Factors influencing energy expenditure in two sub-Arctic seabirds affected directly and indirectly by climate change

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Abstract

Northern regions are impacted disproportionally by climate change, with the Arctic warming at twice the global rate. With the projected increase in temperature, Arctic and sub-Arctic animals are likely to experience strong indirect and direct effects of climate change. Animal health (i.e. physiology) may be a critical early warning signal for impending population change. Identifying what factors elicit metabolic costs and the physiological response to heat stress of an individual is thus crucial to better understand the limitations in how animals can cope with climate change. Seabirds are highly sensitive to changes in their environment and are valuable indicators of marine ecosystem health. Specifically, seabird physiology has been shown to be an early indicator of declining environmental conditions. To better understand seabird physiology, we investigated the factors influencing energy expenditure in two seabird species, one of which is impacted indirectly by climate change via an altered food web and one of which is impacted directly by climate change via overheating. In the first chapter, we investigated the impacts of activity and breeding stage on energy expenditure in black-legged kittiwakes (*Rissa tridactyla*) using doubly-labelled water and biologging techniques. We developed a novel method to measure energy expenditure using time-activity budgets of kittiwakes. As kittiwakes have declined by 90% at this study site in 40 years, with near-zero reproductive success in poor (warm) years due to very long foraging distances, examining constraints on energy expenditure is critical to understand limits associated with foraging. In the second chapter, we investigated the incidence of heat stress at the colony in thick-billed murres (*Uria lomvia*) using 3D printed biophysical models to measure the operative temperature of murres across different microhabitats. We found that murres experience operative temperatures above 21.2 °C, the temperature in which they increase evaporative water loss rates,

on 61% of the days on average (range : 24 – 85%). Operative temperatures ranged from 5.5 °C to 46.5 °C, yet ambient temperature never exceed 23.8 °C. Together, both chapters answer important questions on seabird physiology and lay the path for future studies on conservation physiology. Seabirds are known as indicators of environmental changes, and data from this research can be used to predict how other seabird populations will react to Arctic warming.

Résumé

Les régions Nordiques sont affectées disproportionnellement par les changements climatiques, avec l'Arctique se réchauffant deux fois plus rapidement que la moyenne globale. Considérant l'augmentation de température projetée, les animaux arctiques et subarctiques risquent de subir de forts effets indirects et directs des changements climatiques. La physiologie animale a le potentiel de révéler rapidement les signes avant-gardistes de changements de population imminents. Identifier rapidement les facteurs qui influencent les coûts métaboliques ainsi que les réponses physiologiques causées par le stress thermique d'un individu est crucial afin de mieux comprendre les contraintes auxquelles les animaux feront face dû aux changements climatiques. Les oiseaux marins sont hautement sensibles aux changements au sein de leur environnement et sont donc d'importants indicateurs de la santé des écosystèmes. Mais encore, il a été démontré que la physiologie des oiseaux marins peut agir en tant qu'indicateur du déclin des conditions environnementales. Afin de mieux comprendre la physiologie des oiseaux marins, nous avons examiné les facteurs qui influencent les dépenses énergétiques chez deux espèces, l'une étant affectée indirectement par les changements climatiques via des changements dans leur chaine alimentaire et l'autre directement via surchauffe métabolique. Dans de mon premier chapitre, j'ai examiné l'impact de l'activité et du stade de reproduction sur les dépenses énergétiques chez la mouette tridactyle (*Rissa tridactyla*) à l'aide d'eau doublement marquée et de techniques de biologging. Au cours de ce chapitre, j'ai démontré que les dépenses énergétiques d'un individu peuvent être prédites en fonction de leur budget d'activité. La mouette tridactyle a subi un déclin de 90% à notre site d'étude depuis les 40 dernières années et son succès reproducteur est presque nul lors d'années chaudes dû à leur aire d'alimentation qui augmente de manière drastique. Il est donc crucial de comprendre les contraintes énergétiques de cette espèce. Au cours de mon

deuxième chapitre, j'ai examiné la prévalence du stress thermique chez le guillemot de Brünnich (*Uria lomvia*) à l'aide de modèles biophysiques imprimés en 3D afin de mesurer la température opérative des guillemots dans divers micro-habitats. J'ai démontré que les guillemots subissent des températures opératives au-delà de 21.2 °C, température à laquelle leur taux d'évaporation d'eau augmente de manière drastique, au cours de 61% des journées étudiées (intervalle de 24 à 85%). Malgré le fait que le température ambiante n'aie jamais dépassé 23.8 °C, les températures opératives varient entre 5.5 °C et 46.5 °C. Ensemble, mes deux chapitres répondent à d'importantes questions sur la physiologie des oiseaux marins et déneige le pavé pour de futures études sur la physiologie et la conservation. Les oiseaux marins sont très sensibles aux changements au sein de leur environnement, et les conclusions tirées à partir de notre recherche peuvent être utilisées afin de prédire comment les changements climatiques vont affecter les diverses populations d'oiseaux marins.

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Contribution of Authors

I designed and conducted all experiments of this thesis with the help of my supervisors Dr. Kyle Elliott and Dr. Emily Choy, and guidance from my committee members, Dr. Grant Gilchrist and Dr. Oliver Love. I collected all data for both chapters, with the help of the field crew on Middleton Island 2021 and Coats Island 2022.

For my first chapter, my supervisors and Ms. Shannon Whelan helped with the manuscript revision and provided support for the analyses, Dr. Scott Hatch provided resources and access to the Middleton Island and Dr. Catherine Hambly and Dr. John Speakman validated my doubly-labelled water results independently in their lab.

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List of Abbreviations

ABS: acrylonitrile butadiene styrene

BMR: basal metabolic rate

C_{max}: maximum conductance

C_{min}: minimum conductance

DEE: daily energy expenditure

DLW: doubly-labelled water

EWL: evaporative water loss

FMR: field metabolic rate

GLS: global location sensors

GPS: geographic positioning system

MMR: maximum metabolic rate

ODBA: overall dynamic body acceleration

PETG: polyethylene terephthalate glycol

TBMU: thick-billed murre

T_e: operative temperature

T_a: ambient temperature

TNZ: thermoneutral zone

UCT: upper critical temperature

VIF: variance inflation factor

WBF: wingbeat frequency

Introduction

The northern regions are impacted disproportionately by climate change, with the Arctic warming twice as fast as the planetary average (Dillon et al., 2010). The effects of climate change have been documented in many species, but tend to focus on indirect effects, such as impacts on species interactions (Oswald and Arnold, 2012, Walther et al., 2002, Mellard et al., 2022). Indirect effects of climate change can involve changes in species distribution, often resulting in increased competition, modifications to predator-prey relationships, and increases in parasitism. In the Arctic, novel indirect effects have been documented in Arctic foxes (*Vulpes lagopus*), which now compete with invasive red foxes (*Vulpes vulpes*) (Gallant et al., 2012). In seabirds, increased predation by polar bears (*Ursus maritimus*) has been observed as the ice-free period increases and bears have to rely on alternative food sources rather than seals to survive (Iverson et al., 2014, Smith et al., 2010). Yet, the direct effects of climate change should not be neglected.

Climate change has the potential to affect species directly by impacting on their metabolic processes, potentially resulting in heat stress – defined as a sudden change in the rate of evaporative water loss - in species living in arid or hot climates or even cold-adapted species living in rapidly warming habitats (Conradie et al., 2019, O'Connor et al., 2022, Choy et al., 2021, Kelly et al., 2014, Stitt et al., 2014). The direct effects of climate change have arguably the capacity to impact species much faster than indirect effects. Whereas heat stress has been documented in multiple arid and desert species of birds, little is known about the capacity of Arctic animals to tolerate heat (Rezende and Bacigalupe, 2015, Choy et al., 2021, O'Connor et al., 2022). In arid wildlife, the effects of heat stress have been fairly well documented, and the projected impact of climate change ranges from mass death as observed in flying foxes (*Pteropus spp.*) during heat waves (Ratnayake et al., 2019), to a significant decrease in breeding success as observed in many arid bird species (Conradie et al., 2019, Albright et al., 2017).

In the context of climate change, seabirds can be good indicators of environmental changes as they are highly sensitive to changes in their environment (Furness and Camphuysen, 1997). The role of seabirds as sentinels of the sea has been highlighted in many studies (Grémillet and Boulinier, 2009, Furness and Camphuysen, 1997, Brisson-Curadeau et al., 2017, Aguirre and Tabor, 2004). Seabirds indicate early signs of shifts in environmental conditions, including shifts in marine species composition (Gaston et al., 2003, Sydeman et al., 2017) and trends in contaminants and pollutants (Albert et al., 2019, Choy et al., 2022, Braune, 2007). Consequently, seabirds are a highly relevant group to study both the direct and indirect effects of climate change.

Although seabirds are sensitive to change, different species are likely to experience different pressures of climate change. The black-legged kittiwake (*Rissa tridactyla*) is a gull species (Family Laridae) with a circumpolar distribution (Hatch, 2009). Kittiwakes are highly pelagic gulls that forage only on fish and marine invertebrates present at the surface of the water (Hatch, 2009). With projected increase in sea surface temperature (Alexander et al., 2018), kittiwakes are most at risk of experiencing indirect effects of climate change at their southern range limit as their food source moves further north and prey capture become increasingly challenging as prey fishes speed increases with temperature (BirdLife International, 2019, Osborne et al., 2020, Grady et al., 2019). The thick-billed murre (*Uria lomvia*), an alcid species, is the most abundant seabird in the Canadian Arctic (Gaston and Hipfner, 2000, Gaston et al., 2012). Murres have extremely low heat tolerance, exhibiting signs of heat stress at temperatures as low as 21.2 °C under laboratory conditions (Choy et al., 2021). With the projected increase in temperature and their low capacity to tolerate heat, murres are at risk of experiencing the direct effects of climate change (Choy et al., 2021, Gaston et al., 2002). Altogether, both kittiwakes and murres evolved in a similar environment, yet they are likely to experience different effects of climate change, making these two species highly interesting study species.

In this thesis, I investigated the factors that influence energy expenditure and heat stress in two Arctic seabirds which are affected differently by climate change: the black-legged kittiwake and the thick-billed murre. In the first chapter, I investigated the impacts of behaviours and breeding stages on energy expenditure in black-legged kittiwakes using doubly-labelled water and biologging techniques. In the second chapter, I investigated the incidence of heat stress at the colony in thick-billed murres using 3D printed biophysical models to measure the operative temperature – integrated temperature of an environment as perceived by an individual (Bakken, 1976) - of nesting murres across different microhabitats.

Literature review

Climate change

Climate change is a well-known phenomenon characterized by an increase in environmental CO_2, leading to a rise in ambient temperature, also referred to as global warming (Aizebeokhai, 2009). This global rise in temperature has had severe cascading effects on ecosystems. With ambient temperature increasing, sea surface temperature has increased accordingly, leading to a global rise in sea level of approximately 3.4 mm yearly as warm water expands and glaciers melt (Aizebeokhai, 2009). On top of the visible effects of sea-level rise, such as flooding, the increase in sea surface temperature has led to a reduction in nutrient upwelling as the warm layer of water separates from the colder benthic waters (Hassol and Corell, 2006, Grémillet and Boulinier, 2009). Similarly, glacial melt due to warmer temperatures has led to a freshening of oceans as a large volume of freshwater is introduced into the ocean (Hassol and Corell, 2006, Grémillet and Boulinier, 2009). The salinity gradient between the fresh surface water from glacial melt and the salty benthic waters contributes to the reduction of nutrient mixing. Together, the increase in sea surface temperatures and glacial melt have caused a shift in nutrient composition and an increase in harmful algal blooms (Hassol and Corell, 2006, Grémillet and Boulinier, 2009). On land, the effects of global warming can also be noticed, with the Arctic greening as glaciers melt and the shrubification of the Arctic tundra (Walther et al., 2002, Mellard et al., 2022). Those changes are now shaping many facets of the Earth, but the effects of global warming are felt disproportionally in some regions of the world, such as in high latitudes (Dillon et al., 2010).

Indirectly, climate change has impacted wildlife through changes in species interactions. With rising temperatures, the Arctic is melting fast and the ice-free periods are getting longer, enabling southern species to expand their range further north (Walther et al., 2002, Mellard et al., 2022). The poleward migration of wildlife has led to changes in species interactions such as increased competition, predation, parasitism, and phenological mismatches (Oswald and Arnold, 2012, Walther et al., 2002, Mellard et al., 2022).

Climate change and wildlife

Due to climate change, species range expansion is becoming increasingly frequent, leading to increases in competition between species that share similar niches. The case of the red fox (*Vulpes vulpes*) and Arctic fox (*Vulpes lagopus*) illustrates this problem well (Gallant et al., 2012, Elmhagen et al., 2017). Red foxes have been increasing their presence in the north over the past decade. As both red fox and Arctic fox exploit the same resources, both species are now competing for prey where their ranges overlap. As red foxes are physically bigger, they require a larger territory to sustain their energy needs and are stronger competitors than Arctic foxes, sometimes even killing their competitor, resulting in an overall decline in Arctic foxes in some areas (Gallant et al., 2012, Elmhagen et al., 2017).

