stress than observed for mortality and could have impacts on future reproductive success through carry-over effects (Salton et al. 2015).

A possible mechanism for this is individuals failing to have sufficient energy reserves to attempt breeding attempts, thus having future effects on recruitment to populations (Harrison et al. 2011, Shoji et al. 2015).

Extended periods of time at high levels of energy expenditure can expose individuals to risks such as reduced breeding success or higher levels of stress hormones (Welcker et al. 2015, Hennin et al. 2016). Therefore, considering the frequency of these expensive days is important. Even if a population is able to maintain their population size and weight distribution, there could still be long term effects of chronic energetic stress, including reduced foraging behaviour and efficiency (Cottin et al. 2014). While not presented here, the IBM developed here stores the energetic costs of every simulated day for every individual as part of its outputs. This enables the user to examine the periods of the simulation where energy expenditure is highest. This could allow for identification of periods known as energetic bottlenecks, where individuals have to work harder to survive while being faced with reduced availability of resources (Piersma 2002, Fort et al. 2009). Identifying these periods could allow for concessions to be made specifically in these time periods to reduce stress. For example, in populations of species where displacement from ship traffic is a concern, vessel traffic could be reduced in these windows. Identification of such timeframes could allow for continued development, while minimising the impacts to individuals.

Studies have shown that displacement caused by windfarms has led to areas with a previously high density of individuals now being occupied at a much lower density (Heinänen et al. 2020, Dierschke et al. 2016a, Vilela et al. 2020). There are two possible explanations of these findings. The first is that the individuals which previously occupied these areas have perished (Masden 2010). The second possibility is that those previously occupying the areas have shifted their distribution, so have moved beyond the scope of surveys. If this is the case, then there would be a much higher density in the remaining suitable habitat (Heinänen et al. 2020). Consequently, it would be logical to assume greater competition for resources and thus a lower overall foraging efficiency in these areas. Increased competition and habitat loss are the simulated drivers which lead to lower foraging efficiency simulated in this study (Lamb et al. 2017). Therefore, there is a need to verify and quantify the exact nature of displacement to better understand which modelled scenario best reflects that faced by the population under study. An alternative hypothesis is that individuals are able to relocate away from the footprint of windfarms with no adverse effect. This could be possible in conditions where food and available habitat are not a limiting factor, but are unlikely given the current levels of stress placed upon the marine environment (Croxall et al. 2012, Mazaris et al. 2019)

While our model is among the first to provide a tangible measure on the effects of displacement for marine birds and one of the first formal assessments for RTDs, we acknowledge that there are a few key assumptions that we have made in order to generate our results and reach our conclusions. Currently, the model computes individuals on the scale of a day given their state at the beginning of that day. This means that body mass and SST do not change within a day, therefore individuals will respond to stress (in the form of weight loss) on the following day. However, it may be the case that individuals begin responding to stress immediately after the event. This could potentially increase the time that individuals are able to compensate for stress. Secondly, in this specific application of the model to the RTD, we assume that the behavioural response to displacement is flight. While it is the case that displacement leads to individuals moving from the area, this movement may also be in the form of swimming or passive movement with tides, rather than flight. This especially may be the case for RTDs, as they are specially adapted to life on the water (Gayk et al. 2018). In the case the cost of displacement being swimming as opposed to flight, the cost would be around 4 times lower. Finally, the model works on the assumption of a fixed population of non-breeding individuals with no immigration or emigration. We only focus on simulating individuals which arrive at our study commencement date, however some individuals may move on larger spatial scales, if the local conditions are very poor in a given year. Satellite tracking of RTDs has shown limited movement when individuals arrive in the core wintering area, but a capability to move large geographic distances during migration (Dorsch et al. 2019).

The current framework simulates all individuals as operating within a fixed space with equal environmental properties. A more advanced model would allow for environmental heterogeneity and the exploration of consequences beyond displacement from windfarms (Searle et al. 2018). Creating a spatially explicit IBM to model displacement will require both a finer understanding of the larger and smaller scale movements of the study species but also a better quantification of the foraging habitat in terms of its value to marine birds (Warwick-Evans et al. 2018, Chimienti et al. 2020). This is very challenging, as it requires a high level knowledge of: fine-scale distribution, resource distribution and ecological knowledge on resource use. Furthermore, fine-scale movements of non-breeding birds are also not well known, with many studies making use of course-scale geolocation techniques (Buckingham et al. 2022, Gatt et al. 2021, Pelletier et al. 2020). For example, in the case of RTDs, there is currently information available on the distribution and course scale movements of RTDs across the globe (McCloskey et al. 2018, Dorsch et al. 2019, Duckworth et al. 2022), but to parameterise a spatially explicit IBM, details on fine scale movements are required. Specifically, knowledge on both the daily movements with and without displacement are needed (Peschko et al. 2020). Such knowledge would allow for better apportioning the costs of movements following displacement and the consideration of changes to foraging efficiency based on local densities. Inevitably, improving on the model presented here would be large task requiring extensive further study on the fundamental ecology of RTDs, which have proven a difficult organism to study in large numbers (O'Brien et al. 2020). Furthermore, this situation is not at all unusual for non-breeding marine birds (Baker et al. 2022). However, using the best currently available data and robust modelling methods to produce predictions on the consequences of displacement now, is much preferable to waiting years for further developments and likely reaching the same results (Nicholson and Possingham 2007). The model presented here would also benefit from further validation on species where there is more available data on demographic rates. Current validation of this model was carried out by ensuring the model with no stress replicated the behaviour budgets of observed individuals. However, such tests are circular, as this data was used in the parameterisation.

Making assessments now does not remove the need for the development of a more sophisticated model capable of expanding on the principles presented here and having the flexibility to work across a range of marine bird species. This need is primarily driven by the consequences of displacement and other anthropogenic threats remaining undefined for many species (Garthe and Hüppop 2004, Dierschke et al. 2016b). Many of the rates and equations used in this IBM have been chosen as they are able to broadly encapsulate the allometric relationships across most aquatic bird species (Ellis and Gabrielsen 2002). This means, with some further modification, the IBM presented here could be used on other species where empirical lab-based studies on metabolic and thermodynamic rates have not yet been derived (Ellis and Gabrielsen 2002). Furthermore, the stressors parameterised here, could easily be transferred and attributed to other threats. For example, increased fishing activity could be integrated into this model, by accounting for additional displacement from ships and reducing foraging efficiency based on a lower prey availability, due to competition with fishing vessels (Grémillet et al. 2016).

In summary, this study has presented the first full IBM capable of simulating stress applied to marine birds during the non-breeding season. The model is flexible in the approach taken and can be parametrised in a way to integrate a wide range of marine threats. As a practical example, we have demonstrated the level of resilience of RTDs. This example has shown that in cases where wind farms exclude populations from less than 40% of the total foraging area, the consequences of displacement on mortality are likely to be small. However, sub-lethal effects of displacement on energetic stress and body mass of individual are apparent with lower levels of stress that might otherwise be hard to detect. This IBM currently provides the only avenue to produce estimates on the indirect effects of displacement and so the framework presented here may play a key role in providing figures required by windfarm developers in addressing the consequences of wind farm construction on wildlife.

References

ANDERSEN, J. H., AL-HAMDANI, Z., HARVEY, E. T., KALLENBACH, E., MURRAY, C. and STOCK, A. 2020. Relative impacts of multiple human stressors in estuaries and coastal waters in the North Sea-Baltic Sea transition zone. -*Science of the Total Environment,* **704**: 15.

BAKER, B., MEADOWS, M., RUFFINO, L. and ANDERSON, O. R. 2022. Towards better estimates of Manx shearwater and European storm-petrel population abundance and trends, demographic rates and at-sea distribution and behaviour. JNCC, Peterborough.

BARDSEN, B. J., HANSSEN, S. A. and BUSTNES, J. O. 2018. Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird. -*Ecosphere,* **9**: 22.

BATES, D., MÄCHLER, M., BOLKER, B. and WALKER, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. -*Journal of Statistical Software; Vol 1, Issue 1 (2015),* **67**: 1-48.

BAUER, E., ZIMMERMANN, J., BALDINI, F., THIELE, I. and KALETA, C. 2017. BacArena: Individual-based metabolic modeling of heterogeneous microbes in complex communities. -*PLOS Computational Biology,* **13**: e1005544.

BERLING, T. V. and SURWILLO, I. 2022. Facing the double crisis: geopolitics and climate change put a strain on the Baltic Sea Region energy security. *TESPA Briefs.* Trans European Policy Studies Association, Brussels, Belgium.

BIVAND, R. and LEWIN-KOH, N. 2022. maptools: Tools for Handling Spatial Objects.

BLACK, J., DEAN, B. J., WEBB, A., LEWIS, M., OKILL, D. and REID, J. B. 2015. Identification of important marine areas in the UK for red-throated divers (*Gavia stellata*) during the breeding season. JNCC, Peterborough.

BLOOR, P., THOMPSON, A. and STILL, D. 2020. Review of consented offshore wind farms in the Southern North Sea harbour porpoise Special Area of Conservation. Department for Business, Energy & Industrial Strategy.

BRAITHWAITE, J. E., MEEUWIG, J. J. and HIPSEY, M. R. 2015. Optimal migration energetics of humpback whales and the implications of disturbance. -*Conservation Physiology,* **3**: 5.

BROWN, J. M., BOUTEN, W., CAMPHUYSEN, K. C. J., NOLET, B. A. and SHAMOUN-BARANES, J. 2023. Energetic and behavioral consequences of migration: an empirical evaluation in the context of the full annual cycle. -*Scientific Reports,* **13**: 1210.

BUCKINGHAM, L., BOGDANOVA, M. I., GREEN, J. A., DUNN, R. E., WANLESS, S., BENNETT, S., BEVAN, R. M., CALL, A., CANHAM, M., CORSE, C. J., HARRIS, M. P., HEWARD, C. J., JARDINE, D. C., LENNON, J., PARNABY, D., REDFERN, C. P. F., SCOTT, L., SWANN, R. L., WARD, R. M., WESTON, E. D., FURNESS, R. W. and DAUNT, F. 2022. Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. -*Marine Ecology Progress Series,* **684**: 181-197.

BUCKINGHAM, L., DAUNT, F., BOGDANOVA, M. I., FURNESS, R. W., BENNETT, S., DUCKWORTH, J., DUNN, R. E., WANLESS, S., HARRIS, M. P., JARDINE, D. C., NEWELL, M. A., WARD, R. M., WESTON, E. D. and GREEN, J. A. 2023. Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. -*Journal of Avian Biology,* **2023**: e03018.

CHIMIENTI, M., DESFORGES, J.-P., BEUMER, L. T., NABE-NIELSEN, J., VAN BEEST, F. M. and SCHMIDT, N. M. 2020. Energetics as common currency for integrating high resolution activity patterns into dynamic energy budget-individual based models. -*Ecological Modelling,* **434**: 109250.

CLEASBY, I. R., WAKEFIELD, E. D., BEARHOP, S., BODEY, T. W., VOTIER, S. C. and HAMER, K. C. 2015. Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. -*Journal of Applied Ecology,* **52**: 1474-1482.

COTTIN, M., MACINTOSH, A. J. J., KATO, A., TAKAHASHI, A., DEBIN, M., RACLOT, T. and ROPERT-COUDERT, Y. 2014. Corticosterone administration leads to a transient alteration of foraging behaviour and complexity in a diving seabird. -*Marine Ecology Progress Series,* **496**: 249-262.

COULSON, J. C., MONAGHAN, P., BUTTERFIELD, J. and DUNCAN, N., B. 1983. Seasonal changes in the Herring Gull in Britain: Weight, moult and mortality. *Ardea*. 71: 235-244.

CROXALL, J. P., BUTCHART, S. H. M., LASCELLES, B., STATTERSFIELD, A. J., SYMES, A., TAYLOR, P. and SULLIVAN, B. 2012. Seabird conservation status, threats and priority actions: A global assessment. -*Bird Conservation International,* **22**: 1-34.

DAUNT, F., FANG, Z., HOWELLS, R., HARRIS, M., WANLESS, S., SEARLE, K. and ELSTON, D. 2020. Improving estimates of seabird body mass survival relationships. *Scottish Marine and Freshwater Science reports*. **11**: 54

DIERSCHKE, V., FURNESS, R. W. and GARTHE, S. 2016a. Review: Seabirds and offshore wind farms in European waters: Avoidance and attraction. -*Biological Conservation,* **202**: 59-68.

DIERSCHKE, V., FURNESS, R. W. and GARTHE, S. 2016b. Seabirds and offshore wind farms in European waters: Avoidance and attraction. -*Biological Conservation,* **202**: 59-68.

DIERSCHKE, V., FURNESS, R. W., GRAY, C. E., PETERSEN, I. K., SCHMUTZ, J., ZYDELIS, R. and DAUNT, F. 2017. Possible behavioural, energetic and demographic effects of displacement of red-throated divers. -*JNCC Report,* **605**.

DORSCH, M., BURGER, C., HEINÄNEN, S., KLEINSCHMIDT, B., MORKŪNAS, J., NEHLS, G., QUILLFELDT, P., SCHUBERT, A. and R., Ž. 2019. German tracking study of seabirds in areas of planned offshore wind farms at the example of divers. -*Final report on the joint project DIVER, FKZ*

0325747A/B, funded by the Federal Ministry of Economics and Energy (BMWi) on the basis of a decision by the German Bundestag.

DREWITT, A. L. and LANGSTON, R. H. W. 2006. Assessing the impacts of wind farms on birds. -*Ibis,* **148**: 29-42.

DUCKWORTH, J., O'BRIEN, S., PETERSEN, I. K., PETERSEN, A., BENEDIKTSSON, G., JOHNSON, L., LEHIKOINEN, P., OKILL, D., VÄISÄNEN, R., WILLIAMS, J., WILLIAMS, S., DAUNT, F. and GREEN, J. A. 2022. Winter locations of red-throated divers from geolocation and feather isotope signatures. -*Ecology and Evolution,* **12**: e9209.

DUNN, R. E., WANLESS, S., DAUNT, F., HARRIS, M. P. and GREEN, J. A. 2020. A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. -*Scientific Reports,* **10**: 5993.

DUNN, R. E., WHITE, C. R. and GREEN, J. A. 2018. A model to estimate seabird field metabolic rates. -*Biology Letters,* **14**: 20180190.

EDNEY, A. J. and WOOD, M. J. 2020. Applications of digital imaging and analysis in seabird monitoring and research. -*Ibis,* **163**: 317-337

ELLIS, H. I. and GABRIELSEN, G. W. 2002. *Energetics of free-ranging seabirds,* Boca Raton, FL, CRC Press.

FORT, J., GRÉMILLET, D. and PORTER, W. P. 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. -*Journal of Experimental Biology,* **212**: 2483-2490.

FURNESS, R. W., WADE, H. M. and MASDEN, E. A. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. -*Journal of Environmental Management,* **119**: 56-66.

