# The secret lives of murres: movement and behaviour across the full annual cycle of thick-billed murres (*Uria lomvia*)

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#### Abstract

Seabirds are used as an indicator of marine ecosystems, as they are amenable to monitoring due to breeding in large colonies on land while depending on the ocean for food. The ability to directly study these mobile marine predators while at sea has been challenging until recently. Advances in biologging have led to an explosion of new research that tracks individual animal movement and behaviour in unprecedented detail through space and time. This revolution is providing new opportunities to study how individuals interact with their environment and examine how individual behaviour scales up to population processes. In this thesis, I employ a range of biologging methods to study thick-billed murres (Uria lomvia) over multiple temporal and spatial scales, from daily movements constrained by central-place foraging during the breeding season to changes in seasonal distributions in response to climate change over four decades. Our ability to track wildlife has increased to the point that techniques for analyzing these data are becoming a significant barrier to answering ecological questions. In Chapter 3, I compared six methods of classifying seabird behaviour from accelerometer data, collected on two species of seabird with different styles of flight and modes of foraging. Accurate daily activity budgets can be generated from accelerometer data using multiple methods; therefore, identifying a suitable behavioural classification method should not be a barrier to using accelerometers in studies of seabird behaviour and ecology. In Chapter 4, I applied this approach to long-term biologging with temperature-depth-light recorders to examine how marine habitat influences behaviour and energetics of thick-billed murres in winter. In the northwest Atlantic Ocean, murres showed significant within and among individual flexibility to exploit two distinct habitats: cold water along the Labrador and Greenland shelves and warm water in the Labrador Basin. Within these two habitats, murres adopted different strategies to cope with the energetic constraints of winter.

Climate change is altering the marine environment at a global scale, with some of the most dramatic changes occurring in Arctic regions; these changes may affect the distribution and migration patterns of marine species throughout the annual cycle. Building on this winter behavioural analysis, in Chapter 5 I used a species distribution model to show that the non-breeding distribution and migration phenology of thick-billed murres has likely already shifted in response to climate change. The greatest distribution changes have occurred during fall, where the predicted distribution has shifted 211 km west and 50 km north per decade since 1981. Chapters 4 and 5 focused on data from a single colony, Chapter 6 used multi-colony GPS tracking to examine foraging behaviour across multiple populations. I used GPS tracking data collected from 29 thickbilled and common murre (Uria aalge) colonies across the North Atlantic Ocean basin, to model how foraging range increases with colony size during chick-rearing. The strong relationship between colony size and foraging range means that important foraging habitat for some colonial species can be delineated based solely on population estimates. This result represents an important example of how ecological theory, can inform conservation and management in colonial breeding species. This thesis demonstrates how biologging tools can be used to study ecological questions about wildlife across a range of temporal and spatial scales that were inconceivable using traditional observational methods, contributing to our ability to understand ecological process and conserve wildlife species in the face of anthropogenic change.

#### Résumé

Les oiseaux marins sont de bons indicateurs de la santé des écosystèmes marins puisqu'ils nichent en colonies denses, dépendent de l'océan pour se nourrir et qu'il est possible de suivre leurs déplacements. Néanmoins, notre capacité à suivre les déplacements de ces prédateurs marins pose quelques problèmes logistiques lorsque ces derniers se déplacent au large. De récents avancements en micro-technologie ont menés à une explosion de recherche ayant pour but de suivre le comportement et les mouvements d'animaux sauvages à l'échelle individuelle avec une précision spatiale et temporelle inégalée. Cette révolution a créé de nouvelles opportunités afin d'étudier comment les animaux interagissent avec leur environnement ainsi que d'examiner comment le comportement d'un individu se transmet au niveau d'une population. Dans cette thèse, j'utilise une variété de méthodes micro-technologiques afin d'étudier le Guillemot de Brünnich (Uria lomvia) à plusieurs échelles temporelles et spatiales. Dans le chapitre 3, je compare six méthodes de classifications comportementales chez les oiseaux marins, utilisant des données d'accéléromètres provenant de deux espèces ayant différents styles de vol et méthodes de recherche de nourriture. Il existe plusieurs méthodes pour analyser des données d'accéléromètre afin de générer des budgets d'activité précis. Dans le Chapitre 4, j'applique cette approche aux suivis à long-terme utilisant des enregistreurs de température, de profondeur et de lumière afin d'examiner l'effet de l'habitat marin sur le comportement et les dépenses énergétiques des Guillemots de Brünnich en hiver. Dans le nord-ouest de l'Atlantique, les guillemots ont une flexibilité individuel et populationnel significative, quant à l'exploitation d'habitats distincts, soit le long de la plate-forme continentale entre le Labrador et le Groenland, où l'eau est froide ou dans le bassin du Labrador, où l'eau y est chaude. En fonction de l'habitat dans lequel les guillemots évoluent, ils utilisent une variété de stratégies afin de maintenir leurs coûts énergétiques constants

au fil de l'hiver. À partir de mon analyse de comportement hivernal, j'utilise dans le Chapitre 5 un modèle de distribution d'espèces pour démontrer que la distribution autre qu'en période de reproduction et la phénologie lors de la migration des Guillemots de Brünnich ont probablement déjà été affectées par les changements climatiques. Les changements de distributions les plus marqués surviennent en automne, où la distribution prédite se déplace de 211 km vers l'ouest et de 50 km vers le nord à chaque décennie, et ce depuis 1981. Les Chapitres 4 et 5 portent sur les données provenant d'une seule colonie, contrairement au Chapitre 6 qui utilise les données GPS provenant de plusieurs colonies afin de comparer le comportement de recherche de nourriture entre plusieurs populations. J'ai utilisé des pistes GPS provenant de 29 colonies de Guillemots de Brünnich et Guillemots de Troïl (Uria aalge) situés dans le bassin de l'Océan Nord-Atlantique afin de modéliser l'augmentation de l'aire d'alimentation en fonction de la grosseur de la colonie lors de l'élevage des poussins. La forte relation entre la grosseur d'une colonie et son aire d'alimentation implique que l'aire d'alimentation principale pour une espèce coloniale peut être délimitée à partir de la grosseur de cette colonie uniquement. Cette thèse démontre comment l'utilisation de micro-technologies permet d'étudier des questions écologiques liées à la faune à une échelle temporelle et spatiale qui nous était impensable lors de l'utilisation de méthodes traditionnelle d'observation, contribuant ainsi à améliorer notre habilité à comprendre les processus écologiques et à préserver la vie sauvage face aux changements anthropogéniques.

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#### **Contribution to original knowledge**

Rapidly evolving technology for tracking wildlife over multiple spatial and temporal scales is dramatically changing approaches to wildlife ecology. In this thesis, I contribute to knowledge with original tracking data, new methods for analysis of these data, and the application of both to basic and applied questions in seabird ecology. In particular, Chapters 4 and 5 examine behaviour and distribution of thick-billed murres outside of the breeding season, a period in the annual cycle of most seabirds that is still relatively unknown.

This thesis contributes significant new data about the year-round distribution and behaviour of thick-billed murres. These datasets are, or will be, made publicly available with the publication of the four manuscripts in this thesis (Chapters 3-6). This includes new GPS, accelerometer, and dive data from breeding birds collected at Coats Island, Nunavut (Chapters 3 and 6), and, year round geolocator tracking and temperature-depth-recorder (TDR) data (Chapters 4 and 5) from the same population. Data collected as part of this thesis have already been contributed to multiple international collaborations studying and have been used in co-authored publications (Davidson et al. 2020, Albert et al. 2021), demonstrating the value of this contribution to ecological knowledge.

Throughout this thesis, I develop novel analytical techniques for using biologging data to address ecological questions and conservation concerns. Chapter 3 describes new methods for analyzing accelerometer from seabirds, with applications to behavioural and energetic research. Chapter 5 applies species distribution models in a novel way to address the lack of historical baseline data on non-breeding distributions of seabirds. Chapter 6 adopts an analytical approach used in dispersal ecology to address a fundamental question in seabird foraging ecology.

#### **Contribution of authors**

Chapter 3 is published in Ecology and Evolution (Patterson et al. 2019). The concept for this study was developed by K. Elliott and myself. K. Elliott and I collected data for thick-billed murres, with logistical support from G. Gilchrist. L. Chiver, S. Hatch, and K. Elliott collected data for black-legged kittiwakes. I completed all analysis and wrote the manuscript. All authors provided editorial comments on the manuscript.

Chapter 4 is formatted for submission to Functional Ecology. The concept for this study was developed by all authors. K. Elliott and I collected data for thick-billed murres, with logistical support from G. Gilchrist. I completed all analysis and wrote the manuscript. G. Gilchrist, G. Robertson, D. Fifield, A. Hedd, and K. Elliott provided editorial comments on the manuscript.

Chapter 5 is publised in Marine Ecology Progress Series (Patterson et al. 2021). The concept for this study was developed my K. Elliott, G. Gilchrist, and myself. All authors contributed to collecting data for this study, either directly in the field or through logistical and funding support. I completed all analysis and wrote the manuscript. G. Gilchrist, A. Gaston, and K. Elliott provided editorial comments on the manuscript.

At the time of submission, Chapter 6 had been submitted to Current Biology and was invited for revision following peer review. The concept for this study was developed K. Elliott, G. Gilchrist, A. Gaston, and myself. All authors contributed data for this study. I completed all analysis and wrote the manuscript. All authors provided editorial comments on the manuscript.

#### 1. Introduction

Understanding what determines the distribution and abundance of animals is central to wildlife ecology (Elton 1927). The study of ecology should include investigation of the physiology and behaviour of the species, examining the environment in which it is found, and measurement of the number of individuals within the population (Andrewartha & Birch 1954). Andrewartha and Birch (1954) divided an individual's environment into four components: weather, food, other individuals, and a place to live. Climate change and other anthropogenic stressors are influencing all of these environmental components (Hoekstra et al. 2004, Cury et al. 2011, Post et al. 2013, Poloczanska et al. 2013, Ripple et al. 2014). Within this conservation context, ecological studies on the distribution and abundance of wildlife are as important as ever.

Until recently, most highly mobile organisms were only observable over short time scales, often restricted to specific stages of their annual cycle or life cycle. This is especially true for migratory marine species that spend all, or part, of their time at sea, away from human observers. Biological observations on these species were constrained spatially and temporally to coastal, ship-based, and aerial surveys; while important, these techniques only provide a snapshot of where individual organisms are and what they are doing. Developments in biologging technology, deploying spatial and environmental sensors on wildlife, over the last 50 years have dramatically increased our ability to make continuous observations of highly mobile species wherever they go (Hays et al. 2016, Brisson-Curadeau et al. 2017, Sequeira et al. 2019, Bernard et al. 2021, Williams & Ponganis 2021). This coincides with equally dramatic advances in our ability to continuously observe the physical environment at a global scale through remote sensing (Rose et al. 2015, Goddijn-Murphy et al. 2021). Combining these relatively new data types allows ecologists to address long-standing

ecological questions in new ways, from individual behaviour to population processes over spatial scales from daily movements to annual migrations. Biologging combined with remote sensing provides novel opportunities to study wildlife behaviour and physiology, and connect this directly to the individual's environment.

The non-breeding stages of the annual cycle for most wildlife species have historically received less attention than the breeding stage (Marra et al. 2015a, Rushing et al. 2016), in no small part because of the difficulty in observing individuals over long spatial and temporal scales. The advent of biologging methods that can be used to follow individuals year-round is contributing to our knowledge of the full annual cycle of many species (Bridge et al. 2011). All organisms face trade-offs in the time and energy available for different functions throughout the year (McNamara & Houston 2008). A species' ability to adjust timing and energetic investment in breeding, and the time-scale over which the costs of these adjustments persist, will be important determinants of how that species responds to environmental change (McNamara & Houston 2008). Wildlife ecologists increasingly recognize the importance of migratory connectivity and carry-over effects between seasons in regulating populations (Webster et al. 2002, Norris 2005, Harrison et al. 2011). Biologging methods that measure spatial distribution and individual activity are fast becoming essential tools for linking wildlife behaviour, energetics, and environmental conditions across the annual cycle.

Seabirds are considered important indicators of marine environments because of their broad distribution, their role as marine predators, and their accessibility for monitoring while breeding on land (Cairns 1988, Piatt et al. 2007, Cury et al. 2011). Seabirds are among the most threatened groups of birds; globally 31% of seabird species are considered threatened and 47% have declining population trends (Croxall et al. 2012, Dias et al. 2019). By extending monitoring of seabirds while

at sea, biologging increases the potential of using them as indicators of marine ecosystems (Burger & Shaffer 2008, Brisson-Curadeau et al. 2017).

Arctic marine species are facing interactive effects of climate change and a concurrent increase in anthropogenic activity in this region (Poloczanska et al. 2013, Sydeman et al. 2015). Arctic air and water temperatures have increased dramatically, and sea ice cover has declined, in the last few decades (Meredith et al. 2019). Climate change is contributing to changes in the physical environment of marine species, as well as changing trophic interactions that alter food-web dynamics (Post et al. 2013, Hop & Gjøsæter 2013). Declining sea ice cover is increasing human access to Arctic regions, leading to increased threats to marine species from shipping, fisheries, mining, and oil and gas development (Harsem et al. 2015, Melia et al. 2016, Andrews et al. 2017, Tai et al. 2019).

Thick-billed murres (*Uria lomvia*; hereafter, murres) are a long-lived, circumpolar seabird (Gaston & Hipfner 2020), which is considered an important indicator of Arctic marine ecosystems (Mallory et al. 2006, Barry et al. 2010, Michel et al. 2012). Murres undertake a short and highly seasonal breeding period (Jun-Aug), followed by a non-breeding period at sea (Sep-May) in Arctic or sub-Arctic regions, where they experience reduced food availability, limitations on foraging time associated with day length, and harsh climatic conditions. This thesis applies multiple biologging methods to understand the full-annual cycle of thick-billed murres.

Tri-axial accelerometers provide continuous, high-resolution measurements of acceleration due to gravity and movement in three dimensions (Brown et al. 2013). Accelerometers are small, light-weight, and have low power consumption, which means biologgers that include accelerometers can be used to obtain detailed behavioural data over longer durations on smaller organisms than can be obtained with more conventional sensors, such as GPS (Brown et al. 2012). Use of

accelerometers in ecological research is still limited, due to the significant analytical challenges in working with these rich data. Chapter 3 develops and compares six techniques for classifying seabird behaviour from accelerometer tracks, using data from thick-billed murres (*Uria lomvia*) and black-legged kittiwakes (*Rissa tridactyla*). The objective of this chapter was to identify accurate methods of behavioural classification that can be used to generate daily activity budgets of seabirds from accelerometers.

Thick-billed murres are arguably among the most intensively studied seabird species in the world (Gaston & Nettleship 1981, Gaston & Hipfner 2020); nevertheless, relatively little is known about this species' behaviour and habitat requirements outside of the breeding season. Until the advent of biologgers that could track-year round movements, information about the winter distribution of this species came primarily from band recoveries collected from murre hunting (Donaldson et al. 1997). Early deployments of geolocators to track the year-round movements of murres revealed more diverse distribution and winter habitat use than suspected from banding recoveries (Gaston et al. 2011). Chapter 4 combines spatial tracking data from geolocators with temperature-depth-recorders that provide detailed behavioural data during winter. This chapter examines how thick-billed murres survive challenging winter conditions in sub-Arctic areas when cold ocean temperatures increase energetic costs and reduced day length limits opportunity for foraging.

Climate change is altering the marine environment worldwide (Hoegh-Guldberg & Bruno 2010), changing the phenology and distribution of marine flora and fauna (Poloczanska et al. 2013). Because there are limited baseline data on the at-sea distribution of pelagic species, it is difficult to assess how much these changes have already altered distributions. Chapter 5 uses existing (Gaston et al. 2011, McFarlane Tranquilla et al. 2015) and newly collected geolocator tracking data to develop a species distribution model (SDM) that predicts the non-breeding distribution of

thick-billed murres from Coats Island, Nunavut. This model was used to hindcast the likely nonbreeding distribution of thick-billed murres between 1982 and 2019, and assess the extent to which climate change may have already altered the non-breeding range and migration phenology of a population of this species.

During breeding, colonial seabirds are constrained to foraging close to their colonies, making them particularly vulnerable to anthropogenic activity and climate change during this stage of their annual cycle. In 1963, Ashmole proposed that intraspecific competition leads to prey depletion around colonies, causing reproductive success to decline as breeding adults are required to spend more time and energy to find prey farther from the colony (Ashmole 1963). Chapter 6 tests if foraging distributions of chick-rearing seabirds scale with increasing colony size, as predicted by Ashmole's theory. This chapter uses multi-colony GPS tracking data collected from chick-rearing thick-billed and common murres (*Uria algaa*) collected at 29 breeding colonies throughout the North Atlantic Ocean.

#### 2. Literature review

Wildlife biology can contribute to management of marine resources by documenting how different species use marine environments, and identifying areas that are important to specific populations or communities of marine wildlife (Crowder & Norse 2008, Douvere 2008). This literature review will examine two common traits of seabirds – central place foraging and migration – within the context of climate change. The review will consider examples of how biologging tools have been used to answer questions about these themes in Arctic species, with a specific focus on thick-billed murres (*Uria lomvia*; hereafter, murres), which are the model species studied within this thesis.

Understanding how species interact with their physical and biological environment is a fundamental goal in ecology (Andrewartha & Birch 1954, Hutchinson 1957). This is especially important as anthropogenic activity and global climate change are increasingly affecting these interactions. Arctic marine species face multiple stressors from global climate change (Post et al. 2013, Poloczanska et al. 2013), which is simultaneously causing dramatic changes to the environments on which these species depend while also creating new opportunities for human development in the North. Within marine environments, increased commercial fishing pressure is affecting prey availability and trophic dynamics (Smith et al. 2011, Cury et al. 2011), while increased shipping activity creates disturbances and mortality risks for marine wildlife (Huntington 2009, Schwemmer et al. 2011).

Time and energy trade-offs play a central role in life-history theory, especially for wildlife exposed to pulsed resources (Stearns 1992, McNamara & Houston 2008). Wildlife living in seasonal environments have developed a diversity of responses for dealing with changes in conditions and resources, including such divergent strategies as reduced energy use during some seasons –

hibernation or torpor to decrease metabolic requirements during periods of scarcity (Geiser 2020) – and reduced time spent at particular locations – migration to follow seasonal patterns in climate and food availability (Somveille et al. 2015). Population regulation, adaptation, and competition could be driven by conditions during one or many stages of a species' annual cycle; therefore, these ecological processes can only be fully understood by considering the full annual cycle (Fretwell 1972, Wiens 1977, Newton 2004).

The introduction of animal-borne data loggers (biologgers) is one of the most significant changes in wildlife science to occur within the last 50 years (Hebblewhite & Haydon 2010). Biologging changes the perspective of data collection from Eulerian sampling, where the sampling frame is pre-determined by the observer, to Lagrangian sampling, where the sampling frame is determined by the observed (Tremblay et al. 2009, Phillips et al. 2019). This change in perspective is particularly important for the study of highly mobile marine species that can travel over large spatial scales and use pelagic habitats away from human observers (Hays et al. 2016). Ecological inference from early biologging studies was initially limited by small sample sizes and technological constraints; however, as technologies improve and become more accessible larger sample sizes from multiple populations and species increase the scope of questions that can be addressed with these methods (Sequeira et al. 2019).

#### Thick-billed murres

Thick-billed murres are a long-lived, circumploar seabird (Figure 2.1) that migrates between arctic and subarctic breeding colonies in summer to winter in the marginal ice zone or ice-free subarctic waters (Gaston & Hipfner 2000). Murres experience a short and highly seasonal breeding period followed by wintering in challenging conditions that include reduced food availability, limitations on foraging time associated with day length, and harsh climatic conditions. Murres are among the most abundant arctic seabird species and play an important role in arctic food webs. (Conservation of Arctic Flora and Fauna 1996, Gaston & Hipfner 2000). While murres are considered a low conservation concern globally, some regional populations are in decline (Frederiksen et al. 2016), and murres have been identified as a priority species within the circumpolar flyway (Johnston et al. 2014). They are also harvested for subsistence and recreation in Nunavut, Newfoundland, Labrador, and Greenland (Merkel & Barry 2008). This harvest can play an important role in population regulation (Wiese et al. 2004). Like other pelagic seabirds, murres face multiple threats outside of the breeding season including over-hunting, fuel and oil spills, chronic pollution, competition with fisheries, fisheries by-catch, and changes to habitat and prey populations associated with climate change (Gaston & Hipfner 2000, Wiese et al. 2004, Smith & Gaston 2012, Frederiksen et al. 2016). Developing effective strategies to manage these risks requires knowledge of year-round distributions, habitat requirements, and interactions between life history stages (Ådahl et al. 2006, Marra et al. 2015a, Carneiro et al. 2020).



Figure 2.1. Thick-billed murre flying at a breeding colony on Coats Island, Nunavut. Photo taken by Douglas Noblet.

#### Central place foraging

Breeding seabirds are central place foragers that must return to the nest after each foraging trip. Energy gained while foraging is constrained by the costs associated with travel between the nest and suitable foraging patches (Schoener 1971, Orians & Pearson 1979, Houston & McNamara 1985). Indeed, many species are central place foragers for at least part of their lifecycle, examples include colonial insects (Holway & Case 2000), denning mammals (Doncaster & Woodroffe 1993), nesting birds (Houston 1987), and even humans (Houston 2011). The intensity of central place foraging constraints depends on interactions between time, distance, and energy, all of which are mediated by a species' biology and the individual's environment. Central place foragers must choose prey patches and prey items that maximize energy delivered to the central place while minimizing other costs incurred during foraging, such as energy expended during travel, time away from the central place, and risk of predation (Krebs 1980, Houston & McNamara 1985).

In 1963, Ashmole proposed that intraspecific competition leads to prey depletion around colonies, causing reproductive success to decline as breeding adults are required to spend more time and energy acquiring prey farther from the colony (Ashmole 1963, Rowan 1965). Ashmole's Halo Theory has become a central idea in studies of foraging by breeding seabirds. The hypothesis predicts that, assuming equal distribution and abundance of food, birds at larger colonies should forage farther from their nests than those from small colonies during the same breeding stage. Higher rates of energy gained are predicted at more distant patches, but distant patches require longer travel times (Houston et al. 1996). Prey depletion close to the colony should lead to increased foraging effort at large colonies, as birds must travel farther from the colony to locate prey (Ashmole 1963, Gaston et al. 1983a, Hunt et al. 1986, Cairns 1992, Lewis et al. 2001). Intraspecific competition at large seabird colonies increases energetic costs for the parents, which

is thought to limit colony size for many species by reducing reproductive success (Ashmole 1963, Birt et al. 1987, Gaston et al. 2007). Lower reproductive success and growth rate have been associated with colony size in multiple seabird species (Gaston et al. 1983a, Hunt et al. 1986). While studies that directly test for prey depletion around seabird colonies are exceedingly difficult, correlative evidence for this has been found in cormorants (Birt et al. 1987), kittiwakes (Ainley et al. 2003), and boobies (Weber et al. 2021).

Building on Ashmole's Halo Theory, ecologists have proposed that intraspecific competition for food during the breeding season is an important determinant of the at-sea distribution of seabirds during the breeding season and the spatial distribution of seabird colonies (Furness & Birkhead 1984, Cairns 1989). The size of gannet, puffin, cormorant, and kittiwake colonies in the United Kingdom was negatively correlated with the number of conspecifics breeding at nearby colonies (Furness & Birkhead 1984). Cairns (1989) further developed a 'hinterland model,' which predicts that, "breeding pelagic birds forage only in waters closer to their own colony than to any other." Multi-colony GPS tracking and habitat modelling of seabirds in the United Kingdom have demonstrated that the number of pairs breeding at a source colony and the size and distribution of neighbouring colonies influence the distribution of birds at sea (Grecian et al. 2012, Wakefield et al. 2013, 2017).

Murres have life-history characteristics that make them uniquely well suited to studies of Ashmole's Halo Theory. Murres are single-prey loaders that have a limited capacity to increase chick provisioning without incurring additional energetic costs on adults (Gaston & Nettleship 1981, Houston et al. 1996). Murres have open nests sites that require continuous attendance by one parent, limiting the time available for foraging. Energetic flight costs of murres are among the highest recorded for any species (Elliott et al. 2013). These acute energetic and temporal

constraints are thought to contribute to a unique intermediate fledging strategy, where murrelings leap from their nesting ledges at 25% of adult size (Ydenberg 1989, Elliott et al. 2017), observed in only three species of alcids: thick-billed murres, common murres (*Uria aalge*), and razorbills (*Alca torda*). Globally, murres nest in colonies ranging in size from hundreds to over a million pairs (Irons et al. 2008, Barry et al. 2010, Gaston et al. 2012, 2017); this natural variation provides opportunities to study the effect of colony size on foraging behaviour.

Studies of central place foraging and Ashmole's Theory initially focused on observations made at the colony and on theoretical modelling (Lewis et al. 2001, Gaston et al. 2007). Biologging techniques allow ecologists to directly measure the spatial distribution of seabirds around colonies, particularly using GPS tracking devices that provide high-resolution and precise spatial measurements (Grecian et al. 2012, Brisson-Curadeau et al. 2017, Wakefield et al. 2017). Lower resolution tracking methods, like satellite transmitters and geolocators, can provide this information for wide-ranging pelagic species that make multi-day foraging trips from their colonies (Weimerskirch et al. 1997, Hindell et al. 2020). Along with spatial distribution, spatial tracking devices provide detailed data on movement rates which can be used to estimate foraging effort and foraging locations (Patterson et al. 2016, Torres et al. 2017, McClintock et al. 2020). Non-spatial sensors, like accelerometers and temperature-depth-recorders, can provide detailed data about foraging behaviour in pursuit diving species like murres (Elliott et al. 2008, Brisson-Curadeau et al. 2021)

#### Migration

Migratory species move among, and within, seasonal ranges in response to changes in the availability of suitable habitat; the timing and extent of these movements depend on an interplay

between the environment and individual state (McNamara & Houston 2008). Effective management of migratory species requires knowledge of their distribution and habitat requirements through the entire year (Harrison et al. 2011, Woodworth et al. 2017). Environmental conditions and anthropogenic activity throughout a species' range can contribute to population trends and demographic processes observed during one annual stage (Fretwell 1972, Norris 2005). Synchronized changes in population size across multiple colonies have provided evidence Arctic seabird populations are regulated by conditions experienced on shared wintering grounds (Gaston 2003, Irons et al. 2008, Descamps et al. 2013). Survival of pre-breeders away from their colonies may also play an important role in population growth rates for species with high adult survival (Frederiksen et al. 2021). Hunting, oil pollution, and fisheries by-catch are human activities that can influence population size and growth rate in murres on their wintering grounds (Tasker et al. 2000, Wiese et al. 2004, Merkel & Barry 2008, Anderson et al. 2011). Management of theses sources of mortality would benefit from better understanding of winter distributions and habitat associations.

During each stage of the non-breeding season, murres face different internal and external constraints. Murres undergo a complete, flightless moult immediately after leaving the colony; facing increased energetic costs for feather replacement and thermoregulation at a time when movement is restricted and males are still provisioning flightless young (Davoren et al. 2002, Elliott & Gaston 2014, Burke et al. 2015). In winter, increased costs of thermoregulation coincide with reduced daylight to limit potential foraging time (Fort et al. 2009, 2013, Moe et al. 2021), while winter storms and unpredictable ice conditions can restrict access to prey (McFarlane Tranquilla et al. 2010). Reproductive success in murres declines with lay date and female condition may play an important role in controlling timing of laying (Hipfner et al. 1997, 1999, Hipfner
2001); therefore, timing of migration and spring habitat use may be important factors in determining reproductive success, and delayed breeding may be associated with increased costs during the post-breeding period.

Wintering distributions of murres from multiple colonies in Canada have been tracked using geolocators (Gaston et al. 2011, McFarlane Tranquilla et al. 2013, Frederiksen et al. 2016). Murres from colonies in Hudson Bay, Coats Island and Digges Island, spend most of the year in northern Hudson Bay and Hudson Strait (Nov-May) and winter in oceanic zones of the northern and central Labrador Sea (Dec-Apr) (McFarlane Tranquilla et al. 2013). Changes in sea-ice cover in Hudson Bay and Hudson Strait could influence the timing of migration and non-breeding distribution for these populations. Declining ice cover also creates potential for increased marine transportation through Hudson Strait or to the Port of Churchill (Prowse et al. 2009, Smith & Stephenson 2013), which could increase threats to these murres while at sea. Human harvest of murres primarily occurs during winter off the coasts of Newfoundland, Labrador, and Greenland (Merkel & Barry 2008), management of harvests requires knowledge of the distribution and habitat use of murres year-round. Previous studies on the non-breeding distributions of murres focused primarily on the over-winter (Nov-Feb) period and limited habitat analysis to quantifying occurrence within broad oceanographic regions. More detailed information on non-breeding habitat associations, site fidelity, and migration schedules are needed to inform marine spatial planning for these populations.

Year-round multi-species tracking has demonstrated that movements of marine predators can be predicted by the physical oceanographic environment (Block et al. 2011), these relationships can be used to inform marine spatial planning (Hindell et al. 2020) and to predict impacts of climate change (Hazen et al. 2013). Data from biologging studies provide continuous sampling of a

species' distribution and habitat preference with less spatial and temporal bias than other visual surveys, especially in pelagic habitats where direct observation is difficult (Dambach & Rödder 2011, Engler et al. 2017).

#### Climate change and seabirds

Ocean warming can influence marine species distributions directly, through species physiological constraints, and indirectly, through species interactions (Winder & Schindler 2004, Sydeman et al. 2012, Post et al. 2013, Piatt et al. 2020). Direct effects of climate warming in seabirds can include changes in sea ice cover that influence access to habitat, increased energetic costs and decreased foraging opportunities associated with wind and storms, and changing thermal habitats within breeding areas. Species that forage in close association with sea ice, such as dovekies (*Alle alle*) and ivory gulls (*Pagophila enurnea*), face the loss of foraging habitat during the breeding season, if marginal ice zones recede outside of the foraging range that can be easily accessed from existing colonies (Gilg et al. 2016, Jakubas et al. 2017). However, the converse can also occur, where available foraging habitat is usually constrained by the presence of sea ice around the colony and declining sea ice cover created additional foraging opportunities close to the colony (Gaston et al. 2005).