The increased temperature in the Arctic has also led to longer ice-free seasons (Grémillet and Boulinier, 2009). In the last three decades, the ice-free season in Hudson Bay has lengthened by approximately two months (Iverson et al., 2014) directly impacting ice-dependent species and indirectly affecting their alternative prey. Polar bears (*Ursus maritimus*) rely heavily on sea ice to hunt as they feed primarily on seals and other marine species (Wiig et al., 2008). To prepare for the ice-free season, polar bears make fat reserves during the winter while feeding on rich food such as seals to get through the ice-free season (Iverson et al., 2014). Unfortunately, longer ice-free seasons have forced polar bears to rely more on alternative, less nutritious food sources such as seabird eggs (Wiig et al., 2008, Iverson et al., 2014). As a result, species such as common eiders (*Somateria mollissima*) and thick-billed murres (*Uria lomvia*) are victims of acute predation events at their colonies as polar bears feed more frequently on their eggs and chicks (Iverson et al., 2014).

Although the indirect effects of climate change are posing a real threat to Arctic wildlife, the direct effects of increasing temperature are likely to impact Arctic wildlife much earlier (Grémillet and Boulinier, 2009, Choy et al., 2021). Arctic endotherms have high thermoregulatory costs as they have to physiologically adapt to living in a cold and harsh environment (Irving and Krog, 1954). Some of these adaptations include shorter limbs and thicker coats or dark plumage that reduce heat loss (Irving and Krog, 1954). Unfortunately, these adaptations now come at a cost as the increased capacity of Arctic wildlife to retain heat can lead to overheating and limits breeding investment as temperatures increase (Nord and Nilsson, 2019, Grémillet et al., 2012).

Energy expenditure and physiology

Energy expenditure can be separated into two main categories: basal metabolic rate (BMR) and field metabolic rate (FMR). The basal metabolic rate can be defined as the minimum energy required to maintain bodily functions under non-growing and post-absorptive conditions (Ricklefs et al., 1996). On the other hand, the field metabolic rate encompasses all of the energy required by the animal; in other words, it represents both the inactive and active parts of energy expenditure (Ricklefs et al., 1996).

Energy expenditure and the cost of life

Energy is a common currency for any living organism, and studies dating as early as 1905 have shown an interest in understanding how energy is acquired and expended. Indeed, Atwater (1905) was the first to show that heat loss, which was used to quantify energy expenditure, was strongly linked with oxygen consumption and carbon dioxide production in animals. In early medicine, changes in basal metabolic rate were also used to diagnose thyroid illnesses in humans (Danforth Jr and Burger, 1984). The use of thyroid hormones as a proxy for basal metabolic rate has now been validated in an array of species, including mammals and birds (Welcker et al., 2013, Elliott et al., 2013). Over the years, energy expenditure has been used to further our understanding of complex organisms. Thus, understanding how animals use energy is critical to understanding their ecology and consequently, how they might acclimatize to changes in their environment.

Reproduction is a costly event for many animals, especially birds, which must deliver food to a central place (Elliott et al., 2009). During breeding, individuals balance investment in their offspring against investment in their subsequent survival (Sibley and Calow, 1986, Williams, 1966). In the case where parents cannot balance their investment, allostatic overload is reached, meaning that external requirements are higher than what an individual can cope with (Wikelski and Cooke, 2006). Energy expenditure is driven by internal (e.g., breeding stage) and external (e.g., wind, temperature) factors. Understanding how each of those factors impacts an individual's metabolism can be crucial to identify physiological limitations, such as why and when the allostatic overload might occur, and how animals may cope with such limitations.

For animals, energy expenditure and intake will vary across seascapes and landscapes, depending on variables such as the spatial distribution of food patches, wind currents, and ambient temperature, creating dynamic energyscapes (Shepard et al., 2013, Wilson et al., 2012, Elliott et al., 2014). Individual variation in daily energy expenditure is also linked to varying activity budgets (Jodice et al., 2003, Ricklefs et al., 1996, Green et al., 2009, Dunn et al., 2020). However, other factors, such as breeding stage (and its impact on resting metabolism) and environmental conditions (such as thermoregulation) may also determine energyscapes.

Effect of environmental variations on metabolism and operative temperature

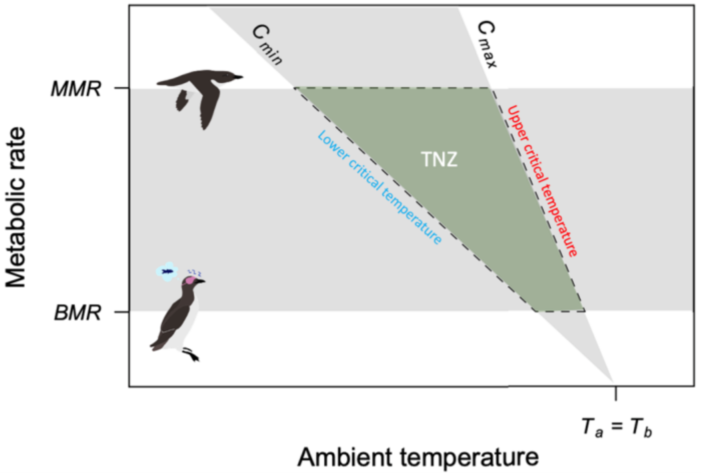

Image 1: Thermal neutral zone (TNZ; green) limited on each side by the minimum (C_{min}) and maximum conductance (C_{max}) of a given individual and at the top and bottom by the basal metabolic rate (BMR) and maximum metabolic rate (MMR). Figure adapted from Rezende and Bacigalupe (2015).

Energy expenditure in homeotherm can be tightly linked to environmental conditions. As homeotherm maintain a constant body temperature (thermoneutral zone), fluctuations in environmental temperature often results in metabolic adjustments (Abreu-Vieira et al., 2015, Rezende and Bacigalupe, 2015). As per the Scholander model (1950), energetic costs towards thermoregulation are null when within the thermoneutral zone (Image 1), until either the lower or upper range of the thermoneutral zone is reached (Rezende and Bacigalupe, 2015). While within the thermoneutral zone, individuals passively maintain their body temperature using methods such as vasoconstriction and evaporative water loss (Rezende and Bacigalupe, 2015, Abreu-Vieira et al., 2015, Ricklefs et al., 1996). However, if temperatures increase and reach a point above the upper critical temperature (UCT), individuals must actively thermoregulate by using heat dissipation behaviours such as wing spreading and panting to avoid hyperthermia (Abreu-Vieira et al., 2015, Ricklefs et al., 1996).

Due to climate change, heat waves are increasing in frequency and duration across the globe (Hassol and Corell, 2006), leading to hyperthermia in many wildlife species (Choy et al., 2021, Ratnayake et al., 2019, von Biela et al., 2020, O’Connor et al., 2018, O'Connor et al., 2022, Conradie et al., 2019). In situations of hyperthermia, where an individual’s body temperature increases in response to ambient temperature, the temperature gradient between an individual’s body temperature and the environment is reduced, leading to reduced heat loss to the environment (Rezende and Bacigalupe, 2015, Abreu-Vieira et al., 2015). To cope with the reduced heat gradients, individuals physiologically respond to re-establish that gradient and ease heat loss to the environment (Choy et al., 2021, Abreu-Vieira et al., 2015, Rezende and Bacigalupe, 2015). Physiological responses can involve increased respiratory frequency, vasodilation, sweating, etc. By increasing their respiratory frequency, heat can be dissipated via evaporation during respiration, ultimately cooling the body (Rezende and Bacigalupe, 2015). Similarly, individuals can increase their rate of evaporative heat loss via vasodilation, where the blood vessels increase in diameter and approach the skin's surface, enabling them to exchange heat with the environment more easily (i.e., convective heat loss). In some species, sweating also enables their body to cool faster and take advantage of other environmental factors, such as wind, to help increase evaporative cooling (Rezende and Bacigalupe, 2015).

Although species can physiologically adapt to actively cool their body, such adaptations can be energetically costly (Abreu-Vieira et al., 2015). According to the "heat dissipation limit" theory, endotherms' sustained energy expenditure, measure via caloric intake, is restrained by the rate at which an individual can dissipate heat (Speakman and Król, 2010). This theory is supported by a series of studies on mammalian lactation, where milk production was limited by the mother's capacity to dissipate heat rather than by resource availability (Speakman and Król, 2010). Evidence of the heat dissipation limit theory has also been demonstrated in birds, where feather-trimmed parents increased their reproductive performance (Tapper et al., 2020, Nord and Nilsson, 2019). Thus, animals can be limited by their capacity to tolerate hyperthermia. When exposed to high ambient temperature, heat stress, expressed as a sudden increase in evaporative water loss rate, occurs (Choy et al., 2021). Ultimately, heat stress and the increased energy requirements of thermoregulation impair other body processes sometimes even resulting in death (Ratnayake et al., 2019, von Biela et al., 2020, Stitt et al., 2014, Kelly et al., 2014). In chinook salmon (*Oncorhynchus tshawytscha*), a study revealed that over half of the salmon studied exhibited heat stress, ranging from increased energy expenditure to death in some cases (von Biela et al., 2020). Similarly, death due to heat stress has been documented in thousands of flying foxes (*Pteropuss* spp.) in Australia (Ratnayake et al., 2019).

Conservation physiology

Although physiology is often used to gain fundamental knowledge on a species' body process, physiology also offers a great tool for species conservation, both pre-emptively and retroactively (Wikelski and Cooke, 2006, Ellis et al., 2012, Cooke et al., 2021). Retroactively, studies on the physiological state of an individual or a population can provide insight of the efficiency of newly established conservation and management measures (Wikelski and Cooke, 2006). Although studies based on behavioural observations, species distribution and population demographics can provide some cues on the efficacy of some conservation measures, the physiology of an individual or a population provides a much more sensitive tool to study animal responses (Wikelski and Cooke, 2006, Cooke et al., 2014). On top of being a useful tool for retrospective assessment of conservation strategies, physiology can also inform us on the effects of change before changes at the population level can be observed (Wikelski and Cooke, 2006).

Indeed, physiology can indicate population decline before said decline is observable (Ellis et al., 2012, Cooke et al., 2014). In the context of climate change, animals suffer the long-term effects of environmental stressors (i.e. increase in temperature), on top of an increased exposure to acute stressors (i.e. increase frequency in extreme climatic events). Whereas the exposition to acute stressors is often observable via distinct changes in behaviour and increased mortality, the exposition to long-term stressors is often undetected and thus neglected (Wikelski and Cooke, 2006, Ratnayake et al., 2019).Yet, the sublethal effects of long-term stressors can ultimately lead to a decline in population (Conradie et al., 2019). In the context of climate change, studying physiology enables us to better understand the impact of environmental stressors on wildlife, and thus enable us to better predict how animals will be impacted by climate change (Ellis et al., 2012, Wikelski and Cooke, 2006, Cooke et al., 2021).

Use of biologging to study behaviour and energetics

Studying wildlife can be challenging, especially when species cannot be easily observed. To solve this challenge, researchers use miniaturized animal-borne devices to track wildlife remotely, also called biologging devices. Biologging devices have been used as early as the 1960s when dive-depth recorders deployed on Weddell seals (*Leptonychotes weddelli*) shed light on their diving patterns in an ice-covered habitat (Kooyman, 1965). The use of biologging devices in early years was restricted to large-bodied animals as the size and weight of the devices did not allow deployments on small vertebrates (Kooyman, 2004). Furthermore, the spatial resolution of some biologging devices was not precise enough to capture small-scale movements (e.g., foraging) but was rather limited to large-scale movements (e.g., migration (Kooyman, 2004)). However, recent technological advancements, such miniaturization of devices and increased spatiotemporal resolution, now enable us to deploy devices on a wide range of animals, ranging from hummingbirds to whales (Rafiq et al., 2021, Ropert-Coudert and Wilson, 2005, Elliott, 2016).

Using biologging to track complex behaviour

Biologging devices have been used extensively to track both the location of an animal and also its behaviour. Geographic positioning systems (GPS) are satellite-based systems that infer position via triangulation. Loggers using GPS (GPS loggers) can be used to infer position, ground speed, and distance travelled and are frequently used to track small to large-scale movements (Chung et al., 2021). Also commonly used are accelerometers that measure body acceleration on one or multiple axes. Accelerometers can be used to measure fine-scale movements and many parameters such as body angle, wingbeat frequency, prey capture, and more (Brisson-Curadeau et al., 2021, Sato et al., 2015, Yoshino et al., 2020). Unlike GPS loggers, accelerometers do not depend on satellites and thus can be used underwater (Chung et al., 2021). Other biologging devices are also frequently used in ecology, such as solar global location sensors (GLSs), acoustic recorders, video loggers, and more. By being paired with the proper statistical analyses, biologging devices have greatly advanced the field of behavioural ecology, enabling researchers to gain valuable insight on species that could not be studied using traditional methods, such as behavioural observations (Chung et al., 2021, Rafiq et al., 2021).