GABRIELSEN, G. 1996. Energy expenditure of breeding common murres. -*Canadian Wildlife Service Occasional Paper,* **91**: 49-58.

GARTHE, S. and HÜPPOP, O. 2004. Scaling possible adverse effects of marine wind farms on seabirds: Developing and applying a vulnerability index. -*Journal of Applied Ecology,* **41**: 724-734.

GATT, M. C., GRANADEIRO, J. P. and CATRY, P. 2021. Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. -*Journal of Avian Biology,* **52**.

GAYK, Z. G., LE DUC, D., HORN, J. and LINDSAY, A. R. 2018. Genomic insights into natural selection in the common loon (*Gavia immer*): evidence for aquatic adaptation. -*BMC Evolutionary Biology,* **18**: 64.

GRÉMILLET, D., PÉRON, C., KATO, A., AMÉLINEAU, F., ROPERT-COUDERT, Y., RYAN, P. G. and PICHEGRU, L. 2016. Starving seabirds: unprofitable foraging and its fitness consequences in

Cape gannets competing with fisheries in the Benguela upwelling ecosystem. -*Marine Biology,* 163: 35.

GRIMM, V., BERGER, U., DEANGELIS, D. L., POLHILL, J. G., GISKE, J. and RAILSBACK, S. F. 2010. The ODD protocol: A review and first update. -*Ecological Modelling,* 221: 2760-2768.

GRIMM, V. and RAILSBACK, S. F. 2005. *Individual-based Modeling and Ecology,* Princeton, Princeton University Press.

GUSATU, L. F., YAMU, C., ZUIDEMA, C. and FAAIJ, A. 2020. A Spatial Analysis of the Potentials for Offshore Wind Farm Locations in the North Sea Region: Challenges and Opportunities. -*ISPRS International Journal of Geo-Information,* 9: 96.

HARRISON, X. A., BLOUNT, J. D., INGER, R., NORRIS, D. R. and BEARHOP, S. 2011. Carry-over effects as drivers of fitness differences in animals. -*Journal of Animal Ecology,* 80: 4-18.

HEINÄNEN, S., ŽYDELIS, R., KLEINSCHMIDT, B., DORSCH, M., BURGER, C., MORKŪNAS, J., QUILLFELDT, P. and NEHLS, G. 2020. Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. -*Marine Environmental Research*: 104989.

HENNIN, H. L., BÊTY, J., LEGAGNEUX, P., GILCHRIST, H. G., WILLIAMS, T. D. and LOVE, O. P. 2016. Energetic Physiology Mediates Individual Optimization of Breeding Phenology in a Migratory Arctic Seabird. -*The American Naturalist,* 188: 434-445.

IRWIN, C., SCOTT, M., S., HUMPHRIES, G. and WEBB, A. 2019. HiDef report to Natural England - Digital video aerial surveys of red-throated diver in the Outer Thames Estuary Special Protection Area 2018. *Natural England Commissioned Reports*.

KAZIL, J., MASAD, D. and CROOKS , A. 2020. *Utilizing Python for Agent-Based Modeling: The Mesa Framework,* Switzerland, AG, Springer Nature.

KELSEY, E. C., FELIS, J. J., CZAPANSKIY, M., PEREKSTA, D. M. and ADAMS, J. 2018. Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. -*Journal of Environmental Management,* 227: 229-247.

KLEINSCHMIDT, B., BURGER, C., BUSTAMANTE, P., DORSCH, M., HEINÄNEN, S., MORKŪNAS, J., ŽYDELIS, R., NEHLS, G. and QUILLFELDT, P. 2022. Annual movements of a migratory seabird—the NW European red-throated diver (*Gavia stellata*)—reveals high individual repeatability but low migratory connectivity. -*Marine Biology,* 169: 114.

LAMB, J. S., SATGÉ, Y. G. and JODICE, P. G. R. 2017. Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. -*Ecology and Evolution,* 7: 6469-6481.

LANGTON, R., DAVIES, I. M. and SCOTT, B. E. 2014. A simulation model coupling the behaviour and energetics of a breeding central place forager to assess the impact of environmental changes. -*Ecological Modelling,* **273**: 31-43.

LIKER, A., PAPP, Z., BÓKONY, V. and LENDVAI, Á. Z. 2008. Lean birds in the city: body size and condition of house sparrows along the urbanization gradient. -*Journal of Animal Ecology,* **77**: 789-795.

MARQUES, A. T., BATALHA, H. and BERNARDINO, J. 2021. Bird Displacement by Wind Turbines: Assessing Current Knowledge and Recommendations for Future Studies. -*Birds,* **2**: 460-475.

MARTIN-SILVERSTONE, E., VINCZE, O., MCCANN, R., JONSSON, C. H. W., PALMER, C., KAISER, G. and DYKE, G. 2015. Exploring the Relationship between Skeletal Mass and Total Body Mass in Birds. -*PLOS ONE,* **10**: e0141794.

MASDEN, E. A. 2010. Assessing the cumulative impacts of wind farms on birds. University of Glasgow.

MAZARIS, A. D., KALLIMANIS, A., GISSI, E., PIPITONE, C., DANOVARO, R., CLAUDET, J., RILOV, G., BADALAMENTI, F., STELZENMÜLLER, V., THIAULT, L., BENEDETTI-CECCHI, L., GORIUP, P., KATSANEVAKIS, S. and FRASCHETTI, S. 2019. Threats to marine biodiversity in European protected areas. -*Science of The Total Environment,* **677**: 418-426.

MCCLOSKEY, S. E., UHER-KOCH, B. D., SCHMUTZ, J. A. and FONDELL, T. F. 2018. International migration patterns of red-throated loons (*Gavia stellata*) from four breeding populations in Alaska. -*PLoS ONE,* **13**: 1-15.

MCKINNEY, R. A. and MCWILLIAMS, S. R. 2005. A new model to estimate daily energy expenditure for wintering waterfowl. -*The Wilson Bulletin,* **117**: 44-55, 12.

MCLANE, A. J., SEMENIUK, C., MCDERMID, G. J. and MARCEAU, D. J. 2011. The role of agent-based models in wildlife ecology and management. -*Ecological Modelling,* **222**: 1544-1556.

MENDEL, B., SCHWEMMER, P., PESCHKO, V., MÜLLER, S., SCHWEMMER, H., GARTHE, S. and MERCKER, M. 2019. Operational offshore wind farms and associated ship traffic cause profound changes in distribution patterns of Loons (*Gavia* spp.). -*Journal of Environmental Management,* **231**: 429-438.

MILLER, J. A. O., FURNESS, R. W., TRINDER, M. and MATTHIOPOULOS, J. 2019. The sensitivity of seabird populations to density-dependence, environmental stochasticity and anthropogenic mortality. -*Journal of Applied Ecology,* **56**: 2118-2130.

MORRIS, D., ANDRES, O., AYERS, R., BROWN, A., ELISA, C., KEITH, C., STEPHEN, D., LIAM, F., FLATMAN, S., GREENWOOD, N., HAVERSON, D., TOM, H., KIERAN, H., SIMON, J., ROSS, J., JULIAN, M., MEADOWS, B., PEARCE, D., JOHN, P., SOPHIE, P., DAVID, R., NATASHA, T., WILLIAMS, O. and WRIGHT, S. 2016. Temperature of the water column. In: SCIENCE, C. F. E. F. A. A. (ed.).

MURPHY, K. J., CIUTI, S. and KANE, A. 2020. An introduction to agent-based models as an accessible surrogate to field-based research and teaching. -*Ecology and Evolution,* **10**: 12482-12498.

NATURAL ENGLAND. 2010. Natural England's Response to London Array OWF Year 3 Ornithological Monitoring Report. *THE INFRASTRUCTURE PLANNING (EXAMINATION PROCEDURE) RULES - East Anglia ONE North Offshore Wind Farm.* Natural England.

NICHOLSON, E. and POSSINGHAM, H. P. 2007. Making conservation decisions under uncertainty for the persistence of multiple species. -*Ecological Applications,* **17**: 251-265.

O'BRIEN, S., RUFFINO, L., JOHNSON, L., LEHIKOINEN, P., OKILL, D., PETERSEN, A., PETERSEN, I. K., VÄISÄNEN, R., WILLIAMS, J. and WILLIAMS, S. 2020. Red-throated diver energetics project: 2019 field season report. -*JNCC Report,* **637**.

PATTERSON, A., GILCHRIST, H. G., ROBERTSON, G. J., HEDD, A., FIFIELD, D. A. and ELLIOTT, K. H. 2022. Behavioural flexibility in an Arctic seabird using two distinct marine habitats to survive the energetic constraints of winter. -*Movement Ecology,* **10**: 45.

PELLETIER, D., SEYER, Y., GARTHE, S., BONNEFOI, S., PHILLIPS, R. A. and GUILLEMETTE, M. 2020. So far, so good… Similar fitness consequences and overall energetic costs for short and long-distance migrants in a seabird. -*PLOS ONE,* **15**: e0230262.

PESCHKO, V., MERCKER, M. and GARTHE, S. 2020. Telemetry reveals strong effects of offshore wind farms on behaviour and habitat use of common guillemots (*Uria aalge*) during the breeding season. -*Marine Biology,* **167**: 118.

PICKLES, M., CORI, A., PROBERT, W. J. M., SAUTER, R., HINCH, R., FIDLER, S., AYLES, H., BOCK, P., DONNELL, D., WILSON, E., PIWOWAR-MANNING, E., FLOYD, S., HAYES, R. J., FRASER, C. and TEAM, H. S. 2021. PopART-IBM, a highly efficient stochastic individual-based simulation model of generalised HIV epidemics developed in the context of the HPTN 071 (PopART) trial. -*PLOS Computational Biology,* **17**: e1009301.

PIERSMA, T. 2002. Energetic Bottlenecks and Other Design Constraints in Avian Annual Cycles. -*Integrative and Comparative Biology,* **42**: 51-67.

PIORKOWSKI, M. D., FARNSWORTH, A. J., FRY, M., ROHRBAUGH, R. W., FITZPATRICK, J. W. and ROSENBERG, K. V. 2012. Research priorities for wind energy and migratory wildlife. -*The Journal of Wildlife Management,* **76**: 451-456.

R CORE TEAM. 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

REID, J. M., TRAVIS, J. M. J., DAUNT, F., BURTHE, S. J., WANLESS, S. and DYTHAM, C. 2018. Population and evolutionary dynamics in spatially structured seasonally varying environments. -*Biological Reviews,* **93**: 1578-1603.

ROBINSON, D. T., BROWN, D. G., PARKER, D. C., SCHREINEMACHERS, P., JANSSEN, M. A., HUIGEN, M., WITTMER, H., GOTTS, N., PROMBUROM, P., IRWIN, E., BERGER, T., GATZWEILER, F. and BARNAUD, C. 2007. Comparison of empirical methods for building agent-based models in land use science. -*Journal of Land Use Science,* **2**: 31-55.

SALTON, M., SARAUX, C., DANN, P. and CHIARADIA, A. 2015. Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. -*Royal Society Open Science,* **2**: 140390.

SEARLE, K. R., MOBBS, D. C., BUTLER, A., FURNESS, R. W., TRINDER, M. N. and DAUNT, F. 2018. Finding out the Fate of Displaced Birds. *Scottish Marine and Freshwater Science*, pp. 149.

SHAFFER, J. A. and BUHL, D. A. 2016. Effects of wind-energy facilities on breeding grassland bird distributions. -*Conservation Biology,* **30**: 59-71.

SHOJI, A., ARIS-BROSOU, S., CULINA, A., FAYET, A., KIRK, H., PADGET, O., JUAREZ-MARTINEZ, I., BOYLE, D., NAKATA, T., PERRINS, C. M. and GUILFORD, T. 2015. Breeding phenology and winter activity predict subsequent breeding success in a trans-global migratory seabird. -*Biology Letters,* **11**: 20150671.

SUN, Y., LI, M., SONG, G., LEI, F., LI, D. and WU, Y. 2017. The role of climate factors in geographic variation in body mass and wing length in a passerine bird. -*Avian Research,* **8**: 1.

VILELA, R., BURGER, C., DIEDERICHS, A., NEHLS, G., BACHL, F., SZOSTEK, L., FREUND, A., BRAASCH, A., BELLEBAUM, J., BECKERS, B. and PIPER, W. 2020. Divers (*Gavia* spp.) in the German North Sea: Changes in Abundance and Effects of Offshore Wind Farms.

VIRTANEN, E. A., LAPPALAINEN, J., NURMI, M., VIITASALO, M., TIKANMÄKI, M., HEINONEN, J., ATLASKIN, E., KALLASVUO, M., TIKKANEN, H. and MOILANEN, A. 2022. Balancing profitability of energy production, societal impacts and biodiversity in offshore wind farm design. -*Renewable and Sustainable Energy Reviews,* **158**: 112087.

WARWICK-EVANS, V., ATKINSON, P. W., WALKINGTON, I. and GREEN, J. A. 2018. Predicting the impacts of wind farms on seabirds: An individual-based model. -*Journal of Applied Ecology,* **55**: 503-515.

WELCKER, J., SPEAKMAN, J. R., ELLIOTT, K. H., HATCH, S. A. and KITAYSKY, A. S. 2015. Resting and daily energy expenditures during reproduction are adjusted in opposite directions in free-living birds. -*Functional Ecology,* **29**: 250-258.

ZHANG, S., XUE, Y., ZHOU, X., ZHANG, X., LIU, W., LI, K. and LIU, R. 2022. State of the Art: High-Performance and High-Throughput Computing for Remote Sensing Big Data. -*IEEE Geoscience and Remote Sensing Magazine,* **10**: 125-149.

Chapter 8 General discussion

Key findings

In this thesis, I have explored the behaviour and ecology of the red-throated diver (RTD), through both the breeding and non-breeding seasons. This work has provided the first insights and knowledge into aspects of the ecology of this poorly understood species. Chapter 2 showed that even a tag recovered from a single individual provided good insight on RTD diving capabilities. This initial work was expanded on further in Chapters 3 and 4 where I looked at the breeding season foraging behaviour and overwinter distributions, respectively. These chapters showed that, across the year, the species demonstrates differing survival strategies, both spatially and temporally, with changes in both behaviour and energy budgets. Chapter 5 built on the work for Chapter 4 and explored how changes in foraging strategy and diet could be linked to isotope values across spatial scales. The energetic costs of winter survival strategies were explored in more detail in Chapter 6, where I created energetic models to look at daily energy expenditure differences through time across the three populations. This work also demonstrated a robust methodology to quantify energy expenditure from behaviour budgets for species with relatively sparse data. Through this work, I have made significant contributions to the knowledge base for a previously understudied species. Finally, the consequences of additional stress on body condition and survival were assessed in Chapter 7, where I built an Individual Based Model (IBM) to simulate the behaviours and energetics of individuals. This facilitated building a framework to quantitatively assess the consequences of additional stress of theoretical populations of free-living marine birds. The IBM is constructed to be broad in its potential applications, but was applied specifically to the problem of RTD displacement to demonstrate the practicalities of the model. I believe this thesis has highlighted an approach to progress from understanding little on the ecology of a species into modelling the consequences of anthropogenic effects. Broadly, this method involved gathering the relevant data and relying on allometric relationships to fill knowledge gaps, before subsequently applying an IBM approach to quantify displacement.