Winter storms are expected to increase in the North Atlantic, a hotspot for multiple seabird species (Montevecchi et al. 2012, Davies et al. 2021), as a result of climate change. Mass mortality events associated with winter storms are well known in seabirds (Clairbaux et al. 2021, Shepard 2021) Climate indices associated with increased wind and storms in the North Atlantic also correlate with reduced adult survival of common (Votier et al. 2005) and thick-billed murres (Smith & Gaston 2012). Alcids in particular have high wing-loading and fast flight speeds, which makes

them sensitive to wind conditions (Elliott et al. 2014, Shepard et al. 2019). Accelerometers combined with GPS tracking provide new opportunities to study how energetic costs are effected by wind. Multi-species tracking of the year-round movements of five species of seabirds in the North Atlantic, combined with bioenergetics modelling, found that winter storms limit feeding opportunities in winter (Clairbaux et al. 2021). For thick-billed murres, unusually high day time temperatures during breeding (>20 °C), combined with increased parasitism from mosquitoes, was thought to contribute to adult mortality and reproductive failure (Gaston & Elliott 2013). This species has limited heat tolerance, making them susceptible to increasing maximum air temperatures at breeding sites (Choy et al. 2021).

Indirect effects of climate change on seabirds include shifts in phenology, changes in prey distribution and abundance, and interspecific competition (Sydeman et al. 2012, 2015, Dias et al. 2019). Ocean warming has clear bottom-up climate influences on lower trophic levels, but can also influence species interactions (predation and competition) at higher trophic levels (O'Connor et al. 2009, Lynam et al. 2017). For example, a persistent marine heat wave in the North Pacific created an 'ectothermic vise' for birds and mammals that feed on forage fish, by simultaneously reducing the quality and quantity of prey at lower trophic levels (phytoplankton, zooplankton, and forage fish) and increasing metabolic demands, and therefore competition from, of ectothermic ground fish (von Biela et al. 2019, Piatt et al. 2020). This unusual and extreme climate event was associated with die-offs of common murres (Piatt et al. 2020) and Cassin's auklets (*Ptychoramphus aleuticus*) (Jones et al. 2018), with ecosystem changes recorded across all trophic levels (Suryan et al. 2021).

Mismatches between breeding phenology and resource availability is a potential effect of climate change on wildlife (Visser et al. 2004, Both et al. 2009, Thackeray et al. 2016). A global meta-

analysis of seabirds found that breeding populations have not adjusted timing of breeding in response to rising sea surface temperatures (Keogan et al. 2018). Cassin's auklets that rely on copepods, Neocalanus cristatus, as a major prey item, have reduced breeding success in warmer years because the timing of peak availability of prey was linked to spring ocean temperatures, such that in warm years N. cristatus were not available during the nestling growth period (Hipfner 2008). Similar mismatches in timing of breeding and prey availability have been observed between Rhinocerous auklets (Cerorhinca monocerata) and Japanese anchovy (Engaulis japonicas), where timing of breeding was linked to spring air temperature while timing of prey availability was driven by winter surface pressure in the North Pacific Ocean (Watanuki et al. 2009). These phenological mismatches are likely to occur in species that rely on climate cues to initiate migration and breeding that are uncoupled from the conditions that control the timing of prey availability, and the directions and rates of change in cues are different. Timing of breeding in three seabird species at a colony in the North Sea was correlated with climate conditions occurring over different spatial scales for migrating and resident species (Frederiksen et al. 2004). Species that time breeding based on photoperiod, and have highly specialized diets, may be most susceptible to phenological mismatches due to climate change (Frederiksen et al. 2004, Keogan et al. 2018).

The timing of spring ice melt influences the timing of seasonal peaks in marine productivity in Arctic ecosystems (Ferland et al. 2011). These changes in phenology can affect migratory species that need to time migration and nest initiation so that food is available and accessible on arrival in breeding ranges and the timing of hatching coincides with peak prey availability (Anderson et al. 2013, Descamps et al. 2019). For thick-billed murres at the southern portion of their range, low sea ice years are correlated with reduced chick growth rate (Gaston et al. 2005). In Arctic and sub-Arctic marine food webs, a change in forage fish composition from a system dominated by Arctic

cod (*Boreogadus saida*) to one dominated by capelin (*Mallotus villosus*) (Hop & Gjøsæter 2013) is expected with climate change. This pattern has already been observed in diets of thick-billed murres (Provencher et al. 2012) and Arctic char (*Salvelinus alpinus*) (Ulrich & Tallman 2021). For murres, this shift in diet is associated with a decline in energy delivered to chicks (Smith & Gaston 2012). Thick-billed murres breeding in the low Arctic already appear to be experiencing effects of climate change on phenology and trophic interactions.

The combination of spatial tracking methods, auxiliary sensors that can record continuous measurements of animal behaviour and environmental conditions, and satellite-derived remote sensing products have the potential to advance our understanding of how seabirds interact with their environment throughout the year (Goddijn-Murphy et al. 2021). The application and integration of these tools in seabird research can contribute to understanding of climate change impacts on seabirds, as well as other conservation priorities (Rose et al. 2015).

# **3.** A comparison of techniques for classifying behaviour from accelerometers for two species of seabird

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Short title: Classifying seabird behaviour from accelerometry

## Abstract

The behaviour of many wild animals remains a mystery, as it is difficult to quantify behaviour of species that cannot be easily followed throughout their daily or seasonal movements. Accelerometers can solve some of these mysteries, as they collect activity data at a high temporal resolution (< 1 sec), can be relatively small (< 1 g) so they minimally disrupt behaviour, and are increasingly capable of recording data for long periods. Nonetheless, there is a need for increased validation of methods to classify animal behaviour from accelerometers to promote widespread adoption of this technology in ecology. We assessed the accuracy of six different behavioural assignment methods for two species of seabird, thick-billed murres (Uria lomvia) and black-legged kittiwakes (*Rissa tridactyla*). We identified three behaviours using tri-axial accelerometers: standing, swimming and flying, after classifying diving using a pressure sensor for murres. We evaluated six classification methods relative to independent classifications from concurrent GPS tracking data. We used four variables for classification: depth, wing beat frequency, pitch and dynamic acceleration. Average accuracy for all methods was greater than 98% for murres, and 89% and 93% for kittiwakes during incubation and chick rearing, respectively. Variable selection showed that classification accuracy did not improve with more than two (kittiwakes) or three (murres) variables. We conclude that simple methods of behavioural classification can be as accurate for classifying basic behaviours as more complex approaches, and that identifying suitable accelerometer metrics is more important than using a particular classification method when the objective is to develop a daily activity or energy budget. Highly accurate daily activity budgets can be generated from accelerometer data using multiple methods and a small number of accelerometer metrics; therefore, identifying a suitable behavioural classification method should not be a barrier to using accelerometers in studies of seabird behaviour and ecology.

## Introduction

Developments in biologging technology have greatly advanced our ability to study wildlife throughout their ranges, without restrictions and bias imposed by human observation and accessibility (Cagnacci, Boitani, Powell, & Boyce, 2010; Hebblewhite & Haydon, 2010). Traditional methods for measuring animal activity involve direct observation of animals in the field, which is labour intensive. Direct observation limits the scale of observations to times and locations where focal species are accessible to biologists, and creates opportunity for bias if focal animals, or their predators and prey, change behaviour in response to the presence of observers (MacArthur, Geist, & Johnston, 1982; Quiros, 2007). Measuring animal activity with accelerometers overcomes most of these challenges by continuously logging activity wherever the individual goes, and, if small enough, with very little impact on the animal's behaviour (Wilmers et al., 2015). Accelerometers have been used to answer a wide-range of ecological questions relating to prey capture (Sato et al., 2015), energetics (Robson, Chauvaud, Wilson, & Halsey, 2012; Elliott, Chivers, et al., 2014), physiology (Watanuki, Niizuma, Geir, Sato, & Naito, 2003), migration strategies (Bishop et al., 2015; Wiemerskirch, Bishop, Jeanniard-du-Dot, Prudor, & Sachs, 2016); but perhaps the most widespread application of accelerometers is in obtaining timeactivity budgets (Brown, Kays, Wikelski, Wilson, & Klimley, 2013; Berlincourt, Angel, & Arnould, 2015).

Combined with other sensors, accelerometers provide a powerful tool to understand the relationships between animal behaviour, energetics, and the environment. Many GPS tracking studies infer animal behaviour from path geometry, collecting locations at very high intervals to obtain detailed tracks to support inferences about animal behaviour based on path trajectories (Grémillet et al., 2004; Ryan, Petersen, Peters, & Grémillet, 2004; Weimerskirch, Le Corre, &

Bost, 2008; Wakefield, Phillips, & Matthiopoulos, 2009; Mendez et al., 2017). Pairing GPS and accelerometer sensors could reduce the frequency of required GPS fixes, extending the battery life for longer deployments without sacrificing detailed behavioural data. Satellite and light-based tracking methods record locations with low temporal resolution (geolocators) and at irregular intervals (satellite transmitters), which precludes inference about detailed behaviour. If these methods were coupled with accelerometers, then it would be possible to track species over large spatial scales for extended time-periods with high temporal resolution. This type of detailed, long-term tracking of animal movements and behaviours will allow robust inference about animal ecology and how species interact with their environments (Wakefield et al., 2009; Cagnacci et al., 2010)

The ease with which biologists can deploy tracking devices to study the movements of wild animals has exceeded the ability of biologists to categorize, analyze and interpret the volume of data these efforts have generated. Widespread adoption of accelerometers to measure animal behaviour is inhibited by limited validation, which has contributed to a lack of consensus on analysis methods. A host of methods have been proposed for classifying animal behaviour from accelerometer data (Supplementary materials), including movement thresholds (Moreau, Siebert, Buerkert, & Schlecht, 2009; Shamoun-Baranes et al., 2012; Brown et al., 2013), histogram analysis (Collins et al., 2015), k-means cluster analysis (Sakamoto et al., 2009; Angel, Berlincourt, & Arnould, 2016), k-nearest neighbour analysis (Bidder et al., 2014), classification and regression trees (Shamoun-Baranes et al., 2012), neural networks (Nathan et al., 2012; Resheff, Rotics, Harel, Spiegel, & Nathan, 2014), random forests (Nathan et al., 2012; Bom, Bouten, Piersma, Oosterbeek, & van Gils, 2014; Pagano et al., 2017), hidden Markov models (Leos-Barajas et al., 2016), expectation maximization (Chimienti et al., 2016), and super machine learning (Ladds et al., 2017). At least three custom software applications are available for classifying animal behaviour from trained accelerometer data: AcceleRater (Resheff et al., 2014), G-sphere (Wilson et al., 2016), and Ethographer (Sakamoto et al., 2009). Many of these methods use machine-learning techniques that are difficult to interpret because underlying processes are opaque. Numerous accelerometer-derived metrics have been employed as predictors in classification models, often without any critical evaluation of their value in improving classification accuracy. We reviewed 15 similar studies that classified animal behaviour from accelerometers, to identify common accelerometer metrics used in classifications (Supplementary materials). These studies used between 1 and 147 different variables in their classification models; the median number of parameters included was seven. Using large numbers of predictor variables may make classifications unnecessarily complex, potentially discouraging biologists from adopting this tool, and make methods developed on one data set less generalizable to other studies. Simpler approaches may appear inadequate in comparison to sophisticated analyses, while many complex methods can be difficult for most ecologists to implement.

Identifying an appropriate classification technique is further complicated because most methods are based on small sample sizes, with limited or no validation of classification accuracy. In a sample of 15 studies, only ten attempted to validate their classifications, only six had sample sizes of more than 10 individuals from the same species, and five studies used data from less than 5 individuals from some species for analysis (Supplementary materials). Many classification methods rely on training data acquired through direct observation of free-living (Nathan et al., 2012), domesticated (Moreau et al., 2009), or captive (Pagano et al., 2017) animals. Training data can be challenging or impossible to collect for wide-ranging species like seabirds, with some species travelling hundreds of kilometers in a single foraging trip. Observations of captive animals are unlikely to represent the full range of animal behaviour for species that move over large spatial scales (Pagano et al., 2017). There is a need for robust unsupervised classification methods and for alternative approaches to developing training and validation data sets for species, such as most seabirds, that cannot be observed directly in the wild.

We compared six different methods for classifying behaviour using accelerometer data from two seabird species: thick-billed murres (Uria lomvia) and black-legged kittiwakes (Rissa tridactyla). In this study, we focus on comparing methods for classifying the main behaviours (flying, swimming, on colony, and diving) that comprise a daily activity budget for two seabird species. Daily activity budgets have been widely used in studies of seabird behaviour (Ropert-Coudert et al., 2004), energetics (Birt-Friesen, Montevecchi, Cairns, & Macko, 1989), and ecology (Furness & Camphuysen, 1997); identifying robust methods for calculating daily activity budgets from accelerometer data should contribute to wider application of this technology. Accelerometer deployments were paired with GPS data loggers and GPS tracks were used to validate the accuracy of accelerometer-based classifications. High-resolution GPS data are already widely used for behavioural classification in free-living birds, thus, these data provide a good option for validating classifications on a large number of individuals engaging in a full range of natural activities. Our analysis focused on identifying coarse-scale behaviours: resting on colony, flying, swimming, and diving (for murres). Quantifying these behaviours is useful for many seabird studies and these behaviours can be inferred from high-resolution GPS tracks. We compared overall accuracy and behaviour-specific accuracy for each species. We also considered the effect of breeding stage (incubation vs. chick rearing) on classification accuracy; although behaviour in general should not change between breeding stages, the frequency of different behaviours can change, and factors such as level of activity and posture while at the nest could change, affecting our ability to

accurately identify these behaviours. To determine if classification method affects estimates of energy expenditure we also used daily activity budgets from each classification to calculate daily energy expenditure (DEE). Finally, we used variable selection to assess whether or not models using more predictor variables perform better than models with fewer variables and to identify the variables that make the greatest contribution to improvements in classification accuracy for each species.

## Methods

## Tagging methods

We deployed GPS-accelerometers (Axy-trek, Technosmart, Rome, Italy; 18 g) on 21 incubating and 19 chick-rearing murres breeding at Coats Island, in 2018. Murres were captured using a noose pole and biologgers were attached to the back feathers using TESA tape (TESA 4651, Hamburg, Germany). Murres were released at the capture site and re-captured between 2 and 4 days later to retrieve data loggers. The biologgers were programed to collect GPS locations at 1 min intervals, depth at 0.1 m resolution and 1 Hz intervals, acceleration in three axes at 25 Hz, and temperature at 1 Hz. Note that deployment of similar tags altered dive duration, flight costs, and chick feeding rates (Elliott, Davoren, & Gaston, 2007; Elliott, Le Vaillant, et al., 2014). As all individuals should be similarly impacted, these tag effects should not affect the results of this study.

We deployed tri-axial accelerometers (Axy-3, Technosmart, Rome, Italy; 3.2 g), paired with GPS biologgers (CatTraQ, Catnip Technologies, USA; 14 g), on black-legged kittiwakes at Middleton Island, Alaska, USA, in 2013. Data were collected from 17 incubating and 19 chick-rearing kittiwakes. Both biologgers were attached to the back feathers of kittiwakes using Tesa tape (TESA 4651, Hamburg, Germany). Kittiwakes were released at the capture site and re-captured between 1 and 3 days later to retrieve data loggers. The biologgers were programed to collect GPS locations at 30 sec intervals and tri-axial acceleration at 25 Hz. Deployment of these tags had no impact on reproductive success and survival, but altered flight duration (Chivers, Hatch, & Elliott, 2016). As all individuals should be similarly impacted, these tag effects should not affect the results of this study.

#### Accelerometer-derived metrics

We focused on three types of accelerometer-derived metrics for behaviour classifications: wing beat frequency, pitch, and dynamic acceleration. We chose variables that we thought would be related to the target behaviours based on our prior knowledge of the study species. We calculated wing beat frequency (WBF) by extracting the dominant frequency in the Z-axis using a Fast Fourier Transform (FFT) over a 5-second moving window. The FFT was performed using the '*fft*' function in base R. The peak frequency in the Z-axis can detect signals that represent motion other than flying (such as walking or sea surface waves), however, for simplicity we refer to this as WBF going forward, as this was the signal we were interested in extracting from the accelerometer. Birds in flapping flight should display characteristic frequencies in vertical motion while travelling.

Pitch measures vertical body angle based on the static acceleration (acceleration averaged over time) of all three axis (Table 3.1). We expected pitch to change between different behaviours, because the body angle of a bird will change between time on land, swimming, and flight. All pitch values were corrected for differences in device orientation by standardizing acceleration measurements to a pitch of  $0^{\circ}$  for periods of presumed flight (WBF between 6 – 9 Hz for murres and 3 – 6 Hz for kittiwakes) (Elliott, Chivers, et al., 2014), when all birds should have a similar and consistent body orientation (Watanuki et al., 2003; Chimienti et al., 2016).

Dynamic body acceleration integrates the amount of dynamic acceleration (i.e. after removing the static component due to gravity and associated with posture) over a fixed time period, and can be used as an index of movement (Shepard, Wilson, Quintana, et al., 2008). Dynamic body acceleration can be measured along each axis individually, or as a composite of all three axes using overall dynamic body acceleration (ODBA, Table 3.1). For murres, we used standard deviation of

the overall dynamic acceleration,  $(SD_{ODBA})$  as a measure of overall activity level. For kittiwakes, initial data exploration indicated that there was greater relative variability in the Z-axis than in the ODBA, therefore, we used standard deviation in the Z-axis (SD<sub>Z</sub>) to measure activity level.

Table 3.1 describes the accelerometer metrics calculated from accelerometers; all of these metrics have been used in prior studies classifying animal behaviour from accelerometers (Shamoun-Baranes et al., 2012; Chimienti et al., 2016; Pagano et al., 2017). Murre classifications also used depth to identify periods of diving. We calculated pitch and dynamic acceleration using a 2-sec moving window (Shepard, Wilson, Halsey, et al., 2008) and wing beat frequency using a 5-sec window, for both species. Once accelerometer statistics were calculated, we subsampled all data to 1 sec intervals to reduce processing time during classification, and because our behaviours of interest occurred at intervals greater than 1 second. All summary statistics are reported as mean  $\pm$  standard deviation.

Statistic	Label	Equation	Description
Static acceleration	$S_X, S_Y, S_Z,$	$\frac{\sum X}{n}, \frac{\sum Y}{n}, \frac{\sum Z}{n}$	Average acceleration in each axis, calculated over a 2-sec moving window
Pitch	Pitch	$tan^{-1}\left(\frac{S_X}{\sqrt{S_Y^2 + S_Z^2}}\right) * \frac{180}{\pi}$	Vertical orientation of the body angle
Dynamic acceleration	$D_X, D_Y, D_Z,$	S <sub>X</sub> - X, S <sub>Y</sub> - Y, S <sub>Z</sub> - Z	Residual acceleration in each axis, calculated over a 2-sec moving window
Overall dynamic body acceleration	ODBA	$ D_X  +  D_Y  +  D_Z $	Dynamic acceleration summed across all three axes
Standard deviation of dynamic acceleration in Z- axis	SD <sub>Z</sub>	$\sqrt{\frac{1}{N}\sum_{i=1}^{N} \left(Dz_i - \frac{\sum Dz}{n}\right)^2}$	Variation in the dynamic acceleration in the Z-axis
Standard deviation of overall dynamic body acceleration	SD <sub>ODBA</sub>	$\sqrt{\frac{1}{N}\sum_{i=1}^{N} \left(ODBA_{i} - \frac{\sum ODBA}{n}\right)^{2}}$	Variation in the dynamic acceleration in the ODBA
Wing beat frequency	WBF		Dominant frequency in the Z- axis, calculated using a 5-sec moving window
Depth	Depth		Meters below sea level

*Table 3.1 Accelerometer-derived metrics calculated prior to behavioural classifications. Only pitch, SDz, SD*<sub>ODBA</sub>, WBF, and depth were used in classifications, other statistics shown were calculated to obtain final classification parameters.

#### Accelerometer track segmentation

We used a behaviour-based track segmentation approach for classification (Bom et al., 2014; Collins et al., 2015). Cliff-nesting murres and kittiwakes must fly to travel between their nest site and foraging areas at sea, therefore, periods of flying should separate colony behaviour from swimming behaviour. For murres, dives are separated from flights by periods of swimming. We used this prior knowledge of seabird behaviour to segment tracks into periods of consistent behaviour. We first classified diving (murres) and flying (murres and kittiwakes) from the 1-sec sampled data using each method. Any behaviour that occurred for less than 3 seconds was reassigned to the previous behaviour class and each period of presumed behaviour was assigned a unique segment ID. For practical reasons, we imposed a maximum length of 120 seconds on each segment. This ensured that if a transition between behaviours was missed, the error wold not propagate beyond 120 sec. This upper limit also ensured that each type of behaviour was represented proportionally in the data. Incubation bouts typically last for many hours, while bouts of flying or diving could last seconds or minutes, so even though most of the birds spend a majority of their time at the nest, there would be relatively few bouts of colony behaviour relative to other types of behaviour. Within each segment, we recalculated movement metrics using mean pitch and mean dynamic acceleration.

## Accelerometer classification – supervised

We used three supervised classification methods: histogram segregation (HS), random forests (RF), and neural networks (NN).

## *Histogram segregation (HS)*

We adapted a histogram segregation (HS) approach from Collins et al. (2015). We used density plots to visualize the distribution of each variable sequentially. Characteristic peaks and valleys in the distribution were used to identify break points for different behaviours. Each behaviour was classified using a stepwise approach, once the locations had been assigned to a behaviour these locations were not considered for the next variable. We first classified 'diving' (murres only) and 'flying' using depth and WBF. Accelerometer data were then broken down into segments of continuous behaviour and we calculated average pitch and average dynamic acceleration within each segment. Remaining 'unknown' segments were classified to 'swimming' and 'colony' based on peaks in histograms for these two variables. Each track was classified individually

## Neural network (NN)

We used the classifications from the HS method to train the neural network (NN) models. We did not use the GPS data for training the model because we wanted to test classification approaches that could be applied when GPS data are not available for model training. We randomly chose ten tracks for each species, then, randomly selected 1000 data points within each behaviour class from each of these tracks to make a training dataset. This trained model was used to predict classifications for all tracks within each data set. NN models were run with 5 hidden nodes using the R Package '*nnet*', version 7.3-12 (Venables & Ripley, 2013).

## Random forest (RF)

The random forest (RF) method used the same training data set described above for the NN model. We ran the RF models using the R package 'randomForest', version 4.5-14 (Liaw & Wiener, 2002).

#### Accelerometer classification – unsupervised

We also used three unsupervised classification methods: k-means cluster analysis (KM), expectation maximization (EM), and Hidden Markov Models (HMM). For each method, we ran analysis with between 3 and 6 classes and visually examined the classifications to decide on the number of classes that best identified the behaviours of interest. When we identified more than three (kittiwakes) or four (murres) behaviour classes, classes were grouped into the behaviours of interest based on expected patterns in behaviour.

#### K-means (KM)

The KM classification was performed in two steps. For murres, dives were identified manually by classifying all data with depth below -1 m as 'diving'. A KM classification was performed on WBF to identify two classes, and the class with higher WBF was labelled as 'flying'. We then segmented all data into bouts of 'diving' (murres only), 'flying' and 'unknown' behaviour. Within segments of continuous behaviour, we calculated the average pitch and dynamic acceleration. A second KM classification was performed on the remaining 'unknown' segments with average pitch and dynamic acceleration as input variables. We used the natural logarithm of dynamic acceleration, and both variables were scaled to their range prior to analysis. The KM classification was performed on all tracks at once. Analysis was run using the '*kmeans*' function in base R.

#### *Expectation maximization (EM)*

The EM classification was performed in two steps. For murres, dives were identified manually by classifying all data with depths below -1 m as 'diving'. An EM classification was performed on WBF to identify two classes; the class with higher WBF was labelled as 'flying'. We then segmented all data into bouts of 'diving' (murres only), 'flying' and 'unknown' behaviour. Within segments of continuous behaviour, we calculated the average pitch and dynamic acceleration. A

second EM classification was performed on the remaining 'unknown' segments, with average pitch and dynamic acceleration as input variables. We used the natural logarithm of dynamic acceleration, and both variables were scaled to their range prior to analysis. EM classification was performed on all tracks for each species at once EM analysis was conducted using the R package '*Rmixmod*' package, version 2.1.1 (Langrognet, Lebret, Poli, & Iovleff, 2016). We considered Gaussian models with free proportions; BIC was used to identify the best model.

#### Hidden Markov models (HMM)

HMMs require data that are sampled at equal intervals, for this reason, we did not use the track segmentation approach described above. Instead, average accelerometer values for WBF, pitch, dynamic acceleration and depth were taken for 5-second intervals (murres) and 10-second intervals (kittiwakes). A shorter interval was used for murres to preserve short inter-dive bouts. We used the R package 'momentuHMM' (McClintock & Michelot, 2018) to fit Hidden Markov Models. For murres, depth data were converted to a binary variable, where data with depth less than -1 m received a value of 1 and depths greater than -1 received a value of 0, this was modelled using a Bernoulli distribution. A full description of the distributions and starting values used for each behaviour and variable is provided in Table 3.2 and Table 3.3. We fixed transition probabilities between colony-swimming, swimming-colony, colony-diving, diving-colony, diving-flying, and flying-diving to zero. The most likely behavioural states were obtained from the model using the Viterbi algotrithm (McClintock & Michelot, 2018).

Table 3.2 Starting values for the state-dependent probability distribution parameters for variables used in the hidden Markov model to classify behaviour of thick-billed murres.

Variable	Family	Link	Parameter	Colony	Diving	Flying	Swimming
Pitch	Normal	Identity	Mean	30	-5	0	-5
		Log	SD	20	50	5	10
$SD_{ODBA}$	Exponential	Log	Rate	25	5	2.5	5
WBF	Log normal	Identity	Location	0.5	2	9	2
		Log	Scale	0.5	0.5	0.2	0.5
		Logit	Zero-mass	0.9	0.9	0.1	0.9
Depth	Bernoulli	Logit	Probability	1 x 10 <sup>-12</sup>	1 - (1 x 10 <sup>-12</sup> )	1 x 10 <sup>-12</sup>	1 x 10 <sup>-12</sup>

Table 3.3 Starting values for the state-dependent probability distribution parameters for variables used in the hidden Markov model to classify behaviour of black-legged kittiwakes.

Variable	Family	Link	Parameter	Colony 1	Colony 2	Flying	Swimming
Pitch	Normal	Identity	Mean	35	10	0	5
		Log	SD	10	10	5	5
$SD_Z$	Log normal	Identity	Location	0.05	0.05	0.6	0.15
		Log	Scale	0.5	0.5	0.5	0.5
		Logit	Zero-mass	0.9	0.9	0.1	0.1
WBF	Log normal	Identity	Location	0.5	2	9	2
		Log	Scale	0.5	0.5	0.2	0.5
		Logit	Zero-mass	0.9	0.9	0.1	0.9

## **GPS** classification

## Thick-billed murre

We used GPS and depth sensor data to validate murre behaviour classifications. Locations requiring a calculated ground speed greater than 30 m/s were excluded from analysis (0.1% of all GPS locations), because these were potential GPS errors. If depth was below -1m, data were labelled as diving. Remaining locations with a calculated ground speed greater than 2 m/s were classified as flying. At relatively high sampling rates (i.e. <100 secs), like those used in this study, the calculated ground speed and instantaneous speeds are expected to be highly correlated (Elliott, Chivers, et al., 2014). Locations within 250 m of the nest were classified as colony and all remaining locations were classified as swimming. Following this initial classification, each bout of continuous behaviour was assigned a unique identifier. Data were examined for obvious classification errors based on temperature, duration of behaviour, and behavioural context (prior and subsequent behaviours). Swimming bouts within 3 km of the colony with a high average temperature (>10 °C) were examined as potential colony locations. Only 0.6% of GPS locations were manually reclassified.

Because the GPS data were collected at a lower temporal resolution (60 sec for murres and 30 sec for kittiwakes) than the accelerometer analysis (1 sec), the GPS classification would be slower to respond to a change in behaviour. For example, a murre that transitions from flying to swimming halfway between two GPS fixes would be classified as still flying during the next location, however the accelerometer could pick up this change in behaviour at the time it occurred. To deal with this difference in sampling rate, we identified periods when the GPS indicated a transition from one behaviour to another. All data points within 60 sec of a GPS transition between colony, flying, or swimming were labelled as transitions and excluded from further analysis. Transitions between diving and swimming were not excluded, because the pressure sensor collected depth data at 1 sec intervals. In total, 11.0% of GPS locations were excluded for murres because they were identified as periods of transition between behaviours.

## Black-legged kittiwake

GPS data were used to validate kittiwake behaviour classifications. Locations requiring a ground speed greater than 20 m/s or more than 10-min between fixes were excluded from analysis (0.4% of locations), because these were potential GPS errors. Locations with a calculated ground speed greater than 3 m/s were classified as flying. Locations on Middleton Island were classified as colony, and all remaining locations were classified as swimming. Kittiwakes can spend significant time on tidal flats and sand bars around Middleton Island (K. Elliott, personal observation); in these locations, birds could be swimming or loafing depending on tide heights and these behaviours could not be differentiated based on the GPS data alone. Therefore, we excluded all locations within 500 m of the island from the analysis. This reduced the total GPS data set by 11.1%; this step was important to minimize uncertainty and potential for errors in our validation data. Similar to murres, all locations within 30 sec of a change in behaviour were labelled as transitions (13.5%) and excluded from the analysis.

#### Classification accuracy

We subsampled the accelerometer data to 1 min (murres) and 30 sec (kittiwakes) to match the resolution of the GPS data and used a confusion matrix to calculate the overall accuracy and the balanced accuracy for each behaviour. Confusion matrices and measures of accuracy were calculated using the R package *carat* (Kuhn, 2016). We used mixed-effects models, with bird identity as a random effect, to test for differences in the classification accuracy among methods

and between breeding stages. Accuracy data were logit transformed prior to analysis. We used the R package *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2016) to run the models and the *lsmeans* package (Lenth, 2016) to calculate parameter estimates, 95% confidence intervals (CI) and for pairwise comparisons.