The applications of biologging devices are wide and have expanded past simple behavioural monitoring. On top of advancing the field of behavioural ecology, the use of biologging devices has expanded to other fields, such as ecological energetics. In Atlantic fur seals (*Arctocephalus gazella*), triaxial accelerometers that monitor the frequency of mouth opening have been used to infer the rate at which prey are captured (Viviant et al., 2014). Video loggers mounted on Adelie penguins *(Pygoscelis adeliae),* aided in identifying important diet shifts (Thiebot et al., 2016), and accelerometers mounted on cormorants' tail have been used to estimate energy expenditure (Stothart et al., 2016, Wilson et al., 2006). Overall, the field of biologging has provided means to study environmental systems using seabirds as environmental health monitors (Brisson-Curadeau et al., 2017).

Methodology: Biophysical models to measure operative temperature

Concepts of operative temperature

Operative temperature can be defined as the integrated temperature of an environment as perceived by an individual (Bakken, 1976). Thus, a measure of operative temperature not only considers ambient temperature itself, but also the various pathways of heat exchange (convection, conduction, radiation; Bakken, 1976; Shine, 2001) that can be influenced by other environmental factors (e.g. wind, contact with the substrate, solar radiation; (Bakken, 1976)). To illustrate this concept, we can imagine a day where an ambient temperature of 20 °C with a bright sun and no wind versus another day at 20 °C with strong winds and dense cloud cover. Due to increased solar radiation and low conductive heat loss, an individual is likely to experience a higher temperature during the first day, that is, due to a higher operative temperature. Whereas on the second day, the operative temperature is likely to be lower as there is no heat gain from solar radiation and increased heat loss via evaporative cooling. In the context of hyperthermia, individuals cannot change ambient temperature, but can physiologically and/or behaviourally adjust to reduce their operative temperature via increasing heat exchange with their environment.

Biophysical models and the copper model

Biophysical models are commonly used to assess operative temperature in animals. Designed to represent a given species in three dimensions, biophysical models must thermally respond to various environmental factors in a way to mimic their live counterparts. Relying on the physical properties of materials, biophysical models usually mimic the size, shape, position, and colour of a given specimen (O'Connor et al., 2018, Shine and Kearney, 2001, Bakken, 1976). Biophysical models enable us to capture fine-scale variation in the environment that cannot be perceived by mathematical or statistical models to assess operative temperature (Bakken, 1992).

Biophysical models have been used widely as early as the 1960s where exoskeletons, freeze-dried animals, and taxidermic mounts were fitted with thermocouples to measure operative temperature (Church, 1960, Bakken, 1976). However, these models had low heat conductance due to the material used for mounting and were highly variable over time as the biological tissues changed with desiccation (Bakken, 1992). In 1973, Porter et al. produced an alternative model by using hollow electroformed copper models (Porter et al., 1973). Due to its highly conductive nature, the copper models became the standard for biophysical models. Still used today, copper models are made of thin copper which is electroformed around a wax core of a given shape. Once formed, the wax core can be melted out leaving a hollow copper model resembling a given animal (Bakken, 1992). Once the right shape is achieved, these models can then be painted or fitted with pelts or feathers to obtain a lifelike model (Shine and Kearney, 2001, Bakken, 1992, O'Connor et al., 2018). Although the copper model is the most widely used biophysical model, they are often costly, involve the use of toxic chemicals, and are complex to produce making them hard to produce for medium to large-scale experiments (Shine and Kearney, 2001, Watson and Francis, 2015).

The use of 3D printed models to assess operative temperature

With the advancement of technology, 3D printing is now easy and accessible to the general public at a reasonable cost and enables us to easily print complex structures of almost any shape and size (Watson and Francis, 2015). In the context of biophysical models, 3D printing enables us to have better control of the output and renders a reproducible and scalable product. Using open-access software (e.g., Blender), 3D-printed models can be designed to resemble a given specimen. By adjusting the printing parameters, all details of the final product (i.e., printing material, wall thickness, infill) can be controlled to ensure constant heat transfer properties and product reproducibility (Watson and Francis, 2015). Produced at a lower cost than copper models, 3D printed models offer a reasonable alternative for larger-scale experiments where the cost of large-scale production is lower (Watson and Francis, 2015). Although fairly novel, 3D-printed biophysical models have been used successfully to measure operative temperature in rufous-cheeked nightjars (*Caprimulgus rufigena*; (O'Connor et al., 2018) and snow buntings (*Plectrophenax nivalis;* (O'Connor et al., 2022)).

Seabirds as indicators

Seabirds as indicators of environmental change

Studying the marine environment can be challenging due to its size and the complex interactions that occur, yet seabirds have proven to be valuable indicators of the marine ecosystem's health (Brisson-Curadeau et al., 2017, Aguirre and Tabor, 2004, Furness and Camphuysen, 1997, Cairns, 1988). Seabirds sample the ocean daily and are highly sensitive to changes (Furness and Camphuysen, 1997, Montevecchi, 2007). Thus, changes in marine health are likely to be detected immediately in seabirds' colonies, where birds' behaviour, reproductive success, and survival can indicate the extent to which the ecosystem is changing (Furness and Camphuysen, 1997, Montevecchi, 2007). Seabird behaviour can be used to track changes in fish populations and distribution (Brisson-Curadeau et al., 2017). Using seabirds to track environmental change has proven to be effective, and comes with much lower costs than the use of traditional methods such as research vessels (Furness and Camphuysen, 1997). Thus, studying seabirds can provide insights not only into seabird ecology but also into environmental health itself (Aguirre and Tabor, 2004).

Unfortunately, seabird sensitivity to changes comes at a cost as they now represent the most threatened group of birds (Croxall et al., 2012). Seabirds live both on land and at sea, meaning that they are impacted by both marine threats (e.g., bycatch and severe marine weather) and terrestrial threats (e.g., invasive species, light pollution, diseases) (Croxall et al., 2012, Dias et al., 2019). A recent assessment of seabird threats demonstrated that over half of seabird species are globally declining, out of which 31% have been declared as globally threatened (Croxall et al., 2012).

Threats to seabirds

Humans exert significant stress on the marine environment, resulting in clear consequences on the marine ecosystem (Halpern et al., 2008). Human activities, such as fisheries, transport, and oil exploitation have strongly impacted the marine environment, resulting in rapid shifts in food regimes for seabirds (Lieske et al., 2020, Grémillet and Boulinier, 2009). Pollution linked with human activities in the ocean, such as oil pollution from ships, plastic pollution, and light pollution, have also caused serious declines in seabird populations (Lieske et al., 2020). Although such threats are often thought of as localized and affecting only specific species or groups of seabirds, these threats often have a larger spread than anticipated, and end up posing a widespread threat to many seabird species and families (Lieske et al., 2020).

Seabirds are also heavily impacted by climate change. As a result of anthropogenic climate change, increasing air temperatures have caused the warming of sea surface temperatures. High sea surface temperature has caused a decline in overall sea surface productivity, in part through a reduction of nutrient upwelling (Grémillet and Boulinier, 2009). Overall, changes in seasonality and nutrient distribution affect the food web and cascade down to shift the food regime, where bottom-up effects have the potential of affecting the whole food web (Grémillet and Boulinier, 2009). Seabirds are top marine predators and are heavily affected by bottom-up effects. Changes in environmental condition impact seabirds' reproductive success, foraging and breeding range, metabolic processes (e.g., heat stress), and other traits (Oro, 2014, Choy et al., 2021). Such effects are especially felt in the Arctic regions, as the effects of global warming are magnified at the poles.

Study Species: Black-legged kittiwakes

The black-legged kittiwake (*Rissa tridactyla*) is circumpolar seabird species in the Laridae family. Within its circumpolar distribution, kittiwakes are separated into two subspecies, *Rissa tridactyla tridactyla* present in the Atlantic and *Rissa tridactyla pollicaris* present in the Pacific (Hatch, 2009). Kittiwakes are highly pelagic seabirds, spending the majority of their time at sea, and come to land almost exclusively to breed (Hatch, 2009, Hatch et al., 1993). During the breeding season, kittiwakes nest on cliffs and lay between one to three eggs per breeding season and practice biparental care (Hatch, 2009). To feed their chicks and themselves, kittiwakes forage at the surface of the water and catch fish by plunge diving (Hatch, 2009).

Although kittiwakes are widely distributed and are one of the most populous gull species on the planet, their numbers are declining. The species was listed by the IUCN Red List as vulnerable in 2018 (BirdLife International, 2019). Although the current threats are mostly the result of human activities, such as fishing and pollution, climate change is expected to impact on this species and contribute to population declines (BirdLife International, 2019).

Study Species: Thick-billed murres

The thick-billed murre (*Uria lomvia*) is an abundant Arctic seabird in the Alcidae family. It breeds in dense colonies on shear rocky cliffs where it lays a single egg per breeding season (Gaston and Hipfner, 2020). Outside of the breeding season, murres are highly pelagic and spend all of their time at sea where they can dive at great depths (up to 200 m) to forage fish and crustaceans (Gaston and Hipfner, 2000, Gaston and Hipfner, 2020). Murres are cold-adapted and rely on sea ice for foraging and thermoregulation (Gaston and Hipfner, 2020). However, in the summer, murres meet an array of environmental conditions, from the warm cliffs where the sun shines on their black plumage to the Arctic waters for foraging.

With the Arctic warming, murres are facing novel challenges, where their capacity to retain heat comes at the cost of their ability to dissipate heat. Murres experience heat stress at temperatures as low as 21.2 ºC and have the lowest maximum evaporative cooling efficiency ever reported in birds (Choy et al., 2021). Although thick-billed murres are currently listed as a species of least concern by the IUCN Redlist (BirdLife International, 2018), some populations wintering around Iceland and Greenland are declining (Frederiksen et al., 2016), and climate change is expected to impact this species even more via a northward species shift over time (Gaston and Hipfner, 2020).

To summarize, the role of seabirds as sentinels of the sea has been highlighted in many studies (Grémillet and Boulinier, 2009, Furness and Camphuysen, 1997, Brisson-Curadeau et al., 2017, Aguirre and Tabor, 2004). Hence studying species such as kittiwakes and murres can provide insights on the health of Arctic ecosystems. On top of their role as sentinels, both kittiwakes and murres nest in large colonies where individuals can easily be observed, making them ideal study subjects. Seabirds are highly sensitive to changes in their surrounding environment (Grémillet and Boulinier, 2009). As a result, it has been suggested that behaviour can provide valuable insights on ecosystem health (i.e., food supply; Brisson-Curadeau et al., 2017). In the context of climate change, studying seabirds’ physiology can provide insights on marine ecosystem health through the birds' behaviour, on top of gaining valuable insights on how these species, as well as seabirds in general, might adapt to their changing environment.

Note on chapter 1

This chapter corresponds to a manuscript titled “Using accelerometry to develop energy budgets in flight: High flapping flight and low gliding flight costs in a marine gull, the black-legged kittiwake ” that will be sent for publication shortly. This chapter was made in collaboration with the Institute for Seabird Research and Conservation (ISRC) on Middleton Island, managed by Dr. Scott Hatch and Ms. Shannon Whelan, and with the collaboration of the Speakman lab, namely Dr. Catherine Hambly and Dr. John Speakman (University of Aberdeen, Scotland).

Chapter 1

Using accelerometry to develop energy budgets in flight: High flapping flight and low gliding flight costs in a marine gull, the black-legged kittiwake

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Abstract

Energy is a common currency for any living organism, and understanding how animals use energy is critical to understanding their ecology and consequently how they might adapt to changes in their environment. Reproduction is a costly event for many animals, especially birds that must deliver food to a central place. Here, we developed a novel DLW-accelerometry calibration to measure energy expenditure in breeding black-legged kittiwakes (*Rissa tridactyla*). Kittiwakes varied their time-activity budgets throughout the breeding season by increasing time spent in flight and decreasing their time spent on water in chick-rearing compared to both incubation and pre-laying. Time-activity budgets were comparable across pre-laying and incubation, yet kittiwakes significantly increased their energy expenditure during incubation, averaging 752 ± 36 kJ d^{-1} in incubation and 623 ± 33 kJ d^{-1} in pre-laying. We obtained activity-specific metabolic rates for 5 behaviours (i.e., flying, swimming, resting on land, resting at the colony and gliding), and found that energy expenditure measured using our calibration versus measured using DLW did not vary. We conclude that (1) time-activity budgets can be easily obtained from free-ranging individuals to accurately track energy expenditure, (2) energy expenditure is highest in chick-rearing, followed by incubation, showing the cost of reproduction, and (3) flapping flight costs are the highest compared to other behaviours yet gliding flight costs are the lowest with along with the cost of resting at the colony.