Ecological understanding

Previously, the knowledge on the ecology of RTDs was mostly centred around the breeding period (Nummi et al. 2013, Solovyeva et al. 2017, Waldenström 2016), with most insights into non-breeding season behaviour focussing on movements (McCloskey et al. 2018, Okill 1994, Stenhouse et al. 2020). Most understandings of behaviour were either limited in scope (Polak and Ciach 2007) or based on indirect data, such as diet samples (Kleinschmidt et al. 2019, Guse et al. 2009) or ring recoveries (Okill

1994). Here, I added to the current knowledge base on breeding season behaviour; demonstrating how foraging strategies vary temporally and spatially as a breeding attempt progresses (Chapter 3). However, the largest knowledge contributions come from the work on the non-breeding season (Chapters 4 to 6). I have shown how behaviour budgets differed across populations and through the first half of the non-breeding season. These behaviours were also translated into energy budgets (Chapter 6). These results provided the first detailed insight into behaviour, foraging behaviour and energetics for the non-breeding period.

Furthermore, in this thesis I suggest development of future methodologies to relate the ecological understanding gathered here into tangible methods to monitor the species efficiently. Both chapters four and five discuss relating foraging behaviour and moult location to feather isotope signatures. Through these chapters, I suggest creating a robust methodology of how ecology links to observed values of isotopes (St John Glew et al. 2018, Buckingham et al. 2023). This understanding would be generated using a wider spatial scale of the species to create a framework to assign individuals to their moulting sites. Subsequently, this would incorporate the known values of feather isotope signatures across spatially distinct populations and diet types. The applications of this would be two-fold. Firstly, the ability to identify the moulting area of an individual could help understand migration routes and areas where RTDs could be particularly vulnerable to interactions with anthropogenic activity and infrastructure (St John Glew et al. 2018, Gómez-Díaz and González-Solís 2007). Secondly, using isotope values to determine foraging strategy and diet could help us understand to what degree individuals could be affected by changes to availability of different prey species. However, generating these insights to a level of accuracy the proves useful could require further exploration of the environment and prey species. In combination, gaining insights into diet and foraging behaviour could predict the expected levels of stress to populations, by assessing the impacts across the constituent individuals (Richards et al. 2021).

In this thesis, I have focussed on populations of RTDs across northern Europe. However, I believe much of the insight gained will be applicable to populations across the full range of Arctic the species (Chapter 3). Specifically, insights into the capabilities of RTDs to forage both in a benthic and pelagic capacity, likely demonstrates that the species has that capacity across their range. Likewise, the switching of foraging strategies across the breeding season, demonstrated in Chapter 3, could be upheld at other breeding locations. The insights gained here into migration strategies also suggest that populations globally could exist on the resident to migrant spectrum. This specific aspect of RTD ecology is increasingly well studied though, through various deployments of GPS tags (Heinänen et al. 2020, Paruk et al. 2015, McCloskey et al. 2018). However, the additional insights gained here may further contextualise this work as populations may occupy the same geographic space but occupy a different foraging niche.

Overall, building a better ecological understanding can have numerous benefits. Firstly, understanding the ecology of species can have a positive impact on the way people view nature and animals (Whitburn et al. 2020). In fact, through outputs of the work in this thesis, there have been numerous interactions with members of the public. These people have delighted in seeing where the birds they view from the coastline move and how they behave. Using science to forge closer connections between humans and animals could help with future conservation efforts, by making people more responsive to environmental issues (Whitburn et al. 2020). Secondly, improving the understanding the current ecology of species provides a more informative baseline for use in predictive models, which in turn improves their reliability (Meyer and Pebesma 2021). For example, insights into foraging behaviour can give a better understanding about the range of prey species consumed (Divoky et al. 2021). This will allow for models to account for the effects of altered prey resources and ability to switch to new prey items across more accurately. Finally, understanding the ecology of a species allows for prediction of new threats that may impact it. For example, early work on the response of RTDs to anthropogenic structures from an understanding of their ecology led to correct predictions of their strong aversion to offshore wind farms (Fox et al. 2006, Schwemmer et al. 2011).

Individual based model applications

From this thesis, there have been several major outputs which will hopefully play an important role in both research and policy centred around the impact of wind farms in northern Europe on RTDs. However, the development of the IBM in this thesis could be applied to any marine bird species to looking at the consequences of a range of threats. While my work presents the framework specifically with the example of RTDs and offshore wind farms in Chapter 7, it could instead apply to a wide range of other study organisms. For example, the inputs could be adapted to instead generate outputs for guillemots (*Uria aalge*). The energetic and behaviour budgets for this species are well described and ample empirical data is available (Dunn et al. 2022, Buckingham et al. 2022), allowing for predictions for similar levels of displacement presented here. The applications could also be applied more widely, if a more robust approach is taken to adapting the framework. For example, using marine mammals instead of bird species may be possible, if adequate considerations are taken in examining the underlying metabolic scaling equations and behaviour costs. For some seabirds, other IBMs have been constructed (Searle et al. 2018, Warwick-Evans et al. 2018), which could present possible opportunities to compare the outputs of the IBM here to those.

In the context of this thesis, the IBM revealed the resilience of RTDs to low levels of displacement (Chapter 7). With low levels of disturbance to foraging efficiency and behaviour budgets, individuals were able to adapt to the additional pressure. This was primarily due to individuals having some flexibility in foraging strategy, with a large capacity to increase their foraging time to offset displacement. As the levels of stress increased there was first a reduction in body mass of individuals before an increase in mortality at higher levels of pressure. Finally, at higher levels of stress, mortality, mass loss and energetic stress were all shown to be at high levels. These findings primarily suggest a balanced approach is needed to anthropogenic development of the marine habitat. Despite the resilience presented for RTDs, care must be taken to avoid pushing them close to or beyond their capacity to deal with stress. Additionally, many of the non-lethal effects predicted, could be monitored through the breeding season, when individuals are mostly more easily observable. This approach would additionally aid in discovering any carry-over effects on productivity as a by-product of stress in the non-breeding season (Harrison et al. 2011).

There are other IBMs currently available or under development with the aim of addressing the consequences of displacement from windfarms (Searle et al. 2018, Warwick-Evans et al. 2018). However, the model presented here has a unique capability to work outside of a spatial context, during periods when individuals are free of the central place constraint and relatively data deficient species. While this means the outputs are more abstract, it allows for broad estimates of the impacts of stress on species where very little is known, beyond the current behaviour budgets. However, the IBM presented here could have spatial and more detailed behaviour contexts applied, by apportioning threats and food resources across a grid. Individuals will then be parameterised in a way such that they can move between grid squares, both to satisfy their energy requirement and movements post-displacement.

Additionally, the threats presented here could be reconceptualised to explore the impacts of other interactions, such as fisheries, climate change or disease (Croxall et al. 2012, Lewison et al. 2012). Currently, the impact of offshore windfarms is modelled as a reduced foraging activity and/or an increase in flight behaviour. Climate change could also lead to reduced foraging efficiency and higher water temperatures (Franco et al. 2020, Prakash 2021). Therefore, both of these effects could be integrated into the model and in fact, current outputs could instead be interpreted in the light of other threats. However, to fully understand how to parametrise other threats, more empirical studies are required to first see how the threats interact with the foraging efficiency of individuals and populations.

Next steps

Through this thesis there has been some additional insight gained into the breeding season behaviour. However, the majority of the novel insights have been into the non-breeding season. The primary reason behind this is an inability of the tags deployed to accurately assign individuals to the seasonally unique behaviour of nest attendance in the breeding period. In terms of applications of breeding season knowledge wind farm interactions, there is less of a concern for RTDs across this period (Dierschke et al. 2017). This is because their interactions are fewer when compared to the non-breeding period, due to lower utilisation of areas where developments are more abundant. However, future constructions could pose an impact if they are placed in a manner where RTDs will have increased interactions. For example, wind farms placed near their nesting sites (Hovick et al. 2014). In this case, alternative methodologies would be required to accurately assess behaviour, which could include camera traps, GPS or accelerometers, which would provide information on nesting behaviour (Gómez Laich et al. 2008, Bird et al. 2022).

While this thesis has allowed for a wide range of new insights into the ecology of RTDs in the non-breeding period, there remain a few aspects of RTD ecology that lack in empirical study. Firstly, the knowledge of exact movement patterns to a fine spatial and temporal resolution have not yet been described. For future modelling and predictions for the impacts of offshore wind farms, this information is essential to allow for high quality simulations. Distributions of individuals can form an understanding of where they are, their habitat preferences and give some insight into prey density (Karpouzi et al. 2007), which alleviates some uncertainty. However, fine scale movement also provides insight into the probability of individuals moving to new foraging patches or moving into the region of wind farms or ship traffic (Mikami et al. 2022). To gain this fine scale understanding, the deployment of location tracking tags with a high temporal resolution of location fixes would be required (Heinänen et al. 2020). One of the largest issues in the deployment of such tags is the uncertainty of the long-term effects of deployment (Dierschke et al. 2017, O'Brien et al. 2020). This raises moral and ethical considerations in whether such deployments are in the best interest of the species. Alternatives to this could be in the form of newer smaller tags with GPS capabilities which would minimise impacts on individuals. This is important since, due to the poor performance of GLS tags in determining RTD locations, I cannot recommend their continued deployment on this species. As discussed in Chapter 4, these performance issues likely stem from shading of the sensors, driven by resting behaviour during twilight events. I therefore suggest light based methods of geolocation are avoided for RTDs.

Secondly, although this thesis has looked at foraging behaviour, there is still a lack of detailed diet composition across the range of RTDs. Our results have shown a combination of pelagic and benthic foraging strategies and this variety of prey types is generally supported by the literature (Kleinschmidt et al. 2019, Morkūnė et al. 2016). Further advancing this information could be essential in understanding the complicated relationships between foraging efficiency and prey density, depending on the relative abundances of prey species in a given year (Benoit-Bird et al. 2013). Finally, another area of priority work would be a complete understanding of the habitat drivers of foraging opportunities, along with understanding the degree of flexibility RTDs have in moving to new habitat. This work is essential in further modelling the consequences of displacement (Kirkpatrick et al. 2018, Kelsey et al. 2018). In a case where RTDs have a wide range of unutilised habitat and can move to new areas following displacement, this may reduce the estimated effects of disturbance. However, if they are limited to a small area of habitat, which they currently occupy, then the consequences could be vastly underestimated. Either way, addressing these research questions will form an integral part of assessing the future impacts of offshore windfarms on RTDs.

Main conclusions

This thesis has presented many of the first insights into the ecology of red-throated divers and made steps to address the questions of how they may respond to anthropogenic stress. Primarily, this assessment of vulnerability is based on their spatial overlap with current and planned windfarms along with capacity for additional foraging. Our current estimates suggest that while RTDs moving into the North Sea are at the highest risk of encountering developments, they also have a high capacity to handle change. This point was further demonstrated through the IBM.

The novel behaviour and ecological insights into RTDs have been a notable output of this thesis. Prior to this work, the majority of knowledge into the habitat use of divers was based on their two-dimensional use of the marine environment they inhabited. The work here presents much of the first exploration of vertical diving movements, which provided insight into the nature of the benthic and pelagic diving patterns. These foraging patterns showed how spatial and temporal changes to foraging behaviour can manifest. This suggests that populations are adapting to local environmental conditions, which may in turn suggest the species has a degree of adaptability to habitat change both through their annual cycle and across their spatial distribution.

I have identified key areas of future work to inform and create a final model capable of predicting the consequences of displacement in known and unknown habitats. Given the high level of interest, both economically and ecologically in understanding these threats; there will likely be projects addressing these challenges in the next few years. These results will then hopefully form the gold standard for both understanding threats to RTDs, along with other species of marine birds.

General introduction and discussion references

ABADI, F., BARBRAUD, C. and GIMENEZ, O. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. -*Global Change Biology,* **23**: 1353-1359.

ALERSTAM, T., HEDENSTRÖM, A. and ÅKESSON, S. 2003. Long-distance migration: evolution and determinants. -*Oikos,* **103**: 247-260.

ASCH, R. G., STOCK, C. A. and SARMIENTO, J. L. 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. -*Global Change Biology,* **25**: 2544-2559.

BAIRLEIN, F. 2001. Results of bird ringing in the study of migration routes. -*Ardea,* **89**: 7-19.

BAND, W., MADDERS, M. and WHITFIELD, D. 2007. *Developing Field and Analytical Methods to Assess Avian Collision Risk at Wind Farms,* Madrid, Quercus/Libreria Linneo.

BARDSEN, B. J., HANSSEN, S. A. and BUSTNES, J. O. 2018. Multiple stressors: modeling the effect of pollution, climate, and predation on viability of a sub-arctic marine bird. -*Ecosphere,* **9**: 22.

BENOIT-BIRD, K. J., BATTAILE, B. C., HEPPELL, S. A., HOOVER, B., IRONS, D., JONES, N., KULETZ, K. J., NORDSTROM, C. A., PAREDES, R., SURYAN, R. M., WALUK, C. M. and TRITES, A. W. 2013. Prey Patch Patterns Predict Habitat Use by Top Marine Predators with Diverse Foraging Strategies. -*PLOS ONE,* **8**: e53348.

BINDOFF, A. D., WOTHERSPOON, S. J., GUINET, C. and HINDELL, M. A. 2018. Twilight-free geolocation from noisy light data. pp. 1190-1198.

BIRD, J. P., FULLER, R. A., PASCOE, P. P. and SHAW, J. D. S. 2022. Trialling camera traps to determine occupancy and breeding in burrowing seabirds. -*Remote Sensing in Ecology and Conservation,* **8**: 180-190.

BIRDLIFE INTERNATIONAL. 2023. Species factsheet: Gavia stellata.

BLACK, J., DEAN, B. J., WEBB, A., LEWIS, M., OKILL, D. and REID, J. B. 2015. Identification of important marine areas in the UK for red-throated divers (*Gavia stellata*) during the breeding season. JNCC, Peterborough.

BODEY, T. W., CLEASBY, I. R., BELL, F., PARR, N., SCHULTZ, A., VOTIER, S. C. and BEARHOP, S. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. -*Methods in Ecology and Evolution,* **9**: 946-955.

BOLTON, M., CONOLLY, G., CARROLL, M., WAKEFIELD, E. D. and CALDOW, R. 2019. A review of the occurrence of inter-colony segregation of seabird foraging areas and the implications for marine environmental impact assessment. -*Ibis,* **161**: 241-259.