## Daily energy budget

We used an estimate of daily energy expenditure to look at the overall variation among classification methods. Daily energy expenditure (DEE in kJ/d) for murres was calculated following Elliott et al. (2013) as:

$$DEE = 32.0 * t_c + 532.8 * t_f + 100.8 * t_s + 97.2 * t_d$$

Daily energy expenditure for kittiwakes was calculated following Jodice et al (2003), using activity specific metabolic rates for nest attendance, commuting flight, and surface feeding to develop the equation:

$$DEE = 21.0 * t_c + 99.9 * t_f + 25.8 * t_s$$

Where t is time in hours and the subscripts are c = colony, f = flying, s = swimming, and d = diving. We converted metabolic rates from CO<sub>2</sub> production rates (mL CO<sup>2</sup> g<sup>-1</sup> h<sup>-1</sup>) to kJ using an energetic equivalent of 27.33 kJ L CO<sub>2</sub> assuming average kittiwake mass of 416 g (Speakman, 1997; P. G. R. Jodice et al., 2003). We used mixed effects models, with bird ID as random effects, to test for differences in DEE estimates among methods.

## Variable selection

We chose 42 accelerometer statistics used in previous studies (Supplementary materials) to consider in our variable selection analysis; these included raw acceleration values, static

acceleration, dynamic acceleration, minimum, maximum, range, skew, and kurtosis for each axis. We also calculated the trend, as the slope coefficient from a linear regression, and autocorrelation, as the value of the first order autocorrelation function. Each of these statistics was calculated over a 2-second moving window. Finally, we included the dominant frequency for each axis calculated over a 5-second moving window.

We used random forests models to identify which variables contributed the most to classification accuracy and how much adding additional variables improved accuracy. To simulate a realistic training data set, acquired through paired GPS-accelerometer deployments, we trained and tested data from the classified GPS tracks using a random subset of 10 individual tracks for each species. From these tracks, we sub-sampled 1000 locations from each behaviour class to ensure each behaviour was adequately represented in the training data. We used forward selection to identify which accelerometer variables provided the greatest improvement in classification accuracy for models with between 1 and 10 variables. To reduce overall computation time, variable importance from a global model with all variables and all training data was used to identify the 20 most influential variables to include in the variable selection analysis. At each step, we ran 100 simulations with randomly selected training data sets and selected the variable with highest median accuracy over all simulations. We compared model accuracy among the best models with 1 to 10 variables and a global model with all 42 variables. Confidence intervals for model accuracy are based on the 2.5th and 97.5th percentile of all simulations.

## Results

## Classification summary

## Murres

Colony segments were characterized by high pitch ( $37.6^{\circ} \pm 6.1^{\circ}$ ; Figure 3.1) and low SD<sub>ODBA</sub> (0.05 g ± 0.02 g). Swimming segments were characterized by low pitch ( $-7.4^{\circ} \pm 2.5^{\circ}$ ) and high SD<sub>ODBA</sub> (0.28 g ± 0.08 g). Flying segments had high WBF (8.1 Hz ± 0.25 Hz). Diving segments were characterized by depths below -1 m ( $-20.5 \text{ m} \pm 9.0 \text{ m}$ ). Figure 3.2 shows the hierarchical process and average breakpoints used for assigning behaviours with the HS method. We used five total classes in the KM classification for murres: 2 colony, 1 diving, 1 flying, and 1 swimming class. For the EM and HMM classes only 4 classes were necessary to obtain a clear separation of all four behaviours, based on visual examination of the classifications.

## Kittiwakes

Colony segments were characterized by high pitch (29.9 °  $\pm$  11.7 °; Figure 3.3) and low SD<sub>Z</sub> (0.04  $\pm$  0.02 g). Swimming was characterized by low pitch (5.7°  $\pm$  2.9°) and high SD<sub>Z</sub> (0.18  $\pm$  0.04 g). Flying segments had high WBF (4.16 Hz  $\pm$  0.16 Hz). The HS method began by classifying flight with WBF, then colony with SD<sub>Z</sub>, and finally swimming with pitch (Figure 3.4). We used four total classes in the KM, EM, and HMM classifications for kittiwakes: 2 colony classes, 1 flying class, and 1 swimming class.



Figure 3.1 Boxplots showing the distribution of average values of predictor variables for each thick-billed murre behaviour.



Figure 3.2 Diagram showing the average break points and classification hierarchy used in the histogram segregation method for thick-billed murres.



Figure 3.3 Boxplots showing the distribution of average values of predictor variables for each black-legged kittiwakes behaviour.



Figure 3.4 Diagram showing the average break points and classification hierarchy used in the histogram segregation method for black-legged kittiwakes.

## **Classification accuracy**

#### Murres

Mean classification accuracy for each method was greater than 98.3% and accuracy for each individual track was above 92.7% for all methods (Figure 3.5). There was no statistical support for a difference in accuracy among classification methods ( $F_{5, 190} = 1.28$ , p = 0.28). Averaging across breeding status, accuracy was highest using the HS (98.5%; CI = 98.1 - 98.7) method and lowest for the HMM (98.3%; CI = 97.9 - 98.6) method, but this difference was not statistically significant ( $t_{190} = 2.162$ , p = 0.26). Accuracy for all methods was higher for murres with chicks (98.4%, CI = 97.9 - 98.8) than for murres with eggs (98.2%, CI = 97.7 - 98.6); however, there was no evidence that accuracy varied with breeding status ( $F_{1,38} = 0.46$ , p = 0.50) or for an interaction between method and breeding status ( $F_{5, 190} = 0.75$ , p = 0.58).

There was a significant interaction between method and behaviour ( $F_{15,894} = 23.6$ , p < 0.001; Figure 3.6), indicating that some methods were more accurate at classifying certain behaviours than other methods. Average classification accuracy for colony across all methods was 99.1% (CI = 99.5 – 99.7); there were no significant differences in classification accuracy among methods for colony (all p > 0.35). Average classification accuracy for swimming across all methods was 98.7% (CI = 98.4 – 98.9); there were no significant differences in classification accuracy among methods for swimming (all p > 0.06). The HMM method was most accurate for classifying flying (97.9%, CI = 97.4 – 98.3); this was significantly higher than all other methods (NN: 95.3%, CI = 94.3 – 96.2;  $t_{894} = 6.88$ , p < 0.001; HS: 95.3%, CI = 94.3 – 96.2;  $t_{894} = 6.93$ , p < 0.001; RF: 95.3%, CI = 94.3 – 96.2;  $t_{894} = 6.93$ , p < 0.001; RF: 95.3%, CI = 94.3 – 96.2;  $t_{894} = 6.93$ , p < 0.001; KM: 94.3%, CI = 93.1 – 95.4;  $t_{894} = 8.69$ , p < 0.001). For diving, classification accuracy was highest for the HS (99.9 %; CI = 99.8 – 1.00), EM (99.9; CI = 99.8 – 1.00), and KM (99.9%; CI = 99.8 – 1.00)

methods, and lowest for the HMM method (98.2%; CI = 97.8 - 98.6). High classification accuracy for diving is expected, because dives in the GPS data and accelerometer data were both classified using the depth sensor. There was a significant interaction between behaviour and stage ( $F_{3,894} =$ 15.9, p < 0.001). Flying was classified more accurately during chick rearing (96.7%, CI = 95.9 -97.4) than during incubation (94.2%, CI = 92.9 - 95.2;  $t_{38} = 3.92$ , p < 0.001) and there was some evidence that swimming was classified more accurately during chick rearing than incubation ( $t_{38} = -1.91$ , p = 0.06).

## Kittiwakes

There was strong evidence for a difference in classification accuracy among methods (F5,170 = 6.21; p < 0.001) and between breeding stages (F1,34 = 9.41; p = 0.004), there was no support for an interaction between method and breeding stage (F5,170 = 0.41; p = 0.84; Figure 3.5). Averaging across all methods, accuracy during the chick stage was 93.7% (CI = 92.0 - 95.0) while accuracy was 89.5% (CI = 86.7 - 91.7) during the egg stage. For birds with eggs, there were no significant differences among the HMM (90.3%, CI = 87.7 - 92.5), HS (90.0%, CI = 87.3 - 92.3), EM (89.6%, CI = 86.7 - 91.9), RF (89.4%, CI = 86.5 - 91.8), and NN (89.1%, CI = 86.2 - 91.5) methods. The KM (88.2%, CI = 85.1 - 90.8) method was significantly less accurate than the HMM (t170 = -3.87, p = 0.002) and HS (t170 = -3.25, p = 0.02) methods. The absolute difference in accuracy between the most accurate method, HMM, and the least accurate method, KM, was only 2.1%. During the chick rearing stage, there were no differences in classification accuracy among the HMM (94.2%, CI = 92.6 - 95.4), RF (93.7%, CI = 92.0 - 95.1), NN (93.7%, CI = 92.0 - 95.1), HS (93.7%, CI = 92.0 - 95.1), and EM (93.6%, CI = 91.8 - 95.0) methods. Classification accuracy for the KM method (93.0%, CI = 91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -92.0 - 95.1), was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t170 = -91.0 - 94.5) was significantly lower than the HMM (t

3.75, p = 0.003) method. The absolute difference in accuracy between the best and worst classification methods was only 1.2%.

There was no interaction between method and behaviour ( $F_{10,593} = 0.66$ ; p = 0.77), indicating that all methods classified different behaviours with similar accuracy. There was a significant interaction between behaviour-specific accuracy and breeding stage ( $F_{2,593} = 163.0$ ; p < 0.001; Figure 3.6). Colony behaviour was identified more accurately during the chick stage (97.6%, CI = 97.1 – 98.1) than during the egg stage (90.0%, CI = 87.8 – 91.8;  $t_{34} = -10.3$ ; p < 0.001). There was no difference in classification accuracy for swimming across stages (Eggs: 92.2%, CI = 90.5 – 93.7; Chicks: 93.1%, CI = 91.7 – 94.4;  $t_{34} = -1.632$ , p = 0.11). There was also no difference in accuracy of flight classification between stages (Eggs: 88.5%, CI = 83.0 – 88.3; Chicks: 88.5%, CI = 86.3 – 90.5;  $t_{34} = -0.92$ , p = 0.37).



Figure 3.5 Average accuracy of classification methods for thick-billed murre (left) and blacklegged kittwakes (right). Large symbols show group means and error bars are 95% confidence intervals, small symbols are data from each individual. Data are displayed on a logit scale.



Figure 3.6 Average accuracy for thick-billed murre (left) and black-legged kittwakes (right) behaviours; only results from the HS method are shown. Large symbols show group means and error bars are 95% confidence intervals, small symbols are data from each individual. Data are displayed on a logit scale.

#### Daily energy budget

#### *Thick-billed murres*

There was a significant difference in estimates of DEE among methods ( $F_{5,190} = 40.3$ , p < 0.001) and suggestive evidence of an interaction between method and breeding status ( $F_{5,190} = 2.19$ , p = 0.06). For murres with eggs, mean DEE calculated with the RF classification (2112 kJ/day, CI = 1908 - 2315) was lower than DEE calculated with all other methods (EM 2242 kJ/day, CI = 2038) -2446,  $t_{190} = -8.76$ , p < 0.001; HS: 2242 kJ/day, CI = 2038 - 2446,  $t_{190} = -8.76$ , p < 0.001; KM: 2242 kJ/day, CI = 2038 - 2446,  $t_{190} = -8.77$ , p < 0.001; HMM: 2265 kJ/day, CI = 2061 - 2468,  $t_{190}$ = -10.3, p < 0.001; NN: 2272 kJ/day, CI = 2069 - 2476, t<sub>190</sub> = -10.8, p < 0.001). During incubation, the difference between average DEE estimate using the RF method and the NN method, was only 161 kJ or 7.1 % of mean DEE. During chick rearing, mean DEE calculated using the RF (2375 kJ/day, CI = 2161 – 2589) classification was significantly lower than all other methods (KM 2454 kJ/day, CI = 2240 - 2669,  $t_{190} = -5.06$ , p < 0.001; EM: 2455 kJ/day, CI = 2240 - 2669,  $t_{190} = -5.06$ , p < 0.001; HS: 2455 kJ/day, CI = 2241 – 2669,  $t_{190} = -5.11$ , p < 0.001; HMM: 2471 kJ/day, CI = 2257 - 2685,  $t_{190} = -6.11$ , p < 0.001; NN: 2475 kJ/day, CI = 2260 - 2689,  $t_{190} = -6.36$ , p < 0.001). The difference between average DEE estimate during chick rearing using the RF method and the NN method, was only 99 kJ or 4.0 % of mean DEE.

## Kittiwakes

Breeding status had a significant effect on DEE ( $F_{1,37} = 23.5$ , p < 0.001); kittiwakes with chicks (1222 kJ/day, CI = 1116 – 1327) had significantly higher DEE than kittiwakes with eggs (869 kJ/day, CI = 767 – 972). Classification method had a significant effect on estimates of DEE ( $F_{5,185} = 74.8$ , p < 0.001). During incubation, the RF method had significantly lower estimates of DEE (842 kJ/day, CI = 739 - 944) than all other methods (NN: 874 kJ/day, CI = 771 – 977,  $t_{185} = -9.09$ ,

p < 0.001; KM: 875 kJ/day, CI = 772 – 978,  $t_{185}$  = -9.31, p < 0.001; HS: 875 kJ/day, CI = 772 – 978,  $t_{185}$  = -9.32, p < 0.001; HMM: 875 kJ/day, CI = 772 – 978,  $t_{185}$  = -9.35, p < 0.001; EM: 876 kJ/day, CI = 773 – 977,  $t_{185}$  = -9.63, p < 0.001). However, the difference between average DEE estimates during incubation using the RF method and the EM method, which had the highest average DEE estimates, was only 34 kJ or 3.9%.,For kittiwakes with chicks, the RF method (1185 kJ/day, CI = 1080 – 1291) also had significantly lower estimates of DEE than all other methods (HMM: 1229 kJ/day, CI = 1123 – 1334,  $t_{185}$  = -9.09, p < 0.001; HS: 1229 kJ/day, CI = 1123 – 1334,  $t_{185}$  = -9.31, p < 0.001; KM: 1229 kJ/day, CI = 1223 – 1334,  $t_{185}$  = -9.32, p < 0.001; EM: 1229 kJ/day, CI = 1123 – 1334,  $t_{185}$  = -9.35, p < 0.001; NN: 1229 kJ/day, CI = 1224 – 1335,  $t_{185}$  = -9.63, p < 0.001). During chick rearing, the difference between average DEE estimate using the RF method and the NN method, was only 44 kJ or 3.6 % of mean DEE.

#### Variable selection

#### Thick-billed murres

Classification accuracy increased from the best possible model using a single variable, 81.0% (CI = 78.7 – 82.3) to 98.7% (CI = 98.2 – 98.9) accuracy for the best model using three variables. Adding more than three variables to the model did not increase model accuracy (Figure 3.7). Variable selection identified WBF, depth, and static<sub>X</sub>, as the three variables with the greatest influence on classification accuracy. A global model using all 43 candidate variables had 98.8% (CI = 98.2 – 99.1) classification accuracy, which overlaps the accuracy achieved with the three-variable model. Following the same procedure using our original variables, WBF, pitch, depth, and sdODBA, gave comparable accuracy at 98.5% (97.7 – 98.9). Pitch, one of our a priori variables, was the fifth variable after static<sub>X</sub> and skew<sub>Z</sub>. Static<sub>X</sub> and pitch had a correlation coefficient of 0.96 (CI = 0.964 - 0.965; p < 0.001); therefore, these two variables may be largely
interchangeable. Our chosen measure of dynamic acceleration,  $SD_{ODBA}$ , did not rank among the twenty most important variables, indicating that including this metric in our original models may not have contributed to classification accuracy.

## Kittiwakes

Classification accuracy increased from the best possible random forest model using a single variable, 80.7% (CI = 77.8 – 83.0), to the best model using two variables, 92.5% (CI = 90.2 – 93.5). Additional variables did not substantially increase model accuracy (Figure 3.7). A global model using all 42 candidate variables had 93.4% (CI = 91.7 – 94.6) classification accuracy, which overlaps the accuracy achieved with the best two-variable model. Forward selection identified auto-correlation in the Z-axis (ACFz) and WBF as the best predictors in a two-variable model. ACF<sub>Z</sub> had low values during colony segments (0.1  $\pm$  0.1), intermediate values during flying segments (0.5  $\pm$  0.04), and high values during swimming segments (0.7  $\pm$  0.12). As with the initial classification methods, WBF was high during periods of flight and low during periods of swimming or periods on the colony.

Our original model using WBF, pitch and SDz had comparable accuracy, 92.5% (CI = 90.4 – 93.6%), to the top two variable model identified through variable selection. ACF<sub>Z</sub> appeared to measure differences in activity in kittiwake behaviour that were not apparent in pitch or SD<sub>Z</sub>. For both pitch and SD<sub>Z</sub>, average values of pitch and SD<sub>Z</sub> for colony were more similar to swimming than flying, while average values of ACF<sub>Z</sub> for colony and swimming were more distinct than from average values for flying. Since our original model had lower accuracy for swimming and colony behaviour, at least during incubation, ACF<sub>Z</sub> may provide better classification for these behaviours.



Figure 3.7 Change in thick-billed murre (left) and black-legged kittiwake (right) behaviour classification accuracy with additional variables included in random forest models using a forward selection procedure. Black points are medians and error bars are 95% confidence intervals.

# Discussion

We found high classification accuracy using a small number of accelerometer-derived metrics to identify coarse-scale animal behaviour. Accuracy was robust to choice of classification method. Even though there were statistically significant differences in classification accuracy for the methods tested, average accuracy of all methods was high (98% murres, 91% kittiwakes). There were no differences in mean accuracy among methods for murres and relatively small differences in mean accuracy among methods for kittiwakes. Choice of classification method appears to have little impact on classification results. Any of the methods described here should provide a robust classification of the principal behaviour types for murres and kittiwakes. We expect these results to be largely transferable to other species in the same families, and potentially more broadly applicable to other waterbirds that use flapping flight.

We were able to achieve highly accurate and consistent results across all methods using a small set of predictor variables. For both species, including more than two or three predictor variables gave no significant improvement in classification accuracy. Many other studies, particularly those using machine learning methods, include large numbers of predictor variables (Nathan et al., 2012; Ladds et al., 2017). We found that limiting the number of variables greatly reduced analysis time, because files are smaller and models are simpler. Resulting classifications are easier to interpret, especially for unsupervised classifications, because they are based on fewer predictors with an *a priori* relationship to behaviour.

More importantly, we have shown that similar variables – pitch, dynamic acceleration, and WBF – can be used to classify the behaviour of two different seabird species. The predictor variables we selected are likely to be useful in classifying coarse-scale behaviours for a wide range of species,

because changes in pitch, dynamic acceleration, and periodicity are fundamental components of all activity (Shepard, Wilson, Quintana, et al., 2008). Even in non-flying species, locomotion (walking, running, swimming) should have a distinct signature in the frequency domain which would help identify this type of behaviour (Shepard, Wilson, Quintana, et al., 2008). Measures of pitch, dynamic acceleration, and frequency should be a good starting point in any behavioural classification. However, our variable selection identified another variable, ACF<sub>Z</sub> for kittiwakes, which performed slightly better in classifying behaviour for this species, the difference in average accuracy in using this variable was minimal. In the absence of training data to conduct similar variable selection, the types of accelerometer statistics we selected *a priori* for our models are likely to be effective in classifying basic behaviour for a range of species.

That classification accuracy was consistently high is perhaps not a surprising result. Many studies have found higher accuracy when only a small number of general behaviours is considered (e.g. Shamoun-Baranes et al., 2012; Hammond, Springthorpe, Walsh, & Berg-Kirkpatrick, 2016; Ladds et al., 2017). Indeed, the behaviours we considered are readily identifiable in an accelerometer trace using the human eye. The challenge for researchers is developing methods that can automatically, and reliably, label these behaviours. This study is notable because we have demonstrated that these behaviours are easily identifiable using large data set from two different, wide-ranging seabird species, which cannot be easily observed in the wild.

Our classification of murre behaviour benefitted from incorporating data from a pressure sensor to measure depth and identify dives. However, the behaviour specific accuracy for the other three behaviours (colony, flying, and diving) were all greater than 94%, so even if diving was excluded the overall classification accuracy for murres would have been high using our methods. Pressure sensors add little to the weight and size of an accelerometer, so for most diving species there is no

reason not record pressure data along with acceleration. For very small diving species, further development of methods to classify dives and estimate depth using only accelerometer data are needed.

Classification accuracy is not the only factor that should influence choice of classification method. Depending on the research questions being addressed, certain methods may be more appropriate. Hidden Markov models offer advantages, beyond high classification accuracy, that are not achieved with the other methods considered here. Specifically, HMMs account for the serial dependence in an acceleration time series (Leos-Barajas et al., 2016). In this study, we could directly model the expected transitions between our three or four behavioural states by setting priors on the transition probabilities. Indeed, for the other classification methods we used a track segmentation approach to improve our ability to detect broad scale behaviours. Our segmentation approach would not work for species that do not have to transition through one behaviour (e.g. flight) to begin another behaviour. HMMs can also be used to jointly model how external factors influence behaviour (Leos-Barajas et al., 2016). Using other methods, this must be done in as a two-step process, first classifying behaviour and then testing for relationships with external factors. However, the HMMs are arguably the least accessible method we considered; they require sophisticated statistical understanding to implement, and success in behavioural classification depends on carefully specified priors. For applications where behavioural classification is likely to be high, and data will ultimately be summarized at large timescales (e.g. hours, days, or longer), the advantages of using HMMs may not outweigh the costs of implementing this method.

Our methods worked across two different species and breeding stages (incubation vs. chickrearing). Nonetheless, classifications were more accurate with murres than kittiwakes across all methods. Murres have high wing loading and high wing beat frequencies (Pennycuick, 1987; Elliott et al., 2013). As a result, murres only use flapping flight, which is easily defined from accelerometer profiles. Kittiwakes have much lower wing loading and lower wing beat frequencies (Pennycuick, 1987; P. G. Jodice et al., 2006). Murres make rapid, directed flights with few landings on the water, which helps to distinguish flight from swimming in GPS tracks. The more agile kittiwakes change direction and make short, frequent landings while visually searching for prey, which would create more overlap in ground speeds measured by GPS. Simultaneous deployments of GPS-accelerometers with salinity loggers or a magnetometer could help improve validation of kittiwake behaviour classifications and identify accelerometer measures characteristic of gliding flight.

In principle, there should be no difference in the behaviours we classified between incubation and chick rearing, because all of these behaviours occur in all stages of the annual cycle. However, we did find it was more difficult to classify swimming and colony behaviour accurately for incubating kittiwakes than for chick-rearing kittiwakes. For both species, swimming was primarily differentiated from colony using differences in dynamic acceleration and pitch. Kittiwakes build a nest structure to hold their eggs and can be quite active in shifting positions and turning eggs within their nest cup. This activity at the nest and changes in pitch during incubation may have made it more difficult to differentiate incubation from swimming consistently. Additionally, during incubation kittiwakes may spend more time resting on the water, which would have relatively low dynamic acceleration compared to active foraging on the water making it more difficult to discern from time spent at the nest. Variable selection analysis found that ACFz was a stronger predictor of behaviour for kittiwakes than either pitch or SD<sub>Z</sub>. ACF<sub>Z</sub> showed strong differentiation between swimming and colony, making it potentially a more useful variable in classifications for kittiwakes.

For any behavioural classification, the position of the data logger on the animal could influence the utility of certain acceleration measures. For example, a logger mounted on the tail or legs would have a different pitch signature than a logger mounted on the back or stomach, and may show different patterns of dynamic acceleration from the main body. Additionally, variation in how loggers are attached to individual animals can influence the ability to identify different behaviours between tracks. Indeed, in our data the differences in classification accuracy among individuals was significantly larger than the differences in classification accuracy among methods. Therefore, there should be careful consideration of logger position, and consistency in logger attachment, during study design, implementation, and data analysis.

By using a training data set for the RF and NN that only included a sub-sample of individuals, we demonstrated that data from a small number of individuals was transferable to a larger sample of individuals. Acquiring training data for species wide-ranging species like seabirds is an impediment to using supervised classification methods for labelling behaviours. We have demonstrated that a simple supervised classification method can be used to build a training data set for basic behaviours in seabirds. The neural network and random forest approaches have the advantage that classifications can be fully automated without any user input once a training data set has been developed. The use of machine learning techniques for classification of wide ranging species can be limited by the challenges of developing a training data set. With large data sets, a training data set could be developed based on a subsample of data using any of the other four methods described here, and a model based on this training data could be used to classify remaining data.

Wing beat frequency was an important variable in our classifications. Estimating wing beat frequency from accelerometer data requires a sampling frequency that is at least two times higher

than the expected wing beat frequency (or equivalent movement pattern) of the focal species ('the Nyquist frequency'). WBF also has many ecological applications, such as estimating changes in mass after a foraging bout (Sato, Daunt, Watanuki, Takahashi, & Wanless, 2008) and measuring changes in flight costs associated with environmental conditions (Elliott et al., 2013). Flapping flight is one of the most energetically expensive behaviours for seabirds, so accurately quantifying this behaviour is important for energetic estimates. We recommend accelerometer studies on seabirds use a sampling frequency that will allow estimation of wing beat frequency, which is consistent with other authors recommendations for sampling frequencies to adequately sample dynamic body acceleration (Gómez Laich, Wilson, Gleiss, Shepard, & Quintana, 2011). For behavioural classifications, we cannot perceive any strong rationale for sampling at frequencies higher than 2-3 times the expected WBF of a focal species.

Coarse-scale behaviour identification, like the approaches demonstrated here, could be a first step in a hierarchical process of identifying fine-scale behaviours (Leos-Barajas et al., 2016, 2017). Several studies have been successful in distinguishing general behaviours, like the behaviours identified in this paper, but have been less successful in effectively classifying finer scale behaviours associated with prey capture, prey handling and self-maintenance (Shamoun-Baranes et al., 2012; Hammond et al., 2016; Ladds et al., 2017). An initial partitioning into general behaviour classes may simplify the process of defining detailed behaviour profiles, especially where these behaviours occur as a subset within more coarse-scale behaviour. While our results show that accurate classification of basic seabird behaviours can be developed using simple methods and a small group of accelerometer statistics, identifying fine scale behaviour may require independently collected training data, and a larger suite of predictor variables, to capture the unique characteristics of less common behaviours.

# Conclusion

Obtaining reliable activity budgets from free-ranging animals is important for addressing a wide range of questions in wildlife ecology and animal behaviour. Combined with methods for tracking animal location, behavioural classification from accelerometers could be used to examine the relationship between behaviour and environmental conditions over large spatial and temporal scales. We believe that uncertainty about how to classify behaviour from accelerometers has been a barrier to wider use of this technique. Our results demonstrate that general behaviours of seabirds can be classified from acceleration profiles using a range of techniques and a small number of predictor variables. Choice of classification method had a negligible effect on accuracy, therefore, researchers should not be impeded by a need to develop and apply the most advanced classification method, as multiple methods can provide similar results when classifying a small number of common behaviours. However, this finding may not hold in cases where the objective is to identify more detailed types of behaviour than the broad classes considered here. Where the goal of classification is to develop a daily activity budget or estimate daily energy expenditure, then simple classification methods are likely adequate, at least for waterbirds that primarily use flapping flight. Where the goal is to examine how different factors effect behaviour, the HMM approach may be preferable because this approach can be used to directly test the effect of predictor variables on behaviour.

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## **Conflict of interest**

None declared.

## Data accessibility

Data used in this analysis and R scripts for behavioural classifications have been archived at <a href="https://datadryad.org/">https://datadryad.org/</a> (doi:10.5061/dryad.2hf101c).

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# Linking statement

The previous chapter developed and compared methods of classifying seabird behaviour from accelerometer traces, with the goal of promoting greater adoption of this type of biologging technology in ecological studies. Accelerometers can provide detailed activity budgets, with the potential for long-term tracking deployments during times of year when individuals may be hard to observe. The next chapter uses biologging data collected from year-round deployments of temperature-depth-recorders on thick-billed murres to examine the effect of habitat and climate variation on behavior and energetics. This chapter implements this type of behavioural study of seabirds at-sea, when they are largely unobservable, that the previous chapter is designed to support.

# 4. Behavioural flexibility in an Arctic seabird using two distinct marine provinces to survive the energetic constraints of winter

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**Author contributions:** All authors contributed to the conception of this study. AP and KE collected field data, with logistical support from HG. AP conducted all data analysis and interpretation, and prepared the initial manuscript. All authors contributed critically to the drafts.

**Data availability:** Data underlying the results of this study will be made available in an appropriate public archive offering open access and guaranteed preservation prior to publication.

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## Abstract

- Homeothermic marine animals in polar regions face an energetic bottleneck in winter that can be overcome by either using a feasting strategy that maximizes foraging efficiency or a resting strategy that minimizes energy expenditure. With their relatively small body size and limited fat stores, the challenges of short days and cold temperatures at high latitudes are exacerbated for flying seabirds.
- 2. We used light-temperature-depth recorders to examine the role of marine habitat, day length, moon illumination, and the state of the North Atlantic Oscillation (NAO) on strategies thick-billed murres use to survive winter in the Northwest Atlantic, where currents carrying cold polar water mix with warm water from the North Atlantic Current creating strong temperature gradients.
- 3. Murres made regular use of two distinct marine provinces: cold (-0.1 ± 1.2 °C), shallower water along the Labrador and Greenland Shelves and warmer (3.1 ± 0.3 °C), deep water in the Labrador Basin. In the cold shelf water, murres used a feasting strategy, with more flying and less foraging each day, resulting in high daily energy expenditure but also high apparent energy intake; this strategy was most evident in early winter when day lengths were shortest. By contrast, murres in warmer basin water employed a resting strategy, with less time flying and more time foraging under low light conditions (nautical twilight and night). In warmer basin water, murres increased diving at night when the moon was full, likely taking advantage of diel vertically migrating prey.
- 4. Changes in daily NAO had direct effects on the behaviour of murres in warmer basin water: under negative NAO (calmer ocean conditions) murres dove more at night and foraging

efficiency increased, while under positive NAO, murres dove mostly during the day and foraging efficiency declined.

5. The proximity of two distinct marine habitats in this region allows individuals from a single species to use dual (low-energy/high-energy) strategies to overcome winter energy bottlenecks.

# Introduction

Animals of all kinds make seasonal and daily movements to balance energy intake and expenditure. Mobile organisms can regulate their energy balance by periodically occupying environments that increase energy intake or reduce metabolic costs (Armstrong et al., 2013; Campana et al., 2011; Huey, 1991; Swingland & Lessells, 1979). Winter strategies encompass a spectrum that with hibernation at one end, minimizing energy output (Geiser, 2020), and pole-to-pole migration at the opposite end, maximizing energy intake (Egevang et al., 2010; Shaffer et al., 2006). Small-bodied, flying birds have limited capacity to build up energy reserves to cope with challenging environments, so they must adopt strategies that balance energy intake and energy expenditure over relatively short time scales (Clairbaux et al., 2021; Clark & Dukas, 2000; Grémillet, Kuntz, Woakes, et al., 2005).