Introduction

Energy is a limited resource, thus understanding how energy is allocated to various life-history traits is crucial to understanding the ecology of a species(Speakman 1997, Butler et al., 1992, Butler et al., 2004). Energy allocation is usually balanced between survival and reproduction (Forbes et al., 2016). Individuals are constantly weighing the pros and cons of investing in their current reproductive success against their future reproductive success, often resulting in trade-offs (Forbes et al., 2016). If allostatic overload is reached, where more energy is invested than there is available, negative impacts on an individual's reproductive success and/or survival can be observed (Wikelski and Cooke 2006). Hence, understanding how individuals expend energy can provide valuable insights into their physiological constraints, and ultimately their ecology. Nonetheless, measuring energy expenditure remains a challenge for wild animals.

Energy expenditure can be measured using traditional methods such as doubly-labelled water and heart rate loggers (Speakman, 1997, Butler et al., 2004), but also using new methods like accelerometry and time-activity budgets (Stothart et al., 2016, Wilson et al., 2006, Fort et al., 2011). Although the use of doubly-labelled water has been validated in a multitude of species, its use is often limited as it can only measure expenditure over a relatively short period of time (hours to days) and provides a single value of energy expenditure (Butler et al., 2004). Alternatively, heart rate loggers can measure energy expenditure over more variable lengths, but often require invasive surgical implantation that is unfeasible under many conditions (Butler et al., 2004). Thus, the use of biologging devices to track complex behaviour and energy expenditure remotely has increased significantly in the last decade due to technological advancements, making these devices accessible to a wide range of species (Patterson et al., 2019; Fort et al., 2011; Elliot 2016). Overall dynamic body acceleration (ODBA) obtained from accelerometers as a proxy for active energy expenditure has been validated in a few species (Wilson et al., 2006, Wilson et al., 2020). Although ODBA can yield accurate estimates for very active species, this method loses its precision when applied to species that spend a significant amount of time conducting low movement activities (i.e., preening; Fort et al., 2011; Jeanniard-du-Dot 2017). For such species, the use of time-activity budgets has proven to be a more suitable option to accurately estimate daily energy expenditure (Fort et al., 2011; Jeanniard-du-Dot 2017; Wilson et al., 2020).

Time-activity budgets can provide valuable insight into an individual's energy expenditure, granted that activity-specific metabolic rates are known for the species of interest (Collins et al., 2016, Fort et al., 2011; Jeanniard-du-Dot 2017). Measured using GPS-accelerometers, time-activity budgets usually separate an animal's movements into broad behavioural categories that occupy the majority of their time (i.e., resting, swimming, flying, diving, etc.). Although the advancement of technology has made tracking behaviour more accessible, the classification of accelerometry data into behaviours is a challenge. Yet, the use of broad behavioural categories when classifying behaviour has proven to be relatively easy and accessible, as using few predictor variables can yield accurate time-activity budgets (Patterson et al., 2019). Energy expenditure measured via time-activity budgets does not account for environmental variables, but studies comparing different energetic modelling methods demonstrated that time-activity budgets provided the best predictions, even against more complex models (Fort et al., 2011). Once activity-specific metabolic rates have been measured with DLW, time-activity budgets offer a more accessible and less costly method to estimate energy expenditure, especially for species such as seabirds that can be hard to access.

Seabirds are sentinel species of environmental changes both on land, and at sea (Brisson-Curadeau et al., 2017). Black-legged kittiwakes (*Rissa tridactyla*), a widespread sub-Arctic seabird, are suitable candidates when it comes to studying energy expenditure using time-activity budgets as their behaviours can be summed up in a few coarse categories (i.e., flying, swimming, and resting; Collins et al 2015, Collins et al., 2016). Kittiwakes are the most numerous gull species and have been extensively studied throughout their range, and as a result have been identified as a "Focal Ecosystem Component" (CAFF, 2020). However, most kittiwake studies tend to focus on a single breeding stage, chick-rearing, potentially missing some key variations in metabolic rate and time-activity budgets that occur over the whole breeding season (Jodice et al., 2003, Welcker et al., 2013, Elliott et al., 2013). Additionally, kittiwakes are most at risk of experiencing indirect effects of climate change at their southern range limit (i.e., the Gulf of Alaska on the Pacific side) as their food source moves further north and prey capture become increasingly challenging as prey fishes speed increases with temperature (BirdLife International, 2019, Osborne et al., 2020, Grady et al., 2019).

Here, we aimed to create a novel DLW-movement calibration in breeding black-legged kittiwakes (hereafter: kittiwake). To do so, we measured energy expenditure using DLW and deployed GPS-accelerometer. Using our accelerometry data, we classified kittiwake behaviours into five broad categories and obtained precise time-activity budgets. We hypothesized that energy expenditure would vary depending on the activity and predict that flight would be the costliest behaviour and would drive energy expenditure up as time in flight increased. Thus, we also hypothesized that energy expenditure would vary based on breeding stage and that chick-rearing would be the costliest breeding stage, based on time-activity budgets, as kittiwakes have to increase time spent in flight foraging for their chicks. Additionally, we compared models based on time-activity budgets to a model based on overall dynamic body acceleration to predict energy expenditure. We hypothesized that time-activity budget would better predict energy expenditure than overall dynamic body acceleration as kittiwakes are likely to engage in a lot of low movement activities during the breeding season (i.e., preening, incubating, nest attendance, etc.).

Methods

We studied male kittiwakes breeding on Middleton Island, Gulf of Alaska (58″25′N, 146″19′W), from May to July 2021. We studied males nesting on an old radar tower equipped with one-way windows, allowing us to monitor each nest closely with minimal disturbance to the colony. We focussed on males specifically as in a previous publication, we showed that although males and females had comparable energy expenditure, females exhibit high individual variation in pre-laying likely as a result of egg formation (Tremblay et al., 2022). To assess daily energy expenditure, we injected a total of 55 males with doubly-labelled water (DLW) following the two-sample method (Speakman 1997). To assess activity budgets, we equipped all injected males along with an additional 38 control males with GPS-accelerometers during pre-laying (n = 20 DLW, 10 control), incubation (n = 35 DLW, 11 control) and chick-rearing (n = 17 control). We visually identified individuals based on their unique colour band combination and determined sex based on behaviour. All work was approved by the McGill Animal Care Committee (protocol 2016-7814), under state permit 21-089 issued by the Alaska Department of Fish and Game and federal permit MB33779 issued by the US Fish and Wildlife Services.

Doubly-labelled water

We injected DLW (H_2 and O_{18}, 1:2 ratio respectively) following the two-sample method (Speakman, 1997). Upon the first capture, we took a background blood sample (25G, from brachial vein, 3 x 44.7 μL non-heparinised glass capillaries) and injected DLW in the brood patch (27G, 0.5 mL). Once injected with DLW, we equipped each bird with a GPS-accelerometer (details below) and immediately released them. We recaptured individuals 1.5 hours to 3.0 hours post-DLW injection and took an initial blood sample (25G, from brachial vein, 3 x 44.7 μL non-heparinised glass capillaries). Two days later, upon GPS-accelerometer retrieval, we took a final blood sample (25G, from brachial vein, 3 x 44.7 μL non-heparinised glass capillaries). For all blood samples, we immediately flame sealed the whole blood in glass capillaries and stored the samples at room temperature for later analysis.

Measuring isotope ratios

To measure the ratio of DLW isotopes in the bird's blood, we extracted the water from the blood samples and analyzed isotope ratios using a Liquid Water Isotope Analyzer (LWIA; Los Gatos

Research, San Jose; technique demonstrated at: https://www.youtube.com/watch?v=NvIHk_50fYw). We distilled the blood in sealed pastor pipettes and placed them on a hot plate for 48h. Once distilled, we transferred the water into glass vials for analysis using the LWIA. To prevent memory effects where the enrichment level of a given sample affects the measurement of the following sample, we analyzed samples with different enrichment levels separately (background, initial and final samples). Additionally, we set the LWIA to conduct five preparatory injections prior to conducting the five measured injections and used the average value of the five measured injections to estimate the ratio of H^2/H^1 and O^{18}/O^{16}. For each run, we included a low and a high standard used to correct the measured values, thus minimizing error due to variations between batches. All DLW analyses were conducted at McGill University, Montreal, CA.

Calculating CO_2 production

Once we measured the DLW isotope ratio in the bird's blood, we converted ratios of H^2/H^1 and O^{18}/O^{16} to estimates of CO_2 produced over the length of the deployment. We first estimated the mean isotope turnover rate for oxygen and deuterium (k_o and k_d) in parts per million per hour (ppm h^{-1}), using the following formula (Speakman 1997);

$$k = [\ln(I_{initial} - I_{background}) - \ln(I_{final} - I_{background})]/Time \qquad \textit{(eq. 1.1)}$$

where $I_{background}$, $I_{initial}$, and I_{final} correspond to background, initial, and final isotope ratios respectively, in parts per million (ppm), and time corresponds to the time between the initial and final DLW sample in decimal hours. As we used the two-sample method, we make the assumption here that the time at initial sampling corresponds to the time at equilibrium (Speakman 1997).

Next, we estimated the isotope dilution space of oxygen and deuterium (N_o and N_d) in the bird's body using the following equation;

$$N = \frac{Mol_{inj}(I_{initial} - I_{inj})}{(I_{background} - I_{initial})} \qquad \textit{(eq. 1.2)}$$

where Mol_{inj} corresponds to the mols of heavy water injected into the bird, $I_{initial}$ and $I_{background}$ correspond to initial and background isotope ratios in ppm, and I_{inj} corresponds to the estimate of injectate enrichment in ppm. To estimate the body water pool, we assumed that the average between the initial measured dilution space of O_{18} (N_o) and the estimated final dilution space corresponds to the pool size (N).

We then estimated the rate of CO_2 production (mmol CO_2 /h) using the following equation (equation 7.17, Speakman 1997):

$$rCO_2 = \frac{N}{2.078} \cdot (k_o - k_d) - (0.0062 \cdot k_d \cdot N) \qquad \textit{(eq. 1.3)}$$

where N corresponds to the pool size, and k_o and k_d correspond to the isotopes' turnover rates (Equation [7.17] Speakman 1997). We converted mmol of CO_2 into mL of CO_2 per hour by multiplying by 22400. Finally, we converted rates of CO_2 production in daily energy expenditure using an average caloric equivalent from a multi-year study on kittiwakes (27.63 J/ml CO_2; Welcker *et al.*, 2010).

Biologging

We deployed GPS-accelerometers (AxyTrek, Technosmart, Rome, Italy, 8g) on the two central rectrices of black-legged kittiwakes, including some coverts. We fixed the units using superglue, Tesa tape, and zip ties (https://www.youtube.com/watch?v=bjlRK1pSxa8). We programmed the GPS-accelerometer to obtain GPS coordinates every three minutes and measure triaxial acceleration at 25 Hz. Once equipped with a GPS-accelerometer, we released individuals and recaptured them 2 days later. For each individual, we recorded body mass, measured using a Pesola scale (accuracy of ± 5g) and weighing cone, at deployment and retrieval., We calibrated all the units in the field prior to deployment following the '6-O method described in Garde *et al.* (2022).

Tag effect

To assess the impact of tag deployment on the bird's body condition, we conducted a one-tailed paired t-test and compared body mass at deployment against mass at retrieval in both control and DLW treatments (i.e., all individuals). To assess the impact of tag deployment on the bird's reproductive success, we conducted two Fisher's exact tests comparing the hatching success and chick mortality of tagged vs. non-tagged males using the function *fisher.test* from the *stats* package in RStudio (R Core Team 2020). We reported data as mean ± s.e.

Foraging behaviour

To assess foraging behaviour, we analyzed GPS data and identified foraging locations and distances based on the birds' residence in space and time (Tores et al., 2017). Prior to conducting our analysis, we visually cleaned the data by looking at speed and distance from the colony and removing outliers based on the visual assessment of data distribution. Foraging location was identified as areas where birds conducted area restricted search (high space and high time), hence excluding areas where the birds were either commuting (low space and low time) or resting (low space, high time; Torres et al., 2017). We mapped kernel density plots of foraging location (50%, 85%, 95%) with *adehabitatHR* (Calenge, 2006) for each breeding stage to account for differences in foraging distance that could impact the birds' daily energy expenditure and time-activity budgets.

Time-activity budgets

To obtain reliable time-activity budgets from kittiwakes, we first calibrated our accelerometry data for each deployment. Using the '6-O calibration done in the field, we adjusted the amplitude and offset of each axis (x, y, z) so that all units facing the same direction read the same vectorial sum (see Garde et al., 2022). When necessary, we recorded the adjustments of amplitude and offset for each axis of each unit, and transposed said adjustments to whole deployment lengths, allowing us to control for tag error.