BOOTH, C. G., SINCLAIR, R. R. and HARWOOD, J. 2020. Methods for Monitoring for the Population Consequences of Disturbance in Marine Mammals: A Review. -*Frontiers in Marine Science,* **7**.

BOST, C. A., COTTÉ, C., TERRAY, P., BARBRAUD, C., BON, C., DELORD, K., GIMENEZ, O., HANDRICH, Y., NAITO, Y., GUINET, C. and WEIMERSKIRCH, H. 2015. Large-scale climatic anomalies affect marine predator foraging behaviour and demography. -*Nature Communications,* **6**: 8220.

BOYD, C., GRÜNBAUM, D., HUNT JR, G. L., PUNT, A. E., WEIMERSKIRCH, H. and BERTRAND, S. 2017. Effects of variation in the abundance and distribution of prey on the foraging success of central place foragers. -*Journal of Applied Ecology,* **54**: 1362-1372.

BUCKINGHAM, L., BOGDANOVA, M. I., GREEN, J. A., DUNN, R. E., WANLESS, S., BENNETT, S., BEVAN, R. M., CALL, A., CANHAM, M., CORSE, C. J., HARRIS, M. P., HEWARD, C. J., JARDINE, D. C., LENNON, J., PARNABY, D., REDFERN, C. P. F., SCOTT, L., SWANN, R. L., WARD, R. M., WESTON, E. D., FURNESS, R. W. and DAUNT, F. 2022. Interspecific variation in non-breeding aggregation: a multi-colony tracking study of two sympatric seabirds. -*Marine Ecology Progress Series,* **684**: 181-197.

BUCKINGHAM, L., DAUNT, F., BOGDANOVA, M. I., FURNESS, R. W., BENNETT, S., DUCKWORTH, J., DUNN, R. E., WANLESS, S., HARRIS, M. P., JARDINE, D. C., NEWELL, M. A., WARD, R. M., WESTON, E. D. and GREEN, J. A. 2023. Energetic synchrony throughout the non-breeding season in common guillemots from four colonies. -*Journal of Avian Biology,* **2023**: e03018.

CAIRNS, D. K. 1987. Seabirds as Indicators of Marine Food Supplies. -*Biological Oceanography,* **5**: 261 - 271.

CALENGE, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. -*Ecological Modelling,* **197**: 516-519.

CARBONERAS, C., CHRISTIE, D. A. and GARCIA, E. F. J. 2020. Red-throated Loon (G*avia stellata)*. In: HOYO, J., ELLIOTT, A., SARGATAL, J., CHRISTIE, D. A. and DE JUANA, E. (eds.) *Handbook of the Birds of the World Alive.* Lynx Edicions, Barcelona.

CARPENTER-KLING, T., PISTORIUS, P., REISINGER, R., CHEREL, Y. and CONNAN, M. 2020. A critical assessment of marine predator isoscapes within the southern Indian Ocean. -*Movement Ecology,* **8**: 29.

CATALÁN, I. A., AUCH, D., KAMERMANS, P., MORALES-NIN, B., ANGELOPOULOS, N. V., REGLERO, P., SANDERSFELD, T. and PECK, M. A. 2019. Critically examining the knowledge base required to mechanistically project climate impacts: A case study of Europe's fish and shellfish. -*Fish and Fisheries,* **20**: 501-517.

CEIA, F. R., CHEREL, Y., PAIVA, V. H. and RAMOS, J. A. 2018. Stable isotope dynamics (δ13C and δ15N) in neritic and oceanic waters of the North Atlantic inferred From GPS-tracked Cory's shearwaters. -*Frontiers in Marine Science,* **5**.

CERTAIN, G. and BRETAGNOLLE, V. 2008. Monitoring seabirds population in marine ecosystem: The use of strip-transect aerial surveys. -*Remote Sensing of Environment,* **112**: 3314-3322.

CHIMIENTI, M., DESFORGES, J.-P., BEUMER, L. T., NABE-NIELSEN, J., VAN BEEST, F. M. and SCHMIDT, N. M. 2020. Energetics as common currency for integrating high resolution activity patterns into dynamic energy budget-individual based models. -*Ecological Modelling,* **434**: 109250.

CHRISTENSEN-DALSGAARD, S., MAY, R. and LORENTSEN, S.-H. 2018. Taking a trip to the shelf: Behavioral decisions are mediated by the proximity to foraging habitats in the black-legged kittiwake. -*Ecology and Evolution,* **8**: 866-878.

COOK, A. S. C. P., DADAM, D., MITCHELL, I., ROSS-SMITH, V. H. and ROBINSON, R. A. 2014. Indicators of seabird reproductive performance demonstrate the impact of commercial fisheries on seabird populations in the North Sea. -*Ecological Indicators,* **38**: 1-11.

COOKE, S. J., SACK, L., FRANKLIN, C. E., FARRELL, A. P., BEARDALL, J., WIKELSKI, M. and CHOWN, S. L. 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science†. -*Conservation Physiology,* **1**.

CROXALL, J. P., BUTCHART, S. H. M., LASCELLES, B., STATTERSFIELD, A. J., SYMES, A., TAYLOR, P. and SULLIVAN, B. 2012. Seabird conservation status, threats and priority actions: A global assessment. -*Bird Conservation International,* **22**: 1-34.

CRUZ-FLORES, M., MILITÃO, T., RAMOS, R. and GONZÁLEZ-SOLÍS, J. 2018. Using marine isoscapes to infer movements of oceanic migrants: The case of Bulwer's petrel, *Bulweria bulwerii*, in the Atlantic Ocean. -*PLOS ONE,* **13**: e0198667.

DAUNT, F., AFANASYEV, V., SILK, J. R. D. and WANLESS, S. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. -*Behavioral Ecology and Sociobiology,* **59**: 381-388.

DESCAMPS, S., RAMÍREZ, F., BENJAMINSEN, S., ANKER-NILSSEN, T., BARRETT, R. T., BURR, Z., CHRISTENSEN-DALSGAARD, S., ERIKSTAD, K.-E., IRONS, D. B., LORENTSEN, S.-H., MALLORY, M. L., ROBERTSON, G. J., REIERTSEN, T. K., STRØM, H., VARPE, Ø. and LAVERGNE, S. 2019. Diverging phenological responses of Arctic seabirds to an earlier spring. -*Global Change Biology,* **25**: 4081-4091.

DESPREZ, M., CHRISTOPHE, B., HENRI, W., KARINE, D. and STÉPHANIE, J. 2018. Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. -*Functional ecology,* **32**: 2040-2053.

DIERSCHKE, V., FURNESS, R. W. and GARTHE, S. 2016. Review: Seabirds and offshore wind farms in European waters: Avoidance and attraction. -*Biological Conservation,* **202**: 59-68.

DIERSCHKE, V., FURNESS, R. W., GRAY, C. E., PETERSEN, I. K., SCHMUTZ, J., ZYDELIS, R. and DAUNT, F. 2017. Possible behavioural, energetic and demographic effects of displacement of red-throated divers. -*JNCC Report,* **605**.

DIVOKY, G. J., BROWN, E. and ELLIOTT, K. H. 2021. Reduced seasonal sea ice and increased sea surface temperature change prey and foraging behaviour in an ice-obligate Arctic seabird, Mandt’s black guillemot (Cepphus grylle mandtii). -*Polar Biology,* **44**: 701-715.

DORSCH, M., BURGER, C., HEINÄNEN, S., KLEINSCHMIDT, B., MORKŪNAS, J., NEHLS, G., QUILLFELDT, P., SCHUBERT, A. and R., Ž. 2019. German tracking study of seabirds in areas of planned offshore wind farms at the example of divers. -*Final report on the joint project DIVER, FKZ 0325747A/B, funded by the Federal Ministry of Economics and Energy (BMWi) on the basis of a decision by the German Bundestag.*

DREWITT, A. L. and LANGSTON, R. H. W. 2006. Assessing the impacts of wind farms on birds. -*Ibis,* **148**: 29-42.

DUCKWORTH, J., GREEN, J., DAUNT, F., JOHNSON, L., LEHIKOINEN, P., OKILL, D., PETERSEN, A., PETERSEN, I. K., VÄISÄNEN, R., WILLIAMS, J., WILLIAMS, S. and O’BRIEN, S. 2020. Red-throated diver energetics project: preliminary results from 2018/19. -*JNCC Report,* **638**.

DUCKWORTH, J., O'BRIEN, S., PETERSEN, I. K., PETERSEN, A., BENEDIKTSSON, G., JOHNSON, L., LEHIKOINEN, P., OKILL, D., VÄISÄNEN, R., WILLIAMS, J., WILLIAMS, S., DAUNT, F. and GREEN, J. A. 2021. Spatial and temporal variation in foraging of breeding red-throated divers. -*Journal of Avian Biology,* **52**.

DUNN, R. E., GREEN, J. A., WANLESS, S., HARRIS, M. P., NEWELL, MARK A., BOGDANOVA, M. I., HORSWILL, C., DAUNT, F. and MATTHIOPOULOS, J. 2022. Modelling and mapping how common guillemots balance their energy budgets over a full annual cycle. -*Functional Ecology,* **00**: 1-15.

DUNN, R. E., WANLESS, S., DAUNT, F., HARRIS, M. P. and GREEN, J. A. 2020. A year in the life of a North Atlantic seabird: behavioural and energetic adjustments during the annual cycle. -*Scientific Reports,* **10**: 5993.

DUNN, R. E., WHITE, C. R. and GREEN, J. A. 2018. A model to estimate seabird field metabolic rates. -*Biology Letters,* **14**: 20180190.

ELLIS, H. I. and GABRIELSEN, G. W. 2002. *Energetics of free-ranging seabirds,* Boca Raton, FL, CRC Press.

ERIKSSON, M. O. G. and SUNDBERG, P. 1991. The choice of fishing lakes by the Red-throated Diver *Gavia stellata* and Black-throated Diver *G. arctica* during the breeding season in south-west Sweden. -*Bird Study,* **38**: 135-144.

FAYET, A. L., FREEMAN, R., SHOJI, A., KIRK, H. L., PADGET, O., PERRINS, C. M. and GUILFORD, T. 2016. Carry-over effects on the annual cycle of a migratory seabird: An experimental study. -*Journal of Animal Ecology,* **85**: 1516-1527.

FORT, J., PORTER, W. P. and GRÉMILLET, D. 2011. Energetic modelling: A comparison of the different approaches used in seabirds. -*Comparative Biochemistry and Physiology, Part A,* **158**: 358-365.

FOX, A. D., DESHOLM, M., KAHLERT, J., CHRISTENSEN, T. K. and PETERSEN, I. K. 2006. Information needs to support environmental impact assessment of the effects of European marine offshore wind farms on birds. -*Ibis,* **148**: 129-144.

FRANCO, B. C., DEFEO, O., PIOLA, A. R., BARREIRO, M., YANG, H., ORTEGA, L., GIANELLI, I., CASTELLO, J. P., VERA, C., BURATTI, C., PÁJARO, M., PEZZI, L. P. and MÖLLER, O. O. 2020. Climate change impacts on the atmospheric circulation, ocean, and fisheries in the southwest South Atlantic Ocean: a review. -*Climatic Change,* **162**: 2359-2377.

FREDERIKSEN, M., MOE, B., DAUNT, F., PHILLIPS, R. A., BARRETT, R. T., BOGDANOVA, M. I., BOULINIER, T., CHARDINE, J. W., CHASTEL, O., CHIVERS, L. S., CHRISTENSEN-DALSGAARD, S., CLÉMENT-CHASTEL, C., COLHOUN, K., FREEMAN, R., GASTON, A. J., GONZÁLEZ-SOLÍS, J., GOUTTE, A., GRÉMILLET, D., GUILFORD, T., JENSEN, G. H., KRASNOV, Y., LORENTSEN, S.-H., MALLORY, M. L., NEWELL, M., OLSEN, B., SHAW, D., STEEN, H., STRØM, H., SYSTAD, G. H., THÓRARINSSON, T. L. and ANKER-NILSSEN, T. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. -*Diversity and Distributions,* **18**: 530-542.

FROST, T., AUSTIN, G., HEARN, R., MCAVOY, S., ROBINSON, A., STROUD, D., WOODWARD, I., WOTTON, S. and ALLEN, R. 2019. Population estimates of wintering waterbirds in Great Britain. -*British Birds,* **112**: 130-145.

FUDICKAR, A., JAHN, A. and KETTERSON, E. 2021. Animal migration: An overview of one of nature's great spectacles. -*Annual Review of Ecology, Evolution, and Systematics,* **52**: 479-497.

FURNESS, R. W. and CAMPHUYSEN, K. 1997. Seabirds as monitors of the marine environment. -*ICES Journal of Marine Science,* **54**: 726-737.

FURNESS, R. W., WADE, H. M. and MASDEN, E. A. 2013. Assessing vulnerability of marine bird populations to offshore wind farms. -*Journal of Environmental Management,* **119**: 56-66.

GATT, M. C., GRANADEIRO, J. P. and CATRY, P. 2021. Migrants and residents of a long-lived seabird differ in their behavioural response to a stressor. -*Journal of Avian Biology,* **52**.

GEARY, W. L., BODE, M., DOHERTY, T. S., FULTON, E. A., NIMMO, D. G., TULLOCH, A. I. T., TULLOCH, V. J. D. and RITCHIE, E. G. 2020. A guide to ecosystem models and their environmental applications. -*Nature Ecology & Evolution,* **4**: 1459-1471.

GÓMEZ-DÍAZ, E. and GONZÁLEZ-SOLÍS, J. 2007. GEOGRAPHIC ASSIGNMENT OF SEABIRDS TO THEIR ORIGIN: COMBINING MORPHOLOGIC, GENETIC, AND BIOGEOCHEMICAL ANALYSES. -*Ecological Applications,* **17**: 1484-1498.

GÓMEZ, C., LARSEN, T., POPP, B., HOBSON, K. A. and CADENA, C. D. 2018. Assessing seasonal changes in animal diets with stable-isotope analysis of amino acids: A migratory boreal songbird switches diet over its annual cycle. -*Oecologia,* **187**: 1-13.

GÓMEZ LAICH, A., WILSON, R. P., QUINTANA, F. and SHEPARD, E. L. C. 2008. Identification of imperial cormorant Phalacrocorax atriceps behaviour using accelerometers. -*Endangered Species Research,* **10**: 29-37.

GROVES, D. J., CONANT, B., J., K. R., J.I., H. and J.G., K. 1996. Status and Trends of Loon Populations Summering in Alaska, 1971-1993. -*The Condor,* **98**: 189.

GUSE, N., GARTHE, S. and SCHIRMEISTER, B. 2009. Diet of red-throated divers *Gavia stellata* reflects the seasonal availability of Atlantic herring *Clupea harengus* in the southwestern Baltic Sea. -*Journal of Sea Research,* **62**: 268-275.