During winter at high latitudes, low air and water temperatures increase energetic demands for thermoregulation at the same time as shorter day lengths limit opportunities for foraging (Daunt et al., 2006; Grémillet & Wilson, 1999). These challenges are particularly acute for diving seabirds species that spend nearly all of their time on or under water, where heat loss is greater than in air, and also have limited insulation and stored energy reserves in order to retain the ability to fly (Amélineau et al., 2018; Fort et al., 2009, 2013; Richman & Lovvorn, 2011). Highly mobile species, such as seabirds, may switch among different marine habitats during winter to take advantage of more favourable conditions that increase energy intake and/or reduce energetic costs within their wintering areas.

One strategy for species wintering in areas with limited daylight would be to minimize the time required for foraging by locating and exploiting high quality prey patches, a *feasting strategy* 

(Grémillet & Wilson, 1999). In this case, we would expect relatively high dive efficiency and more time spent searching for prey patches above-water in flight. Because there are significant additional locomotion costs associated with flying in search of prey, this feasting strategy should be preferred when prey density is high (Norberg, 1977). Alternatively, species may select habitat and adopt foraging behaviour that minimizes energy expenditure in winter, a *resting strategy* (Norberg, 1977). For marine species, this could mean selecting regions with warmer ocean temperatures that reduce costs of thermoregulation. Because light availability is a critical parameter limiting time available for foraging in winter, a resting strategy would likely depend on extending foraging into periods with lower light availability, (Grémillet, Kuntz, Gilbert, et al., 2005; Grémillet & Wilson, 1999; Moe et al., 2021). Some diving predators take advantage of increased illumination from the moon to forage longer and deeper at night (Elliott & Gaston, 2015; Regular et al., 2011). Foraging strategies that minimize energy expenditure are predicted to be more efficient when prey density is lower (Norberg, 1977).

Thick-billed murres (*Uria lomvia*), hereafter murres, are a widely distributed Arctic seabird species, that is declining through portions of their global range, with some declines apparently linked to wintering areas (Frederiksen et al., 2016). Winter has been proposed as a potential energetic bottleneck for Alcids wintering in the North Atlantic (Amélineau et al., 2018; Fort et al., 2009, 2013). In Canada, murre colony sizes show synchronous patterns, indicating that conditions on shared wintering areas may be important for determining survival and subsequent breeding success (Gaston, 2003). The energetic costs of flight are five times higher than costs of diving or resting on the water in murres (Elliott et al., 2013); therefore, murres must trade-off the costs of flight with the benefits of locating profitable prey patches. Indeed, breeding murres switch to

feeding on amphipods in order to minimize flight costs associated with searching for fish during high winds (Elliott et al., 2014).

A resting strategy that relies on night-feeding would be most beneficial where diel vertical migration (DVM) brings prey into the surface layers of the ocean at depths that are accessible to diving predators at night. This daily migration allows mesopelagic zooplankton and fish to feed in productive surface waters with reduced predation risk from visual predators. Under daylight conditions murres can forage at depths down to 200 m (Gaston & Hipfner, 2000), while at night maximum dive depths are less than 50 m (Regular et al., 2011) and most dives occur in the top 20 m of the water column (Elliott & Gaston, 2015). Because dive depth at night is limited by light availability (Regular et al., 2011), use of a night-feeding strategy is likely influenced by both moon phase and weather, with higher rates of night diving when the moon is full and cloud cover is low. Night-feeding could be a more profitable strategy in deeper water (>200 m), where prey can take refuge below the maximum diving depth of murres during the day. Environmental conditions that contribute to a higher biomass of DVM prey or a shallower active layer at night could promote night-feeding.

Weather can impact the behaviour and foraging of seabirds through increased energetic costs associated with increased wind or through reduced visibility and accessibility of prey (Daunt et al., 2006; Elliott et al., 2014; Finney et al., 1999). The North Atlantic Oscillation is an important climate pattern that is associated with changes in weather and ocean climate in the Northern Hemisphere (Drinkwater et al., 2003; Greatbatch, 2000), which have been shown to have a pronounced influence in both terrestrial and marine ecosystems (Hurrell et al., 2001). The NAO is measured as a the gradient of sea level pressure between the Icelandic low pressure center and the Azores high pressure center, where positive phase is associated with a strong gradient and

negative phase is associated with a weak gradient. Annual and seasonal NAO has been shown to influence seabird adult survival (Grosbois & Thompson, 2005; Sandvik et al., 2005); breeding phenology (Frederiksen et al., 2004); reproductive success and breeding propensity (Thompson & Ollason, 2001); foraging behaviour (Pereira et al., 2020; Thompson & Ollason, 2001); and chick growth rates (Pereira et al., 2020). Positive NAO is associated with strong northwest winds, colder temperatures, less precipitation, higher ice cover, and increased storm activity in the northwest Atlantic (Bader et al., 2011; Hurrell et al., 2003; Mann & Drinkwater, 1994). Climate indices, like the NAO, can be useful in understanding effects of weather on wildlife because they can provide a simplified measure of complex spatial and temporal variability in prevailing weather conditions within a region (Stenseth et al., 2003).

Recent advances in our ability to track murres year-round have demonstrated exceptionally high foraging effort (dive depth and time spent diving) in common murres (*Uria aalge*), a closely related species, wintering in the North Sea (Dunn et al., 2020) and on the Newfoundland and Labrador shelf (Burke & Montevecchi, 2018). Here, we use miniature depth loggers to study thick-billed murres originating from a breeding colony on Coats Island, in northern Hudson Bay (Figure 4.1), which winter in the northwest Atlantic Ocean (Gaston et al., 2011; McFarlane Tranquilla et al., 2013). This globally-significant wintering area is shared by common and thick-billed murres, black-legged kittiwakes (*Rissa tridactyla*), Atlantic puffins (*Fratercula arctica*), and dovekies (*Alle alle*) originating from colonies throughout Arctic and Atlantic Canada, as well as Greenland, Iceland, and Spitsbergen (Clairbaux et al., 2021; Frederiksen et al., 2016; McFarlane Tranquilla et al., 2015). This region is dominated by cold water currents flowing along the Labrador and West Greenland Shelves, relatively warm and deep water of the Labrador Basin in between, and the warmer North Atlantic Current (Gulf Stream) to the south (Figure 4.1).

We examined how marine habitat type, defined by sea surface temperature, influences behaviour and energetics of thick-billed murres during winter. We used measurements of sea surface temperature from leg-mounted temperature-depth-light recorders to assign individuals to three broad habitat classes, which correspond well with the three major ocean systems within the winter range of this population. We then examine how habitat class, day of year, moon phase, and climate conditions (NAO) influenced winter strategies. Specifically, we looked for differences in daily activity budgets, energetics, and diving behaviour, to determine how murres cope with the demands of winter within the marine habitats in their range. Under the feasting strategy we expected murres to spend less time foraging and more time flying per day, because murres are travelling more to locate patches of high quality prey. Under the resting strategy, we expected murres to spend more time foraging under low light conditions (during twilight or nighttime) to compensate for reduced foraging time available during the day.



Figure 4.1. Study area map showing location of the breeding colony at Coats Island (black triangle), in Hudson Bay, the Labrador Shelf, and the Labrador Basin. White arrows indicate the flow of the Labrador Current (LC), the West Greenland Current (WGC), and North Atlantic Current, adapted from (Yashayaev et al., 2021).

# Methods

#### *Temperature-depth-light recorders*

Tracking of murres in winter was initiated by deploying devices on birds in summer while they breed at Coats Island, in Hudson Bay, Nunavut, Canada ( $62.95^{\circ}N$ ,  $82.01^{\circ}W$ ), a colony of 30,000 breeding pairs of thick-billed murres (Gaston et al. 2012). In 2017 (n = 48) and 2018 (n = 45), we deployed LAT2800S geolocator-temperature-depth-recorders (Lotek, Newmarket, ON; 36-mm x 11-mm x 7.2-mm, 5.5-g). Loggers were programmed to collect light level, temperature, depth, and wet/dry state at 10-second intervals. All loggers were deployed on breeding adults captured using a noose pole, while attending an egg or chick. Loggers were retrieved and downloaded during subsequent (one or two) breeding seasons. Analysis for this study focused on January to March in 2018 and 2019. This period coincides with the time of year when all individuals are present within their wintering range.

## Estimating dive behaviour, SST, daily activity rates, and energetics

Dives were defined as any period when depth was at least 5 m. We classified dives into four light categories according to the estimated solar angle at the mean latitude and longitude (average of locations estimates at dawn and dusk) for each individual on each day. Location estimates were obtained using the 'probGLS' package in R (Merkel et al., 2016), a complete description of this analysis is provided in the supplementary material (Table 11.1). Solar elevations were obtained using the 'suncalc' package (Thieurmel & Elmarhraoui, 2019). Classes were day (>0°), civil twilight (0° to -6°), nautical twilight (-6° to -12°), and night (<-12°). We calculated the total time diving within each light category per day.

We estimated the SST based on times when a murre was likely to be swimming at the surface of the water. Initially, we calculated the range of water temperatures experienced during each day based on the 5<sup>th</sup> to 95<sup>th</sup> quantiles of temperature measurements recorded during dives; this range was used to set upper and lower limits on potential SST. Murres were assumed to be at the surface of the water when: the range of temperatures experienced over every 180 sec period was less than  $0.5^{\circ}$ C; the bird was not diving; the tag was not dry; and the temperature was within the range of water temperatures recorded by the tag that day (±1°C). The daily SST estimate was calculated as the mean temperature measured for all at surface data points during each day.

Murres were considered to be flying if the logger was dry for at least 60 seconds and the maximum temperature while dry was less than 7°C. Murres were considered to be resting, with the tagged leg tucked, if the maximum temperature was greater than 7°C. Daily activity rates were calculated for time flying, time foraging (total time in dive bouts), and time resting with the tagged leg tucked. All remaining time was classified as swimming for use in calculating daily energy expenditure (DEE).

We calculated DEE based on daily activity budgets, dive durations, and SST, using the equation from (Burke & Montevecchi, 2018, based on Elliott & Gaston 2014):

$$DEE = 508 * T_f + 3.64 * \left(\sum 1 - e^{\frac{d}{1.23}}\right) + (113 - 2.75 * SST) * T_s + (72.2 - 2.75 * SST) * T_r$$

Where,  $T_f$  is time spent flying per day in hours, d is duration of each dive in minutes, *SST* is sea surface temperature in °C,  $T_s$  is time spent actively swimming in hours, and  $T_r$  is time spent resting on the water in hours. We calculated an apparent energy intake rate assuming that murres are balancing their energy budget over 5-day interval. The apparent energy intake (AEI) rate was based on the 5-day moving averages of DEE and time spent diving:

$$AEI = \frac{DEE_5 * 1/E}{Td_5}$$

Where,  $DEE_5$  is the 5-day rolling average of daily energy expenditure, Td<sub>5</sub> is the 5-day rolling average of time spent diving. E is a constant to correct for assimilation efficiency (73%) of prey items (Brekke & Gabrielsen, 1994).

## Classification of habitat states and habitat distribution

Three thermal habitat states – Cold, Warm, and Warmer – were defined using a hidden Markov model (HMM), with mean daily SST as a predictor variable. A three state model was the minimum number of states required to obtain non-overlapping state distributions. State distributions were modelled using a normal distribution, with initial probability distributions (mean  $\pm$  SD) of -1  $\pm$  3°C (Cold), 3  $\pm$  3°C (Warm), and 8  $\pm$  3°C (Warmer); varying these starting values by  $\pm$ 1°C had no affect on predicted state distributions. Daily transition probabilities among states were modelled as a function of four potential main effects: year (2018 or 2019), day of year, moon illumination, and NAO. AIC was used to identify the most parsimonious model among all combinations of main effects on the transition probabilities. The HMM models were run using the 'momentuHMM' package, version 1.5.2 (McClintock & Michelot, 2018). Model checking was performed by simulating observations from the fitted model and comparing observed data to the expected quantiles and autocorrelation function from the simulated data (McClintock et al., 2020). The Viterbi algorithm was used to assign each point data to one of the three habitat states (McClintock & Michelot, 2018).

We used monthly SST measurements to estimate the spatial distribution of each habitat class within the study area. We extracted environmental data from a  $0.25^{\circ} \times 0.25^{\circ}$  grid within the study

area from Copernicus Marine Service Global Ocean Physics Reanalysis (GLOBAL\_ANALYSIS\_FORECAST\_PHY\_001\_030). We calculated the probability density function for each state based on the SST value of each monthly raster cell and assigned each cell to the state with the highest probability.

#### Statistical analysis

We used generalized linear mixed models (GLMM) to test for effects of habitat type, day of year, moon phase, and daily NAO on the proportion of total time diving during different light conditions (day, civil twilight, nautical twilight, and night), daily activity rates (flying and diving), and energetics (DEE and AEI). We obtained moon illumination based on the fraction of the moon visible on each date, values ranges from 0 (new moon) to 1 (full moon), using the 'suncalc' package (Thieurmel & Elmarhraoui, 2019). Daily NAO values were obtained from the United Prediction States National Weather Service Climate Center (https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao.shtml). Preliminary data analysis showed no evidence of differences in diving, activity budgets, or energetics between males and females, therefore we did not include sex in the analysis.

Models included all two-way interactions between habitat and other main effects (DOY, moon illumination, and NAO). Individual deployment identity and tracking year were included as random effect in all models. Models of dive times and activity times were fit using a beta distribution with a logit link function. For proportion of time diving under different light conditions all four response variables (daylight diving, civil twilight diving, nautical twilight diving, and night diving) were divided by the total time spent diving that day to normalize values between 0 and 1. For daily activity rates the response variables (flying and diving) were divided by 24 hrs to

normalize values between 0 and 1. Where the response variable contained more than 2% zero values in data we included a zero inflation parameter dependent on habitat in the set of candidate models. When less than 3% of the response values had zero values (daylight diving and time diving) we added 1 min of time to response values to fit models without zero inflation. Models of energetics (DEE and AEI) were fit with a Gamma distribution, with a log link function to ensure that parameter estimates were positive. GLMM models were run using the 'glmmTMB' package in R (Mollie et al 2017). Parameter estimates in tables are presented on the link scale ± SE. Model predictions provided in the text are estimated marginal means with 95% confidence intervals on the response scale. GLMM model fits were evaluated using posterior predictive checks with the 'performance' package in R (Lüdecke et al., 2021). Finally, we examined dive depth profiles across habitat class and light category. We calculated the percentage of all dives within each habitat that occurred within 10 m depth categories for each of the four light classes.

# Results

We recovered tracks from 34 murres in 2018 and 20 murres in 2019. The majority of tracks covered the entire winter period (96%), except for two tracks that ended during March. Sample size of tracks was split relatively evenly between males (n = 25) and females (n = 29).

## Habitat classification and physical oceanography

Mean SST within the three habitat states from the HMM was -0.1 °C ( $\pm$  1.2 °C) for Cold water, 3.1 °C ( $\pm$  0.3 °C) for Warm water, and 6.5 °C ( $\pm$  2.4 °C) for Warmer water. The spatial distribution of these habitat states broadly corresponded to the major currents within the Northwest Atlantic (Figure 4.2). The Cold water habitat was primarily located in shelf regions along the Labrador, Newfoundland and Greenland coasts; this habitat corresponds to cold-water carried by the Labrador, West Greenland, and East Greenland Currents (Figure 1, Reverdin et al., 2003). The Warm habitat was located in the deep water of the Labrador Basin. The Warmer water habitat occurred primarily in the south and east extent of the winter range, and includes water from the North Atlantic Current (Reverdin et al., 2003). This distribution of habitat was relatively consistent throughout the study period, except for Mar 2019, when the warmer water habitat intruded farther into the Labrador Basin (Figure 4.2). A detailed comparison of physical oceanographic features associated with the habitat classes is provided in the supplementary material.

#### Murre habitat use and transition probabilities

In both years, the proportion of murres using Cold water was highest in January and March, while use of Warm water peaked in February (Figure 4.3). On average, murres spent 46 days (range = 5-90) in Cold water, with six individuals (11%) staying in Cold water through the entire winter period (Jan 1 – Mar 31). The mean time spent in Warm water was 39 days (range = 0-85) and 87% of tracked murres spent some time in Warm water during winter. Use of Warmer water was low throughout the winter; only 17% of murres spent any time in Warmer water, with mean time of only 5 days (range = 0-64). Cold and Warm water habitat were used at similar rates and the majority of tracked murres, 89%, switched between at least two habitats during winter (Figure 11.2). Transition probabilities were highest between Cold and Warm water (Cold-Warm 0.033, Warm-Cold 0.024). Transitions from either Cold or Warm water to Warmer water had a relatively low probability (Cold-Warmer 0.001, Warm-Warmer 0.003). Transitions probabilities were higher from Warm to Cold and from Warmer to either of the other habitats in 2019 than in 2018. Murres in Warm water were more likely to transition to Cold water when NAO was negative and when moon illumination was higher.


*Figure 4.2. Estimated monthly spatial distribution of the three habitat types - Cold water, Warm water, and Warmer water – identified using the hidden Markov model, for winter 2018 and 2019. Dashed line indicates the 1000 m shelf break.* 



Figure 4.3. The proportion of tracked thick-billed murres from Coats Island, NU, Canada, using each habitat type by date and year in winter (Jan-Mar) of 2018 and 2019. Habitat types were determined using a hidden Markov model with sea surface temperature measured using leg mounted temperature-depth-light recorders, as the observed state.

#### Proportion of time diving and dive depths under different light conditions

Most diving occurred during daylight for murres in both habitats (Figure 4.4); however, daylight diving was more prevalent for murres in Cold water than in Warm water (Figure 4.5, Table 11.2, Table 11.3). The proportion of diving that occurred during daylight increased with DOY in both habitats, but the rate of increase was greater in Warm water than in Cold water. In both habitats, murres made between 10-20% of dives during civil twilight and the proportion of diving during civil twilight declined with DOY. Diving under low light conditions (nautical twilight and night) was more prevalent for murres in Warm water, where murres made a significantly higher proportion of dives under low light conditions in early winter. Short day lengths in early winter apparently limit day light diving in both habitats, but only murres in Warm compensated by increasing the proportion of time diving during nautical twilight and at night.

Moon phase and NAO strongly influenced diving behaviour of murres in Warm water, but had little effect on diving by murres in Cold water (Figure 4.5, Table 11.2, Table 11.3). When the moon phase was bright, murres in Warm water increased the proportion of their diving that happened at night and decreased the proportion of diving that occurred during other light phases. In Warm water, NAO had a strong positive effect on proportion of diving that occurred during the day and a strong negative effect on time diving during nautical twilight and at night. The marginal effect of NAO on timing of diving for murres in Warm water was remarkable: under NAO +2, the vast majority of diving occurred during the day (87%) and night diving was minimal (6%), while under NAO -2, the proportion of time diving at night (27%) was approaching the predicted proportion of diving during the day (36%). Increased moon illumination and negative NAO both contributed to an increased proportion of time diving under low light conditions (nautical twilight and night) by murres in Warm water, but had little or no effect on diving behaviour of murres in Cold water.

The majority of dives occurred during the day in both habitats (Figure 4.6); however, the proportion of dives during the day was much higher in Cold water, 81%, than in Warm water, 62%. Murres in Warm water made a higher proportion of their dives during nautical twilight, 12%, and at night, 14%. Day dives were primarily concentrated between 40-100 m deep in Cold water, while murres in Warm water made deeper dives during the day (70-130 m). Dive depths attenuated with light availability in both habitats; most dives during nautical twilight and at night were less than 20 m deep (Figure 4.6).



Figure 4.4. Predicted proportion of time diving (%) for thick-billed murres in winter, based on time of day (yellow = daylight, green = civil twilight, light blue = nautical twilight, dark blue = night), day of the year, habitat type (Cold or Warm), moon illumination (0 = new, 1 = full) and North Atlantic Oscillation (NAO) index. In the two upper plots, the solid line shows the mean prediction and shaded areas are the 95% confidence interval.



Figure 4.5. Predicted marginal effects of day of year (DOY), moon illumination (0: new moon, 1: full moon) and the North Atlantic Oscillation (NAO) on proportion of time diving during (%) daylight, civil twilight, nautical twilight, and night for thick-billed murres in Cold water (blue) and Warm water (red) habitat in the Northwest Atlantic. Solid lines are predicted marginal means from a generalized linear mixed effects model, shaded areas are 95% confidence intervals, and points are observed daily observations. Note that the y-axis ranges vary among rows.



Figure 4.6. Distribution of dive depths by habitat type (Cold – blue, Warm – red) and light level. Each panel shows the percentage of dives at 10 m depth intervals, values across panels sum to 100 for each habitat type.

#### Daily activity rates

Murres spent an average of 3-6 hours diving per day throughout winter (Figure 4.7). DOY, moon illumination, and NAO all influenced total time diving per, but the affects differed between habitats (Table 11.4, Table 11.5). In Cold water, murres increased the amount of time diving from 3.6 hr/day in early winter to 5.2 hr/day in late winter (Figure 4.8). Given that murres in Cold water primarily forage under high light conditions, this increase in time diving with DOY is likely driven by increased availability of daylight later in winter. In Warm water, there was no effect of DOY on time diving; however, moon illumination had a moderate positive effect on total time diving and NAO had a strong positive effect on total time diving. At NAO -2 murres in Warm water were expected to spend 4.0 hr/day diving, at NAO +2 murres were expected to spend 5.4 hr/day foraging. This could indicate that murres in Warm water were able to forage more efficiently when NAO was negative, when a higher proportion of total dive time occurred at night.

Averaging across predictors, murres spent more time flying in Cold water (0.55 hr/day, CI = 0.51-0.60) than in Warm water (0.34 hr/day, CI = 0.31-0.37, Figure 4.7, Table 11.4). In Warm water, murres doubled the amount of time flying per day from 0.24 hr/day in early winter to 0.48 hr/day in late winter; while DOY had no affect on time flying in Cold water (Figure 4.8, Table 11.5). In both habitats, murres flew less when NAO was more positive. Increased wind associated with positive NAO phases could limit flying by murres throughout their winter range. Moon illumination was included in the top model for time flying, but the sizes of these affects were relatively small.



Figure 4.7. Time spent diving and flying for thick-billed murres in Cold water habitat (blue) and Warm water habitat (red) for 2018 and 2019, Lines show predicted values from generalized linear models, that included fixed effects for habitat, year, day of year, moon, and North Atlantic Oscillation, as well as two-way interactions between habitat and all other predictors. Solid lines are mean estimates and dashed lines are 95% confidence intervals. Points show the observed values for each individual each day. Note that y-axis ranges change among plots.



Figure 4.8. Predicted marginal effects of day of year, moon illumination (0: new moon, 1: full moon) and the North Atlantic Oscillation (NAO) on time spent flying and diving for thick-billed murres in Cold water (blue) and Warm water (red) habitat in the Northwest Atlantic. Solid lines are predicted marginal means from a generalized linear mixed effects model, shaded areas are 95% confidence intervals, and points are observed daily observations.

### **Energetics**

Murres had higher DEE in Cold water, 2589 kJ/day (CI = 2553-2625) than in Warm water, 2268 kJ/day (CI = 2236-2300, Figure 4.9, Table 11.6, Table 11.7). This difference was driven by a combination of additional time flying and the lower SST in the Cold water habitat. DEE declined during the winter in Cold water and increased slightly in Warm water (Figure 4.10). NAO had a negative effect on DEE for murres in both habitats, which can be attributed to the decline in time flying under positive NAO conditions (Figure 4.10).

Apparent energy intake was higher in Cold water, 769 kJ/hr diving (CI = 753-784) than in Warm water, 714 kJ/hr diving (CI = 699-728, Figure 4.9, Table 11.6, Table 11.7). AEI declined with DOY in both habitats; however, the decline was larger in Cold water than Warm water (Figure 4.10). By the end of winter, AEI was similar in both habitats (Figure 4.9). Moon illumination had a modest negative effect on AEI in Warm water, but there was no moon effect in Cold water. NAO had a strong negative affect on AEI in both habitats (Figure 4.10); this means that when NAO was positive, murres in both habitats had lower foraging efficiency, and spent relatively more time diving to meet their estimated DEE.



Figure 4.9. Daily energy expenditure (kJ/day) and apparent energy expenditure (kJ/hour) of thickbilled murres in Cold water habitat (blue) and Warm water habitat (red) for 2018 and 2019. Lines show predicted values from generalized linear models, that included fixed effects for habitat, year, day of year, moon, and North Atlantic Oscillation, as well as two-way interactions between habitat and all other predictors. Solid lines are mean estimates and dashed lines are 95% confidence intervals. Points show the observed values for each individual each day. Note that y-axis ranges change among rows.



Figure 4.10. Predicted marginal effects of day of year, moon illumination (0: new moon, 1: full moon) and the North Atlantic Oscillation (NAO) on daily energy expenditure (DEE) and apparent energy expenditure (AEI) for thick-billed murres in Cold water (blue) and Warm water (red) habitat in the Northwest Atlantic. Solid lines are predicted marginal means from a generalized linear mixed effects model, shaded areas are 95% confidence intervals, and points are observed daily observations.

## Discussion

Marine habitat had strong effects on dive behaviour, daily activity rates, and energetics, such that Cold water was associated with a high-energy feasting strategy and Warm water was associated with a low-energy resting strategy. Murres regularly used two habitat types during winter, Cold water that occurs along the Labrador and Greenland shelves and Warm water within the Labrador Basin. Murres had significant among and within-individual flexibility to exploit these two habitats, which apparently support different strategies for surviving the high energetic costs of winter. Wintering in the Cold shelf water had higher energetic costs associated with thermoregulation and increased flight activity; however, these costs were evidently offset by higher apparent energy intake rates during early winter requiring less foraging each day. The Warm basin water had lower energetic costs, but required murres to spend longer foraging each day, including foraging under low light conditions during nautical twilight and at night.

Murres from our study population occasionally used Warmer water in the North Atlantic current; however, the proportion of tracked murres using this habitat was relatively small, precluding a detailed analysis of behaviour and energetics within this habitat. While murres in our population avoided this Warmer water in mid-North Atlantic, this region does support wintering murres from other colonies (Frederiksen et al., 2016) and is a persistent year-round hotspot for numerous seabird species (Davies et al., 2021).

We found support for the feasting strategy for murres wintering in Cold water habitat. Murres spent the most time flying and the least time foraging in this habitat. Additional flight time and costs of thermoregulation both contributed to higher DEE in Cold water. The most likely reason for increased flying is that murres in this habitat invest more time and energy searching for high quality prey patches. In spite of the increased energetic costs associated with this activity, murres in Cold water spent less time foraging through most of the winter than those in Warm water, leading to higher apparent energy intake. Murres must be able to achieve higher foraging efficiency in this habitat to support this difference in behaviour and energetic costs. This feasting strategy could be susceptible to sudden changes in prey availability, and be especially risky when extreme weather or ice conditions prohibit travelling to areas with better prey conditions. Coastal ice buildup and sustained northeasterly winds have contributed to wrecks of thick-billed murres in Newfoundland, where murres trapped in coastal bays by ice starved within 2-3 days (McFarlane Tranquilla et al., 2015). Similarly, many seabirds wintering in the North Atlantic are vulnerable to extended periods of stormy weather, where wind and rough seas are thought to limit birds ability to forage or access prey over extended periods of time (Clairbaux et al., 2021; Daunt et al., 2006; Frederiksen et al., 2008). Body temperature increases during flight (Torre-Bueno, 1976), particularly for aquatic species with high wing loading (Guillemette et al., 2007). In Cold water habitat, increased flying may have additional benefits for thermoregulation as well as locating prey.

In contrast, murres in Warm water used a resting strategy, expending less energy on flight and thermoregulation but spending more time overall diving for prey. Individuals using an active foraging mode expend more energy and should encounter more prey than individuals using a passive foraging strategy (Huey & Pianka, 1981; Masman et al., 1988; Norberg, 1977). For murres, increasing time searching for prey underwater, rather than in the air, would have significant energetic savings as the costs of diving are comparable to swimming at the surface (Elliott et al., 2013). Passive foraging should be more profitable at low prey density (Norberg, 1977). If prey density is low, and murres are foraging passively to conserve energy, then Warm water habitat has

the additional benefit of reduced energy expenditure on thermoregulation. In both years, use of Warm water peaked in mid-winter (February), potentially because murres move out of Cold water as prey density declines through winter and return to Cold water in March as the time available for foraging during daylight increases.

Murres only dove significantly at night in Warm water; presumably, because in Cold water they were able to meet their daily energy needs during daylight while murres in Warm water could not. Indeed, murres in Warm water increased their night diving effort in response to increased moon illumination (full moon) and weak NAO conditions. We propose that this was a response to increased opportunity to benefit from diel vertical migration when light conditions were favourable for diving at night. Interestingly, murres in Warm water reduced diving during nautical twilight when moon illumination was high but increased it when NAO was positive. Potentially, murres may maximize diving under the fading light conditions of nautical twilight when there is no moonlight but clear skies, but wait for full night conditions when the moon is brighter, or the arrival of DVM prey in shallow water is delayed under full moon conditions. Limited night foraging in Cold habitats could have important climate change implications. If Cold shelf habitat does not support foraging at night, then individuals in this habitat cannot switch to a night foraging strategy as northward range shifts decrease time available for foraging during the day creating a habitat-mediated photic barrier to range shifts (Huffeldt, 2020).