Using the calibrated accelerometry data along with GPS data and bathymetry data, we classified behaviour into five broad behaviours: at the colony, resting on land, swimming, flying, and gliding. We classified behaviours using a Hidden Markov Model using the *momentuHMM* package (McClintock and Michelot, 2018) on RStudio (R Core Team 2020) based on four predictor variables (Figure 1.1); wingbeat frequency (WBF; gamma distribution), presence/absence at the colony (Bernoulli distribution, 1 km radius around the colony), presence/absence on land (Bernoulli distribution), and ground speed (Bernoulli distribution with a 5 km/h threshold). We measured wing beat frequency using a Fast Fourier Transform on the z-axis using the *seabiRd* package (Patterson et al., 2019) and wing beat frequencies of 1 Hz or lower were automatically reclassified as zero Hz. To increase processing speed, we subsampled our accelerometry data at 30-second intervals.

DLW-movement calibration and activity-specific metabolic rate

To obtain activity-specific metabolic rates, we used a model selection approach to assess the best predictors of energy expenditure. We first corrected the values of energy expenditure to a standard mass to control for the effect of variation in body mass on energy costs, as body mass can influence both daily energy expenditure (larger lean body mass would have higher resting and flight costs) and ODBA (heavier birds would have a lower ODBA for the same force generated; Gleiss et al., 2011).

As kittiwakes are sexually dimorphic, we attempted to minimize the effect of body mass by only using males (Helfenstein et al., 2004). Nonetheless, there was a variation in body mass, averaged across deployment and retrieval, during incubation (average: 463 ± 29 g; range: 412.5 – 536 g)

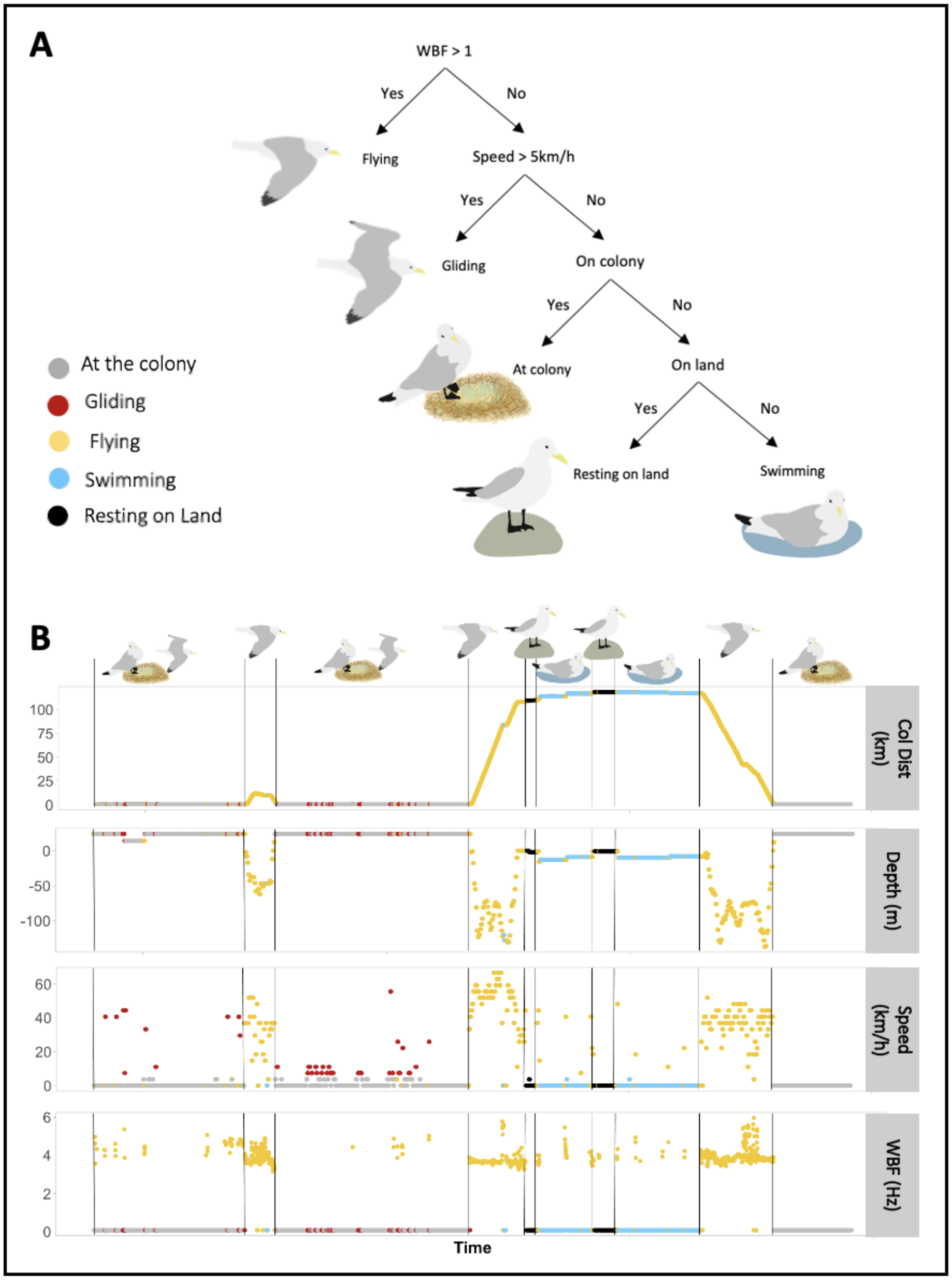

Figure 1.1: A) Behavioural classification using a Hidden Markov Model based on wing beat frequency (WBF), ground speed, presence/absence at the colony and presence/absence on land to classify behaviours in five broad categories (flying, gliding, at colony, resting on land and swimming). **B)** An example track with classification shown with colony distance (km/h), water depth from bathymetry (m), speed (km/h), and wing beat frequency (Hz).

compared with pre-laying (421 ± 19 g; range: 398-463 g). The mass pre- and post-deployment was comparable during incubation but not pre-laying (pooled: R = 0.66; incubation: R = 0.64; pre-laying: R = 0.22). The larger, more variable body mass during incubation is consistent with incubating birds having higher lipid concentrations to increase thermoregulation (incubation of eggs) and fasting duration (during incubation bouts) (Golet and Irons 1999; Jacobs et al., 2011).

To account for the effect of body mass, we standardized the daily energy expenditure of kittiwakes (in kJ d^{-1}) to a body mass of 450 g using the following formula (see Appendix 1):

$$DEE_{std} = DEE_{measured} + (Mass - 450) \cdot 3.30 \quad \textbf{(4).}$$

where $DEE_{measured}$ corresponds to the daily energy expenditure of kittiwakes measured using doubly-labelled water (in kJ d^{-1}) and *Mass* corresponds to the average of the kittiwake's mass at deployment and retrieval (in g). We then used DEE_{std} in time budget models.

To obtain activity-specific metabolic rates, we used a model selection approach to identify the best predictors of standardized energy expenditure using the *MuMIn package* (Barton, 2022). We selected the best model using AICc to account for our small sample size, where the better models have a lower AICc value. Then using models within 2 delta AICc (Burnham and Anderson, 2002), we tested for multicollinearity between the covariates based on variance inflation factor (VIF), where we discarded models with VIFs higher than 10 (Vittinghoff et al., 2011). Covariates considered included; the proportion of time spent in each behaviour (at the colony, on land, swimming, flying, and gliding), the dynamic body acceleration for each behaviour (ODBA; at the colony, on land, swimming, flying, and gliding), the breeding stage (pre-laying and incubation; no DLW injected during chick-rearing) and an intercept set at 0 (Elliot, 2016). We calculated ODBA for each behaviour using the *seabiRd* package (Patterson et al., 2019). We first compared a model based on ODBA to a model based on time-activity budgets, and then used the best of these two models to conduct a model selection and identify the best overall model. Once we identified the best model to predict energy expenditure based on AICc and VIFs, we extracted estimates for each covariate in the model to obtain activity-specific metabolic rates (in kJ d^{-1}) and converted them to kJ d^{-1} g^{-1} by dividing the estimates by 450 g. Values are also reported as multiples of basal metabolic rate (3.49 W; Elliott et al., 2013).

Estimates of daily energy expenditure

Using our activity-specific metabolic rates, we estimated daily energy expenditure for all DLW and control birds (n = 80) using their time-activity budgets obtained from the GPS-accelerometry data. We used the following formula to obtain estimates of daily energy expenditure (Stothart et al., 2016):

$$DEE = MR_{flight} \cdot T_{flight} + MR_{on\,water} \cdot T_{on\,water} + MR_{on\,land} \cdot T_{on\,land} + MR_{Col+Soar} \cdot \left(T_{at\,colony} + T_{soaring} \right) \quad \textbf{(5)}$$

where *MR* (in kJ g^{-1} d^{-1}) corresponds to the activity-specific metabolic rate of each behaviour (time at the colony and gliding pooled together based on model selection results), and *T* corresponds to the proportion of time spent in a given behaviour (% per day).

Statistical Analysis

Out of 93 kittiwakes we deployed GPS-accelerometers on, we retrieved 92 units and obtained 90 usable tracks spread between pre-laying (n = 20 DLW, 10 controls, incubation (n = 34 DLW, 10 controls), and chick-rearing (n = 16 controls). We excluded from the analysis data from 10 deployments for which we did not obtain a ‘6-O calibration in the field, thus preventing us from calibrating these deployments. We used data from 80 GPS-accelerometry deployments, out of which 49 birds had been injected with DLW. By including only the 80 deployments for which we obtained a calibrated deployment, we minimised errors due to tag placement and unit variability. Out of the 55 birds injected with doubly-labelled water, we recaptured 54 individuals and obtained daily energy expenditure estimates for 50 individuals. We excluded one individual who had final levels O^{18} within 2% of background levels (Speakman 1997), one individual whose final sample was destroyed in transport, and an additional two individuals that were mistakenly identified as males, leaving us with a total of 50 individuals with energy measurements from DLW in pre-laying (n = 17) and incubation (n = 33). As previous results showed that incubating males and females have similar activity budgets (Tremblay et al., 2022), we did not exclude the females from the time-activity budget analysis.

Energy expenditure and time-activity budgets

Using RStudio (R Core Team 2020), we modelled energy expenditure from DLW measurements and time-activity budgets against the breeding stage to test for statistical differences across the breeding season. For each linear model, we ran an ANOVA (type II) using the *car* package (Fox and Weisberg, 2019) to test for the direct effects of the breeding stage on energy and activity budgets. If the ANOVA rendered significant results ($\alpha = 0.05$), we also conducted an analysis of least-squares means (LSM) using the *emmeans* package (Russel, 2021) to identify where the significance laid. We reported data as mean ± s.e.

Results

Tag effect

Deployments lasted on average 58.9 ± 2.3 h (range: 39.1 - 122.2 h). Body condition decreased over the length of the deployment for birds injected with DLW, with an average mass loss of 11.73 ± 4.57 g (paired $t_{48} = 2.57$, $p = 0.007$) between deployment and retrieval. We found no effect of deployment on body condition in control birds (- 4.64± 5.87, paired $t_{27} = 0.79$, $p = 0.218$). Additionally, we found no significant effect of tag deployment on hatching success (p = .31, Fisher's exact test) and chick mortality (p = 0.47, Fisher's exact test), with on average 65 ± 3 % of chicks hatching and 53 ± 3% of chick mortality.

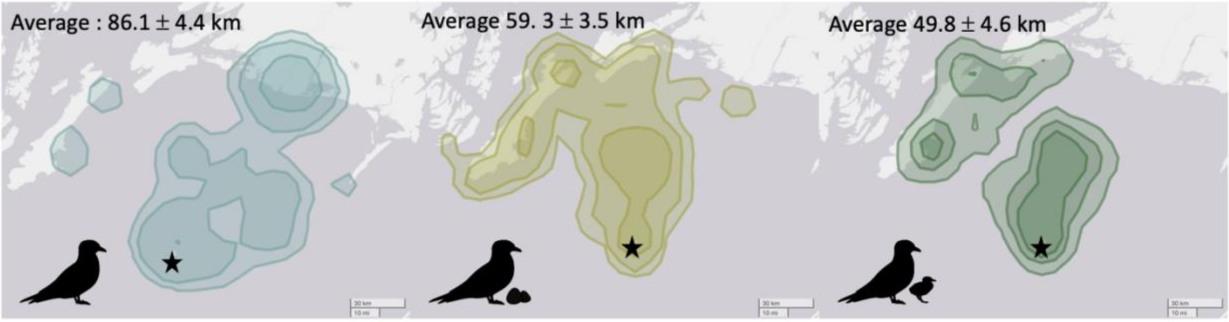

Figure 1.2: Foraging location (50%, 85% and 95% kernel density) of 90 kittiwakes across the breeding season.

Foraging behaviour

Kittiwakes foraged at different distances from the colony throughout the breeding season ($p < 0.0001$), with an average foraging distance of 86.1 ± 4.4 km in pre-laying, 59.3 ± 3.5 km in incubation, and 49.8 ± 4.6 km in chick-rearing (Figure 1.2). Birds foraged at a greater distance from the colony during pre-laying compared to both incubation and chick-rearing and foraged the closest to the colony during chick-rearing (Table S1.1).