HALPIN, L. R., ROSS, J. D., RAMOS, R., MOTT, R., CARLILE, N., GOLDING, N., REYES-GONZÁLEZ, J. M., MILITÃO, T., DE FELIPE, F., ZAJKOVÁ, Z., CRUZ-FLORES, M., SALDANHA, S., MORERA-PUJOL, V., NAVARRO-HERRERO, L., ZANGO, L., GONZÁLEZ-SOLÍS, J. and CLARKE, R. H. 2021. Double-tagging scores of seabirds reveals that light-level geolocator accuracy is limited by species idiosyncrasies and equatorial solar profiles. -*Methods in Ecology and Evolution,* **12**: 2243-2255.

HARRISON, X. A., BLOUNT, J. D., INGER, R., NORRIS, D. R. and BEARHOP, S. 2011. Carry-over effects as drivers of fitness differences in animals. -*Journal of Animal Ecology,* **80**: 4-18.

HAYWOOD, J. C., FULLER, W. J., GODLEY, B. J., SHUTLER, J. D., WIDDICOMBE, S. and BRODERICK, A. C. 2019. Global review and inventory: how stable isotopes are helping us understand ecology and inform conservation of marine turtles. -*Marine Ecology Progress Series,* **613**: 217-245.

HAZEN, E. L., ABRAHMS, B., BRODIE, S., CARROLL, G., JACOX, M. G., SAVOCA, M. S., SCALES, K. L., SYDEMAN, W. J. and BOGRAD, S. J. 2019. Marine top predators as climate and ecosystem sentinels. -*Frontiers in Ecology and the Environment,* **17**: 565-574.

HEINÄNEN, S., ŽYDELIS, R., KLEINSCHMIDT, B., DORSCH, M., BURGER, C., MORKŪNAS, J., QUILLFELDT, P. and NEHLS, G. 2020. Satellite telemetry and digital aerial surveys show strong displacement of red-throated divers (*Gavia stellata*) from offshore wind farms. -*Marine Environmental Research*: 104989.

HIDEF. 2016. Sensitivity of offshore seabird concentrations to oil pollution around the United Kingdom: Report to Oil & Gas UK. *Report to Oil & Gas UK*.

HOBSON, K. A., PIATT, J. F. and PITOCCHELLI, J. 1994. Using stable isotopes to determine seabird trophic relationships. -*Journal of Animal Ecology,* **63**: 786-798.

HOVICK, T. J., ELMORE, R. D., DAHLGREN, D. K., FUHLENDORF, S. D. and ENGLE, D. M. 2014. REVIEW: Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. -*Journal of Applied Ecology,* **51**: 1680-1689.

HUMPHRIES, M. M., THOMAS, D. W. and KRAMER, D. L. 2003. The role of energy availability in mammalian hibernation: A cost-benefit approach. -*Physiological and Biochemical Zoology,* **76**: 165-179.

HUNT, G. L., DRINKWATER, K. F., ARRIGO, K., BERGE, J., DALY, K. L., DANIELSON, S., DAASE, M., HOP, H., ISLA, E., KARNOVSKY, N., LAIDRE, K., MUETER, F. J., MURPHY, E. J., RENAUD, P. E., SMITH, W. O., TRATHAN, P., TURNER, J. and WOLF-GLADROW, D. 2016. Advection in polar and sub-polar environments: Impacts on high latitude marine ecosystems. -*Progress in Oceanography,* **149**: 40-81.

INGER, R. and BEARHOP, S. 2008. Applications of stable isotope analyses to avian ecology. -*Ibis,* **150**: 447-461.

IRWIN, C., SCOTT, M., S., HUMPHRIES, G. and WEBB, A. 2019. HiDef report to Natural England - Digital video aerial surveys of red-throated diver in the Outer Thames Estuary Special Protection Area 2018. *Natural England Commissioned Reports*.

JAEGER, A., LECOMTE, V., WEIMERSKIRCH, H., RICHARD, P. and CHEREL, Y. 2010. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. -*Rapid Communications in Mass Spectrometry : RCM,* **24**: 3456-60.

KARPOUZI, V. S., WATSON, R. and PAULY, D. 2007. Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. -*Marine Ecology Progress Series,* **343**: 87-99.

KELSEY, E. C., FELIS, J. J., CZAPANSKIY, M., PEREKSTA, D. M. and ADAMS, J. 2018. Collision and displacement vulnerability to offshore wind energy infrastructure among marine birds of the Pacific Outer Continental Shelf. -*Journal of Environmental Management,* **227**: 229-247.

KIRKPATRICK, L., GRAHAM, J., MCGREGOR, S., MUNRO, L., SCOARIZE, M. and PARK, K. 2018. Flexible foraging strategies in Pipistrellus pygmaeus in response to abundant but ephemeral prey. -*PLOS ONE,* **13**: e0204511.

KJELLÉN, N. 1994. Moult in relation to migration in birds—a review. -*Ornis Svecica,* **4**: 1-24.

KLEINSCHMIDT, B., BURGER, C., DORSCH, M., NEHLS, G., HEINÄNEN, S., MORKŪNAS, J., ŽYDELIS, R., MOORHOUSE-GANN, R. J., HIPPERSON, H., SYMONDSON, W. O. C. and QUILLFELDT, P. 2019. The diet of red-throated divers (*Gavia stellata*) overwintering in the German Bight (North Sea) analysed using molecular diagnostics. -*Marine Biology,* **166**: 77.

KÜHL, H. S., BOWLER, D. E., BÖSCH, L., BRUELHEIDE, H., DAUBER, J., EICHENBERG, D., EISENHAUER, N., FERNÁNDEZ, N., GUERRA, C. A., HENLE, K., HERBINGER, I., ISAAC, N. J. B., JANSEN, F., KÖNIG-RIES, B., KÜHN, I., NILSEN, E. B., PE'ER, G., RICHTER, A., SCHULTE, R., SETTELE, J., VAN DAM, N. M., VOIGT, M., WÄGELE, W. J., WIRTH, C. and BONN, A. 2020. Effective Biodiversity Monitoring Needs a Culture of Integration. -*One Earth,* **3**: 462-474.

LAMB, J. S., SATGÉ, Y. G. and JODICE, P. G. R. 2017. Influence of density-dependent competition on foraging and migratory behavior of a subtropical colonial seabird. -*Ecology and Evolution,* **7**: 6469-6481.

LAURENSON, K., ATKINS, K., CLARK, B., MORGAN, G., MORGAN, L. and VOTIER, S. 2021. Gannet *Morus Bassanus* ring recoveries suggest shorter migrations than geolocator tracking, but indicate no long-term change in migration distances. -*Bird Study,* **68**: 1-8.

LEWISON, R., ORO, D., GODLEY, B., UNDERHILL, L., BEARHOP, S., WILSON, R. P., AINLEY, D., ARCOS, J. M., BOERSMA, P. D., BORBOROGLU, P. G., BOULINIER, T., FREDERIKSEN, M., GENOVART, M., GONZÁLEZ-SOLÍS, J., GREEN, J. A., GRÉMILLET, D., HAMER, K. C., HILTON, G. M., HYRENBACH, K. D., MARTÍNEZ-ABRAÍN, A., MONTEVECCHI, W. A., PHILLIPS, R. A., RYAN, P. G., SAGAR, P., SYDEMAN, W. J., WANLESS, S., WATANUKI, Y., WEIMERSKIRCH, H. and YORIO, P. 2012. Research priorities for seabirds: improving conservation and management in the 21st century. -*Endangered Species Research,* **17**: 93-121.

LISOVSKI, S., HEWSON, C. M., KLAASSEN, R. H. G., KORNER-NIEVERGELT, F., KRISTENSEN, M. W. and HAHN, S. 2012. Geolocation by light: Accuracy and precision affected by environmental factors. -*Methods in Ecology and Evolution,* **3**: 603-612.

MAGOZZI, S., YOOL, A., VANDER ZANDEN, H. B., WUNDER, M. B. and TRUEMAN, C. N. 2017. Using ocean models to predict spatial and temporal variation in marine carbon isotopes. -*Ecosphere,* **8**: e01763.

MASDEN, E. A., HAYDON, D. T., FOX, A. D. and FURNESS, R. W. 2010. Barriers to movement: Modelling energetic costs of avoiding marine wind farms amongst breeding seabirds. - *Marine Pollution Bulletin,* **60**: 1085-1091.

MASDEN, E. A., HAYDON, D. T., FURNESS, R. W., FOX, A. D., DESHOLM, M. and BULLMAN, R. 2009. Barriers to movement: Impacts of wind farms on migrating birds. -*ICES Journal of Marine Science,* **66**: 746-753.

MAZARIS, A. D., KALLIMANIS, A., GISSI, E., PIPITONE, C., DANOVARO, R., CLAUDET, J., RILOV, G., BADALAMENTI, F., STELZENMÜLLER, V., THIAULT, L., BENEDETTI-CECCHI, L., GORIUP, P., KATSANEVAKIS, S. and FRASCHETTI, S. 2019. Threats to marine biodiversity in European protected areas. -*Science of The Total Environment,* **677**: 418-426.

MCCLOSKEY, S. E., UHER-KOCH, B. D., SCHMUTZ, J. A. and FONDELL, T. F. 2018. International migration patterns of red-throated loons (*Gavia stellata*) from four breeding populations in Alaska. -*PLoS ONE,* **13**: 1-15.

MERKEL, B., PHILLIPS, R. A., DESCAMPS, S., YOCCOZ, N. G., MOE, B. and STRØM, H. 2016. A probabilistic algorithm to process geolocation data. -*Movement Ecology,* **4**: 26.

MEYER, H. and PEBESMA, E. 2021. Predicting into unknown space? Estimating the area of applicability of spatial prediction models. -*Methods in Ecology and Evolution,* **12**: 1620-1633.

MIKAMI, K., KAZAMA, K., KAZAMA, M. T. and WATANUKI, Y. 2022. Mapping the collision risk between two gull species and offshore wind turbines: Modelling and validation. -*Journal of Environmental Management,* **316**: 115220.

MORKŪNĖ, R., LESUTIENĖ, J., BARISEVIČIŪTĖ, R., MORKŪNAS, J. and GASIŪNAITĖ, Z. R. 2016. Food sources of wintering piscivorous waterbirds in coastal waters: A triple stable isotope approach for the southeastern Baltic Sea. -*Estuarine, Coastal and Shelf Science,* **171**: 41-50.

NATURAL ENGLAND. 2010. Natural England’s Response to London Array OWF Year 3 Ornithological Monitoring Report. *THE INFRASTRUCTURE PLANNING (EXAMINATION PROCEDURE) RULES - East Anglia ONE North Offshore Wind Farm.* Natural England.

NORRIS, D. R. 2005. Carry-over effects and habitat quality in migratory populations. -*Oikos,* **109**: 178-186.

NUMMI, P., VÄÄNÄNEN, V., PAKARINEN, R. and PIENMUNNE, E. 2013. The Red-throated Diver (*Gavia stellata*) in human-disturbed habitats - building up a local population with the aid of artificial rafts. -*Ornis Fennica,* **90**: 16-22.

O'BRIEN, S., RUFFINO, L., JOHNSON, L., LEHIKOINEN, P., OKILL, D., PETERSEN, A., PETERSEN, I. K., VÄISÄNEN, R., WILLIAMS, J. and WILLIAMS, S. 2020. Red-throated diver energetics project: 2019 field season report. -*JNCC Report,* **637**.

O'BRIEN, S. H., WILSON, L. J., WEBB, A. and CRANSWICK, P. A. 2010. Revised estimate of numbers of wintering Red-throated Divers Gavia stellata in Great Britain. -*Bird Study,* **55**: 152-160.

O'BRIEN, S., RUFFINO, L., LEHIKOINEN, P., JOHNSON, L., LEWIS, M., PETERSEN, A., PETERSEN, I. K., OKILL, D., VÄISÄNEN, R., WILLIAMS, J. and WILLIAMS, S. 2018. Red-Throated Diver Energetics Project - 2018 Field Season Report. *JNCC Report No. 627.* JNCC, JNCC, Peterborough.

O'BRIEN, S. H., WEBB, A., BREWER, M. J. and REID, J. B. 2012. Use of kernel density estimation and maximum curvature to set Marine Protected Area boundaries: Identifying a Special Protection Area for wintering red-throated divers in the UK. -*Biological Conservation,* **156**: 15-21.

OKILL, J. D. 1994. Ringing recoveries of red-throated divers *Gavia stellata* in Britain and Ireland. -*Ringing & Migration,* **15**: 107-118.

PARUK, D. J. 2008. Nocturnal Behavior of the Common Loon, *Gavia immer*. -*Canadian Field-Naturalist,* **122**.

PARUK, J. D., CHICKERING, M. D., LONG, D., IV, UHER-KOCH, H., EAST, A., POLESCHOOK, D., GUMM, V., HANSON, W., ADAMS, E. M., KOVACH, K. A. and EVERS, D. C. 2015. Winter site fidelity and winter movements in Common Loons (*Gavia immer*) across North America. -*The Condor,* **117**: 485-493.

PEREIRA, J. M., PAIVA, V. H., CEIA, F. R. and RAMOS, J. A. 2020. Facing extremes: Cory's shearwaters adjust their foraging behaviour differently in response to contrasting phases of North Atlantic Oscillation. -*Regional Environmental Change,* **20**: 77.

PETTORELLI, N., LAURANCE, W. F., O'BRIEN, T. G., WEGMANN, M., NAGENDRA, H. and TURNER, W. 2014. Satellite remote sensing for applied ecologists: opportunities and challenges. -*Journal of Applied Ecology,* **51**: 839-848.

PIERSMA, T. 2002. Energetic Bottlenecks and Other Design Constraints in Avian Annual Cycles. -*Integrative and Comparative Biology,* **42**: 51-67.

POLAK, M. and CIACH, M. 2007. Behaviour of black-throated diver *Gavia arctica* and red-throated diver *Gavia stellata* during autumn migration stopover. -*Ornis Svecica,* **17**: 90-94.

POLLET, I. L., RONCONI, R. A., LEONARD, M. L. and SHUTLER, D. 2019. Migration routes and stopover areas of leach's storm petrels *Oceanodroma leucorhoa*. -*Marine Ornithology,* **47**: 55-65.

PORTER, W. P. and KEARNEY, M. 2009. Size, shape, and the thermal niche of endotherms. -*Proceedings of the National Academy of Sciences,* **106**: 19666-19672.

PRAKASH, S. 2021. Impact of Climate change on Aquatic Ecosystem and its Biodiversity: An overview. -*International Journal of Biological Innovations,* **3**.

QI, H., COPLEN, T. B., MROCZKOWSKI, S. J., BRAND, W. A., BRANDES, L., GEILMANN, H. and SCHIMMELMANN, A. 2016. A new organic reference material, l-glutamic acid, USGS41a, for δ13C and δ15N measurements − a replacement for USGS41. -*Rapid Communications in Mass Spectrometry,* **30**: 859-866.