The rapid response of murres to daily changes in NAO could be an indication that effects of NAO on murre behaviour are mediated through weather, specifically wind or cloud cover, which could immediately effect the energetic costs of flight and foraging ability of murres. Other indirect mechanisms of NAO forcing through effects on the food web would likely occur over a longer time scale than what was tested here. DEE and AEI were both higher under negative NAO

conditions; we attribute this relationship to increased time flying during weak NAO. Wind speeds in the Northwest Atlantic are higher under NAO positive conditions (Drinkwater et al., 2003); murres could reduce time flying due to increased wind. This could simultaneously reduce DEE and AEI if murres are limited in their ability to search out prey. Probably the most dramatic results associated with NAO was the marked increase in nocturnal foraging, and concurrent decline in total time foraging, in Warm (basin) water when NAO was negative. We interpret this as increased foraging efficiency at night. Negative NAO is associated with decreased wind in the Northwest Atlantic. This could promote nocturnal foraging if decreased wind allows stratification of surface water layers (Drinkwater et al., 2003), promoting increased plankton growth and greater biomass of DVM. Less wind could also cause reduced turbulence and a thinner active mixing layer at the surface (Sutherland et al., 2014), forcing prey to migrate closer to the surface at night where they would be more accessible to diving murres (Heywood, 1996). Given that our time series of murre behaviour only covers two winters, during which strongly negative NAO conditions occurred infrequently (primarily late-Feb to late-Mar 2018), it is possible that the effect of NAO observed here arise from a single anomalous event that may not be re-occur with additional monitoring.

Given the differences in oceanography and foraging behaviour between the Cold (shelf) and Warm (basin) habitats observed in our study, it is likely that murres target different prey within these marine provinces. Relatively little is known about the winter diet of thick-billed murres, and what sampling has occurred is biased towards murres collected by hunters in coastal waters around Newfoundland and western Greenland (Elliot et al., 1990; Falk & Durinck, 1993; Gaston et al., 1983). Early studies of winter diet reported a shift from predominantly fish and squid in early winter to amphipods and euphausiids in Jan-Mar (Elliot et al., 1990). Invertebrate prey include amphipods (*Parathemisto* spp.), euphasiids (*Thysanoessa* spp.), squid (*Gonatus fabricii*) and

polychaetes (Nereis pelagica), while fish species identified in winter diets include Arctic cod (Boreogadus saida), Atlantic cod (Gadus morhua), capelin (Mallotus villosus), and Northern sandlance (Ammodytes dubius) (Elliot et al., 1990; Falk & Durinck, 1993; Gaston et al., 1983; Moody & Hobson, 2007). Isotopic analysis indicated that thick-billed murres collected around Newfoundland fed on a mix of fish and invertebrate prey in winter, with a higher proportion of invertebrates in their diet than during the breeding season (Moody & Hobson, 2007). Murres collected near Nuuk, Greenland, switched from a diet dominated by fish, primarily capelin, in October to one dominated by crustaceans in March (Falk & Durinck, 1993), similar to trends reported in Newfoundland. In Greenland, murres collected in the southwest had a higher proportion of fish in their stomach contents than murres collected in the northwest (Falk & Durinck, 1993). We found an increase in time spent diving and a decrease in AEI for murres in Cold water through winter, which would be consistent with a switch from fish to crustaceans as observed in these other studies. Myctophids (Benthosema glaciale) are abundant and evenly distributed within the Labrador Sea (Coté et al., 2019; Klevjer et al., 2020; Pepin, 2013). Myctophids are an important prey species for many seabirds that forage nocturnally (Watanuki & Thiebot, 2018) and could be an important component of the diet of murres in the Labrador Sea.

Our results for thick-billed murres show similarities in daily activity rates, daily energy expenditure, and environmental rates to year-round tracking of common murres from two populations the North Atlantic. The distribution of thick-billed murres using Cold water in our study overlapped with the winter distribution of common murres on the Grand Banks (Burke & Montevecchi, 2018). Both species spent similar time flying (COMU: 0.5 hr/day, TBMU: 0.6 hr/day), but thick-billed murres (Cold: 4 hr/day, Warm: 4 hr/day) spent more time diving than common murres (3 hr/day). Similar to thick-billed murres in Cold water in our study, common

murres on the Grand Banks spent minimal time diving at night (3% of total dive time in Dec-Feb). Common murres wintering in the North Sea, reside in warmer (6-8 °C) water than the Cold and Warm habitats used by thick-billed murres in our study (Dunn et al., 2020). In the North Sea, common murres spent very little time flying (0.2 hr/day), a significant amount of time diving (4-5 hr/day), and also engaged in significant night diving (1.2 hr/day) from Dec to Feb (Dunn et al., 2020), similar to murres using the Warm Labrador Basin water in our study. These similarities suggest that a feasting strategy in cold water and a resting strategy in warm water may be consistent among murres from different populations and in different wintering areas.

The juxtaposition of different marine habitats in the Northwest Atlantic may be advantageous to mobile marine predators, like thick-billed murres, by allowing them to match their winter habitat use to individual phenotype, individual condition, and changes in local environment. Whereas many species are only able to choose a single strategy to cope with the polar winter, murres in this population are able to switch habitats and adapt their behaviour to that habitat. Dispersal across thermal gradients in response to individual variation in thermal preference has been linked to phenotype dependent survival rates in lizards (Bestion et al., 2015). Assuming individuals within this population are exhibiting habitat matching, there are potentially three distinct winter phenotypes: warm-water specialists, cold-water specialists, and habitat generalists (Tigano et al. 2018, Tranquilla et al., 2014). The next step is to understand the fitness consequences of these phenotypes, and how those fitness consequences could change with anticipated marine climate change in the coming century.

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# Linking statement

The previous chapter showed how different marine habitats influence energetic costs and behavior in winter. This interaction between species and their physical environment determines the distribution of species at a landscape level. Global climate change is altering the physical environment of marine species through changes in ocean temperature, air temperature, ice cover, and wind patterns. Many species are already shifting their geographic in response to these changes. The previous chapter showed how individuals respond to their physical environment with changes in behavior and energy expenditure. The next chapter uses this correlation between individual movements and physical oceanographic habitat to model the non-breeding distribution of thickbilled murres.

# 5. Northwest range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate

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Short title: Patterson et al.: Range shifts of an Arctic seabird

## Abstract

Climate change is altering the marine environment at a global scale, with some of the most dramatic changes occurring in Arctic regions. These changes may affect the distribution and migration patterns of marine species throughout the annual cycle. Species distribution models have provided detailed understanding of the responses of terrestrial species to climate changes, often based on observational data; biologging offers the opportunity to extend those models to migratory marine species that occur in marine environments where direct observation is difficult. We used species distribution modelling and tracking data to model past changes in the non-breeding distribution of thick-billed murres (Uria lomvia) from a colony in Hudson Bay, Canada, between 1982 and 2019. The predicted distribution of murres shifted during fall and winter. The largest shifts have occurred for fall migration, with range shifts of 211 km west and 50 km north per decade, compared with a 29 km shift west per decade in winter. Regions of range expansions had larger declines in sea ice cover, smaller increases in sea surface temperature, and larger increases in air temperature than regions where the range was stable or declining. Murres migrate in and out of Hudson Bay as ice forms each fall and melts each spring. Habitat in Hudson Bay has become available later into the fall and earlier in the spring, such that habitat in Hudson Bay was available for 21 d longer in 2019 than in 1982. Clearly, marine climate is altering the distribution and annual cycle of migratory marine species that occur in areas with seasonal ice cover.

KEY WORDS: Thick-billed murre · Uria lomvia · Hudson Bay · Species distribution model

## Introduction

Climate change is altering the marine environment worldwide (Hoegh-Guldberg & Bruno 2010), changing the phenology and distribution of marine flora and fauna (Poloczanska et al. 2013). Arctic surface water temperature increased at a rate of 0.5 °C decade<sup>-1</sup> from 1982 to 2017 (Meredith et al. 2019), and surface air temperature has increased twice as fast as the global average in the last 2 decades (Meredith et al. 2019), leading to the rapid loss of sea ice, an important physical stratum for wildlife. Consequently, many Arctic marine species are experiencing changes in distribution, abundance, and phenology, either as a direct response to physical changes in their habitat or indirectly through trophic interactions (Sydeman et al. 2015). For highly mobile, pelagic species, our knowledge of their reaction to habitat changes has been limited by our ability to observe animals at sea, especially outside of the breeding season. Given the strong seasonality in the Arctic, there is an urgent need to measure how habitat use and phenology changes through the annual cycle, to understand how climate change is affecting Arctic marine life.

Ice cover and ocean temperature are important factors determining the large-scale distributions and abundance of marine species (Perry et al. 2005, Post et al. 2013). Ice directly affects polar marine mammals and marine birds by either facilitating or restricting access to prey (Tynan et al. 2009). Changing sea surface temperature (SST) and ice cover in the northwest Atlantic are associated with changes in the growth of Atlantic Salmon (*Salmo salar* L.) (Friedland & Todd 2012), anadromous Arctic charr (*Salvelinus alpinus*) (Michaud et al. 2010), capelin (*Mallotus villosus*) (Carscadden et al. 2001), and Atlantic cod (*Gadus morhua*) (Drinkwater 2005), and, farther north, Arctic cod (*Boreogadus saida*) and zooplankton blooms (Welch et al. 1992, Beaugrand et al. 2003, Darnis et al. 2012). Moreover, seasonal sea ice dynamics also play an important role in the timing of spring phytoplankton blooms, which can be a key factor at the end
of the non-breeding season (Coppack & Both 2002, Søreide et al. 2010, Gaston et al. 2011, Leu et al. 2011, Post et al. 2013). Ocean warming could also have significant effects on the survival and reproductive success of many polar seabird species, through changes in the distribution, abundance, and availability or their prey (Croxall 2002, Sydeman et al. 2015).

Thick-billed murres Uria lomvia (hereafter, murres) are an abundant and widespread Arctic seabird, with a circumpolar distribution. The species is considered an important indicator of Arctic marine ecosystems (Mallory et al. 2006, Barry et al. 2010, Michel et al. 2012). Through much of their range, murres migrate away from breeding areas as ice forms in winter and return as ice recedes in spring. A longer ice-free period could influence the timing and extent of migration by murres, allowing them to remain within their breeding range longer. The decline of sea ice could also affect the availability of ice associated prey (Hop & Gjøsæter 2013), or the timing of peak prey availability relative to key periods of the murres annual cycle, such as chick-rearing. Increasing ocean temperature could affect the distribution, abundance, and size of their prey (Carscadden et al. 2001, Drinkwater 2005, von Biela et al. 2019), while simultaneously increasing competition with predatory fish species (Holsman & Aydin 2015). This type of complex trophic interaction has been suggested as the cause of mass mortality and breeding failure for common murres U. aalge in the northeast Pacific in response to an extended marine heatwave (Piatt et al. 2020). Increased frequency and intensity of storms could increase foraging costs for murres. Many seabird species have been shown to spend more time foraging or have lower feeding rates during inclement weather (Finney et al. 1999, Daunt et al. 2006, Elliott et al. 2014) and winter mortality events have been associated with periods of high wind (Harris & Wanless 1996, Frederiksen et al. 2008).

Species distributions models (SDMs) are important tools for predicting the current, past, and future distributions of wildlife (Elith & Leathwick 2009, Robinson et al. 2011, Dambach & Rödder 2011, Guisan et al. 2013) and have been used widely in terrestrial ecology for the last 30 yrears. They have been used less in marine ecology (Robinson et al. 2011), most commonly for fish and marine mammals (Dambach & Rödder 2011). The proliferation of tracking studies on seabirds provides an opportunity to use SDMs to expand our understanding of habitat use of marine birds at-sea (Engler et al. 2017). Species with high dispersal ability, such as seabirds, are more capable of tracking climate changes than more sedentary species, facilitating modeling of shifts in distribution (Araújo & Pearson 2005). Data from tagging studies provide continuous sampling of a species' distribution and habitat preference with less spatial and temporal bias than other visual surveys, especially in remote habitats where direct observation is difficult (Dambach & Rödder 2011, Engler et al. 2017).

We used SDM and global location sensor (GLS) tracking data to model habitat use and examine past changes in the non-breeding distribution of thick-billed murres from Coats Island, Nunavut, Canada. An SDM was developed for the non-breeding period (September to May) using tracking data collected over 4 non-breeding periods (2007/08, 2008/09, 2017/18, and 2018/19). We used climate and physical oceanography variables to model the non-breeding distribution of thick-billed murres. From this model, we predicted the historical distribution of murres from 1982 to 2019 using remotely sensed climate data. We used these predictions to map murre distributions during 4 non-breeding stages of the murre annual cycle (moult, fall migration, winter, and spring migration) and to test for long-term changes in these distributions. We expected to find that non-breeding distributions have shifted north as a result of warming ocean temperatures and declining sea ice cover, which are known to be occurring within the range of this population. We also tested

for changes in the phenology of habitat availability within Hudson Bay. We expected that more habitat would be available for murres within Hudson Bay in fall and spring, due to declining seaice cover in Hudson Bay. Exploring the extent, magnitude, and direction of these past changes is an important first step to understanding how sensitive this species will be to future climate change.

# Materials and methods

## GLS tracking

Tracking was conducted at Coats Island, in Hudson Bay, Nunavut, Canada ( $62.95^{\circ}$ N,  $82.01^{\circ}$  W), a colony of 30000 breeding pairs of thick-billed murres (Gaston et al. 2012). As part of earlier tracking studies (Gaston et al. 2011, McFarlane Tranquilla et al. 2013), 3 types of geolocators (British Antarctic Survey, Cambridge, UK), namely Mk5 (3.6-g), Mk7 (3.6-g), and Mk13 (1.8-g), were deployed at Coats Island in 2007 (n = 20) and 2008 (n = 20). All Mk loggers recorded maximum light levels at 10-minute intervals, and a subset of these loggers also recorded temperature at 10-min intervals. In 2017 (n = 48) and 2018 (n = 45), we deployed LAT2800S geolocator-temperature-depth-recorders (Lotek, Newmarket, ON; 36 mm x 11 mm x 7.2 mm, 5.5 g) at the same colony. LAT 2800 loggers were programmed to collect light level, temperature, depth, and wet/dry state at 10-second intervals. All loggers were deployed during the summer on breeding adults captured on the nest, using a noose pole, while attending an egg or chick. Loggers were retrieved and data downloaded 1 to 2 yr later, during subsequent breeding seasons.

# Location estimates

For LAT2800S loggers, we summarized maximum-recorded light levels at 5-minute intervals prior to estimating twilights. Twilight was estimated using the threshold method in the 'TwGeos' package (Lisovski et al. 2016). We defined 2 behavioural modes, flying and on water. Flying was defined as any period where the sensor was dry and tag temperature was <5°C; this temperature threshold was used to prevent periods of leg-tucking from being falsely classified as flying (Linnebjerg et al. 2014). Location estimates were calculated using a probabilistic algorithm with the 'probGLS' package in R (version 0.9.5, Merkel et al. 2016). The 'probGLS' method estimated

two locations per daily, at sunrise and sunset. At each time step, 1000 random particles were generated within the defined study area based on the observed twilights, random solar angles between  $-6^{\circ}$  and  $-1^{\circ}$ , and twilight error following a log-normal distribution (shape = 2.49, scale = 0.94). Using 'probGLS', we also incorporated additional information about habitat use and murre behaviour by weighting each random particle based on a land mask, sea ice cover, SST, and movement speed. Because murres do not use, or travel over, land during the non-breeding period, random particles over land received a weight of 0. Because murres cannot remain in areas with complete ice cover, random particles with greater than 90% ice cover (NOAA high-resolution ice cover, NOAA/OAR/ESRL PSL, https://psl.noaa.gov/), were also assigned a weight of 0. For loggers with a temperature sensor (LAT 2800 and MK5), particles were weighted according to the similarity between remotely sensed SST and internal logger temperature (NOAA high resolution SST NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, https://psl.noaa.gov/; Reynolds et al. 2007). Finally, random particles were weighted according to a movement model limiting the distance travelled between consecutive locations based on realistic movement rates for murres; the movement model used different parameters for loggers with wet/dry sensors (LAT2800) that could estimate time spent in flight (Table 12.1). One particle was randomly selected from the possible particles based on the assigned weights. These steps were repeated at each time step until an entire track was generated. The process was repeated to generate 100 possible tracks for each deployment. The most probable track was calculated as the geographic median of possible locations at each time step, and this track was used in mapping and estimates of migration timing. Full details of the parameters used in the probabilistic algorithm are provided in the supplementary material (Table 12.1). We present maps of estimated tracks for each year, based on the most probable tracks estimated above (Figure 5.1).

To compare the timing of migration across tracking years, we calculated the latest date when each bird crossed 70° W in fall and spring. Murres from Coats Island migrate through Hudson Strait, and 70° W represents the halfway point of movement through this corridor. We used mixed effects models to test for difference in migration timing among years, with individual identity as a random factor to account for murres tracked over 2 yr. Mixed effects model were conducted using the 'lme4' package, version 1.1-27 (Bates et al. 2015). Residual and q-q plots were used to check assumptions. The minimum and maximum date when 95% of tracked birds migrated across years were used to summarize the fall and spring migration stages, respectively.

#### **SDMs**

We developed an SDM for the non-breeding period (September to May). SDMs assume that species are at an equilibrium with their environment and that all relevant environmental gradients have been sampled (Elith & Leathwick 2009). Tracking of smaller species is often limited to using GLS devices, which have lower spatial accuracy than other tracking methods (Phillips et al. 2004). Using paired deployments of satellite platform terminal transmitters (PTT) and GLS loggers on black-browed albatrosses (*Thalassarche melanophris*), Quillfeldt et al. (2017) found that device type (PTT versus GLS) had less influence on SDM accuracy and overlap in predicted distributions than the choice of SDM algorithm.

We considered 7 predictor variables in the model: bathymetry, slope, distance from colony (distance), day of year (DOY), sea surface temperature (SST), air temperature (air), sea ice cover (ice), and wind speed (wind). The 3 static environmental variables, bathymetry, slope, and distance from colony were included in the model because they are likely biologically relevant to the species' distribution (Stanton et al. 2012). Bathymetry and slope are both likely to influence the distribution

of prey, even with changing marine climate. Murres are primarily constrained to areas close to the colony during moult and spring migration, therefore distance from the colony was included to ensure this pattern was included in the model. DOY was included as a temporal variable to allow habitat preferences to change through the non-breeding period. Other static variables, i.e. longitude, latitude, and day length, were not included because we were interested in how the species responds to variation in climate (Stanton et al. 2012). Bathymetry data used the ETOPO1 Global Relief Model (https://www.ngdc.noaa.gov/mgg/global/). Slope was calculated from the bathymetry layer using the terrain function in the 'raster' package in R (Hijmans & Van Etten 2016). Daily-mean SST and ice were obtained from the European Space Agency Reprocessed Sea Surface Temperature Analysis (Merchant et al. 2019). Daily-mean air temperature (2 m) and surface wind speed were obtained from NOAA Physical Sciences Laboratory NCEP/NCAR Reanalysis 1 (https://psl.noaa.gov/data/gridded/data.ncep.reanalysis.pressure.html). Bilinear interpolation was used to resample environmental variables to a standard 0.25° spatial resolution, using the 'raster' package (Hijmans & Van Etten 2016).

Our SDM compared environmental predictors at observed locations from murre GLS tracks to available environmental conditions at pseudo-absence locations (Barbet-Massin et al. 2012). To incorporate uncertainty in GLS location estimates into the modelling, all 100 possible tracks generated for each deployment using the probGLS algorithm were included as observed locations. Including all possible locations gives more weight to portions of the tracks where the location is more certain (because all possible locations are more clustered) and less weight to portions of the tracks where the location is less certain (because all possible locations are more dispersed). The mean standard deviation across iterations for any location estimate was 2.1° longitude and 2.0° latitude. Pseudo-absences were randomly sampled from ocean areas within 1,000 km of any location collected within each tracking year. Pseudo-absences were sampled at a 1:1 ratio with observed locations (Barbet-Massin et al. 2012). Areas within 200 km of used locations collected within the same month were excluded from the selection area to ensure that pseudo-absences were outside of areas known to be occupied by murres at that time. For each tracking year, entire tracks from 70% of individuals were randomly assigned as training data and entire tracks from the remaining 30% of individuals were used as test data. Selection areas for pseudo-absences were determined separately for test and training data. Figure 12.1 provides example maps of used locations and pseudo-absences.

We used random forests for our SDM, using the 'ranger' package in R (Wright & Ziegler 2017). The model was fit using the train function in the 'caret' package (Kuhn et al. 2021). We first ran hyper-parameter tuning on a subsample of 5% of the data, considering combinations of the split rule ('gini' and 'extratrees'), minimum node size (5, 10, and 15), and 'mtry' (1 - 7). The area under the receiver operating characteristic curve (AUC) was used to identify the best combination of hyper-parameters on the sample data, and the selected hyper-parameters (mtry = 1, splitrule = extratrees, node size = 5) were used on the full model. The model was fit to the training data using repeated 4-fold cross-validation with 10 repeats, where each fold used 3 tracking years for model training and 1 tracking year for model testing.

Model accuracy was assessed using the AUC, F<sub>1</sub> scores (F1), and the Continuous Boyce Index (CBI). Model accuracy statistics (AUC and F1) are presented from cross-validation used in model fitting, which represents the accuracy in predicting probability of occurrence to unobserved years. We also present model accuracy for withheld test data, which represents accuracy in predicting to tracks of new individuals. AUC and F1 scores were calculated using the 'pROC' package (Robin et al. 2011) and CBI was calculated using the 'ecospat' package (Broennimann et al. 2021).

Variable importance measures were used to assess the relative contribution of each predictor to the model. Variable importance was calculated separately within each stage (moult, fall, winter, and spring), using the 'vip' package (Greenwell et al. 2020), to examine how habitat preferences changed through the non-breeding period. Variable importance measures for each stage were scaled to values between 0 and 100. We calculated accumulated local effects (ALEs) to examine how each environmental variable influenced the predicted probability of use. The ALE shows the relative effect of each predictor variable on the model predictions and this measure is not biased by correlation among predictor variables (Molnar 2019), positive values indicate an increase in mean probability of use and negative values indicate a decrease in the mean probability of use. The ALEs were calculated using the 'ilm' package in R (Molnar 2018); ALE values for each predictor variable are reported for each non-breeding stage, in order to examine how habitat use changes among stages of the annual cycle.

In 2017 and 2018, tracked murres were included in a separate study examining the effects of increased reproductive investment on non-breeding behaviour. Prior to developing the SDM described above, we tested if treatments applied in that study had any influence on the SDM (see Table 12.2). After confirming that there was no effect of treatment, all tracks from 2017 and 2018 were included in the final model.

## Distributions by non-breeding stage

We compared predicted distributions for the 4 life-history stages: moult, fall migration, winter, and spring. Stage-specific distributions were calculated by predicting murre occurrence from the SDM at 3 day intervals over the period 1982–2019, then calculating the median predicted probability of use for each raster cell in each stage for each year. To quantify changes in the

distribution of habitat, the stage-specific range areas were defined using the probability cut-off that included 90% of used locations. To quantify changes in the predicted distributions over time, we calculated a baseline range based on the mean distributions for the period 1982-1989. For each stage, we estimated 8 distribution measures: the total area, percentage overlap with the baseline distribution, median longitude, median latitude, western edge, eastern edge, northern edge, and southern edge. All distribution measurements were made using an Albers equal area projection with central meridian at 60°W and standard parallels at 45°N and 65°W. Range edges were calculated as the 5<sup>th</sup> and 95<sup>th</sup> percentiles of eastings (western and eastern edges) and northings (southern and northern edges) of all raster cells within the range. We used linear regression, with year as a predictor, to test for changes in distribution measures over time. Residual and q-q plots were used to check assumptions of the linear regression; Spearman's correlation tests were used to confirm linear regression results if normality assumptions were not met. A Bonferroni correction was used to account for multiple comparisons on the same seasonal distributions.

To investigate how changes in climate variables contributed to changes in stage-specific distributions, we compared mean values of ice cover, SST, air temperature, and wind speed between the 1980s (1982-1989) and the 2010s (2010-2019). We calculated the predicted distribution within each period, and identified regions where the predicted distribution declined, remained stable, or increased. We randomly sampled 50 points within these regions for each season, extracted the mean climate values for the 2 periods, and calculated the change in mean climate values from the 1980s to the 2010s. We used generalized least squares regression to determine how the change in climate varied among regions where the predicted range had declined, remained stable, or increased. Fixed variance weights for each region were used to account for

unequal variance among regions. Residual and q-q plots were used to check assumptions of the regressions.

#### Fall and spring habitat phenology

Murres that breed in Hudson Bay migrate annually to the northwest Atlantic Ocean. To examine changes in the timing of habitat availability in Hudson Bay in spring and fall, we predicted the amount of suitable habitat in Hudson Bay at 3-day intervals for the years 1982 to 2019. Habitat area was quantified as the area of suitable habitat within the Hudson Bay marine ecoregion (Spalding et al. 2007); suitable habitat was defined, as above, using the probability cut-off from model predictions that included 90% of used locations. We used a non-linear logistic regression curve to model the seasonal decline in habitat availability in fall and the increase in habitat available in spring as a function of DOY. Analysis was performed using the 'nls' function in R. We compared a null model with no effect of year to a model that included a trend with year.

All analysis was done using R version 4.1.0 (R Core Team 2021); p-values <0.05 were considered significant for all parametric tests.

# Results

# Tracking

We recovered data from 90 individuals during the non-breeding seasons over the 4 years of tracking (Table 5.1). Tracked murres followed a similar migration route and used the same wintering area during each year of tracking (Figure 5.1, Figure 12.2-12.5). Immediately following breeding, murres remained in Hudson Bay through the moult in September and October. Murres migrated through Hudson Strait to the Northern Labrador Shelf in November and December. During winter, murres spread out within the Labrador Sea, also reaching the Gulf of St Lawrence, the Eastern Scotian Shelf, the East Greenland Shelf, and the Irminger Sea. They began migrating back through Hudson Strait and into Hudson Bay in April. The track for 1 murre was excluded during moult, because this individual stopped breeding in early August and migrated to the wintering area before moulting.

Mean fall and spring migration occurred on DOY 333 and 117, respectively. There was no difference in migration timing among the 4 years for fall ( $\chi^2 = 2.15$ , p = 0.542) or spring ( $\chi^2 = 1.39$ , p = 0.707). There was significant variation in the timing of migration among individuals each year (Figure 12.6). Murres migrated over a period of 50 days in fall and 42 days in spring. Across the year, 95% of all tracked murres migrated between DOY 308 and 362 day of the year in fall and between DOY 90 and 141 day of the year in spring. We used these dates to summarize habitat use in four stages of the non-breeding period: moult (DOY 245-307), fall migration (DOY 308-362), winter (DOY 363-88), and spring migration (DOY 89-152).

#### **SDMs**

The SDM had good predictive performance across years and individuals. Cross-validation AUC was 98.7% and the F1 score was 94.2%. For the withheld test tracks from 30% of individuals the AUC was 97.2%, the F1 score was 91.2%, and the CBI was 0.82. Ninety percent of used locations were located in areas with a predicted probability of use of 0.7 or higher; therefore, a probability of use of 0.7 was used as a cut-off for estimating suitable habitat.

SST and distance from colony were the 2 most important variables across all four stages (Figure 5.2). In fall, winter, and spring, the probability of use was higher for SST <4°C (Figure 5.3); during moult there was very little effect of SST on probability of use. Probability of use declined with distance from the colony in all stages, with the strongest effects occurring during moult and spring. Bathymetry was an important predictor in all stages; shallow water (<500 m) was preferred during moult, when murres are using shallow areas in Hudson Bay, and deeper water (>2000 m) was preferred in fall, winter, and spring. Air temperature was an important predictor in fall, winter, and spring, with probability of use higher for temperatures <4°C. In winter, probability of use declined with air temperatures less than -12°C. Probability of use declined with increasing ice cover. Slope, DOY, and wind speed contributed the least to the model predictions.

## Predicted distributions within each non-breeding stage

The non-breeding distribution of thick-billed murres closely follows the receding ice, which 'pushes' murres out of Hudson Bay and Hudson Strait into the North Atlantic each year, and which murres then follow back into Hudson Bay each spring following melt (Figure 5.4, Figure 12.7-11.8). Using the SDM to estimate suitable non-breeding habitat from 1982 to 2019, we found significant changes in predicted distributions in fall and winter, with the greatest changes occurring

in fall (Figure 5.5, Table 12.3). Overlap with the baseline range in fall declined by  $0.7 \pm 0.1\%$  yr<sup>-1</sup> (mean ± SE) (Table 12.3). The fall range shifted west by  $21.1 \pm 4.1$  km yr<sup>-1</sup>, occupying all of Hudson Bay by the 2010s, and north by  $5.0 \pm 1.0$  km yr<sup>-1</sup>, with increased use of Hudson Strait, Foxe Basin, and Davis Strait (Figure 5.4). Overlap in the winter distribution declined by  $0.3 \pm 0.08\%$  yr<sup>-1</sup>, and the winter distribution shifted west by  $2.8 \pm 0.7$  km yr<sup>-1</sup> (Table 12.3). The spring range shifted north by  $3.8 \pm 1.3$  km yr<sup>-1</sup>; however, this trend was marginally non-significant (p = 0.06, Table 12.3). The most notable changes in spring distribution came from increased use of Hudson Strait and northern Hudson Bay. Results for all distribution measures are provided in Table 12.3.

Ice cover has declined, while SST and air temperature have increased between the 1980s and the 2010s (Figure 5.6, Table 12.4). The largest changes in ice cover occurred within the fall distribution, where the region of increasing suitable habitat had mean declines of  $21.5 \pm 0.51\%$ . For fall, winter, and spring, ice cover declined more in regions of stable and increasing suitable habitat than in regions of declining suitable habitat. Regions of declining fall suitable habitat had the largest increases in SST (fall:  $1.11 \pm 0.03$ °C), while regions of increasing winter and spring suitable habitat had the smallest change in SST (winter:  $0.27 \pm 0.02$ °C; spring:  $0.05 \pm 0.01$ °C). The largest increases in air temperature occurred in areas of increasing suitable habitat during fall (4.83 ± 0.15°C). For fall, winter, and spring, regions with declining suitable habitat had less change in air temperature than regions of increasing suitable habitat than in areas with stable or declining suitable habitat. For moult, air temperature increased more in regions of increasing suitable habitat. Overall changes in air temperature during moult and spring were of a smaller magnitude than during fall and winter. For winter and spring stages, wind speed tended to increase in areas of increasing suitable habitat.

## Fall and spring habitat phenology

Fall habitat is available later than in the 1980s (F<sub>910, 3</sub> = 126.8, p < 0.001, Figure 5.7). The date when suitable fall habitat reaches the midpoint of decline has increased by 0.38 days per year (SE = 0.03, t =12.83, p < 0.001). There was no evidence that the amount of suitable habitat available at the start of fall (237 ± 1199 km<sup>2</sup>, t = 0.20, p = 0.84) or the rate of habitat decrease through fall ( $0.01 \pm 0.02$ , t = 0.42, p = 0.67) have changed. According to this model, there were 200000 km<sup>2</sup> of suitable habitat available until DOY 344 in 1982, whereas in 2019, the same amount of habitat was available until DOY 358 (mean change: 0.38 d yr<sup>-1</sup>).