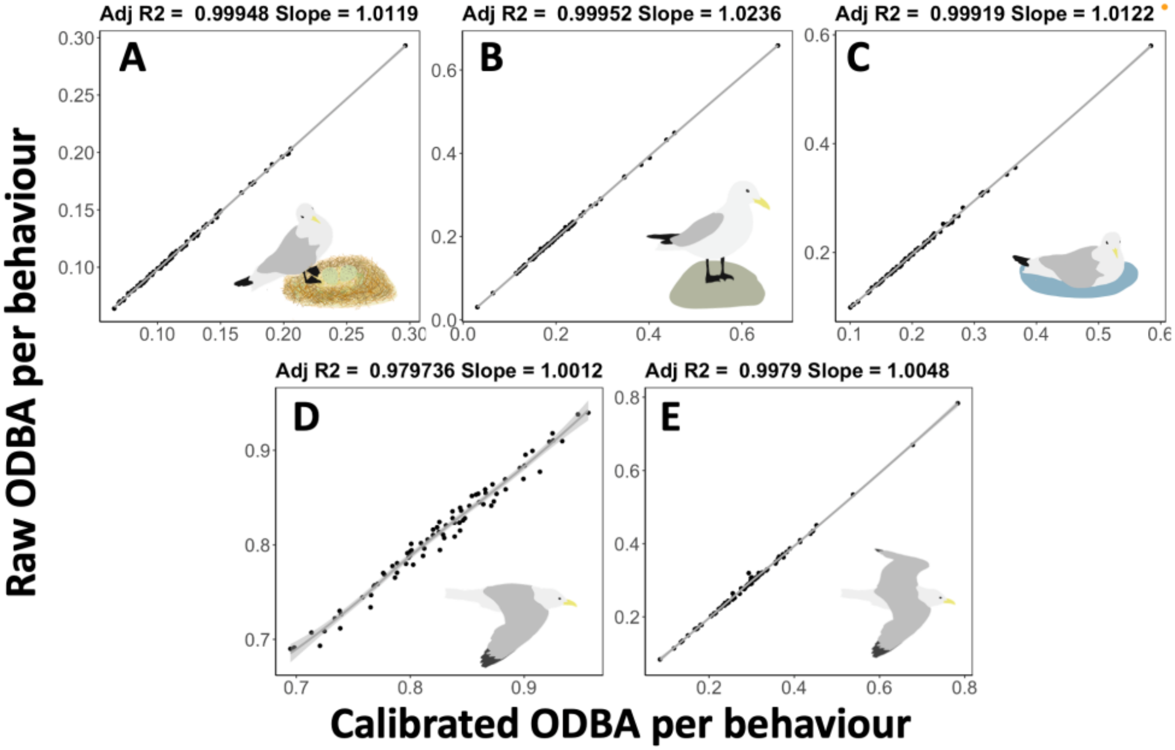

Figure 1.3: Comparison of calibrated vs. raw overall dynamic body acceleration (ODBA) of 80 kittiwakes **a)** at the colony, **b)** resting on land, **c)** swimming, **e)** flying and **f)** gliding/soaring.

Time-activity budgets

ODBA obtained from calibrated data correlates tightly with ODBA obtained from raw data with R^2 ranging from 0.98 to 1.00 (Figure 1.3). Following the calibration, we excluded visible outliers from further analysis, resulting in the removal of one bird, likely as a result of a unit malfunction.

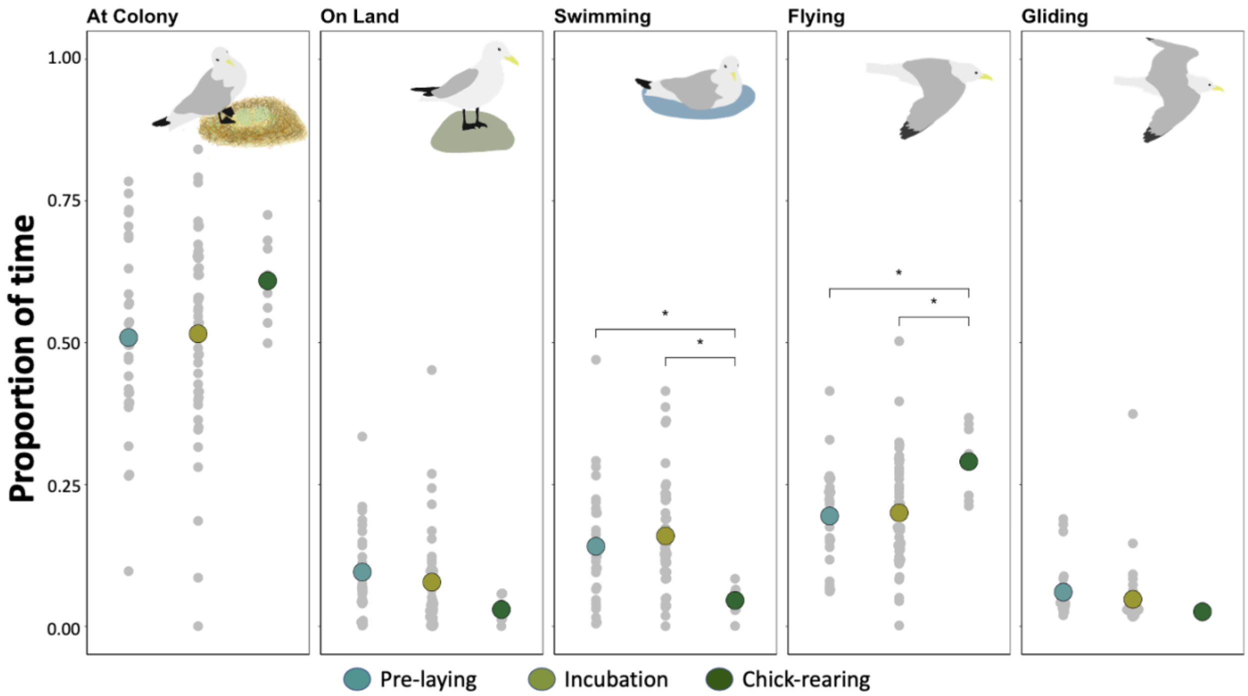

Figure 1.4: Time-activity budgets of 80 kittiwakes throughout the breeding season. Significantly different groups are identified with an asterisk (*).

Kittiwakes varied their time spent flying ($F_{2,77}$ = 3.80 , p = 0.03) and swimming ($F_{2,77}$ = 4.68, p = 0.01) throughout the breeding season. Kittiwakes increased significantly their time spent in flight in chick-rearing compared to pre-laying and incubation (Table S1.1). On average, birds spent 32 ± 2% of their time flying in chick-rearing compared to 25 ± 1% in pre-laying and 22 ± 1% in incubation (Figure 1.4). On the other hand, kittiwakes decreased significantly their time spent swimming during chick-rearing (Table S1.1), with an average of 5 ± 2% of their time compared to 14 ± 2% in pre-laying, and 16 ± 1% in incubation (Figure 1.4). Time spent at the colony did not vary significantly across the breeding stages, with kittiwakes spending on average 53 ± 16% at the colony. Similarly, time spent resting on land did not vary significantly and occupied 8 ± 8% of the kittiwakes' time. Gliding also occupied 4 ± 2% of the kittiwakes' time and did not vary significantly across the breeding stages.

DLW-movement calibration and activity-specific metabolic rate

Based on DLW measurements, kittiwakes increased their daily energy expenditure in incubation compared to pre-laying (129 ± 53.8 kJ d^{-1}, $F_{2, 48} = 376.45$, $p = 0.0$; see Appendix 2, Table S1.2). Using standardized daily energy expenditure (Figure 1.5), we compared models using time-activity budgets, overall dynamic body acceleration (ODBA), and breeding stage (see Table 1.1 for top three models). Models based on time-activity budgets predicted energy expenditure more accurately (Table 1.1), with the best model including time spent flying, swimming, resting on land, and pooled time spent at the colony and gliding (Table 1.1). Using estimates from our best model, we found that kittiwakes spent 3.88 ± 0.94 kJ d^{-1} g^{-1} when in flight, 2.06 ± 0.88 kJ d^{-1} g^{-1} when swimming, 1.24 ± 0.78 kJ d^{-1} g^{-1} when resting on land and 0.56 ± 0.26 kJ d^{-1} g^{-1} when at the colony and gliding (Table 1.2)

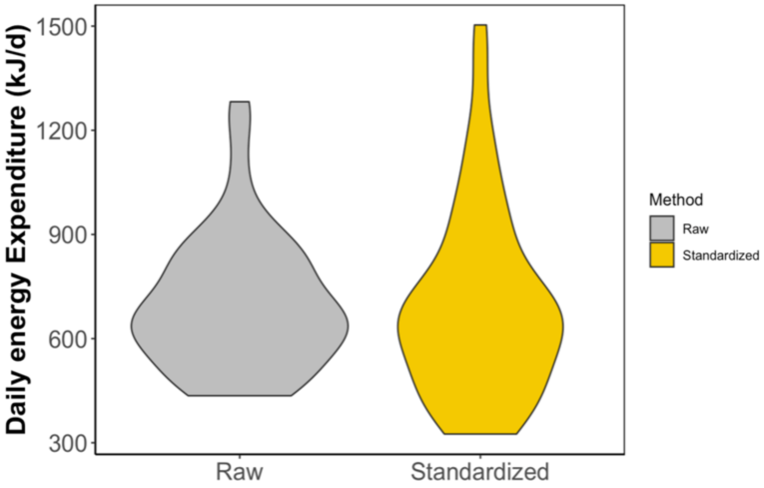

Figure 1.5: Distribution of raw (grey) energy expenditure vs standardized energy expenditure (yellow) - energy expenditure for a kittiwake of 450 g - (kJ d^{-1}) for all 49 kittiwakes injected with doubly-labelled water.

Estimates of daily energy expenditure

There was no significant difference in energy expenditure estimated using the DLW and time-activity budget methods for kittiwakes in both pre-laying and incubation ($F_{1,125}$ = 0.21, p = 0.65; Figure 1.6B). Both methods showed a significant effect of breeding stage on daily energy expenditure ($F_{2,125}$ = 6.4, p = 0.002), and estimates of energy expenditure measured using time-activity budgets showed that kittiwakes, during both incubation and chick-rearing exhibit significantly higher energy expenditure than during pre-laying (Table S1.1). Our results correlate with previous activity-specific metabolic rates (Figure 1.6A) estimated using DLW and behavioural observations (Jodice et al., 2003), and mathematical modelling (Collins et al., 2016).To allow for a comparison between our calibration and Jodice et al. (2003), we converted the activity-specific metabolic rate they obtained using their respective methods, measured in mL CO_2 g^{-1} h^{-1} to kJ g^{-1} d^{-1}, using the same caloric equivalent as described in our methods (see Table 1.2 for more details). Similarly, to compare our values to Collins et al. (2016) values, we converted their values (in kJ h-1 for a 365g individual) to kJ g^{-1} d^{-1} (Table 1.2).

Table 1.1: Models of time-activity budgets and activity-specific overall dynamic body acceleration (ODBA) considered to predict standardized daily energy expenditure (DEE_{std}), using AICc and variance inflection factors (VIFs). In all cases, the intercept was set to

#	**Model**	**AICc**	**ΔAICc**	**R²**	**VIFs**					
					Fly	**Swim**	**Col**	**Rest**	**Glide**	**Col = Glide**
1	DEE_{std} ~ Fly + Swim + Col + Rest + Glide	665.18	0.00	0.92	10.98	4.78	3.59	2.01	9.29	-
2	DEE_{std} ~ Fly + Swim + Rest + Col=Glide	667.18	2.00	0.91	7.86	4.59	-	1.81	-	3.84
3	DEE_{std} ~ Fly_{odba} + $Soar_{odba}$+ $Swim_{odba}$ + Col_{odba}+ $Rest_{odba}$	676.83	11.65	0.81	-	-	-	-	-	-

DEE_{std} : standardized daily energy expenditure
ODBA : overall dynamic body acceleration
VIFs : variance inflection factors

Table 1.2: Activity-specific metabolic rates (kJ d^{-1} g^{-1}) obtained for each behaviour using our best fit model compared to estimates obtained by Jodice *et al.* (2003) for similar behavioural classes.