RHODES, J. R., ARMSWORTH, P. R., IACONA, G., SHAH, P., GORDON, A., WILSON, K. A., RUNTING, R. K. and BRYAN, B. A. 2022. Flexible conservation decisions for climate adaptation. -*One Earth,* **5**: 622-634.

RICHARDS, C., COOKE, R. S. C. and BATES, A. E. 2021. Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. -*Global Ecology and Biogeography,* **30**: 973-986.

RISHWORTH, G. M., TREMBLAY, Y., GREEN, D. B. and PISTORIUS, P. A. 2014. An automated approach towards measuring time-activity budgets in colonial seabirds. -*Methods in Ecology and Evolution,* **5**: 854-863.

RIZZOLO, D. J., SCHMUTZ, J., A., MCCLOSKEY, S. E. and FONDELL, T. F. 2014. Factors influencing nest survival and productivity of red-throated Loons (*Gavia stellata*) in Alaska. -*The Condor*: 574-587.

RIZZOLO, D. J. and SCHMUTZ, J. A. 2007. Egg Flotation Estimates Nest Age for Pacific and Red-Throated Loons. -*Waterbirds: The International Journal of Waterbird Biology*: 207-213.

ROGERS, L. A. and DOUGHERTY, A. B. 2019. Effects of climate and demography on reproductive phenology of a harvested marine fish population. -*Global Change Biology,* **25**: 708-720.

SCHWEMMER, P., MENDEL, B., SONNTAG, N., DIERSCHKE, V. and GARTHE, S. 2011. Effects of ship traffic on seabirds in offshore waters: implications for marine conservation and spatial planning. -*Ecological Applications,* **21**: 1851-1860.

SEARLE, K. R., MOBBS, D. C., BUTLER, A., FURNESS, R. W., TRINDER, M. N. and DAUNT, F. 2018. Finding out the Fate of Displaced Birds. *Scottish Marine and Freshwater Science*, pp. 149.

SHACKELFORD, N., STANDISH, R. J., RIPPLE, W. and STARZOMSKI, B. M. 2018. Threats to biodiversity from cumulative human impacts in one of North America's last wildlife frontiers. -*Conservation Biology,* **32**: 672-684.

SHEN, M., CHEN, J., ZHUAN, M., CHEN, H., XU, C.-Y. and XIONG, L. 2018. Estimating uncertainty and its temporal variation related to global climate models in quantifying climate change impacts on hydrology. -*Journal of Hydrology,* **556**: 10-24.

SKOV, H., HEINÄNEN, S., LOHIER, S., THAXTER, C. B., WILLIAMS, A. E. and BANKS, A. N. 2016. Real-time species distribution models for conservation and management of natural resources in marine environments. -*Marine Ecology Progress Series,* **542**: 221-234.

SMITH, R. J., BENNUN, L., BROOKS, T. M., BUTCHART, S. H. M., CUTTELOD, A., DI MARCO, M., FERRIER, S., FISHPOOL, L. D. C., JOPPA, L., JUFFE-BIGNOLI, D., KNIGHT, A. T., LAMOREUX, J. F., LANGHAMMER, P., POSSINGHAM, H. P., RONDININI, C., VISCONTI, P., WATSON, J. E. M., WOODLEY, S., BOITANI, L., BURGESS, N. D., DE SILVA, N., DUDLEY, N., FIVAZ, F., GAME, E. T., GROVES, C., LÖTTER, M., MCGOWAN, J., PLUMPTRE, A. J., REBELO, A. G., RODRIGUEZ, J. P. and SCARAMUZZA, C. A. D. M. 2019. Synergies between the key biodiversity area and systematic conservation planning approaches. -*Conservation Letters,* **12**: e12625.

SOLOVYEVA, D., PARUK, J., TASH, J., VARTANAYN, S., DANILOV, G., POSPEKHOV, V. and EVERS, D. 2017. Post-breeding densities, population sizes and lake size partitioning of loon species in western Chukotka, Russia. -*Contemporary Problems of Ecology,* **10**: 621-631.

ST JOHN GLEW, K., WANLESS, S., HARRIS, M. P., DAUNT, F., ERIKSTAD, K. E., STRØM, H. and TRUEMAN, C. N. 2018. Moult location and diet of auks in the North Sea inferred from coupled light-based and isotope-based geolocation. -*Marine Ecology Progress Series,* **599**: 239-251.

STENHOUSE, I. J., BERLIN, A. M., GILBERT, A. T., GOODALE, M. W., GRAY, C. E., MONTEVECCHI, W. A., SAVOY, L. and SPIEGEL, C. S. 2020. Assessing the exposure of three diving bird species to offshore wind areas on the U.S. Atlantic Outer Continental Shelf using satellite telemetry. -*Diversity and Distributions,* **26**: 1703-1714.

STRØM, H., DESCAMPS, S., EKKER, M., FAUCHALD, P. and MOE, B. 2021. Tracking the movements of North Atlantic seabirds: Steps towards a better understanding of population dynamics and marine ecosystem conservation. -*Marine Ecology Progress Series,* **676**: 97-116.

THOMPSON, D. L., JOHNSON, L., WILLIAMS, J. and LEHIKOINEN, P. 2022. Red-throated diver energetics project: 2021 field season report. *JNCC Report*, JNCC Peterborough.

TOMLINSON, S., ARNALL, S. G., MUNN, A., BRADSHAW, S. D., MALONEY, S. K., DIXON, K. W. and DIDHAM, R. K. 2014. Applications and implications of ecological energetics. -*Trends in Ecology & Evolution,* **29**: 280-290.

TRAVIS, J. M. J., DELGADO, M., BOCEDI, G., BAGUETTE, M., BARTOŃ, K., BONTE, D., BOULANGEAT, I., HODGSON, J. A., KUBISCH, A., PENTERIANI, V., SAASTAMOINEN, M., STEVENS, V. M. and BULLOCK, J. M. 2013. Dispersal and species' responses to climate change. -*Oikos,* **122**: 1532-1540.

TREMBLAY, Y., BERTRAND, S., HENRY, R. W., KAPPES, M. A., COSTA, D. P. and SHAFFER, S. A. 2009. Analytical approaches to investigating seabird–environment interactions: a review. -*Marine Ecology Progress Series,* **391**: 153-163.

TREMBLAY, Y., CHEREL, Y., OREMUS, M., TVERAA, T. and CHASTEL, O. 2003. Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds. -*Journal of Experimental Biology,* **206**: 1929-1940.

UHER-KOCH, B. D., SCHMUTZ, J. A. and WRIGHT, K. G. 2015. Nest visits and capture events affect breeding success of Yellow-billed and Pacific loons. -*Condor,* **117**: 121-129.

VOTIER, S. C., GRECIAN, W. J., PATRICK, S. and NEWTON, J. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: Results from GPS-PPT tracking, radio-tracking and stable isotope analysis. -*Marine Biology,* **158**: 355-362.

WALDENSTRÖM, J. 2016. Does the breeding performance differ between solitary and colonial breeding Red-throated Loons Gavia stellata in the core area of the Swedish population?

WARWICK-EVANS, V., ATKINSON, P. W., WALKINGTON, I. and GREEN, J. A. 2018. Predicting the impacts of wind farms on seabirds: An individual-based model. -*Journal of Applied Ecology,* **55**: 503-515.

WEISS, F., FURNESS, R. W., MCGILL, R. A. R., STRANGE, I. J., MASELLO, J. F. and QUILLFELDT, P. 2009. Trophic segregation of Falkland Islands seabirds: Insights from stable isotope analysis. -*Polar Biology,* **32**: 1753-1763.

WHITBURN, J., LINKLATER, W. and ABRAHAMSE, W. 2020. Meta-analysis of human connection to nature and proenvironmental behavior. -*Conservation Biology,* **34**: 180-193.

WHITE, A. F. and DAWSON, R. D. 2021. Can diet composition estimates using stable isotope analysis of feathers predict growth and condition in nestling mountain bluebirds (*Sialia currucoides*)? -*Ecology and Evolution,* **11**: 15273-15288.

Wildlife and Countryside Act 1981. *69.* UK Public General Acts, United Kingdom of Great Britan and Northern Ireland.

WILLIAMS, J. J. and NEWBOLD, T. 2020. Local climatic changes affect biodiversity responses to land use: A review. -*Diversity and Distributions,* **26**: 76-92.

WILSON, R. P., CULIK, B. M., KOSIOREK, P. and ADELUNG, D. 1998. The over-winter movements of a chinstrap penguin (Pygoscelis antarctica). -*Polar Record,* **34**: 107-112.

YERKES, T., HOBSON, K. A., WASSENAAR, L. I., MACLEOD, R. and COLUCCY, J. M. 2008. Stable isotopes (δD, δ13C, δ15N) reveal associations among geographic location and condition of alaskan northern pintails. -*The Journal of Wildlife Management,* **72**: 715-725.

YODA, K. 2019. Advances in bio-logging techniques and their application to study navigation in wild seabirds. -*Advanced Robotics,* **33**: 108-117.

ZUBEROGOITIA , I., ZABALA, J. and MARTÍNEZ, J. E. 2018. Moult in Birds of Prey: A Review of Current Knowledge and Future Challenges for Research. -*Ardeola,* **65**: 183-207, 25.

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Without these contributions we would still be lacking in knowledge of so many areas for this species. Projects like this are special, because they allow us to answer and explore questions in both an applied and natural history context. As I said in the discussion, I think natural history studies can have a profound effect on people’s connection to nature. I’d love to see the benefits of this reflected more in the literature as well as more mechanisms to move our work into the wider public.

There was an incredibly wide array of RTD experts who made the data collection of this project possible and I am immensely grateful for the time they put in. The work they do is vital for projects like these and the enthusiasm throughout the whole process has been uplifting. In addition to those included in the author lists of the chapters above, there were numerous other volunteers who helped across the sites. I would also like to specifically thank Aevar, Guðmundur, Logan and Moray for hosting me during my field work in Shetland and Iceland. I learnt a lot and really enjoyed my time with you all. I also really appreciated the fun detours Aevar took me on during my time in Iceland.

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Chapter 9 Supplementary materials

Chapter 3 Supplementary materials

FIGURE 9.1 CHAPTER 3, SUPPLEMENTARY FIGURE 1

Comparison of the candidate models for each of the response variables tested in this paper. ▪ *represents the variable was present in the model. Tables show the best fitting model first then the ΔAIC values in relation to the best fitting model. In cases where multiple models had ΔAIC<2, the most parsimonious model was selected.*

i. dive duration, family=gaussian

Site	Random effect for individual	K	ΔAICc
▪	▪	5	0
	▪	3	19.16

ii. log(bout duration), family=gaussian

Site	Random effect for individual	K	ΔAICc
▪	▪	5	0
	▪	3	6.06

iii. log(maximum dive depth), family=gaussian

Site	Random effect for individual	K	ΔAICc
▪	▪	5	0
	▪	3	9.49

iv. number of dives in a bout, family=gaussian

Site	Random effect for individual	K	ΔAICc
▪	▪	5	0
	▪	3	7.07

v. proportion of U-shaped dives, family=binomial

Site	Dive duration	Site : Dive duration	Random effect for individual	K	ΔAICc
▪	▪	▪	▪	7	0
▪	▪		▪	5	153.71
	▪		▪	3	161.43
▪			▪	4	2184.32
			▪	2	2191.22

vi. daily time spent foraging, family=gaussian

Site	Time	Site:Time	Random effect for individual	K	ΔAICc
▪			▪	5	0
▪	▪		▪	6	0.01
▪	▪	▪	▪	8	1.17
			▪	3	4.02
	▪		▪	4	4.39

vii. proportion of IDZ dives, family=binomial

Site	Time	Site:Time	Random effect for individual	K	ΔAICc
▪	▪	▪	▪	7	0
▪	▪		▪	5	11.03
	▪		▪	3	32.81
▪			▪	4	256.81
			▪	2	381.06

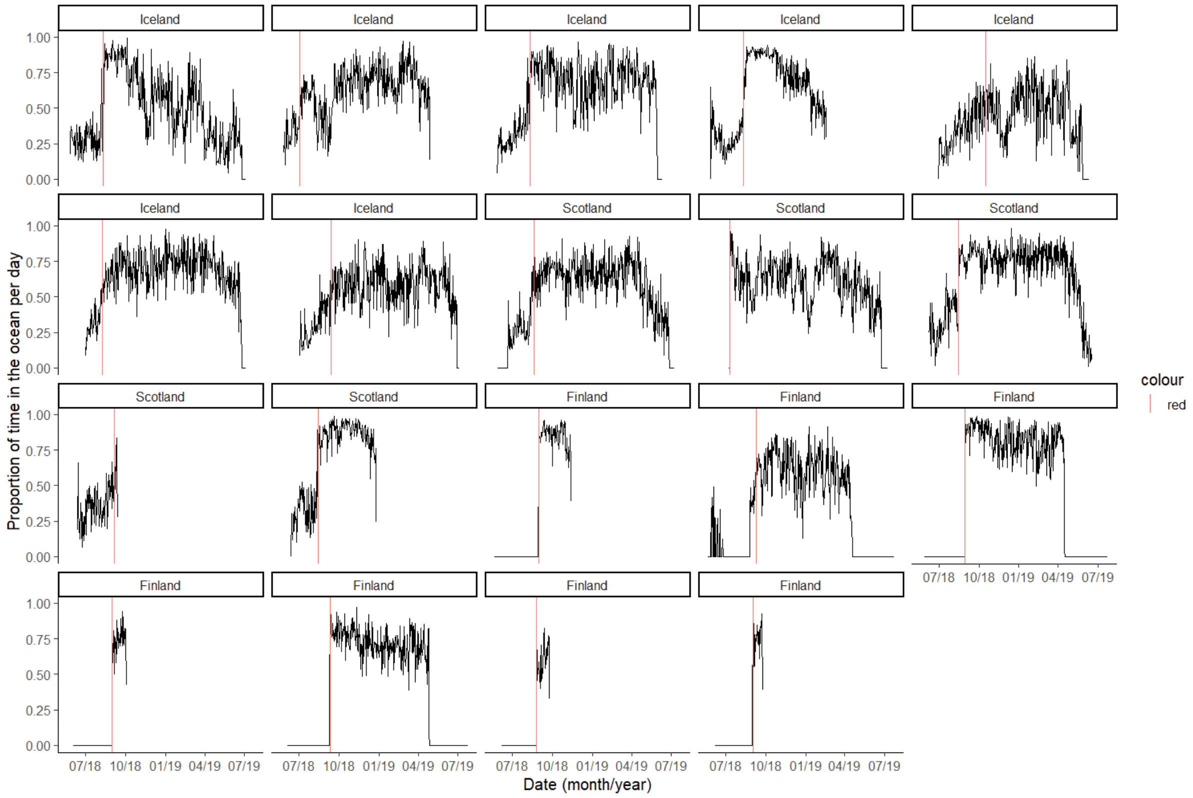

FIGURE 9.2 CHAPTER 3, SUPPLEMENTARY FIGURE 2

Proportion of time the saltwater immersion loggers were wet per day throughout the deployment period. Red lines show the estimated end of summer using a cut-off. This cut-off was defined as the first day of five continuous days with greater than 45% of the records showing immersion in saltwater.