More spring habitat is now available earlier than in the 1980s ( $F_{1141, 3} = 20.3$ , p < 0.001, Figure 5.7). The mean asymptote for spring suitable habitat increased by  $3846 \pm 778 \text{ km}^2 \text{ yr}^{-1}$  (t = 4.94, p < 0.001). There was no evidence that the date when habitat reaches its midpoint ( $-0.004 \pm 0.06$  d; t = -0.06, p = 0.95) or the rate of habitat increase through spring ( $0.07 \pm 0.05$ ; t = 1.48, p = 0.14) have changed. According to this model, 200000 km<sup>2</sup> of suitable habitat were available on DOY 112 in 1983 and on DOY 106 in 2019 (mean change:  $-0.16 \text{ d yr}^{-1}$ ).

# Discussion

Since 1982, the predicted distribution of murres from Coats Island during fall and winter has shifted north and west. SST, air temperature, and ice cover were important climate variables within our SDM, which accurately predicted the distribution of murres during the non-breeding period. Range expansion was associated with declining sea ice cover and warmer air temperatures, while range contraction was associated with increasing SST. The greatest changes in distribution have occurred in the fall, where habitat available in Hudson Bay has increased substantially. Other recent studies have predicted that unchecked anthropogenic climate change will result in a northward shift in the winter distribution of multiple seabird species in the North Atlantic (Clairbaux et al. 2021); our study shows that climate change has already contributed to shifts in the non-breeding distribution of thick-billed murres from Coats Island.

Our SDM approach assumes that the murre niche is at equilibrium and that we characterized the relevant components of the niche, and, thus, that the statistical relationship between environmental variables and murre distribution measured by our SDM can be extrapolated backward in time (Elith & Leathwick 2009). This latter assumption may not be valid if murres have more phenotypic flexibility than is captured in our training data, or if murres have adapted their habitat preferences in response to changing climate conditions. The SDM was developed using a limited set of climate predictors that are available for the entire period 1982-2019; these variables likely do not capture all elements of the niche of murres during the non-breeding period. In particular, non-breeding distributions are likely driven by biotic interactions, like the distribution of prey, for which we did not have the relevant information (murre non-breeding season diet and the relevant fish and invertebrate distributions at depth are poorly known). Nonetheless, many fish and invertebrate distributions are strongly associated with SST and sea ice cover (Perry et al. 2005, Søreide et al.

2010); as such, a central assumption is that our model should capture these biotic interactions indirectly.

SDMs based on climate data are best suited for coarse-scale modelling of widely distributed, mobile species (Robinson et al. 2011). Finer-scale modelling of habitat use and ecological interactions by murres will require more precise tracking methods (e.g. GPS loggers), which are not yet feasible for year-round deployment on this species. However, despite the uncertainty inherent in the GLS locations, we believe this SDM provides useful information on current and historic distributions of murres because the predicted distributions and habitat associations identified using this model agree with current knowledge of the species' biology (Gaston & Hipfner 2020, Moody & Hobson 2007, Fort et al. 2013).

There have been substantial changes in the timing of modelled habitat availability for murres in Hudson Bay over the last 38 yr. The average date when fall habitat declines to less than 200000 km<sup>2</sup> has increased by 3.8 d decade<sup>-1</sup>, and the date when spring habitat reaches 200000 km<sup>2</sup> has advanced by 1.6 d decade<sup>-1</sup>. Therefore, murres could spend 21 more days in Hudson Bay in 2019 than in 1982. The murres tracked in our study demonstrated significant among-individual variation in the timing of migration in and out of Hudson Bay in the fall (range: 50 d) and spring (range: 42 d). This indicates that individual condition or preference play an important role in the timing of migration for this species. Increased availability of habitat within Hudson Bay could have a positive effect on murres, by allowing greater flexibility in the timing of migration. Any potential benefit of increased access to Hudson Bay, however, could be offset by changes in the food web associated with on-going changes to the marine climate (Hoover et al. 2013a,b) or increased competition (Piatt et al. 2020). Transient benefits of climate change and sea-ice loss have been documented for other ice-associated Arctic species (Laidre et al. 2020).

Studies of climate change impacts on phenology tend to focus on changes to spring phenology (Askeyev et al. 2007, Wolkovich et al. 2012, Parmesan et al. 2013, Gallinat et al. 2015, Kolářová & Adamík 2015). Our study highlights an example of an Arctic population that is experiencing the greatest climate change induced impacts on phenology during the fall. Conditions during fall can play an important role in population demographics by influencing juvenile survival and determining condition of both adults and juveniles at the onset of winter, when many species face harsh environmental conditions. For murres, delayed fall migration could provide post-breeding adults with more time to complete their flightless moult and gain body reserves, while also providing juvenile murres more time to grow and gain experience flying and foraging before undertaking their first migration. It takes breeding murres approximately 50 d after egg-laying to raise a chick to nest departure (Gaston & Hipfner 2020) and an additional 35 d at sea before chicks are independent (Elliott et al. 2017). This limits the time during which murres can begin nesting and successfully raise young. Increased time with suitable habitat within the breeding range could increase the window when murres can successfully breed. Our study supports the growing consensus that autumn phenology can be as sensitive as spring phenology to changing climates, especially for species which must undergo a feather moult before migration (Jenni & Kéry 2003, Brisson-Curadeau et al. 2020).

Many migratory species depend on matching the timing of breeding with seasonal peaks in resource availability in order to achieve successful breeding (Perrins 1970, Cushing 1990). The timing of ice-off is an important determinant of peak production in Arctic regions (Legendre et al. 1981); therefore, the changing spring conditions could influence the ideal timing of breeding. The modelled habitat conditions that correspond to migrating back to Hudson Bay are occurring earlier now than 38 years ago. Murres at Coats Island breed earlier in years with less ice cover in Hudson

Bay (Gaston et al. 2005) and the mean laying date has advanced by 0.25 days per year since 1990 (S. Whelan, unpubl. data), indicating that murres are able to advance breeding in response to changing climate conditions. As murres now have 21 more days of suitable habitat available within Hudson Bay, and seem to be tracking the increased availability of spring habitat to avoid a mismatch, it may appear that climate change is advantageous. However, changing marine climate in Hudson Bay has altered prey composition during the chick-rearing period (Gaston et al. 2003) and may bring in competitors (Gaston & Woo 2008), leading to lower chick growth rates and ultimately fitness.

Our model identified important non-breeding regions for murres from Coats Island, which show consistently high use at a multi-decadal scale, and could be important for marine spatial planning to mitigate the impacts of increased marine activities. During the non-breeding period, murres from Coats Island were most concentrated during moult when their range was restricted to central Hudson Bay. This is a critical stage in their annual cycle, when they are flightless and the fathers are caring for dependent offspring. Moult is the time of year when distribution is determined more by the static variable distance from colony, than by climatic variables, and also the period (outside of the breeding season) when, because of temporary flightlessness, murres have the least flexibility to alter their distribution in response to changing conditions. This could make murres sensitive to changes in prey conditions at this time of year. Hudson Bay has relatively low levels of human activity, specifically shipping, which could pose risks to moulting murres through by-catch or oil pollution. However, shipping in Hudson Bay and Hudson Strait is expected to increase, including in regions that overlap with the moult distribution (Pizzolato et al. 2016, Dawson et al. 2018).

The wintering habitat that we have identified for murres from Hudson Bay, includes habitat for a significant portion of the global population of thick-billed murres (Frederiksen et al. 2016) as well

as many other seabird species (Mallory et al. 2008, Frederiksen et al. 2012, Hedd et al. 2012, Linnebjerg et al. 2013, Fifield et al. 2017, Amélineau et al. 2018). Conditions during winter probably play an important role in population regulation of murres (Gaston 2003). Across their annual range, the wintering area is the region where murres from Coats Island experience the greatest overlap with anthropogenic threats such as shipping, fisheries by-catch (Davoren 2007), chronic and acute oil pollution (Wiese & Ryan 2003), and hunting (Gaston & Robertson 2010). Modelling winter habitat use, as we have done here, is an important step in developing marine spatial planning of offshore wintering areas for seabirds. The extent to which murres can shift their winter distribution northward may be affected by day length. As murres forage primarily, though not exclusively, during daylight (Regular et al. 2011, Dunn et al. 2020), northern range shifts would involve a decrease in the amount of time available for foraging in daylight. A comparison of winter energy expenditure and dive behaviour of thick-billed murres and common murres wintering in regions with and without polar night, showed that wintering in an area with polar night resulted in higher daily energy expenditure and reduced foraging opportunities for common murres (Fort et al. 2013).

Diversity of responses among populations within a species can enhance its resilience (Sydeman et al. 2015). Our analysis focused on habitat changes for a population of murres close to the southern edge of their range. Other populations in northern parts of the range faced with similar environmental changes may experience a different response. For example, colonies in the Canadian High Arctic are more constrained by sea ice during the breeding season (Gaston et al. 2005). Earlier ice-off dates around these colonies could lead to improved reproductive success for these populations. Negative effects for populations within some portions of the breeding range may be offset at the species level by positive effects in other regions. However, to the extent that

large portions of the murre population share common wintering areas and conditions during the winter play an important role in adult survival (Frederiksen et al. 2016), this could create greater sensitivity to climate change at the species level.

Mapping the distribution of populations outside of the breeding season is a key priority for the conservation of marine birds. Long-term data on winter distributions of pelagic seabirds were, until recently, limited to data collected from band recoveries and vessel surveys, which are biased in the Arctic by low spatial and temporal coverage. In contrast, our SDM was effective at predicting stage-specific distributions of murres across years and individuals and is an improvement over the more common approach using utilization distributions to map species ranges, which are limited by the relatively small number of tracked individuals. The SDM approach is more likely to identify the entire distribution, which could otherwise be missed. In dynamic marine environments, an SDM can account for significant inter- and intra-annual variation in habitat by predicting distributions over multiple time-periods. Our study demonstrates the advantage of including year-round tracking as part of long-term monitoring programmes to facilitate improved understanding of non-breeding distributions, habitat requirements, and the effects of environmental variability and climate change on population demographics (Carneiro et al. 2020).

# Data availability

The GLS tracking data used in the current study are available in the Movebank Data Repository, https://doi.org/10.5441/001/1.p1m75qn1 (Patterson et al. 2021a). The species distribution model and predicted distributions from this study are available in Dryad, https:// doi. org/ 10.5061/ dryad.4qrfj6qbk (Patterson et al. 2021b).

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Table 5.1. Sample sizes of thick-billed murres tracked from Coats Island, Nunavut, Canada, during each non-breeding period and a summary of fall and spring migration timing; migration was measured as the date each individual track crossed 70° W. DOY: day of the year

	Recovery rate	Individuals tracked	Fall Migration (DOY)		Spring Migration (DOY)	
Year	(%)	(Number of locations)	Mean (± SD)	Range	Mean $(\pm SD)$	Range
2007/08	90	18 (9679)	$335\pm15.2$	304 - 361	$119\pm6.45$	104 - 132
2008/09	57	10 (4208)	$336\pm13.5$	317 - 356	$116\pm18.7$	87 - 136
2017/18	71	35 (17521)	$329\pm11.4$	310 - 359	$117\pm15.3$	96 - 145
2018/19	60	27 (9485)	$334\pm17.0$	308 - 364	$117\pm14.6$	100 - 141



Figure 5.1. Geolocator tracks of thick-billed murres from Coats Island, Nunavut, Canada. Each line shows the most probable track of 1 individual, with lines coloured to show month of the tracking year (September to May). The red points show the location of the colony. Monthly distribution maps for all 4 years of tracking are provided in Figure 12.2-12.5.



Figure 5.2. Relative importance of environmental predictors for the species distribution model within each stage of the non-breeding period of thick-billed murres. Variable importance is scaled between 0 and 100 for each stage. SST: sea surface temperature; DOY: day of the year



Figure 5.3 Accumulated local effects for each environmental predictor. Positive values indicate a positive effect on the mean probability of occurrence of thick-billed murres and negative values indicate a negative effect; SST: sea surface temperature



Figure 5.4. Predicted distributions of thick-billed murres from Coats Island 1982–1989 and 2010–2019, within each stage of the non-breeding period. Shading shows the median distribution across each stage and time period for probability of use greater than 0.5. Lines indicate the 1982–1989 distribution. Black points show the centroid of the predicted distribution in 1982–1989 and white points show the centroid of the predicted distribution in 2010–2019. Maps of all decades are available in Figure 12.8-12.9.



Figure 5.5. Long-term trends in measures of stage-specific distribution of thick-billed murres, predicted from the species distribution model. Black points show the estimated value for each year, lines show long-term trends, and shaded areas are 95% confidence intervals. Detailed results of linear regressions are provided in Table S3. All distribution measurements were made using an Albers equal area projection with central meridian at 60° W and standard parallels at 45° N and 65° W.



Figure 5.6. Change in climate variables within areas where the distribution of thick-billed murres has declined, remained stable, or increased during moult, fall migration, winter, and spring migration between the 1980s (1980–1989) and the 2010s (2010–2019). Points are the mean change in habitat and error bars are 95% confidence intervals; SST: sea surface temperature.



Figure 5.7 Timing of (left) fall habitat decline and (right) spring habitat increase in Hudson Bay. Points and dashed lines show predicted habitat by date based on the stage-specific species distribution models. Solid lines show the average trend in habitat phenology based on the logistic regression models. For visual clarity, only every second year is plotted.

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# Linking statement

The ability to predict where species will occur on the landscape is a pre-requisite for conservation measures. For colonial breeding species, there are different constraints on distribution during the breeding and non-breeding seasons. The previous chapter used correlations with habitat characteristics to predict non-breeding distributions. The next chapter develops a process-based model to predict foraging distributions around colonies during the breeding season. Together these two chapters aim to increase understanding of what regulates the distribution of thick-billed murres throughout the year.

# 6. Foraging range scales with seabird colony size

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### Summary

Density dependent prey depletion around breeding colonies has long been proposed as an important factor controlling the population dynamics of colonial animals<sup>1,2</sup>. Colony size often varies over several orders of magnitude within the same species and can include millions of individuals per colony<sup>3,4</sup>; as such, colony size likely plays an important role in determining the individual behaviour of its members and how the colony interacts with the surrounding environment<sup>4</sup>. Using tracking data from murres (Uria spp.), the world's most densely breeding seabirds, we show that the frequency distribution of foraging trip ranges scales to the 0.31 power of colony size during the chick-rearing stage, consistent with Ashmole's theory<sup>1,2,5</sup>. Whereas the strongest evidence for Ashmole's theory in seabirds has been from species that search in two dimensions, we extend this idea to pursuit-divers that use the third dimension. This pattern was consistent across colonies varying in size over three orders of magnitude and distributed throughout the North Atlantic region. The strong relationship between colony size and foraging range means that important foraging areas for some colonial species can be efficiently delineated based solely on population estimates. Protected areas covering the foraging ranges of the 17 largest colonies would safeguard two-thirds of the North Atlantic population; currently, only two of those colonies have significant coverage by marine protected areas. Our results represent an important example of how theoretical models, in this case Ashmole's version of central place foraging theory, can be applied to inform conservation and management in colonial breeding species.

## **Results and discussion**

#### Colony size-foraging range relationship

Colonial breeding is pervasive among seabirds – occurring in 95% of species<sup>6</sup> – and densitydependent prey depletion around breeding colonies has long been proposed as an important factor controlling population dynamics. In 1963, Ashmole proposed that intraspecific competition leads to prey depletion around colonies, causing reproductive success to decline as breeding adults are required to spend more time and energy to find prey farther from the colony<sup>1,7</sup>. The hypothesis predicts that, assuming equal distribution and abundance of food, birds at larger colonies should forage farther from their nests than those from small colonies during the same breeding stage. Foraging range should increase with colony size to the 0.5 power, because, assuming an equal density of birds, the area available for foraging is proportional to the square of distance from the colony<sup>8,9</sup>. Although prey depletion is widely assumed to limit colony size in seabirds, based on geographical distributions of colonies and variation in trip durations or daily energy expenditure with colony size<sup>8,10–12</sup>, direct measurements of the relationship between colony size and foraging range are scarce, with some exceptions<sup>13</sup>. While several studies have shown that prey is less abundant near colonies<sup>14–16</sup>, a link with colony size is necessary to provide support for Ashmole's theory.

To examine these ideas, we used GPS tracking data (5,304 foraging trips) collected from common (*Uria aalge*) and thick-billed murres (*Uria lomvia*) at 29 colonies, ranging in size from 900 to 470,000 breeding pairs, within the North Atlantic region (Figure 6.1, Figure 13.1, Table 13.1). Murre colonies range in size over five orders of magnitude, from hundreds to millions of pairs<sup>17,18</sup>. High flight costs, delivery of single prey items to chicks, and open breeding sites that necessitate

continuous nest attendance to protect offspring make murres particularly sensitive to increases in foraging range that reduce parental provisioning rates<sup>19–21</sup>. Only data from birds in the chick-rearing stage of breeding at the colony were included in the analysis, as this is the breeding stage when feeding rates are highest and intraspecific competition is expected to have the greatest effect on foraging range<sup>19,22</sup>. In total, our study included 1,174 separate GPS deployments between 2009 and 2020, with a median of 81 foraging trips per site (range = 7-1,537, Methods). We calculated the maximum horizontal distance from the colony for each foraging trip (hereafter, trip distance). Common and thick-billed murres are closely related species with similar morphology, behaviour, and energetics<sup>17,18</sup>; therefore, we expected them to exhibit a similar relationship between foraging range and colony size. We found no difference in the distribution of trip distances or spatial segregation between thick-billed and common murres at colonies where both species were tracked simultaneously (Methods, Table 13.2); tracking and colony size data from both species were therefore combined in all subsequent analyses.

We developed a foraging range model to describe the two dimensional distribution of foraging trips with distance from the colony as a function of colony size. We followed the dispersal kernel paradigm, where the distribution of dispersers within a population is expected to follow a probability density function and the parameter estimates of these distributions are used to model general ecological relationships related to dispersal<sup>23–25</sup>. The distribution of foraging trip distances around each colony conformed most closely to a Weibull distribution (Methods). The scale parameter ( $\lambda$ ) of the Weibull distribution increased with colony size (F<sub>1,27</sub> = 42.23, p <0.0001) to the exponent 0.31 (95% CI = 0.29-0.33) of colony size (Figure 6.2a, Methods); this exponent was significantly different from the expected value of 0.5 (linear hypothesis test: F<sub>1,27</sub> = 16.3, p = 0.0004). Across all colonies, the mean shape parameter (k) was 1.35 (95% CI = 1.33-1.44), with

no significant relationship to colony size ( $F_{1,27} = 3.20$ , p = 0.09, Methods). The foraging range model predicted that 95% of foraging trips occur within 34.1 km (95% CI = 31.5-35.2) and 97.3 km (95% CI = 89.6-101.1) for colonies of 10,000 and 300,000 pairs, respectively (Figure 6.2b). For 19 colonies with sufficient tracking data to estimate a representative foraging area using utilization distributions, the mean overlap between the observed and predicted 95% foraging areas was 60.5% (mean Dice's similarity: 0.605, SD = 0.097; Figure 6.3; Methods).

The geographic extrapolation of our foraging range model assumes that birds use the whole area within their colony's foraging radius. However, as prey are likely to be unevenly distributed, we could expect birds to make repeated, directed trips to highly profitable prey patches within that radius, which might result in significantly closer or farther foraging distributions and total exploited areas than predicted by our model. If a consistent foraging hotspot, such as a fish spawning site, is available, then many individuals may travel to that hotspot regardless of distance. For example, common murres in Atlantic Canada exploit dense concentrations of spawning capelin (Mallotus villosus) during chick-rearing, making directed trips during active spawning; when these prey are not available, however, murres respond by foraging over a wider area<sup>26,27</sup>. Under this scenario, the directionality of foraging trips should be highly concentrated, with less of a relationship to colony size. There was no correlation between the fit of the foraging range model and the circular variance in trip bearings (r = -0.213, p = 0.27), which does not support the hypothesis that sites where individuals make more consistent foraging trips have less predictable foraging distributions (Methods, Figure 13.4). Variance in trip bearings was positively related to the total number of trips recorded (r = 0.602, p < 0.001) and the number of years of tracking (r =0.445, p = 0.015, Figure 13.4). Tracking studies tend to have small sample sizes and short duration. Over the short-term, small samples may be insufficient to describe the foraging range during a period of constant conditions; individuals tracked may not visit all the areas utilised by the wider population during that period, or even by themselves at times before or after the deployment. Increasing variance in trip direction with number of trips and years of tracking indicates that over time, trips will occupy more of the potential range.

The strength of the relationship between foraging distribution and colony size over a substantial number of colonies, spanning an entire ocean basin, provides convincing evidence for Ashmole's theory that intraspecific competition for food is an important factor contributing to negative density-dependence in colonial seabirds, including deep-diving species that can exploit all three dimensions. Previous multi-colony studies generally focused on surface feeding species (especially sulids), sampled over a much smaller geographical range, and a smaller range of colony sizes (<75,000 pairs)<sup>8,11–13,28</sup>; although work on Adelie penguins is a notable example for diving species<sup>10,12</sup>. Our study is remarkable in showing that Ashmole's Halo theory extends to pursuit diving species that forage in three dimensions and that the relationship between colony size and foraging range applies across an entire ocean basin. The cost of commuting between foraging areas and breeding sites increases with distance for breeding adults, which can constrain chick growth at larger colonies<sup>29</sup>, because the time between feedings increases<sup>21</sup>. Multiple studies have proposed that foraging range should scale with the 0.5 exponent of colony size<sup>8,9,28,30</sup> because foraging area scales with the square root of foraging range; however, the scaling factor in our study was lower, at 0.31 (95% CI = 0.29-0.33). This could result from systematic differences in habitat quality that also correlate with colony size, namely that colony size is positively correlated with foraging conditions. Alternatively, the lower exponent may arise from predation pressure exerted in three dimensions. Murres are pursuit divers that can forage at depths over 200 m<sup>17</sup>, therefore foragers may trade-off costs of flying farther to locate prey by making more, deeper dives while remaining

closer to the colony<sup>31,32</sup>. Similar scaling is likely to exist among other species, but values will depend on their foraging ecology and environment; further studies across different taxa of central place foragers may reveal more general patterns. The recent proliferation of tracking studies provide the opportunity for large-scale multi-colony and multi-species studies to better understand this fundamental ecological relationship.

#### Predicting murre foraging ranges throughout the North Atlantic

There are an estimated 7,356,000 pairs of murres breeding at 412 colonies (larger than 500 pairs) within the North Atlantic region (Table 13.5). With so many colonies, it is clearly not feasible to directly measure colony-specific foraging radii using GPS tracking; therefore, estimating range from colony size data, which are easier to collect and more widely available, offers a pragmatic alternative to infer potential utilisation distributions during chick-rearing. Using the foraging range model described above, we estimate that the 95% foraging area (FA<sub>95</sub>) for all murre colonies in the North Atlantic is 689,000 km<sup>2</sup>, with FA<sub>95</sub> of individual colonies ranging in size from 87 km<sup>2</sup> to 38,600 km<sup>2</sup> (Figure 6.4, Methods). There are 17 colonies (5% of all colonies) with at least 100,000 breeding pairs; these colonies account for 57% of the total North-Atlantic murre population and have a combined FA<sub>95</sub> of 342,000 km<sup>2</sup>. Because the foraging radii of some larger colonies encompasses smaller neighbouring colonies, the estimated areas within the radii are utilised by 63% of breeding murres in the North-Atlantic, demonstrating that protecting even a relatively small proportion of colonies could protect much of the regional population.

We compared predicted foraging areas (FA<sub>95</sub>) to the World Database of Protected Areas  $(WDPA)^{33}$ , to evaluate the level of protection for foraging areas of the North Atlantic murre population. The WDPA may not include all protected areas and does not reflect other effective

management actions that may be in place within different jurisdictions; however, it provides a useful starting point for evaluating the level of potentially effective species protection in place. Forty-four percent of all colonies, representing 61% of the population, have less than 10% of their FA<sub>95</sub> within protected areas and 14% of colonies (12% of the population) have no overlap with protected areas. Only 16% of colonies, accounting for 5% of the population, have at least 90% of their FA<sub>95</sub> within protected areas. Among the 17 largest colonies, only two have more than 50% of their FA<sub>95</sub> within protected areas and 10 colonies have less than 10% of their FA<sub>95</sub> within protected areas and 10 colonies have less than 10% of their FA<sub>95</sub> within protected areas and 10 colonies have less than 10% of their foraging range, this would help safeguard foraging areas for two-thirds of the North Atlantic population of murres during the breeding season. Of course, the effectiveness of a marine protected area for any seabird species depends on the management prescriptions related to specific activities including hunting, fisheries, tourism, and shipping<sup>34,35</sup>; nevertheless, this analysis illustrates the utility of the foraging range model for informing any area-based conservation measures

Foraging range is a widely used tool for identifying critical habitat around seabird colonies<sup>30,36,37</sup>. Thaxter et al.<sup>37</sup> proposed using species-specific foraging ranges to inform Marine Protected Areas around seabird colonies. Our study shows that colony size can be used to inform estimates of foraging range for species that occur in colonies that range in size over multiple orders of magnitude. Modelling foraging distributions based on colony size has the advantage of being generalizable over a broad geographical and ecological scale, as represented in this study. The fundamental constraints imposed by colony size and the energetic costs associated with commuting trips are not flexible, so we would expect the relationship between colony size and foraging range to persist, at least once colony size has returned to equilibrium, in spite of changes in local environmental conditions. Marine spatial planning should, of course, also consider local

foraging conditions where these data area available, as exceptionally long foraging trips have been observed among auk species of the Northern Isles of the United Kingdom<sup>13</sup>, where low forage fish availability has contributed to declining seabird populations<sup>38</sup>. While our dataset is noteworthy in its size, it still represents direct tracking at only 7% of the murre colonies within the North Atlantic, which demonstrates the limitations of predicting foraging habitat through direct tracking of such a widely distributed species. Generalizable models, informed by ecological theory, represent an important contribution to informing conservation for such species on a large scale. This an important example of how behavioural theory, in this case Ashmole's halo, a special case of central place foraging theory, can be applied to inform conservation and management<sup>39</sup>.

**Data and code availability statement** Tracking data used in this study will be made available in a public repository. Code used in this analysis will be made available on GitHub.

**Author contributions** All authors contributed data and edited the paper. A.P., H.G.G. and K. E. conceived of and led the project. A.P. conducted the analysis and drafted the paper.

Competing interests The authors declare no competing interests.

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Figure 6.1 The distribution of murre colonies with GPS tracking data used in this study. Point size indicates estimates of colony size. Inset maps provide detailed views of GPS tracking data for common (green) and thick-billed (purple) murres. All maps use Lambert Conformal Conical projection and inset maps are plotted on the same scale.



Figure 6.2. Relationship between colony size and mean foraging range (left) modelled using a Weibull distribution (mean =  $\lambda\Gamma[1 + 1/k]$ , where  $\lambda = 0.88*Cs0.31$ , k = 1.35, Cs = colony size, and  $\Gamma$  is the gamma function). Points show observed mean foraging range for individual colonies, with point size scaled to the number of trips recorded at each site and colours indicating colonies of common murre (green), thick-billed murre (purple), and mixed species (orange) colonies; the solid line shows the predicted relationship between foraging range and colony size; the shaded area shows the 95% confidence region for this relationship. Examples of predicted foraging trip density distributions for a range of colony sizes (right). Each coloured line shows the predicted density of foraging trip distances for a given colony size. Closed points and open points, respectively, show the distance at which 50% and 95% of foraging trips would occur.



Figure 6.3. Overlap between predicted foraging distribution (open polygons) based on the foraging range model and observed foraging distribution (filled polygons) based on the mean utilization distribution of all GPS tracks from each site. The 95% (orange) and 50% (red) foraging areas are shown. Dice's similarity for each colony is given in the top-right corner (see Methods).



Figure 6.4. Predicted 95% foraging ranges for common (COMU) and thick-billed murre (TBMU) colonies throughout the North Atlantic region. Marine protected areas from the World Database of Protected Areas<sup>33</sup> are shown in yellow. Colonies were considered mixed if both thick-billed and common murres accounted for at least 5% of the total breeding population size.

## Methods

No statistical methods were used to predetermine sample size. The experiments were not randomized and the investigators were not blinded to allocation during experiments and outcome assessment. All analyses were conducted using R version  $4.1.0^{40}$ . All statistical tests used two-sided p-values.

#### **GPS** tracking

Foraging trips were defined as any continuous period of movement more than 1 km from the colony that lasted at least 20 minutes. For each foraging trip, we calculated the maximum horizontal distance from the colony (hereafter, trip distance). Details on study site locations and tracking sample sizes are provided in Table 13.1 and maps of all tracks are shown in Figure 13.1.

### Combining trips from common and thick-billed murres

We used two-sample Kolmogorov-Smirnov tests to determine if there was a difference in the distribution of foraging trip distances for common and thick-billed murres, when both species were tracked from the same colony. There was no significant difference in the distribution of maximum foraging distance between the two species (Table 13.2). Foraging trips for common and thick-billed murres overlapped geographically in all cases where both species were tracked simultaneously (Figure 13.1). Based on these results, tracks of common and thick-billed murres were combined in all analyses.

### Foraging range model

We used maximum likelihood estimation to fit five potential probability density functions (halfnormal, exponential, lognormal, Gamma, and Weibull distributions) to the trip distances from each colony<sup>41</sup>. Following Bullock et al<sup>25</sup>, AICc was used to identify which distributions that had the best fit to data from all colonies and we assessed goodness of fit using Nakagawa and Schielseth's<sup>42</sup> general  $r^2$ :

$$r^{2} = 1 - \frac{\sum_{i=1}^{n} (\hat{y}_{i} - y_{i})^{2}}{\sum_{i=1}^{n} (y_{i} - \bar{y})^{2}}$$

where, *n* is the number of observations,  $y_i$  is the *i*th observed value,  $\hat{y_i}$  is the *i*th predicted value, and  $\overline{y}$  is the mean predicted value. Observed values were the 10<sup>th</sup> percentiles of the observed trip distances at each colony and predicted values were the 10<sup>th</sup> percentiles of fitted distributions. We used  $r^2 \ge 0.7$  as a threshold for a good fit between predicted and observed values<sup>25</sup>. The Weibull distribution was among the distributions with AICc  $\le 4$  at 62% of sites, 97% of sites had an  $r^2 \ge$ 0.7, and the Weibull distribution had a median  $r^2$  of 0.96 (Table 13.3). The half-normal and lognormal distributions were also competitive at 55% of sites, based on AICc, and had  $r^2 \ge 0.7$  at more than half of all sites. Based on these results, we examined the relationship between colony size for the Weibull, lognormal, and half-normal distributions.