DEEstd ~ Rest + Swim + Fly + (Col.Soar) ***Adj R2= 0.90***			*Jodice et al. (2003)*		*Collins et al. (2016)*	
Behaviour	***Estimate ± s.e.*** kJ g^{-1} d^{-1}	**× BMR***	***Behaviour***	***Estimate*** kJ g^{-1} d^{-1}	***Behaviour***	***Estimate*** kJ g^{-1} d^{-1}
Rest	1.24 ± 0.78	1.77	Loafing near colony	0.92	Nest attendance	0.89
Swim	2.06 ± 0.88	2.94	Surface feeding	1.51	Swim	1.24
Fly	3.88 ± 0.94	5.54	Commut. flight Search. flight (Averaged)	5.37	Fly	3.17
Col.Soar	0.56 ± 0.26	0.80	Nest attendance Loafing near colony (Averaged)	1.07	Nest Attendance	0.89

* BMR = 0.70 kJ g^{-1} d^{-1} (from Elliott *et al.* 2013; 3.49 W for average weight of 432 g)

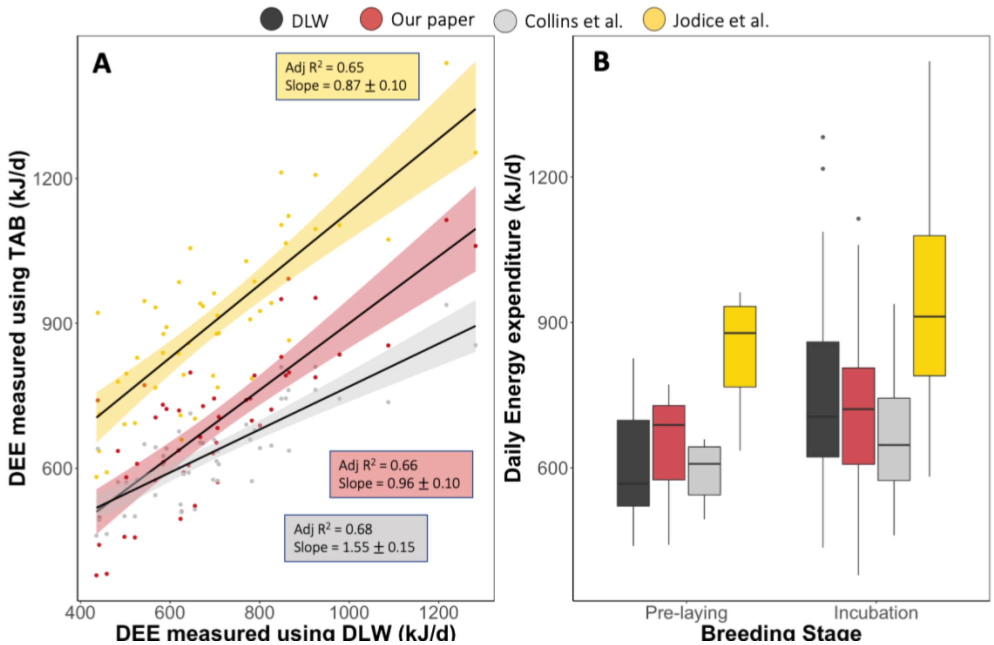

Figure 1.6: Comparison of daily energy expenditure (kJ d^{-1}) in 49 kittiwakes measured using time-activity budgets using activity-specific metabolic rates from our paper (red), Collins et al. (2016;

grey) and Jodice et al. (2003; yellow) **A)** to energy expenditure measured using doubly-labelled water and **B)** per breeding stage.

Discussion

Using time-activity budgets and measurements of energy expenditure via doubly-labelled water, we obtained activity-specific metabolic rates to estimate energy expenditure in breeding black-legged kittiwakes. Measurements of energy expenditure using doubly-labelled water showed that male kittiwakes increased their energy expenditure in incubation compared to pre-laying (Figure 1.6). Although time-activity budgets suggested that chick-rearing would be the costliest stage due to the increased time spent flying (Figure 1.4), energy expenditure estimated via time-activity budgets showed that both incubation and chick-rearing are costlier than pre-laying (Figure 1.6B). Energy expenditure measured via doubly-labelled water and time-activity budgets both yielded similar results (Figure 1.6A-B), and results from our calibration correlated with a previous time-activity budget calibration obtained via behavioural observations (Figure 1.6A; Jodice et al., 2003).

We found that the tag affected the body condition of doubly-labelled water birds only, likely as a response to increased stress from the additional handling compared to the control birds. As we used the two-sample method (Speakman 1997) to obtain more accurate measurements of energy expenditure, kittiwakes injected with doubly-labelled water were recaptured 1.5-3 hours after the first capture. Although we did not test for differences in time-activity budgets between treatments, this additional capture (2-4 minutes handling time) might have resulted in an increased time spent flying as a response to the additional stress. Nevertheless, we found no effect of treatment on breeding success between DLW, control, and non-tagged birds. Our measurements of energy expenditures from doubly-labelled water are within the normal range for kittiwakes; hence, we believe that tagging did not affect our results (Gabrielsen et al., 1987, Jodice et al., 2003, 2002, Collins et al., 2016). Furthermore, the tag effect we detected highlights the need for our DLW-accelerometry calibration in kittiwakes as measuring energy using DLW can affect the kittiwake's body condition negatively, unlike the deployment of GPS-accelerometers only.

Using data from our GPS-accelerometer deployments, we showed that kittiwakes foraged closer to the colony as the breeding season progressed; however, kittiwakes increased their time spent in flight during chick-rearing, likely due to more numerous foraging trips (Rishworth and Pistorius 2015, Osborne et al., 2020). In chick-rearing, kittiwakes forage for both themselves and to provide for their chicks, hence a larger portion of their time is spent foraging, resulting in shifts in time-activity budgets. Other studies on incubating and chick-rearing kittiwakes showed a similar pattern in time-activity budgets, where kittiwakes increased their time spent in flight and reduced time on the water during chick-rearing compared to incubation (Collins et al., 2016, Tremblay et al., 2022).

Although the shift in time-activity budgets during chick-rearing is reflected in the energy expenditure of kittiwakes through an increase in daily cost, the increased cost of incubation compared to pre-laying cannot be attributed to a significant increase in time spent in flight. Indeed, we found that the activity budgets of kittiwakes are similar during both pre-laying and incubation, yet energy expenditures were significantly higher in incubation compared to pre-laying (Table S1.1). This shift in energy expenditure may be attributed to the higher thermoregulatory costs associated with incubation, such as increased metabolism to keep their eggs warm, or increased heat exchange with the environment through the brood patch resulting in birds having to maintain a higher body temperature (Welckers et al., 2013). Measurements of resting metabolic rates using triiodothyronine (a thyroid hormone) suggest that kittiwakes have higher metabolic costs during incubation compared to pre-laying (Elliott et al., 2013, Welcker et al., 2013, Tremblay et al., 2022). This increased cost of incubation was also observed in our previous study that compared time-activity budgets and energy expenditure in both male and female kittiwakes (Tremblay et al., 2022).

Although we used males exclusively in this study, we believe that our calibration is valuable to estimate energy expenditure in both breeding males and females, with the potential exception of pre-laying. Indeed, in a previous publication (Tremblay et al., 2022), we have found evidence of high individual variation in energy expenditure in prey-laying females likely as a response to egg formation (Whelan et al., 2021, Creelman and Storey, 1991). Otherwise, it has been shown that there is no significant difference between males' and females' energy expenditure during incubation and chick-rearing when accounting for differences in time-activity budget and mass (Tremblay et al., 2022, Thomson et al., 1998). We suggest that further research on the energetic costs of pre-laying females is needed to elucidate the cost of egg formation in kittiwakes. Furthermore, we acknowledge that our calibration for the cost of soaring and colony attendance yielded estimates below published values of BMR for kittiwakes (Elliot et al., 2013), but we believe that our values are correct as previous measurements of BMR were likely driven up by handling stress. Thus, we are confident that our DLW-movement calibration can yield accurate estimates of energy expenditure for males and females outside of the egg formation period. Altogether, our data highlights the importance of measuring energy expenditure directly in the wild, due to handling stress in captivity.

To our knowledge, our study is the first to classify gliding in kittiwakes using GPS-accelerometry data. Although gliding occupies only a small portion of the kittiwakes' time-activity budgets, we believe that pooling flight and gliding into a single behavioural category could lead to errors when estimating energy expenditure from time-activity budgets. As results from our model selection indicated, the energy expended when gliding is more similar to the energy expended when at the colony (i.e., nest attendance) than during flapping flight. Our behavioural classification also identified key metabolic differences between kittiwake resting on land, on water, and at the colony. Thus, selecting species-appropriate behavioural categories can prove to be crucial when estimating energy expenditure based on time-activity budgets.

Although we succeeded at obtaining five behavioural categories that are broad enough yet explained most of the variation in energy expenditure, we acknowledge that the classification used three types of data, namely GPS, accelerometry and bathymetry data. This methodological choice was the results of analytical challenges faced when analyzing behavioural data from a plunge-diving species with high variability in its flying behaviour, where using metrics of accelerometry only yielded poor results. We recognize that this adds a level of complexity as some of our behavioural classes may not be obtainable by using solely one type of data (i.e. resting on land vs. resting on water), but we also believe that using five behavioural categories ultimately enabled us to better predict energy expenditure based on time-activity budgets.

Our estimates of energy expenditure obtained using our calibration correlate with energy estimates calculated using the most frequently used calibration to date (Figure 1.6; Jodice et al., 2003). Absolute values of energy expenditure differed among studies with our calibration yielding consistently lower energy expenditures estimates. This difference in absolute values may be a result of the different methods used to obtain time-activity budgets (behavioural observations, smaller sample size, etc.) for the calibration and/or individual variation between the Middleton Island colony and Shoup Bay colony (Jodice et al., 2003). Estimates of energy expenditure obtained using our calibration and Collins et al. (2016; Figure 1.6) estimates obtained via a mathematical model showed similar estimates. We believe that our calibration advances the field of energetics by offering a more accessible method as it uses broad and easily identifiable behavioural categories. With the advancement of biologging technologies, our capacity to follow animals' behaviour has improved, yet identifying precise behaviours often requires complex models and confirming such behavioural classifications using observations is often not possible when working with seabirds.

Overall, we created a novel DLW-movement calibration for breeding kittiwakes that offers a less restrictive and less invasive way to measure energy expenditure than other traditional methods such as heart-rate loggers and DLW. The calibration produced will facilitate the estimation of daily energy expenditure using only GPS-accelerometers, reducing the impact on animals, researcher effort, and expense relative to traditional DLW methods. Using broad behavioural categories, time-activity budgets can be easily obtained from free-ranging individuals to measure energy expenditure. Seabirds are highly sensitive to changes in their surrounding environment (Wolf et al., 2016, Grémillet and Charmantier 2010). As a result, it has been suggested that behaviour can provide valuable insights into ecosystem health (Brisson-Curadeau et al., 2017). Studying energy expenditure using time-activity budgets can provide insights into marine ecosystem health through the birds' behaviour, on top of gaining valuable insights into how seabirds respond to their changing environment.

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Appendix 1: Supplementary Methods

Supplementary method for mass correction

Due to variation in mass, we looked at the effect of mass on daily energy expenditure for the pooled data, as well as each breeding stage individually. For the pooled data, we considered both power law (Log (DEE) = 1.91 ± 0.45 * Log (Mass) – 5.14 ± 2.80; t_{47} = 4.209; p = 0.0001; R^2 = 0.27) and linear (DEE = 3.30 ± 0.71 * (Mass) – 780 ± 319; t_{47} = 4.65, $p < 0.0001$; R^2 = 0.32) relationships, where significance tests are given for the slopes. Given the variation in body mass between the two stages, we also considered the stages separately. For incubation, both power law (Log (DEE) = 2.03 ± 0.68 * Log (Mass) – 5.89 ± 4.16; t_{30} = 3.00; p = 0.005; R^2 = 0.23) and linear (DEE = 3.61 ± 1.08 * (Mass) – 917 ± 503; t_{30} = 3.33, p = 0.002; R^2 = 0.27) relationships were significant. For pre-laying, neither power law (Log (DEE) = 0.29 ± 1.16 * Log (Mass) + 4.63 ± 7.00; t_{15} = 0.25; p = 0.81; R^2 = 0.00) nor linear (DEE = 0.57 ± 1.64 * (Mass) + 358 ± 690; t_{15} = 0.35, p = 0.73; R^2 = 0.01) relationships were significant. Given that the power law explained less of the variation than the linear relationship (and the similarity between both relationships), we only included the linear relationship going forward, which we applied on the pooled data given the similarity between the regression lines for incubating and pooled data.

Appendix 2: Supplementary Results

Table S1.1: Summary of least square means test on linear models looking at the effects of the breeding stage on foraging distance and time-activity budgets and estimated energy expenditure of 90 kittiwakes.