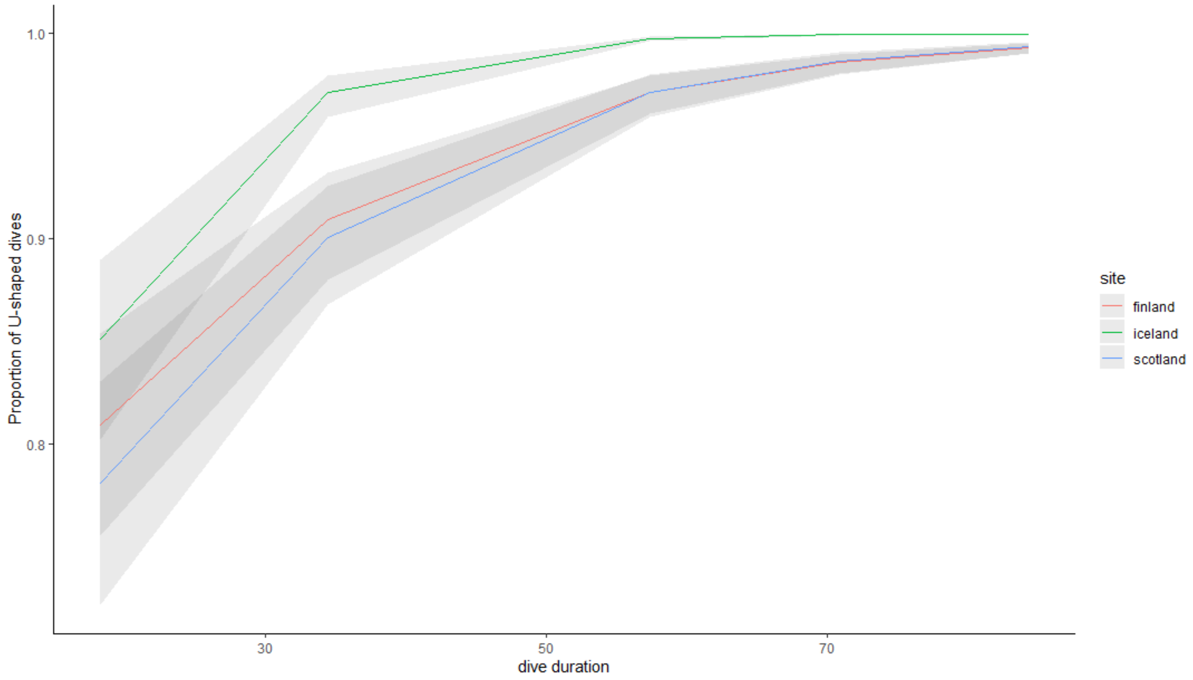

FIGURE 9.3 CHAPTER 3, SUPPLEMENTARY FIGURE 3

The model output from the best model explaining the proportion of U-shaped dives across three sites against the dive duration. The likelihood of detecting a U-shaped dive increases as dive duration increases as there are more data points per dive.

TABLE 9-1 CHAPTER 3, SUPPLEMENTARY TABLE 1

Number of red-throated divers captured and tags recovered across the three study sites.

Site	GLS and TDR deployed	Birds recaptured	GLS recovered	Working GLS tags	TDR recovered	Working TDR tags	Birds with both a TDR and GLS tags
Finland	31	10	10	7	8	8	6
Scotland	31	9	9	5	8	8	4
Iceland	12	8	8	7	7	7	6

Chapter 5 Supplementary materials

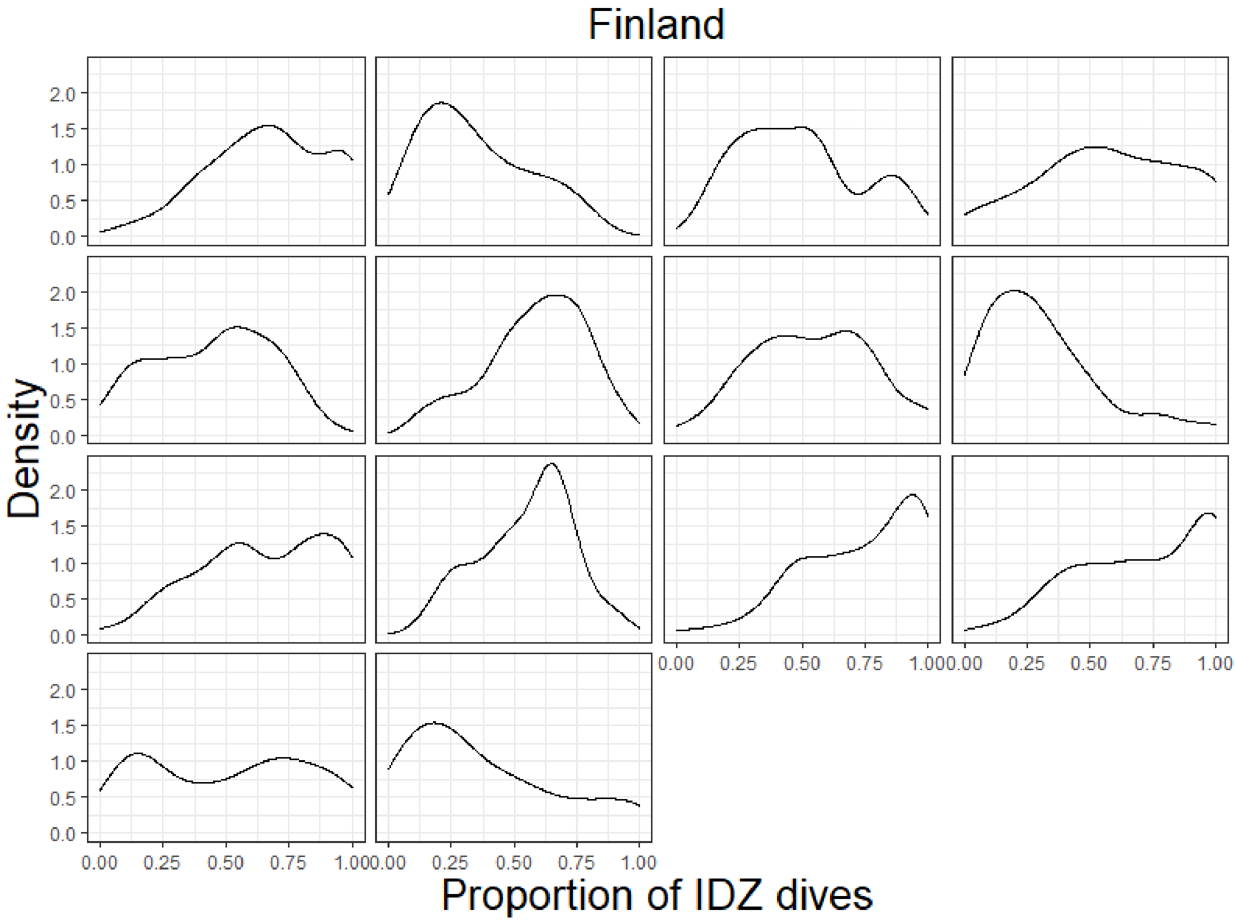

FIGURE 9.4 CHAPTER 5, SUPPLEMENTARY FIGURE 1A

A density histogram showing the proportion of IDZ dives in each bout, where the number of bouts within was over eight for the Finland population of RTD. The bandwidth is the standard deviation of the smoothing kernel for each panel, which itself is generated from a Gaussian distribution. Bouts are not weighted for the number of dives within them.

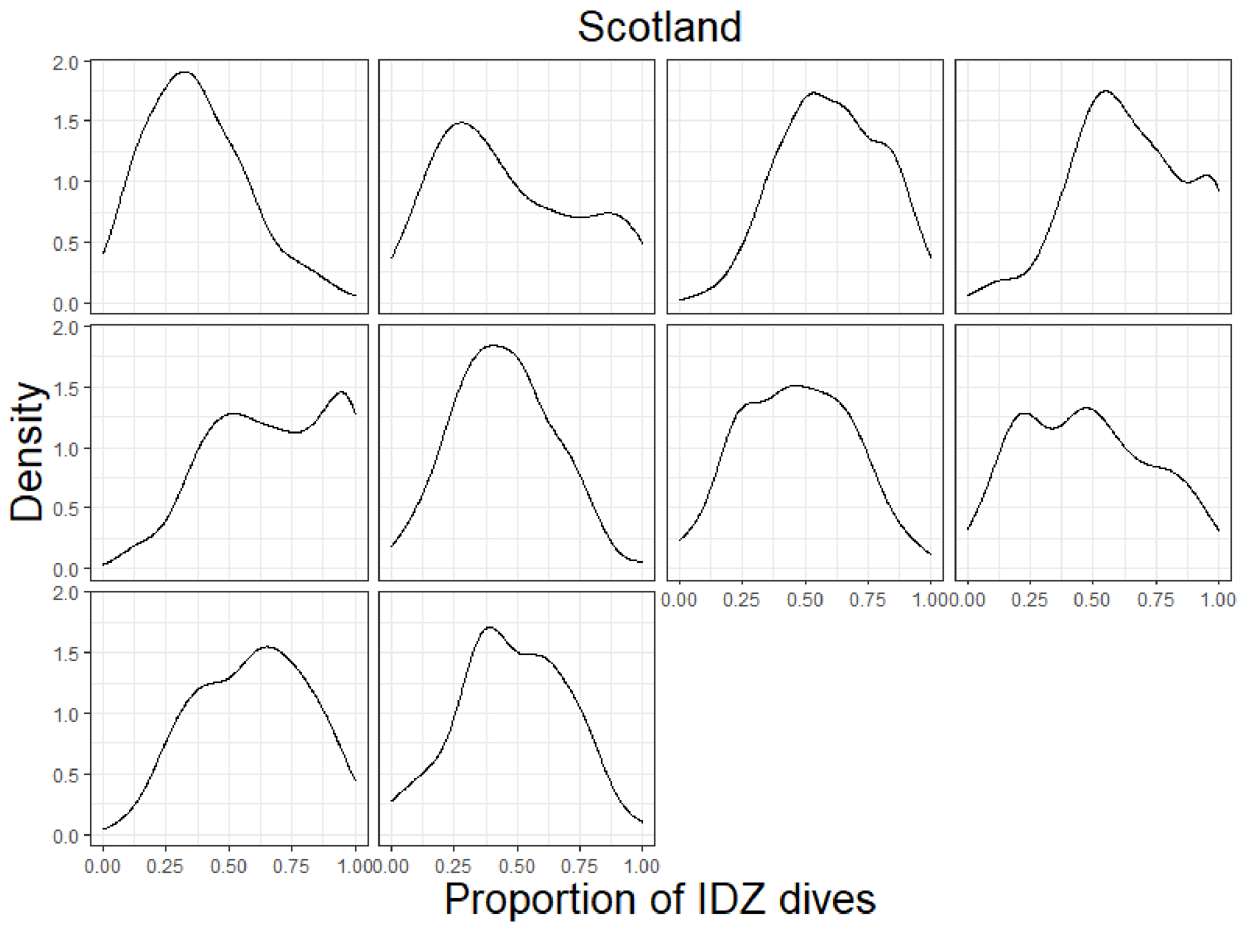

FIGURE 9.5 CHAPTER 5, SUPPLEMENTARY FIGURE 1B

A density histogram showing the proportion of IDZ dives in each bout, where the number of bouts within was over eight for the Scotland population of RTDs. The bandwidth is the standard deviation of the smoothing kernel for each panel, which itself is generated from a Gaussian distribution. Bouts are not weighted for the number of dives within them.

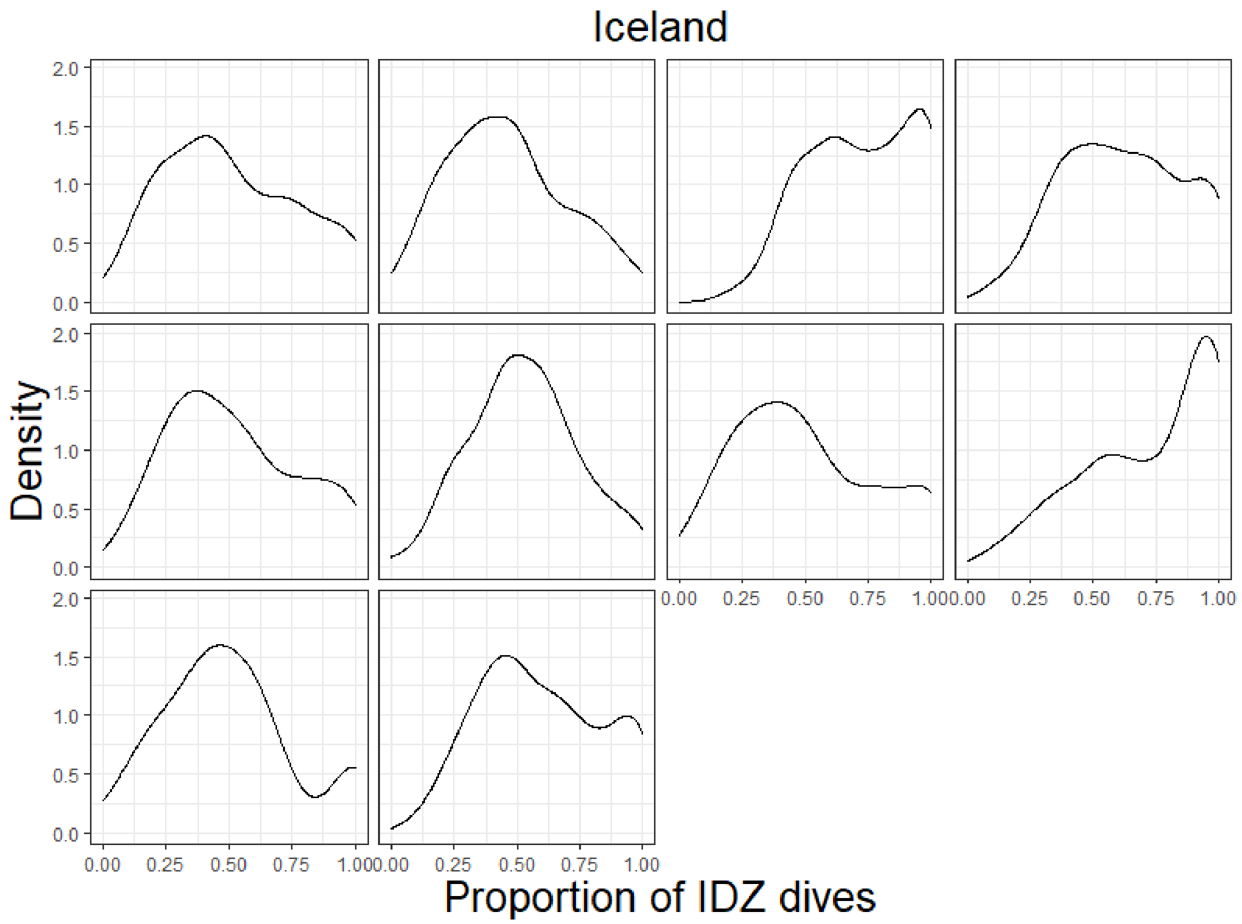

FIGURE 9.6 CHAPTER 5, SUPPLEMENTARY FIGURE 1C

A density histogram showing the proportion of IDZ dives in each bout, where the number of bouts within was over eight for the Iceland population of RTDs. The bandwidth is the standard deviation of the smoothing kernel for each panel, which itself is generated from a Gaussian distribution. Bouts are not weighted for the number of dives within them.