We used weighted least squares (WLS) regression to examine the relationship between colony size and the distribution parameters. Colony size and distribution parameters were log transformed for analysis. The log of number of trips was included as a weighting parameter to account for greater uncertainty in distributions at sites with smaller sample sizes. Non-parametric bootstrapping was used to calculate uncertainty in all parameter estimates; we generated 500 bootstrap datasets by resampling *n* trips from each colony with replacement, where *n* is the number of trips recoded per site.

All three distributions had a significant relationship between colony size and at least one fitted parameter (Table 13.4, Figure 13.2). The estimated exponents for the relationships were similar

for each distribution (lognormal  $\mu = 0.28$ , half-normal  $\sigma = 0.30$ , and Weibull  $\lambda = 0.31$ ). For the Weibull distribution, there was not a significant relationship between the shape parameter, k, and colony size (F = 3.20, p = 0.08). The location,  $\mu$ , and scale,  $\sigma$ , parameters of the lognormal distribution were both positively associated with colony size; however the effect of colony size on  $\mu$  was larger than the effect on  $\sigma$ . Foraging range predictions using the Weibull and half-normal distributions were similar for all quantiles greater than 0.5 (Figure 13.2). Predictions from the lognormal distribution had a higher density of trips close to the colony and a fatter tail predicting more trips at farther distances than the other two distributions.

The Weibull distribution had the best fit for data from the largest number of colonies (Figure 13.3). For this reason, the Weibull foraging range model was used in all subsequent analyses and results from this model are reported in the main text. Figure 13.3 shows the observed and predicted distributions of foraging trips for each colony.

#### Comparing foraging range model to utilization distributions

GPS tracks were linearly interpolated to 5 min intervals, so that each location would be given the same weight in kernel density estimates. Only deployments with a minimum of 20 off colony locations (>1 km) were included in the analysis. We calculated kernel density with the adehabitatHR package<sup>43</sup> using a 400 x 400 km area centred on the colony with a 2 x 2 km grid resolution, in the Albers Equal Area projection. Kernel smoothing parameters were calculated separately for each individual using the *ad hoc* method and utilization distributions were averaged across all individuals within each colony. We defined the foraging area based on the 95% volume contour of the kernel density estimate, after excluding any areas that overlap with land.

We used bootstrapping to determine which sites had enough tracking data to estimate a consistent foraging area. For each site, we resampled tracks 500 times with replacement, at increasing sample sizes from 5 to the original number of tracks from the colony. For sites with more than 50 tracks, we re-sampled up to 50 tracks and for each sample, we calculated the total area of the 95% foraging area. For each sample size, we calculated the coefficient of variation (CV) in the estimated foraging areas, and sites with a minimum CV less than 0.25 were included in analysis of foraging area. We could estimate a consistent foraging area for 19 sites. The mean sample size required for a consistent utilization distribution was 11 tracks (SD = 12.9, range = 5-53); however, sample size was not the sole determinant of consistency as the sample size for sites where a consistent UD could not be estimated overlapped this range.

The probability of murres foraging at each raster cell was calculated on the same grid used in estimating UDs based on the probability density function of the Weibull distribution (Table 13.3), with the scaling parameter for each colony estimated from the colony size (Cs) as  $\lambda = 0.88 * \text{Cs}^{0.31}$ , and k = 1.35. We calculated the predicted 95% foraging area based on all cells with a probability of use of at least 0.05. Predicted foraging areas were compared to observed foraging areas using Dice's Similarity Coefficient<sup>28</sup> s:

$$s = \frac{2A(UD_0 \cap UD_P)}{A(UD_0) + A(UD_P)}$$

where,  $A(UD_0)$  and  $A(UD_P)$  are the observed and predicted foraging areas.

### Variance in trip bearings

We calculated the bearing between the colony and the farthest foraging location within each trip using the 'geosphere' package<sup>44</sup>. For each colony, we calculated the variance in bearings using the

'circular' package<sup>45</sup>. We used Spearman's correlation tests to examine factors associated with the relationship between variance in trip bearings and the absolute residuals from the foraging range model; the number of trips measured per site; and the number of years of tracking data per site (Figure 13.4).

### Predicting foraging ranges within the North Atlantic murre population

We used existing data sources and consultation with regional experts to compile colony size data for murre colonies in the North Atlantic between 75°W and 75°E (Table 13.5). We used the foraging range model described above to estimate the 95% foraging range of all colonies with at least 500 breeding pairs. We mapped the 95% foraging area (FA<sub>95</sub>) for each colony by creating a spatial buffer around the colony center with a radius of FA<sub>95</sub> and subtracting any areas that intersected land<sup>46</sup>. We then calculated the area within the FA<sub>95</sub> buffer zone of all colonies and determined their percent overlap with marine protected areas in the World Database of Protected Areas<sup>33</sup>. All overlap analysis was performed using an Albers Equal Area Projection.

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## 7. Discussion

The study of wildlife ecology has been evolving rapidly with the development of new biologging approaches (Hays et al. 2016, Sequeira et al. 2019, Bernard et al. 2021). This revolution has coincided with a period of increased conservation concern about the effect of human activity on climate (Poloczanska et al. 2013, Sydeman et al. 2015), habitat (Hoekstra et al. 2004, Fischer & Lindenmayer 2007), and species interactions (O'Connor et al. 2009, Cury et al. 2011). The application of biologging approaches has incredible potential to advance wildlife ecology and conservation; although, there is also a risk of ecologists being overwhelmed by the quantity of data obtained through biologging (Hebblewhite & Haydon 2010). This thesis developed and applied biologging approaches to address ecological and conservation questions with a particular focus on thick-billed murres, an indicator species for Arctic marine ecosystems.

I used a range of biologger types that measure spatial distribution (GPS and geolocator), individual behaviour (accelerometer and temperature-depth-recorder), and local environmental conditions (temperature sensors) to link individual behaviour and energetics with spatial distribution and habitat. Chapters 4, 5, and 6 cover all components of the annual cycle of adult murres. The research presented here scales up from high-resolution behaviour of individuals (Chapter 3), to population scale behaviour and distribution (Chapters 4 and 5), to examine spatial distribution at a meta-population level (Chapter 6). I considered how intra-specific competition affects distributions around colonies during the breeding season (Chapter 6) and how environmental conditions affect distribution during the non-breeding season (Chapter 5). For the non-breeding season, I also examined how climate and weather influence distribution and behaviour within seasons (Chapter 4) and across four decades (Chapter 5).
Obtaining reliable activity budgets from free-ranging animals is important for addressing a wide range of questions in wildlife ecology. Biologgers with additional sensors that measure animal behaviours, like flight and foraging, can expand the ecological applications of tracking studies, beyond measuring where individuals go to understanding how they are interacting with different habitats (Cooke et al. 2004, Bestley et al. 2013). In Chapter 3, I developped and compared six techniques for classifying seabird behaviours from accelerometer loggers. All analytical methods had high classification accuracy for two species, thick-billed murres and black-legged kittiwakes, with different flight and foraging styles, demonstrating that activity budgets defined from accelerometers are robust to classification technique. In Chapter 4, I applied a similar classification approach to generate daily activity budgets and daily energy expenditure from sensors that measured temperature, depth, and wet-dry state through the winter. These logger data showed that marine habitat, climate variability, and moon phase all influence behavior and energetics at this challenging time of year.

Prior to the advent of long-term biologging for this species, it was assumed that thick-billed murres wintered primarily within the marginal ice-zone along the continental shelf (Gaston et al. 1983b, Elliot et al. 1990, Donaldson et al. 1997). Early geolocator tracking of this species showed that murres are more widely distributed and use a broader range of marine habitat in winter than previously known (Gaston et al. 2011, McFarlane Tranquilla et al. 2013). Chapter 4 of this thesis provides some of the first data on how environmental conditions in winter influence foraging behaviour, activity budgets, and energetics for this species. Murres showed flexibility to switch between two distinct marine habitats during winter. Habitat type had important effects on foraging behaviour and energy budgets. Winter conditions are important for determining survival of adults and pre-breeding juveniles (Gaston 2003, Smith & Gaston 2012, Frederiksen et al. 2016) and can

also influence reproductive performance in subsequent years for some species (Catry et al. 2013, Marra et al. 2015b, Fayet et al. 2016). Given the on-going and anticipated effects of climate change on marine ecosystems, including declining sea-ice cover, increased sea and air temperatures, and increased storm activity (Meredith et al. 2019), it is critical to understand the relationship between habitat, behaviour, and ultimately survival. Year-round tracking of spatial distribution and individual behaviour is an essential tool for investigating these relationships.

The two chapters examining murres during the non-breeding period (Chapters 4 and 5) both demonstrated the importance of marine climate in determining distribution and behaviour when murres are not constrained by central-place foraging. Sea surface temperature, air temperature, and ice cover all influenced the seasonal range through fall migration, winter, and spring migration. Changes in these physical habitat attributes have likely already altered migration timing and spatial distributions of murres from sub-Arctic populations like Coats Island. Belugas (Delphinapterus *leucas*) in Eastern Hudson Bay showed different habitat use and fall migration timing in response to sea surface temperature (Bailleul et al. 2012). In European Shags (Phalacrocorax aristotelis), winter foraging by females was correlated with timing of breeding the following spring (Daunt et al. 2006). Phenological responses of polar seabird species to climate change are complex, with examples of geographical and phylogenetic variation (Barbraud & Weimerskirch 2006, Descamps et al. 2019). Given the diverse foraging strategies of murres within different marine habitats (Chapter 4) and variability in migration timing (Chapter 5) observed in this thesis, continued tracking of year-round behaviour and migration of murres in this population would provide useful insight into the factors that control migration phenology in Arctic marine species.

A central goal of ecology is to identify general rules that predict behaviour and distributions of wildlife. This thesis has demonstrated two examples of murre behaviour that show consistent

patterns across large spatial scales and populations. Chapter 4 described differences in foraging behaviour and energetics that were associated with different marine ecosystems, defined by sea surface temperature. Comparing these results to recent studies that tracked common murres during winter, showed similar foraging behaviour in this closely related species. Common murres wintering in warmer water in the North Sea (Dunn et al. 2020), displayed a similar resting strategy to the thick-billed murres using warm water in the Labrador Basin. While common murres wintering in cold water on the Grand Banks in the northwest Atlantic, appear to use a similar feasting strategy as thick-billed murres wintering in the same cold water region, with more time flying and somewhat less time diving (Burke & Montevecchi 2018). Chapter 6 showed there is a consistent pattern of scaling between colony size and the foraging distribution of thick-billed and common murres at colonies throughout the North Atlantic, in spite of the large geographic and environmental differences among colonies. These are both examples of individuals of the same, or closely related, species responding to environmental gradients, sea surface temperature in winter and intraspecific competition during chick-rearing, in consistent ways. Chapter 6 leveraged an extensive archive of GPS tracking collected at multiple colonies over more than a decade, to reexamine a fundamental question in foraging ecology. Collecting similar long-term, multipopulation data on year-round movements and behaviour would provide valuable insights into the ecology of migratory marine species (Sequeira et al. 2019, Carneiro et al. 2020).

## 8. Conclusion

Biologging techniques have revolutionized wildlife science by enabling observation of individual movement and behaviour in high-resolution over longer time scales and larger spatial scales than was conceivable to earlier ecologists (Wilmers et al. 2015). This change has been especially valuable for studying migratory species that travel large distances each year (McKinnon & Love 2018) and marine species that spend much of their time away from land and under water, where they are nearly unobservable by humans (Hays et al. 2016, Roncon et al. 2018). This field also faces challenges as ecologists develop methods for analyzing 'big data' generated by biologgers and work to integrate biologging with existing ecological theory (Hebblewhite & Haydon 2010).

The non-breeding period has long been neglected in seabird ecology (Webster et al. 2002, Marra et al. 2015a); biologging approaches demonstrated in this thesis provide powerful tools to address this gap in our knowledge. In particular, biologging methods that combine spatial tracking with behavioural data, such as those used in Chapter 4, can contribute significantly to our understanding migration, habitat use, and annual survival. Technological constraints on tracking devices still limit the tools available for year-round tracking of many species; wildlife ecologists need to continue working to develop biologgers that can fully address this gap. For small-bodied, deep-diving species, like murres, this means a developing logger that can provide GPS-level accuracy through winter without inhibiting behaviour or thermoregulation.

I employed multi-year (Chapter 5) and multi-colony (Chapter 6) tracking data sets to address largescale ecological questions about climate change and foraging theory. Applying long-term, multipopulation, and multi-species tracking data sets to answer ecological questions and conservation issues is becoming more common (Sequeira et al. 2019, Carneiro et al. 2020, Hindell et al. 2020). I contend that the greatest potential of biologging to contribute to wildlife ecology as a discipline would be realized best by incorporating regular tracking of wildlife into on-going long-term studies. Ecologists ability to use tracking data to address large-scale questions also depends on developing infrastructure to standardize and archive data collected using different platforms, and also make tracking data searchable to facilitate connecting researchers to existing data (Davidson et al. 2020, Sequeira et al. 2021).

Understanding species behaviour and how it is influenced by its environment are key elements of wildlife ecology (Elton 1927, Andrewartha & Birch 1954). Biologging has greatly expanded ecologists capacity to observe individual movement, behaviour, and energetics in natural systems. Combined advances in biologging of wildlife and remote sensing of the environment have created opportunities to address long-standing questions about the relationship between wildlife species and their environment. This thesis applied these approaches to link individual behaviour and energetics, measured in fine detail, to ecological processes occurring over many decades and at colonies across an entire ocean-basin.

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## 10. Supplementary materials for Chapter 3

Study	Species	n	Accelerometer Measures	Predictor Variables	Behaviours Identified	Classification Methods	Accuracy (%)
Gómez Laich et al 2009	Imperial cormorant ( <i>Phalacrocorax atriceps</i> )	14	Pitch, acceleration, standard deviation, frequency	7	8	Thresholds	-
Moreau et al 2009	Goat ( <i>Capra aegagrus</i> hircus)	3	Acceleration, inclination	4	3	Thresholds	Eating: 87 - 93 Resting: 68 - 90 Walking: 20 - 92
Nathan et al 2011	Griffon vulture ( <i>Gyps</i> fulvus)	43	Mean, standard deviation, skewness, kurtosis, maximum, minimum, ACF, trend, square root of sum-of-squares, pair-wise correlation, ODBA, inclination, azimuth	38	7	Linear discriminant analysis (LDA), support vector machines (SVM), classification and regression trees (CART), random forests (RF), artificial neural networks (ANN)	ANN: 84.8 CART: 86.0 LDA: 86.7 RF: 90.9 SVM: 87.0
Shamoun- Baranes et al 2012	Oystercatcher (Haematopus ostralegus)	3	GPS speed, pitch, roll, maximum dynamic acceleration, mean dynamic acceleration, frequency, dominant power spectrum	17	3, 8	Classification trees	3 Behaviours: 86.8 8 Behaviours: 73.6
Bidder et al 2014	Badger (Meles meles), Camel (Camelus dromedaries), Cheetah (Acinonyx jubatus), Imperial cormorant (Phalacrocorax atriceps), Dingo (Canus hupus dingo), Kangaroo (Macropus rufus), Wombat (Lasiorhinus latifrons), Humon (Homo sanians)	5, 1, 1, 14, 1, 1, 1, 1, 1	Acceleration	3	5	K-nearest neighbour	Badger: 71 Camel: 82 Cheetah: 77 Cormorant: 77 Dingo: 83 Kangaroo: 91 Wombat: 76 Human: 95
Bom et al 2014	Crab plover ( <i>Dromas</i> ardeola)	22	Mean, standard deviation, maximum, minimum, skewness, kurtosis, dominant power spectrum, trend, dynamic acceleration, overall dynamic body acceleration	31	8	Random forest	Inactive: 95 Fly: 89 Walk: 88 Handle: 84 Search: 78
Resheff et al 2014	Griffon vulture ( <i>Gyps</i> fulvus)	nr	Mean, standard deviation, skewness, kurtosis, maximum, minimum, normalized, covariance,	52	6	Artificial neural network (ANN), decision tree, linear-support vector	ANN: 84.8 Decision tree: 77.7 LDA: 80.8

## Table 10.1. Summary of recent studies that used accelerometers to classify animal behaviours.

Study	Species	n	Accelerometer Measures	Predictor Variables	Behaviours Identified	Classification Methods	Accuracy (%)
			correlation, mean difference, standard deviation difference, dynamic acceleration, overall dynamic body acceleration, wave amplitude, line crossings, 25th percentile, 50th percentile, 75th percentile			machine (LSVM), linear/quadratic discriminant analysis (LDA), nearest neighbours, radial basis function for support vector machine (RBF SVM), random forest (RF)	LSVM: 80.1 Nearest neighbour: 80.5 RF: 84.0 RBF SVM: 82.6
Berlincourt et al 2015	Short-tailed shearwater (Puffinus tenuirostris)	10	Static acceleration, dynamic acceleration, pitch, continuous wavelet transformation, speed		5	Ethographer	-
Collins et al 2015	Black-legged kittiwake (Rissa tridactyla)	6	Pitch, standard deviation	2	3	Histogram segregation	Flying: 97.9 On land: 97.5 On water: 97.5
Chimienti et al 2016	Razorbills ( <i>Alca torda</i> ), Common guillemots ( <i>Uria aalge</i> )	2, 5	Acceleration, depth, vertical speed, static acceleration, dynamic acceleration, pitch, amplitude, pitch variance	7	5,7	Expectation maximization	-
Hammond et al 2016	Alpine chipmunk ( <i>Tamais</i> alpinus) Lodgepole chipmunk ( <i>Tamais speciosus</i> )	20	Mean , variance, minimum, maximum, covariance, spectral features		2-5	Hidden semi-Markov model, optimum- threshold baseline, support vector machine learning	2 Behaviours: 89.9 3 Behaviours: 81.6 4 Behaviours: 73.5 5 Behaviours: 73.3
Leos-Barajas et al 2016	Blacktip reef shark ( <i>Carcharhinus</i> <i>melanopterus</i> ), Verreaux's eagle ( <i>Aquila</i> <i>verreauxii</i> )	1, 1	Overall dynamic body acceleration, minimum specific acceleration	1	2	Hidden Markov model	-
Cianchetti- Benedetti et al 2017	Scopoli's shearwater (Calonectris diomedea)	60	Vectorial dynamic body acceleration, static acceleration	2	3	Thresholds	-

Study	Species	n	Accelerometer Measures	Predictor Variables	Behaviours Identified	Classification Methods	Accuracy (%)
Ladds et al 2017	Australian fur seal (Arctocephalus pusillus doriferus), New Zealand fur seal (Arctocephalus forsteri), Sub-antarctic fur seal (Arctocephalus tropicalus), Australian sea lion (Neophoca cinerea)	2, 3, 1, 6	Mean, median, minimum, maximum, range, standard deviation, skewness, kurtosis, absolute value, inverse covariance, trend, 10 <sup>th</sup> percentile, 90 <sup>th</sup> percentile, square root of sum of squares, pairwise correlation, inclination, azimuth, dynamic body acceleration, partial dynamic body acceleration, vectorial dynamic body acceleration	147	4, 6	Random forest, gradient boosting machine, logistic regression, super machine learning	4 Behaviours: 85.1 6 Behaviours: 73.6
Pagano et al 2017	Polar bear (Ursus maritimus)	7	Static acceleration, dynamic acceleration, overall dynamic body acceleration, dominant power spectrum, frequency, magnitude, wet/dry status	25	10	Random forest	Resting: 97.3 Walking: 97.1 Swimming: 88.7 Running: 70.9
## 11. Supplementary materials for Chapter 4

#### Geolocator estimates used to determine solar angle

For location estimates, we summarized maximum-recorded light levels at 5-minute intervals prior to estimating twilights. Twilight times were estimated using the threshold method in the 'TwGeos' package (Lisovski et al. 2016). We defined two behavioural modes, flying and on water. Flying was defined as any period where the sensor was dry and tag temperature was less than 5°C; this temperature threshold was used to prevent periods of leg-tucking from being falsely classified as flying (Linnebjerg et al. 2014). Location estimates were calculated using a probabilistic algorithm that incorporates data from twilight estimates, a land-sea mask, sea surface temperature, and movement rates in order to generate more realistic estimates of seabird positions from geolocators (Merkel et al. 2016, Halpin et al. 2021). Location estimates were constrained to be over water with less than 90% ice cover within each 0.25° x 0.25° raster cell. We also included sea surface temperature (NOAA High Resolution SST NOAA/OAR/ESRL PSL, https://psl.noaa.gov/, Reynolds et al. 2007) matching in location estimates. Full details of the parameters used in the probabilistic algorithm are provided in the supplementary material (Table 11.1).

Parameter	Value
Light threshold <sup>1</sup>	175
Solar range (°)	-6 to -1
Speed – Fly (m/s)	
Mean	15
SD	5
Max	25
Speed – On water (m/s)	
Mean	1
SD	1.3
Max	5
SST SD (°C)	0.1
Max SST difference (°C)	2
Spring equinox (days)	-21 to 14
Fall equinox (days)	-14 to 21
Ice concentration cut-off (%)	90
Boundary box (°)	-110W, -10W, 30N, 75N

*Table 11.1. Parameter values used in the probGLS model to estimate locations from temperaturedepth-light loggers.* 

<sup>1</sup>Unitless values specific to tag model.

#### Physical oceanographic characteristics of the habitat classes

We used bathymetry and oceanographic models to examine the spatial distribution and physical oceanography of the habitat classes defined from the HMM. We extracted environmental data from a 0.25° x 0.25° grid within the study area (40°-70° N and 35-75°W). Bathymetry was obtained from ETOPO1 Global Relief Model (https://www.ngdc.noaa.gov/mgg/global/). Monthly SST, ice cover concentration, mixed layer depth (MLD), sea surface height (SSH), and current velocity were obtained from Copernicus Marine Service Global Ocean Physics Reanalysis (GLOBAL\_ANALYSIS\_FORECAST\_PHY\_001\_030). We calculated the probability density function for each state based on the SST value of each monthly raster cell and assigned each cell to the state with the highest probability. We compared physical oceanography of the three habitat classes using density plots, medians, and inter-quartile ranges.

The three habitats identified from the HMM were also associated with differences in other physical oceanographic habitat characteristics within the Northwest Atlantic, in addition to SST (Figure 11.1). Cold water habitat was primarily located over shelf water (-233 m; IQR = -470 to -114 m), had a shallower mixed layer depth (33 m; IQR = 20 to 46 m), higher sea surface height (-0.53 m; IQR = -0.71 to -0.45 m), and more ice cover (22%; IQR = 0.4 to 77%) than the other two habitats. Warm water habitat was relatively deep (-3200 m; IQR = -3400 to -2700 m) and ice-free (0.0%; IQR = 0 - 0.2%), with a deeper mixed layer (216 m; IQR = 142 to 421 m) and lower sea surface height (-1.04 m; IQR = -1.1 to -0.99 m) than the Cold water habitat. The Warmer water habitat had the deepest bathymetry (-3450 m; IQR = -4200 to -2700 m), no ice cover (0.0%), intermediate mixed layer depth (145 m; IQR = 102 to 203) and intermediate sea surface height (-0.92 m; IQR = -0.99 to -0.67). Current velocities overlapped for the three habitat classes.



Figure 11.1. Maps showing physical oceanographic characteristics – sea surface temperature (SST), bathymetry, ice cover, mixed layer depth (MLD), sea surface height (SSH), and current velocity – within the study area for Feb 2018. Density plots show the distribution of each variable by habitat type at sample points throughout the study period (Jan-Mar, 2018 and Jan-Mar 2019). Oceanographic data from Copernicus Marine Service, GLOBAL\_REANALYSIS\_PHY\_001\_030. The white outlines show the state boundaries for Feb 2018 as shown in Figure 4.2.



Figure 11.2. Plots of estimated sea surface temperature (SST) experienced during winter by each individual murre. Points are coloured according to the habitat state classification from a hidden Markov model with three states: Cold (blue), Warm (yellow), and Warmer (red).



Figure 11.2 (cont). Plots of estimated sea surface temperature (SST) experienced during winter by each individual murre. Points are coloured according to the habitat state classification from a hidden Markov model with three states: Cold (blue), Warm (yellow), and Warmer (red).



Figure 11.2 (cont). Plots of estimated sea surface temperature (SST) experienced during winter by each individual murre. Points are coloured according to the habitat state classification from a hidden Markov model with three states: Cold (blue), Warm (yellow), and Warmer (red).

Table 11.2. AIC model comparison for generalized linear mixed effects models of proportion of time diving during daylight, civil twilight, nautical twilight, and night. Predictor variables in model formulae are H = habitat, D = day of year, M = moon illumination, N = NAO. ZI refers to models that included zero-inflation parameters. All models included random effects for year and deployment id. Column names refer to the number of parameters in each model (K), log-likelihood (LL), Akaike's Information Criterion (AIC), delta AIC ( $\Delta AIC$ ), and AIC weight. Only the ten models with the lowest AIC and the null model are shown.

Model	K	LL	AIC	ΔΑΙΟ	wAIC
$Day \sim H + D + M + N + H:D + H:M + H:N$	11	2928	-5833.2	0.0	1.00
$Day \sim H + D + M + N + H:D + H:N$	10	2912	-5804.3	28.8	0.00
$Day \sim H + D + N + H:D + H:N$	9	2895	-5771.8	61.4	0.00
$Day \sim H + D + M + N + H:M + H:N$	10	2861	-5701.3	131.9	0.00
$Day \sim H + D + M + N + H:N$	9	2843	-5667.1	166.0	0.00
$Day \sim H + D + N + H:N$	8	2821	-5626.2	207.0	0.00
$Day \sim H + D + M + N + H:D + H:M$	10	2806	-5591.4	241.8	0.00
$Day \sim H + D + M + N + H:M$	9	2783	-5548.4	284.8	0.00
$Day \sim H + D + M + N + H:D$	9	2779	-5539.7	293.5	0.00
$Day \sim H + D + M + N$	8	2757	-5497.6	335.6	0.00
$Day \sim 1$	4	2323	-4637.4	1195.7	0.00
$Civil \sim H + D + M + N + H:D + H:M, ZI \sim 1$	11	5790	-11557.0	0.0	0.41
$Civil \sim H + D + M + N + H:D + H:M, ZI \sim H$	12	5790	-11555.6	1.4	0.20
$Civil \sim H + D + M + N + H:D + H:M + H:N$	12	5790	-11555.2	1.9	0.16
$Civil \sim H + D + M + H:D + H:M, ZI \sim 1$	10	5787	-11554.3	2.7	0.10
$Civil \sim H + D + M + N + H:D + H:M + H:N, ZI \sim H$	13	5790	-11553.7	3.3	0.08
$Civil \sim H + D + M + H:D + H:M, ZI \sim H$	11	5787	-11552.9	4.2	0.05
$Civil \sim H + D + M + N + H:M + H:N, ZI \sim 1$	11	5782	-11541.3	15.8	0.00
$Civil \sim H + D + M + H:M, ZI \sim 1$	9	5780	-11541.1	15.9	0.00
$Civil \sim H + D + M + N + H:M, ZI \sim 1$	10	5781	-11541.0	16.0	0.00
$Civil \sim H + D + M + N + H:M + H:N, ZI \sim H$	12	5782	-11539.9	17.2	0.00
$Civil \sim 1, ZI \sim 1$	5	5321	-10631.1	926.0	0.00
Nautical $\sim$ H + D + M + N + H:D + H:M + H:N, ZI $\sim$ H	13	4643	-9260.8	0.0	1.00
Nautical $\sim$ H + D + M + N + H:D + H:M, ZI $\sim$ H	12	4628	-9231.6	29.2	0.00
Nautical $\sim$ H + D + M + N + H:D + H:N, ZI $\sim$ H	12	4614	-9203.8	57.0	0.00
Nautical $\sim$ H + D + M + N + H:M + H:N, ZI $\sim$ H	12	4606	-9188.4	72.4	0.00
Nautical $\sim$ H + D + M + N + H:M, ZI $\sim$ H	11	4601	-9179.4	81.4	0.00
Nautical $\sim$ H + D + M + N + H:D, ZI $\sim$ H	11	4601	-9179.4	81.4	0.00
Nautical $\sim$ H + D + M + H:D + H:M, ZI $\sim$ H	11	4599	-9177.0	83.8	0.00
Nautical $\sim$ H + D + M + H:M, ZI $\sim$ H	10	4582	-9143.5	117.3	0.00
Nautical $\sim$ H + D + M + N + H:N, ZI $\sim$ H	11	4580	-9137.9	122.9	0.00
Nautical $\sim$ H + D + M + H:D, ZI $\sim$ H	10	4576	-9132.2	128.6	0.00
Nautical $\sim 1, ZI \sim 1$	5	3904	-7797.5	1463.3	0.00
Night $\sim$ H + D + M + N + H:D + H:M + H:N, ZI $\sim$ H	13	-247	520.9	0.0	0.96
Night $\sim$ H + D + M + N + H:M + H:N, ZI $\sim$ H	12	-252	527.1	6.3	0.04
Night $\sim$ H + D + M + N + H:D + H:N, ZI $\sim$ H	12	-256	536.2	15.4	0.00
Night $\sim$ H + D + M + N + H:N, ZI $\sim$ H	11	-259	540.2	19.3	0.00
Night $\sim$ H + M + N + H:M + H:N, ZI $\sim$ H	11	-266	554.3	33.4	0.00
Night $\sim$ H + D + M + N + H:D + H:M, ZI $\sim$ H	12	-269	562.9	42.1	0.00
Night $\sim$ H + D + M + N + H:M, ZI $\sim$ H	11	-271	563.4	42.5	0.00
Night $\sim$ H + M + N + H:N, ZI $\sim$ H	10	-275	569.5	48.7	0.00
Night $\sim$ H + D + M + N, ZI $\sim$ H	10	-280	580.4	59.6	0.00
Night $\sim$ H + M + N + H:M, ZI $\sim$ H	10	-281	581.6	60.8	0.00
Night ~ 1, $ZI \sim 1$	5	-652	1314.0	793.1	0.00

Parameter	Day	Civil	Nautical	Night
Conditional terms				
(Intercept)	-1.20 (0.08)	-1.62 (0.04)	-2.94 (0.07)	-2.27 (0.15)
DOY	0.01 (0.001)	-0.01 (0.000)	-0.006 (0.001)	-0.003 (0.002)
Moon	0.01 (0.05)	0.01 (0.03)	0.02 (0.06)	0.12 (0.15)
NAO	0.03 (0.03)	-0.03 (0.01)	0.001 (0.03)	0.08 (0.08)
HabitatWarm	-1.34 (0.08)	0.36 (0.05)	1.64 (0.07)	0.70 (0.17)
DOY:HabitatWarm	0.01 (0.001)	-0.003 (0.001)	-0.01 (0.001)	-0.01 (0.003)
Moon:HabitatWarm	-0.40 (0.07)	-0.20 (0.05)	-0.57 (0.07)	0.76 (0.18)
NAO:HabitatWarm	0.58 (0.04)	0.05 (0.02)	-0.22 (0.04)	-0.61 (0.09)
Zero-inflation terms				
(Intercept)		-3.91 (0.15)	-0.76 (0.04)	1.67 (0.06)
HabitatWarm		-0.18 (0.23)	-1.99 (0.10)	-1.62 (0.07)

Table 11.3. Parameter estimates for time spent diving during daylight, civil twilight, nautical twilight, and night. Values are parameter estimates ( $\pm$  SE), shown on the logit-link scale, from generalized linear mixed effects models. Only parameters included in the most parsimonious models (Table 11.2).

Table 11.4. AIC model comparison for generalized linear mixed effects models of daily time flying and diving. Predictor variables in model formulae are H = habitat, D = day of year, M = moon illumination, N = NAO. ZI refers to models that included zero-inflation parameters. All models included random effects for year and deployment id. Column names refer to the number of parameters in each model (K), log-likelihood (LL), Akaike's Information Criterion (AIC), delta AIC ( $\Delta AIC$ ), and AIC weight. . Only the ten models with the lowest AIC and the null model are shown.

Model	K	LL	AIC	ΔΑΙΟ	wAIC
$Fly \sim H + D + M + N + H:D + H:M, ZI \sim H$	12	10700	-21375.6	0.0	0.32
$Fly \sim H + D + N + H:D, ZI \sim H$	10	10698	-21375.2	0.4	0.26
$Fly \sim H + D + M + N + H{:}D,  ZI \sim H$	11	10698	-21373.9	1.7	0.14
$Fly \sim H + D + M + N + H{:}D + H{:}M + H{:}N,  ZI \sim H$	13	10700	-21373.7	1.9	0.12
$Fly \sim H + D + N + H:D + H:N, ZI \sim H$	11	10698	-21373.4	2.2	0.11
$Fly \sim H + D + M + N + H{:}D + H{:}N, ZI \sim H$	12	10698	-21372.1	3.5	0.05
$Fly \sim H + D + H:D, ZI \sim H$	9	10690	-21362.6	13.0	0.00
$Fly \sim H + D + M + H{:}D + H{:}M, ZI \sim H$	11	10692	-21361.5	14.1	0.00
$Fly \sim H + D + M + H{:}D, ZI \sim H$	10	10691	-21361.0	14.6	0.00
$Fly \sim H + D + M + N + H{:}D + H{:}M,ZI \sim 1$	11	10686	-21349.1	26.5	0.00
$Fly \sim 1, ZI \sim 1$	5	10528	-21045.1	330.5	0.00
$Dive \sim H + D + M + N + H:D + H:M + H:N$	11	6173	-12324.3	0.0	0.50
$Dive \sim H + D + M + N + H:D + H:N$	10	6172	-12324.1	0.2	0.46
$Dive \sim H + D + N + H:D + H:N$	9	6169	-12319.5	4.8	0.05
$Dive \sim H + D + M + N + H:D$	9	6161	-12304.4	19.9	0.00
$Dive \sim H + D + M + N + H:D + H:M$	10	6162	-12303.6	20.8	0.00
$Dive \sim H + D + N + H:D$	8	6159	-12302.1	22.2	0.00
$Dive \sim H + D + M + N + H:M + H:N$	10	6145	-12270.1	54.2	0.00
$Dive \sim H + D + M + N + H:N$	9	6144	-12270.0	54.3	0.00
$Dive \sim H + D + M + H:D$	8	6142	-12267.3	57.0	0.00
$Dive \sim H + D + H:D$	7	6141	-12267.2	57.1	0.00
Dive $\sim 1$	4	5951	-11893.7	430.6	0.00

Parameter	Diving	Flying
Conditional terms		-
(Intercept)	-1.736 (0.035)	-3.667 (0.050)
DOY	0.005 (0.000)	-0.001 (0.001)
Moon	0.019 (0.022)	0.024 (0.043)
NAO	0.011 (0.012)	-0.068 (0.017)
HabitatWarm	0.237 (0.036)	-0.769 (0.070)
DOY:HabitatWarm	-0.004 (0.001)	0.008 (0.001)
Moon:HabitatWarm	0.049 (0.033)	-0.133 (0.069)
NAO:HabitatWarm	0.080 (0.017)	
Zero-inflation terms		
(Intercept)		-2.96 (0.10)
HabitatWarm		0.65 (0.12)

Table 11.5. Parameter estimates for time spent diving and flying. Values are parameter estimates  $(\pm SE)$ , shown on the logit-link scale, from generalized linear mixed effects models. Only parameters included in the most parsimonious models are shown (Table 11.4).

Table 11.6. AIC model comparison for generalized linear mixed effects models of daily energy expenditure (DEE) and apparent energy intake (AEI). Predictor variables in model formulae are H = habitat, D = day of year, M = moon illumination, N = NAO. ZI refers to models that included zero-inflation parameters. All models included random effects for year and deployment id. Column names refer to the number of parameters in each model (K), log-likelihood (LL), Akaike's Information Criterion (AIC), delta AIC ( $\Delta AIC$ ), and AIC weight. Only the ten models with the lowest AIC and the null model are shown.

Model	K	LL	AIC	ΔΑΙC	wAIC
$DEE \sim H + D + M + N + H:D + H:M$	10	-29706	59431.8	0.0	0.30
$DEE \sim H + D + N + H:D$	8	-29708	59431.8	0.0	0.30
$DEE \sim H + D + M + N + H:D$	9	-29708	59433.5	1.7	0.13
$DEE \sim H + D + M + N + H:D + H:M + H:N$	11	-29706	59433.8	2.0	0.11
$DEE \sim H + D + N + H:D + H:N$	9	-29708	59433.8	2.0	0.11
$DEE \sim H + D + M + N + H:D + H:N$	10	-29708	59435.5	3.7	0.05
$DEE \sim H + D + H:D$	7	-29720	59453.3	21.6	0.00
$DEE \sim H + D + M + H:D + H:M$	9	-29718	59454.1	22.4	0.00
$DEE \sim H + D + M + H{:}D$	8	-29719	59454.3	22.5	0.00
$DEE \sim H + D + M + N + H:M + H:N$	10	-29721	59461.5	29.7	0.00
$DEE \sim 1$	4	-30322	60652.5	1220.7	0.00
$AEI \sim H + D + M + N + H{:}D + H{:}M$	10	-26984	53988.9	0.0	0.58
$AEI \sim H + D + M + N + H:D + H:M + H:N$	11	-26984	53989.6	0.7	0.40
$AEI \sim H + D + M + N + H{:}D$	9	-26989	53996.1	7.3	0.02
$AEI \sim H + D + M + N + H:D + H:N$	10	-26989	53997.5	8.6	0.01
$AEI \sim H + D + N + H:D$	8	-26997	54009.2	20.3	0.00
$AEI \sim H + D + N + H:D + H:N$	9	-26997	54011.0	22.1	0.00
$AEI \sim H + D + M + N + H:M + H:N$	10	-27003	54026.4	37.5	0.00
$AEI \sim H + D + M + N + H:M$	9	-27008	54033.6	44.7	0.00
$AEI \sim H + D + M + N + H{:}N$	9	-27008	54033.9	45.1	0.00
$AEI \sim H + D + M + N$	8	-27012	54039.4	50.5	0.00
AEI ~ 1	4	-27771	55550.6	1561.7	0.00

Table 11.7. Parameter estimates for daily energy expenditure (DEE) and apparent energy expenditure (AEI). Values are parameter estimates ( $\pm$  SE), shown on the log-link scale, from generalized linear mixed effects models with Gamma distribution. Only parameters included in the most parsimonious models are shown (Table 11.6).

Parameter	DEE	AEI
(Intercept)	7.8835 (0.0077)	6.8706 (0.0124)
DOY	-0.0005 (0.0001)	-0.0043 (0.0001)
NAO	-0.0104 (0.0021)	-0.0738 (0.0038)
HabitatWarm	-0.1672 (0.0073)	-0.1232 (0.0143)
DOY:HabitatWarm	0.0008 (0.0001)	0.0016 (0.0002)
Moon		-0.0082 (0.0101)
Moon:HabitatWarm		-0.0460 (0.0151)

### 12. Supplementary materials for Chapter 5

#### SUPPLEMENTARY MATERIAL

# Northward range shifts and shorter wintering period of an Arctic seabird in response to four decades of changing ocean climate

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Short title: Range shifts of an Arctic seabird

	LAT 2800S	MK5	MK7
Light threshold <sup>1</sup>	175	12	12
Solar range (°)		-6 to -1	
Speed – Fly (m/s)			
Mean	15	3	3
SD	5	5	5
Max	25	15	15
Speed – On water (m/s)			
Mean	1	3	3
SD	1.3	5	5
Max	5	15	15
SST SD (°C)	0.1	0.1	
Max SST difference (°C)	2	2	
Spring equinox (days)		-21 to 14	
Fall equinox (days)		-14 to 21	
Ice concentration cut-off (%)		90	
Boundary box (°)		-110W, -10W, 30N, 75N	

Table 12.1. Parameter values used in GLS location estimates for the three types of loggers used in this study.

<sup>1</sup>Unitless values specific to tag model.



Figure 12.1. Maps showing the distribution of used locations (yellow) and pseudo absences (purple) for the 2017/18 tracking year. Pseudo absences were selected from all areas within 1,000 km of any observed location within each tracking year, excluding areas within 200 km of used locations collected within the same month.



Figure 12.2. Monthly movements of thick-billed murres tracked from Coats Island (red point), Nunavut, Canada, during the 2007/08 non-breeding period.



*Figure 12.3.* Monthly movements of thick-billed murres tracked from Coats Island (red point), Nunavut, Canada, during the 2008/09 non-breeding period.



Figure 12.4. Monthly movements of thick-billed murres tracked from Coats Island (red point), Nunavut, Canada, during the 2017/18 non-breeding period.



Figure 12.5. Monthly movements of thick-billed murres tracked from Coats Island (red point), Nunavut, Canada, during the 2018/19 non-breeding period.



Figure 12.6. Longitude by date for each individual thick-billed murre track. Colours represent tracks of different individuals. The dashed horizontal line indicates 70°W, which was used to measure eastward migration in fall and westward migration in spring.

#### Effect of experimental treatment on model accuracy and variable importance

In 2017 and 2018, tracked murres were included in a separate study examining the affects of increased reproductive investment on non-breeding behaviour. Within this experiment, 33% of nests had their egg removed during early incubation, to force females to relay; 33% of nests had both adults handicapped by clipping the five outer primaries to the length of the 6<sup>th</sup> primary; and 33% of nests were in the control group. Initial exploration of the spatial distribution of locations for birds from each treatment showed significant overlap in the non-breeding distributions of control, delay, and handicap murres.

To test if experimental treatments applied to murres in the 2017 and 2018 had any effect of SDM, we ran a separate models on data for tracks from only these two years. One models included the eight predictor variables described in the main manuscript, and the other model included an additional variable for experimental treatment. We compared accuracy for a model including treatment as a predictor and a model without treatment. We compared accuracy for each of these models, using AUC, F1 score, and the Continuous Boyce Index, to determine if treatment influenced model predictions. We also calculated variable importance for all predictors in the model including treatment as an effect, to determine if treatment was useful in predicting murre distributions within any season.

Including treatment in the SDM did not improve model accuracy using any metric (Table 12.2). Variable importance of treatment was less than 2.2 in all seasons (Figure 12.7), supporting the conclusion that experimental treatment did not affect model predictions.

Table 12.2. Species distribution model accuracy including and excluding experimental treatment as a predictor variable. Accuracy measures are area-under-curve (AUC), F1 statistic (F1), and the Continuous Boyce Index (CBI).

Model	AUC	F1	CBI	
Including treatment	98.1	93.1	91.1	
Excluding treatment	98.9	93.7	92.8	



Figure 12.7. Relative importance of environmental predictors for the species distribution model including treatment as a predictor. Variable importance is scaled between 0-100 for each stage.



Figure 12.8. Predicted seasonal distributions of thick-billed murres from Coats Island from 1989 -2019, by decade. Shading shows the median distribution across each season and time period for probabilities greater than 0.5. Lines indicate the 1982-1989 distribution relative to the each decade. Black points show the median distribution in 1982-1989 and white points show the median distribution in each decade.



Figure 12.9. Predicted seasonal distributions of thick-billed murres from Coats Island from 1989-2019, by decade. Shading shows the median distribution across each season and time period for probabilities greater than 0.5. Lines indicate the 1982-1989 distribution relative to the each decade. Black points show the median distribution in 1982-1989 and white points show the median distribution in each decade.

Table 12.3. Summary of comparisons for changes in predicted distributions of thick-billed murres from Coats Island over time, by season. Intercepts (mean  $\pm$  SE) represent parameter estimates for 1982; slopes (mean  $\pm$  SE) are estimated change per year. Area is the total area with a median probability of use of at least 70%. Overlap is the percent overlap of each year's distribution with the average distribution from 1982 – 1989. Easting and northing are the center (median) of each range. Edges are the 5<sup>th</sup> and 95<sup>th</sup> percentiles of eastings and northings within each distribution. All spatial analysis was performed using an Albers Equal Area projection with central meridian at 60°W and standard parallels at 45°N and 65°W.

Parameter	Intercept	Slope	F	p-value	r <sup>2</sup>
Moult (Sep-Oct)	-	-			
Area (1,000 km <sup>2</sup> )	774.97 (12.85)	0.35 (0.60)	0.34	1.000	-0.02
Overlap (%)	99.1 (0.8)	-0.055 (0.039)	1.98	1.000	0.03
Easting (km)*	-1351.42 (6.33)	0.05(0.29)	0.03	1.000	-0.03
West edge (km)*	-1769.53 (2.51)	0.018 (0.12)	0.02	1.000	-0.03
East edge (km)	-1008.29 (14.37)	1.26 (0.67)	3.55	0.541	0.07
Northing (km)	795.52 (7.11)	0.29 (0.33)	0.75	1.000	-0.01
South edge (km)	312.69 (6.92)	0.91 (0.32)	8.06	0.059	0.16
North edge (km)	1205.50 (28.17)	1.91 (1.31)	2.13	1.000	0.03
Fall (Nov-Dec)					
Area (1,000 km <sup>2</sup> )	1315.78 (70.85)	8.57 (3.29)	6.76	0.107	0.13
Overlap (%)	84.3 (0.03)	-0.75 (0.14)	28.10	<0.001	0.42
Easting (km)	37.49 (88.619)	-21.07 (4.13)	26.10	<0.001	0.40
West edge (km)	-1242.45 (72.59)	-11.56 (3.38)	11.70	0.012	0.22
East edge (km)	563.03 (39.26)	-7.77 (1.83)	18.10	0.001	0.32
Northing (km)	578.60 (20.50)	4.96 (0.95)	27.00	<0.001	0.41
South edge (km)	-119.44 (33.72)	6.74 (1.57)	18.50	0.001	0.32
North edge (km)	1070.63 (27.26)	6.13 (1.27)	23.40	<0.001	0.38
Winter (Jan-Mar)					
Area (1,000 km <sup>2</sup> )	1072.40 (42.52)	4.56 (1.98)	5.36	0.212	0.11
Overlap (%)	92.7 (1.8)	-0.27 (0.08)	10.20	0.024	0.20
Easting (km)	486.41 (15.45)	-2.86 (0.72)	15.80	0.003	0.29
West edge (km)	44.32 (14.9)	-2.79 (0.69)	16.20	0.002	0.29
East edge (km)	856.88 (13.57)	-2.25(0.63)	12.80	0.008	0.24
Northing (km)	332.67 (16.71)	0.52 (0.78)	0.44	1.000	-0.02
South edge (km)	-708.03 (71.09)	0.66 (3.31)	0.04	1.000	-0.03
North edge (km)	964.94 (33.60)	4.12 (1.56)	6.96	0.098	0.14
Spring (Apr-May)					
Area (1,000 km <sup>2</sup> )	471.76 (49.02)	-0.56 (2.28)	0.06	1.000	-0.03
Overlap (%)	62.5 (4.1)	-0.31 (0.19)	2.54	0.958	0.04
Easting (km)	-423.45 (126.14)	-6.58 (5.87)	1.26	1.000	0.01
West edge (km)	-1359.58 (42.67)	-2.34 (1.98)	1.39	1.000	0.01
East edge (km)	358.41 (36.07)	-2.39 (1.68)	2.03	1.000	0.03
Northing (km)	770.74 (28.80)	3.79 (1.34)	8.02	0.060	0.16
South edge (km)*	59.00 (64.36)	-1.13 (2.99)	0.14	1.000	-0.02
North edge (km)	1284.45 (19.57)	0.78 (0.91)	0.74	1.000	-0.01

\* Residual plots indicated a violation of the normality assumption, the non-significant relationship with year was confirmed using a Spearman's correlation test.

Table 12.4. Changes in environmental variables between the 1980s (1982-1989) and 2010s (2010-2019) for regions where habitat distribution was stable, declining, or increasing within each season. Table shows the mean (SE) change in each environmental variable between the 1980s and 2010s for each season. Superscript letters indicate which regions had a significant difference in change in each climate variable for each season.

Climate variable	Season	Declining	Stable	Increasing	F	p-value	r <sup>2</sup>
Ice cover (%)	Moult	-1.16 (0.2) <sup>a</sup>	-0.23 (0.09) <sup>b</sup>	-1.88 (0.67) <sup>a</sup>	11.88	<0.001	0.14
	Fall	-0.48 (0.28) <sup>a</sup>	-13.74 (1.32) <sup>b</sup>	-21.46 (0.51) <sup>c</sup>	674.35	<0.001	0.82
	Winter	-0.98 (0.19) <sup>a</sup>	-9.48 (1.15) <sup>b</sup>	-16.65 (0.8) <sup>c</sup>	202.38	<0.001	0.62
	Spring	-6.78 (1.01 ª	-12.22 (0.75) <sup>b</sup>	-9.49 (0.5) <sup>c</sup>	9.91	<0.001	0.12
SST (°C)	Moult	0.72 (0.02) <sup>a</sup>	0.68 (0.06) <sup>a</sup>	0.79 (0.04) <sup>a</sup>	1.99	0.14	0.03
	Fall	1.11 (0.03) <sup>a</sup>	0.79 (0.05) <sup>b</sup>	0.49 (0.03) <sup>c</sup>	<i>99.41</i>	<0.001	0.52
	Winter	0.83 (0.01) <sup>a</sup>	0.79 (0.05) <sup>a</sup>	0.27 (0.02) <sup>b</sup>	249.2	<0.001	0.59
	Spring	0.89 (0.08) <sup>a</sup>	0.49 (0.08) <sup>b</sup>	0.05 (0.01) <sup>c</sup>	66.94	<0.001	0.42
Air temperature (°C)	Moult	1.43 (0.02) <sup>a</sup>	1.28 (0.04) <sup>b</sup>	1.77 (0.07)°	17.34	<0.001	0.18
	Fall	1.68 (0.06) <sup>a</sup>	3.97 (0.26) <sup>b</sup>	4.83 (0.15) <sup>c</sup>	200.08	<0.001	0.72
	Winter	0.98 (0.02) <sup>a</sup>	3.27 (0.29) <sup>b</sup>	2.89 (0.21) <sup>b</sup>	69.32	<0.001	0.45
	Spring	0.75 (0.12) <sup>a</sup>	1.2 (0.04) <sup>b</sup>	0.97 (0.05) <sup>a</sup>	9.72	<0.001	0.12
Wind speed (km/hr)	Moult	0.12 (0.01) <sup>a</sup>	0.03 (0.02) <sup>b</sup>	0.09 (0.02) <sup>ab</sup>	5.4	0.01	0.07
	Fall	0.1 (0.07) <sup>a</sup>	0.33 (0.04) <sup>b</sup>	0.28 (0.05) <sup>ab</sup>	4.06	0.02	0.05
	Winter	-0.76 (0.09) <sup>a</sup>	-0.22 (0.1) <sup>b</sup>	0.13 (0.07)°	32.63	<0.001	0.28
	Spring	-0.12 (0.02) <sup>a</sup>	0.12 (0.03) <sup>b</sup>	0.23 (0.02) <sup>c</sup>	69.89	<0.001	0.45

## 13. Supplementary materials for Chapter 6



Figure 13.1. Maps of GPS tracks of common (green lines) and thick-billed murres (purple lines) from all sites included in this study (black points). GPS deployments are from chick-rearing murres. Panels are arranged in order from the smallest to largest colonies. All maps are on the same scale and use the Lambert Conformal Conical projection centred on the longitude of the colony.



Figure 13.1 (cont). Maps of GPS tracks of common (green lines) and thick-billed murres (purple lines) from all sites included in this study (black points). GPS deployments are from chick-rearing murres. Panels are arranged in order from the smallest to largest colonies. All maps are on the same scale and use the Lambert Conformal Conical projection centred on the longitude of the colony.



Figure 13.2. Foraging range model estimates for the half-normal (top), lognormal (middle), and Weibull (bottom) distributions. The left hand column shows the relationship between mean foraging range and colony size. Means for each distribution calculated using the equations in Table 13.3. Points show observed foraging range for each individual colony, where colours indicate type of colony (common murre: green, mixed colony: orange, thick-billed murre: purple), and size indicates weighting by number of trips measured. The solid lines show the predicted mean relationship with colony size from weighted least squares regression and shaded area show the 95% confidence region for each model. Predicted foraging trip density distributions for a range of colony sizes (right column). Each coloured line shows the predicted density of foraging trip distances for a given colony size. Closed points and open points, respectively, show the distance at which 50% and 95% of foraging trips would occur.



Figure 13.3. Predicted (solid line) and observed (dashed lines) foraging trip distributions by distance from colony for each site in the study. Predicted distributions follow the Weibull foraging range model that predicts foraging distribution based on colony size (Cs), where  $\lambda = 0.88 \text{*Cs}^{031}$  and k = 1.35.


*Figure 13.4. Scatterplots of relationship between variance in trip bearings and absolute residuals from linear regression (left), number of trips (center), and number of years (right).* 

Foraging Tracking Colony Country Lon Lat Pairs Trips Deployments Years Fr50 Fr75 Fr95 Cape -76.10 49 2 Graham Canada 72.93 52,000 323 23.8 35.2 53.8 Moore -82.02 62.95 30,000 1537 336 6 28.8 45.5 Coats Canada 18.3 -77.77 62.56 400,000 1074 202 4 33.2 56.1 103.5 Digges Canada -56.53 18,200 139 2 10.4 29.8 41.8 Gannets Canada 53.93 18 2 91.5 Funk Canada -53.19 49.75 472,000 85 16 31 47.2 South Cabot Canada -53.36 49.17 10,000 61 9 2 17.5 34.3 38.0 Gull -52.77 3,500 10 2 14.1 20.7 36.2 Canada 47.27 24 -73.05 6,350 27 1 16.3 30.2 Carey Greenland 76.73 7 22.3 Greenland -70.04 42 10 1 27.5 48.7 110.9 Saunders 76.58 133,000 25 24.3 44.9 74.8 Apparsuit Greenland -56.82 73.79 35,300 6 1 Kippaku Greenland -56.63 73.72 15,000 172 43 4 16 23.9 44.6 Ritenbenk Greenland 800 2 4.3 -51.22 69.8 27 6 3.2 3.9 Kitsissut 7 3 4 Greenland -48.45 60.76 2,390 25 5.4 7.5 Avalliit 1 Grimsey Iceland -18.02 66.57 71,300 61 13 15.9 34.3 59.8 Skoruvik Iceland -14.83 66.39 29,800 7 3 1 56 86.8 117.5 Langanes Iceland -14.54 66.38 15,200 84 17 3 5.2 7.7 39.1 Latrabjarg Iceland -24.53 65.51 344,000 91 29 1 56.3 86.7 147 7 Skrudur Iceland -13.62 64.9 13,100 29 1 8.6 14.8 20.8 Papey Iceland -14.1864.59 3,700 81 20 1 18.8 28.6 36.8 Ossian Norway 12.45 78.93 951 14 4 1 7.6 14.4 81.8 Diabasodden Norway 16.13 78.36 1,220 106 20 3 5.4 7.3 16.8 Bjornoya Norway 19.08 74.33 227,000 229 80 3 47.7 65 95.9 Hornoya Norway 31.15 70.39 26,800 521 137 6 10.8 21 52.6 Karlso Sweden 17.96 57.29 15,700 128 33 4 13.6 23.6 37.5 Copinsay Scotland -2.67 58.9 11,000 31 8 2 3.1 5.8 12.9 Winnifold Scotland -1.88 57.38 19,900 17 4 1 6.2 8.5 14 Fowlsheugh Scotland -2.2 56.92 36,800 31 10 1 18.9 30.2 40.1 Colonsay Scotland -6.23 56.09 15,400 165 44 5 15.6 22.4 35.1 3 Puffin England -4.02 53.32 2,680 148 26 8.9 12.4 22

Table 13.1. Colony sizes and GPS tracking summary for each thick-billed and common murre colony included in this study. Fr50, Fr75, and Fr95 are the observed 50<sup>th</sup>, 75<sup>th</sup>, and 95<sup>th</sup> percentile of foraging trip distances from all foraging trips at each colony.

Table 13.2. Kolmogorov-Smirnov tests for a difference in the distribution of foraging trip distances when both common murres and thick-billed murres were tracked from the same colony.

Colony	Common murre trips (n)	Thick-billed murre trips (n)	D	p-value
Bjornoya	112	117	0.16	0.107
Grimsey	37	24	0.24	0.310
Kitsissut Avalliit	8	17	0.33	0.493
Langanes	49	35	0.16	0.620
Latrabjarg	57	34	0.26	0.093

Table 13.3 The probability density functions (PDF) and means that were fit to the distribution of trip distances (x) from each colony, along with summaries of the number of sites for which each distribution was within 4 AIC of the best distribution and the  $r^2$  was at least 0.7. Trip distance (x) is in kilometers. Symbols  $\lambda$ ,  $\beta$ ,  $\alpha$ ,  $\sigma$ , and  $\mu$  are the fitted parameters for each distribution.  $\Gamma$  is the gamma function. Values in parentheses for  $\Delta AICc \leq 4$  and  $r^2 \geq 0.7$  are the proportion of all colonies that met each criterion.

Distribution	PDF	Mean	∆AICc ≤ 4	$r^2 \ge 0.7$	Median r <sup>2</sup>
Exponential	$\lambda e^{-\lambda x}$	$\frac{1}{a}$	6 (0.21)	20 (0.69)	0.861
Gamma	$\frac{\beta^a}{\Gamma(\alpha)} x^{\alpha-1} e^{-\beta x}$	$\frac{\alpha}{\beta}$	11 (0.38)	28 (0.97)	0.940
Half-normal	$\frac{\sqrt{2}}{\sigma\sqrt{\pi}} \exp\left(-\frac{x^2}{2x^2}\right)$	$\frac{\sigma\sqrt{2}}{\sqrt{\pi}}$	16 (0.55)	20 (0.69)	0.917
Lognormal	$\frac{1}{x\sigma\sqrt{2\pi}}\exp\left(-\frac{(lnx-\mu)^2}{2\sigma^2}\right)$	$exp\left(\mu+\frac{\sigma^2}{2}\right)$	15 (0.52)	26 (0.90)	0.891
Weibull	$\frac{k}{\lambda} \left(\frac{x}{\lambda}\right)^{k-1} e^{-(\lambda)^k}$	$\lambda\Gamma\left(1+\frac{1}{k}\right)$	18 (0.62)	28 (0.97)	0.958

Table 13.4. Relationship between colony size and foraging range using three distributions: lognormal, half-normal, and Weibull. Values for intercepts and slopes are parameter estimates (SE), on the log scale. As there was no significant relationship between colony size and the shape (k) of the Weibull distribution (see text), estimates from the intercept only model are shown in this case.

Distribution	Parameter	Intercept	Slope	<b>F</b> <sub>1,27</sub>	p-value	$r^2$
Lognormal	μ	-0.297 (0.487)	0.282 (0.048)	37.44	< 0.0001	0.56
	σ	0.202 (0.202)	0.072 (0.020)	15.38	< 0.0001	0.34
Half-normal	σ	0.111 (0.510)	0.302 (0.050)	37.10	< 0.0001	0.59
Weibull	k	0.301 (0.057)				
	λ	-0.123 (0.494)	0.308 (0.049)	42.23	< 0.0001	0.60

Region	Number of	Total	Data sources
8	colonies	Population	
Canada	39	2,447,000	CWS-ECCC unpublished data, 47–50
Norway	82	1,438,000	SEAPOP: http://www.seapop.no, Barents Portal:
			http://www.barentsportal.com
Iceland	15	1,016,000	51,52
Russia	59	995,000	Barents Portal: http://www.barentsportal.com
Scotland	126	607,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>
Greenland	18	325,000	<sup>54</sup> Greenland Institute of Natural Resources, Unpublished data
England	13	133,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>
Northern Ireland	3	111,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>
Republic of	19	102,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>
Ireland			
Faroe Islands	13	87,000	55
Wales	18	68,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>
Sweden	4	20,000	O. Olsson, unpublished data
Denmark	1	4,000	O. Olsson, unpublished data
Isle of Man	2	4,000	Seabird Monitoring Programme: https://app.bto.org/seabirds <sup>53</sup>

*Table 13.5. Summary of North Atlantic murre colony numbers, total population (breeding pairs), and data sources. Only colonies with at least 500 breeding pairs are included in this summary.*