Chapter 6 Supplementary materials

TABLE 9-2 CHAPTER 6, SUPPLEMENTARY MATERIALS 1

Table showing the effect of changing the $T_{absolute}$ and $T_{relative}$ temperature cut-off parameters on the behaviours that are defined by them when classifying behaviours in red-throated divers. Parameters are changed by looking at increases and decreases of 25% increments from 50% to 150%. In all cases, the change to the behaviour caused by changing the cut-off value is less than 10% from the original value, demonstrating robustness of the method.

Behaviour: parameter changed	Percentage of cut-off in decision tree									
	50		75		100		125		150	
	Time	% Time	Time	% Time	Time	% Time	Time	% Time	Time	% Time
Resting: $T_{absolute}$	8.72	105	8.53	103	8.29	100	8.04	97	7.78	94
Resting: $T_{relative}$	7.73	93	8.11	98	8.29	100	8.37	101	8.4	101
Flight: $T_{relative}$	0.11	92	0.11	92	0.12	100	0.12	100	0.12	100

Chapter 6, Supplementary Materials 2:

We measured and explored variation in body mass and wing length within and between populations in order to determine the most appropriate way to account for potential size-driven influences on metabolic rates in this species. In this analysis we included data gathered from all individuals that were caught through this study (n= 41, 42, 24 for Finland, Scotland, Iceland respectively), not just those from which data loggers were retrieved. In Scotland, RTDs can be sexed reliably in the field, especially when both individuals in a breeding pair are visible, based on differences in body mass (Okill, French et al. 1989). This revealed a similar number of males (n=18) and females (n=20) were sampled in Scotland. Identification of the sex of all individuals from Scotland and Iceland was not available. Inspection of the distribution of body masses in Finland and Iceland suggested that while between populations there is likely to be a difference in the body mass threshold used to sex this species in the field, that at both of these sites a similar proportion of males and females were sampled. Thus, sex and its potential impact on body mass and wing length was not considered further in this analysis.

We carried out an ANVOA for wing length and body mass to test for differences across the three populations. We also modelled body mass as a function of wing length, site and an interaction between the two, using a linear model. Finally, we carried out Tukey test post-hoc tests to explore differences between populations in all models.

There was strong evidence for differences in body mass between the populations ($F_{(2, 104)}$ = 8.5, p<0.001), with individuals in Finland having a higher body mass than Iceland (p=0.01) and Scotland (p<0.001), but there was no evidence for a difference between Scotland and Iceland (p=0.88) (Supplementary Materials 1, Figure 1). Similarly wing length varied between sites ($F_{(2, 104)}$ = 21.7, p<0.001), with individuals from Finland having a larger wing length than RTDs from Scotland (p<0.001) and Iceland (p<0.001), but no difference between Iceland and Scotland (p=0.36) (Supplementary Materials 1, Figure 2).

There was strong evidence that body mass varied with wing length ($F_{(1, 101)}$ = 156.1, p<0.001) (Supplementary Materials1, Figure 3). However, there was no evidence for an interaction between population and wing length ($F_{(2, 101)}$ = 1.6, p=0.2) (Supplementary Materials 1, Figure 3). The linear model also showed no difference in intercept for any of the sites, even in models built with the interaction term removed (P>0.05 in all pairwise comparisons). Therefore, the relationship between wing morphometrics and body mass was shared across populations, meaning differences in body mass between populations were due to birds being morphometrically bigger, rather than just heavier for example due to different body condition.

Differences in body mass and morphometrics across sites lead to DEE and DEE_T being presented as KJ per unit body mass to the power of the average allometric component from Equation 1 in the main paper ($Mass^{0.7545}$), rather than as just KJ. This allowed comparisons across sites to account for the differences in size and hence mass.

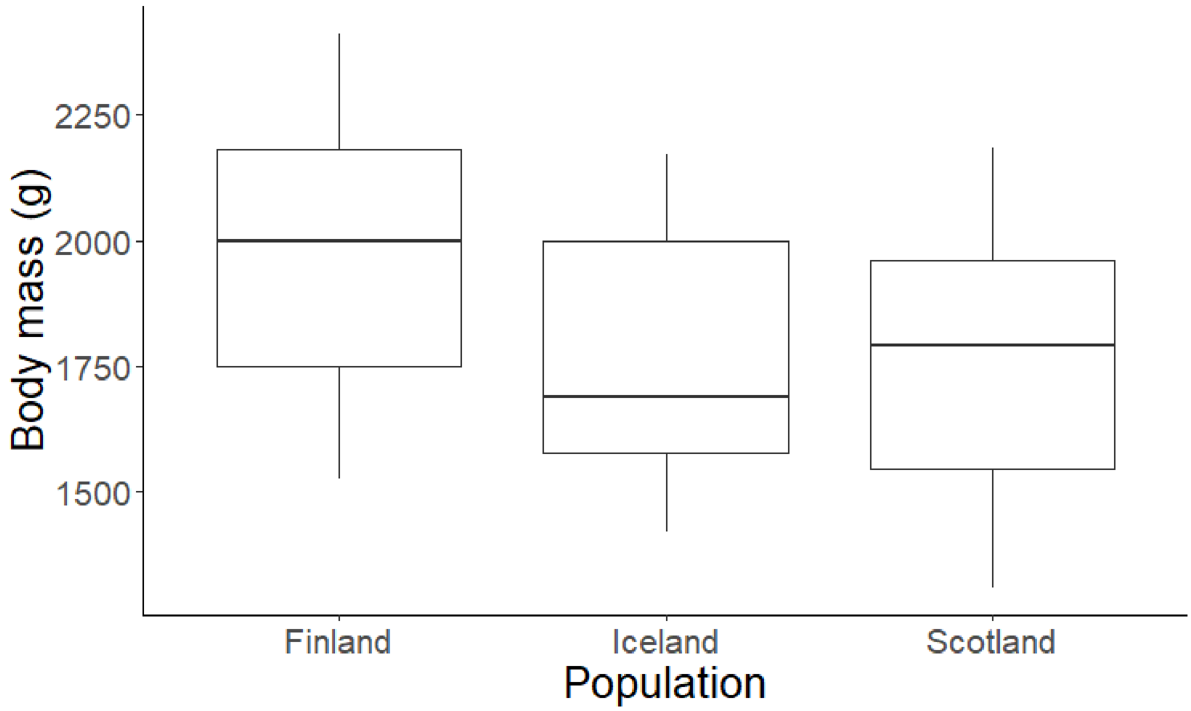

FIGURE 9.7 CHAPTER 6, SUPPLEMENTARY MATERIALS 2, FIGURE 1

Boxplot for the mass of each population.

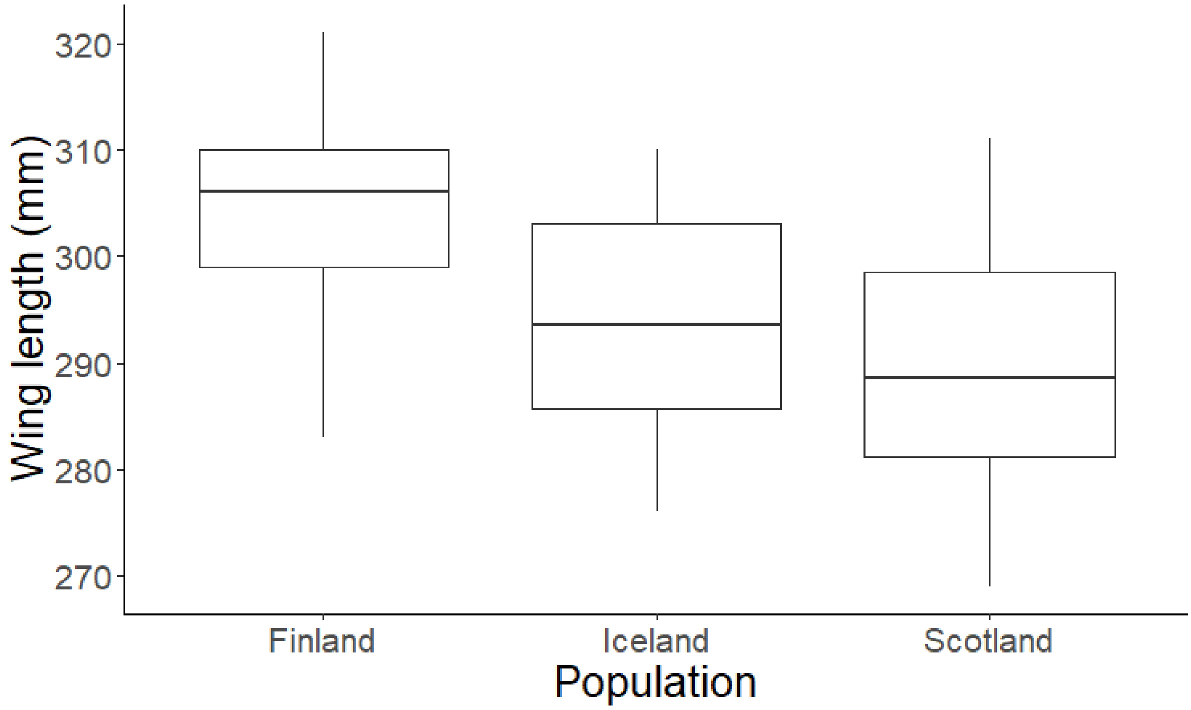

FIGURE 9.8 CHAPTER 6, SUPPLEMENTARY MATERIALS 2, FIGURE 2

Boxplot for the wing lengths of each population.

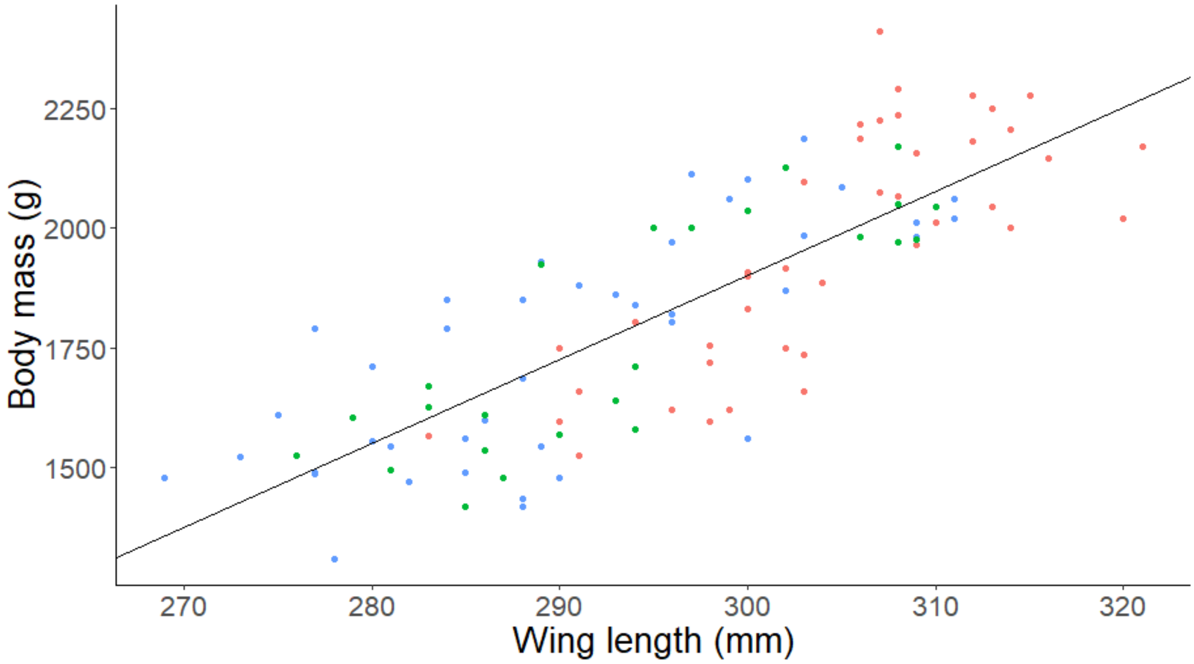

FIGURE 9.9 CHAPTER 6, SUPPLEMENTARY MATERIALS 2, FIGURE 3

*Wing length against the body mass of individuals from the three study populations. The solid lines show the predicted relationship between body mass and wing length. Data points for the populations from Finland, Scotland and Iceland are shown in red, green and blue, respectively. Regression line generated from a model where Body mass = Wing length * 17.5 – 3354.*

References

Okill, J. D., D. D. French and S. Wanless (1989). "Sexing Red-throated Divers in Shetland." Ringing & Migration **10**(1): 26-30.

TABLE 9-3 CHAPTER 6, SUPPLEMENTARY MATERIALS 3

*The final models for each of the modelled response variables, where ▪ indicates the presence of an explanatory variable in the final model. s() indicates a smoothing factor was applies to the predictor and s(by=site) indicates that a separate smoother was applied to each level within the by factor, otherwise the effects are linear. * indicates that the selected model was a simpler form of the best fitting model, within 2 ΔAICc units. Both DEE and* DEE_T *are calculated accounting for body mass.*

Response variable	time	s(time)	s(time, by=site)	site	time:site	Adjusted R^2	AICc weight
DEE	▪			▪	▪	0.27	0.86
Foraging			▪	▪		0.28	0.86
Resting		▪				0.19	0.81
Flying	▪			▪	▪	0.03	0.70
Active on water		▪				0.20	0.38*
Swimming			▪	▪		0.34	0.93
DEE_T			▪	▪		0.93	1

FIGURE 9.10 CHAPTER 6, SUPPLEMENTARY MATERIALS 4

The individual outputs of the best fitting model for the five observed behaviours: foraging, resting, flight, active on water and swimming. Predictions used from these models which lead to negative values are treated as 0 when shown in Figure 3 in the main paper. Finland, Scotland and Iceland are shown in red, blue and green, respectively.