Linear Model	*Variables*	*Estimate ± s.e.*	*P value*
Foraging distance ~ Stage (in km)	Pre-laying – Incubation	26.8 ± 5.6	**<0.0001**
	Pre-laying – Chick-rearing	36.3 ± 6.4	**<0.0001**
	Incubation – Chick-rearing	9.5 ± 5.6	**<0.0001**
Time flying ~ Stage (in %)	Pre-laying – Incubation	-1 ± 2	0.97
	Pre-laying – Chick-rearing	-10 ± 4	**0.03**
	Incubation – Chick-rearing	-9 ± 3	**0.03**
Time swimming ~ Stage (in %)	Pre-laying – Incubation	-2 ± 2	0.7
	Pre-laying – Chick-rearing	10 ± 4	**0.04**
	Incubation – Chick-rearing	11 ± 4	**0.009**
DEE ~ Stage (in kJ d^{-1})	Pre-laying – Incubation	-86.8 ± 27.1	**0.005**
	Pre-laying – Chick-rearing	-103.5 ± 43.6	**0.05**
	Incubation – Chick-rearing	-16.6 ± 42.0	0.9

Table S1.2: Energy expenditure of kittiwakes measured via doubly-labelled water

Breeding Stage	**Sample size** (n)	**Mean ± s.e.** kJ g^{-1} d^{-1}	**Mean ± s.e.** kJ d^{-1}	**Min** kJ d^{-1}	**Max** kJ d^{-1}
Pre-laying	17	1.48 ± 0.08	623 ± 33	439	950
Incubation	33	1.62 ± 0.07	752 ± 36	435	1282
Total	50	1.57 ± 0.05	705 ± 27	435	1282

Linking statement

To better understand how climate change is likely to impact seabird physiology, we investigated the factors influencing energy expenditure in black-legged kittiwakes. As time-activity budgets predicted energy expenditure in kittiwakes, with flight being the costliest behaviour, changes in food webs and foraging range are likely to impact on kittiwakes strongly as temperature increases. Thus, we expect kittiwakes to be more vulnerable to the indirect effects of climate change. In the second chapter, we will take a closer look at the thick-billed murre’s physiological response to varying environmental conditions, more specifically examining incidences of heat stress at the colony. As murres have very low heat tolerance (Choy et al., 2021), we expect that this species is likely to be impacted heavily by the direct effects of climate change via warming temperatures.

Note on chapter 2

This chapter corresponds to a manuscript titled “Dealing with the heat: assessing heat stress in an Arctic seabird using 3D printing” that will be sent for publication shortly. This chapter was made in collaboration with Dr Ryan O’Connor (University of Windsor), David Fifield (ECCC), Dr Glenn Tattersall (Brock University), Dr Francois Vézina (Université du Québec à Rimouski), Dr Oliver Love (University of Windsor), Dr. Anna Hargreaves (McGill University), and both of my supervisors, Dr Kyle Elliott and Dr Emily Choy.

Chapter 2

Dealing with the heat: assessing heat stress in an Arctic seabird using 3D printing

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Abstract

Effects of climate change on Arctic endotherms have focussed primarily on indirect (food web) effects, yet because Arctic animals often have low heat dissipation capacity, the direct effect of warming (overheating) may impact strongly on them. We used 3D printing, infrared imagery and surface temperature loggers, to develop 3D printed biophysical models to assess thick-billed murres' (*Uria lomvia*) operative temperature (integrated temperature of the thermal environment as perceived by an individual) near their southern range limit at Coats Island, Nunavut, Canada. At this sub-Arctic colony, murre models experience operative temperatures above 21.2 °C, the temperature in which they increase evaporative water loss rates, on 61% of the days on average (range : 24 – 85%) with their operative temperatures ranging from 5.5 °C to 46.5 °C even though ambient temperatures never exceed 23.8 °C. Exposure to heat stress was not uniform across the colony. Murres experienced daily evaporative water loss ranging from 3.79 % to 4.61 % of body mass with EWL rates ranging from 1.29 g h^{-1} to 2.18 g h^{-1}, with smaller individuals experiencing high rates of evaporative water loss per hour. Overall, measures of operative temperature were consistently higher than ambient temperature, highlighting the need to consider operative temperature when studying heat stress. Biophysical models are valuable and non-invasive tools to study the effects of heat stress, and can help predict how animals will react to Arctic warming.

Introduction

The Arctic is warming at twice the global average rate, affecting many basic ecological processes (Dobson et al., 2015, Post et al., 2009). With the projected increase in temperature, many studies have shown that Arctic and sub-Arctic animals are experiencing strong indirect effects (changes in species interactions). However, few studies have documented direct effects (changes in metabolic processes) of climate change, perhaps because Arctic temperatures are typically low and, consequently, it is thought that wildlife should be able to cope with such temperatures. Arctic animals are well adapted to withstand extreme cold temperatures due to their capacity to minimize heat loss, but in a warming environment, their limited capacity to dissipate heat can impact on their survival (Oswald and Arnold, 2012). Nonetheless, the indirect effects of climate change on Arctic wildlife have been well documented, including phenological mismatches, shifts in species range, increased parasitism, and more (Iverson et al., 2014, Mellard et al., 2022, Oswald and Arnold 2012, Gallant et al., 2012). Unfortunately, the direct effects of climate change (i.e.: heat stress) on an individual's physiology have received little attention, especially for Arctic species that are assumed to live in environments where they are seldom heat-stressed (Choy et al., 2021, O'Connor et al., 2022, Oswald and Arnold, 2012) and the quality of the data currently available is poor (McKechnie et al., 2017, Boyles et al., 2019). Yet, direct effects have the potential of affecting Arctic wildlife at a much faster rate than indirect effects (O'Connor et al., 2022, Choy et al., 2021).

In seabirds, the breeding season typically corresponds with higher ambient temperatures, especially Polar Regions where birds are exposed to long periods of sunlight. Being endotherms, birds maintain a constant body temperature and use an array of strategies to retain or evacuate heat to remain in their thermoneutral zone, where metabolic costs of thermoregulation are minimal (Scholander et al., 1950). As stated by the heat dissipation limit theory, endotherm's energy output is limited by their capacity to dissipate heat resulting from their metabolism (McKechnie et al., 2021, Speakman and Krol, 2010). Thus, evaporative heat dissipation is essential to tolerate high ambient temperatures in a warming environment. Yet, heat dissipation capacity can result in trade-offs between thermoregulation and other breeding functions, and ultimately can lead to decreased reproductive success (Tapper et al., 2020, Conradie et al., 2019, Oswald and Arnold, 2012, Cook et al., 2020). Cliff-nesting seabirds with little protection from the sun are particularly susceptible to heat stress due to high heat gain with the environment, and regularly experience operative temperatures much higher than air temperatures (Schreiber and Burger, 2001). Moreover, insulation and other physiological adaptations to limit heat loss to cold water is likely to be in evolutionary conflict with adaptations to dissipate heat at nest sites (Oswald and Arnold, 2012; Cook et al., 2020).

While studies on the capacity of Arctic seabirds to tolerate extreme cold are available (Scholander et al., 1950), very limited information is available on their capacity to tolerate heat (Oswald and Arnold, 2012). The thick-billed murre (*Uria lomvia,* hereafter: murre) is a widespread Arctic seabird that nests on cliffs where both adults care for their offspring. During the day, males will incubate the nests for 12h while the female forages, until the female returns to incubate for the night (Gaston and Hipfner, 2020). As murres are diving seabirds, they meet an array of thermal conditions, including the warm sun on their black plumage to the glacial waters where they forage. Murres experience heat stress - a sudden change in evaporative water loss rate - at temperatures as low as 21.2 ºC and have the lowest maximum evaporative cooling efficiency ever measured in birds, presumably reflecting their adaptation to frigid waters (Choy et al. 2021). At temperature of 21.2 °C and above, murres' rate of evaporative water loss (EWL) increases significantly, with higher evaporative water loss rates in smaller individuals (Choy et al., 2021). In the field, mortality in murres has been reported on days with ambient temperature as low as 22 °C due to acute dehydration (Gaston et al., 2002). These results highlight the need for further research on climate change-induced heat stress that murres experience at the colony during the breeding season.

To study heat stress, biophysical models have been used in an array of ectothermic species, and a few endothermic ones as well. Biophysical models are used to assess operative temperature, also defined as the integrated temperature of an environment as perceived by an individual (Bakken, 1976). Operative temperature measured using biophysical models yields a single estimate of temperature that considers the various pathways of heat exchange: convection, conduction, and radiation (Bakken, 1976). Biophysical models must reproduce as accurately as possible a given specimen in terms of the size, shape and colouration to capture the thermal conditions experienced by said specimens (Bakken, 1976, Shine and Kearney, 2001).

As demonstrated by Choy et al. (2021), murres experience heat stress at temperature equal or above 21.2 ºC, but said experiment was conducted under controlled conditions where air temperature equals operative temperature. However, Gaston et al. (2002) found that the black backs of murres could reach temperatures as high as 47 ºC when exposed to full sun with air temperatures as low as 22 ºC, therefore highlighting the importance of studying heat stress of nesting murres in their various microhabitats. Here, we aim to assess incidences of heat stress in thick-billed murres using biophysical models to quantify evaporative water loss while at different colony locations. If murres experience heat stress at the colony, then we predict that the rate evaporative water loss should start increasing at ambient temperature below 21.2 ºC.

Methods

Experimental design

We 3D printed biophysical models to assess the operative temperature of breeding murres. Following rigorous material testing (Appendix 1), we 3D printed our models in polyethylene terephthalate glycol (hereafter PETG; black 1.75 mm PETG filaments from DURAMIC 3D, product # 612677937130) with a wall thickness of 3.2 mm (see Appendix 1). Using freshly dead murres, we measured the spectral reflectance of the white plumage (ventral plumage) and of the black plumage (dorsal plumage, head feathers, and wing coverts) using a hand-held photo spectrometer (Ocean Optics^{TM} Red Tide USB 650) connected to a light source (tungsten–halogen, Ocean Optics^{TM} LS-1). To represent murre colouration as accurately as possible, we painted the models based on our measurements of the spectral reflectance of the murre plumage, and painted the models using Benjamin Moore outdoor paint in colours HC-190 and AC- 195, as their light reflectance values (LVR = 2.48 and LVR = 52.76 respectively) matched the black and the white feathers' reflectance (r = 1.52 ± 1.24 % and r = 47.49 ± 9.60% respectively). To compare against the painted models, we also fitted a subset of models with skin and feathers from dead murres. We mounted the murre skin over the models so that only the bill, legs and base of the models were not covered.

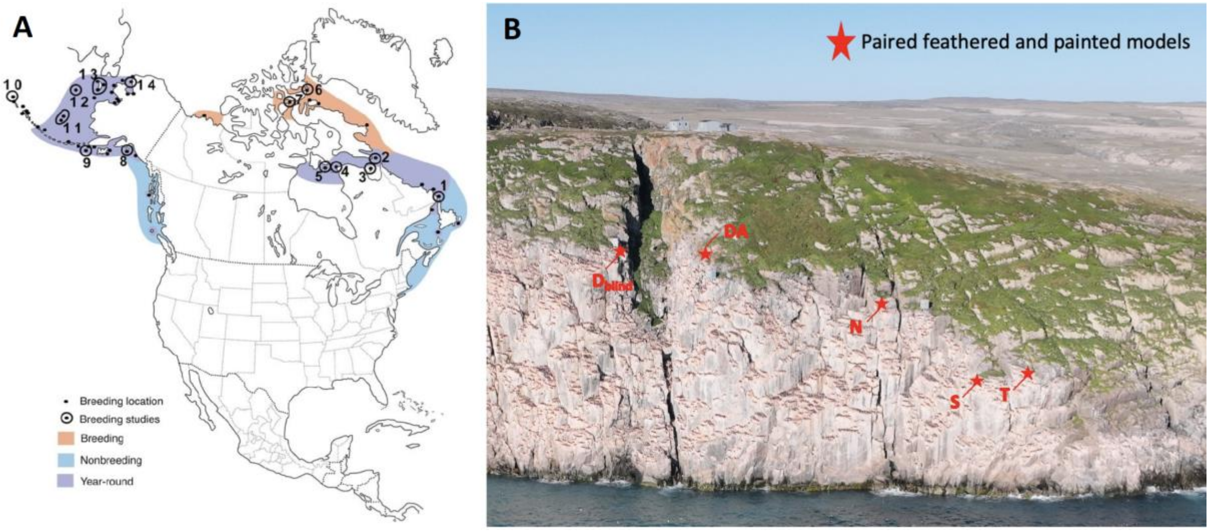


Figure 2.1: A) Range of Thick-billed murre where Coats Island colony corresponds to the breeding study site #5. Map adapted from Bird of the World (Gaston and Hipfner, 2020). **B)** Biophysical models deployed in colony on Coats Island (n = 5 painted and 5 feathered models). Plot names are indicated by the letters linked to the stars, where red stars denote sites where we deployed both a painted and a feathered model.

To investigate incidences of heat stress in breeding murres, we quantified the operative temperatures experienced by murre models on Coats Island (62°35′N 082°45′W), Nunavut, at five locations (Figure 2.1) representing the range of environments occupied by breeding murres near the upper edge of the colony where heat stress is predicted to be the greatest (Gaston and Elliott, 2013) between 10 July and 7 August 2022. For each location, we deployed a painted and a feathered model together to enable us to compare the performance of both models, and ultimately validate the use of the painted models for murres. Coats Island hosts 30,000 breeding pairs of murres which are located at the southern end of the species' range, and therefore, are exposed to warmer temperatures than at higher latitudes. Using our measurements of operative temperature, we also predicted evaporative water loss in murres subjected to varying environmental conditions across difference microclimates throughout the breeding season.

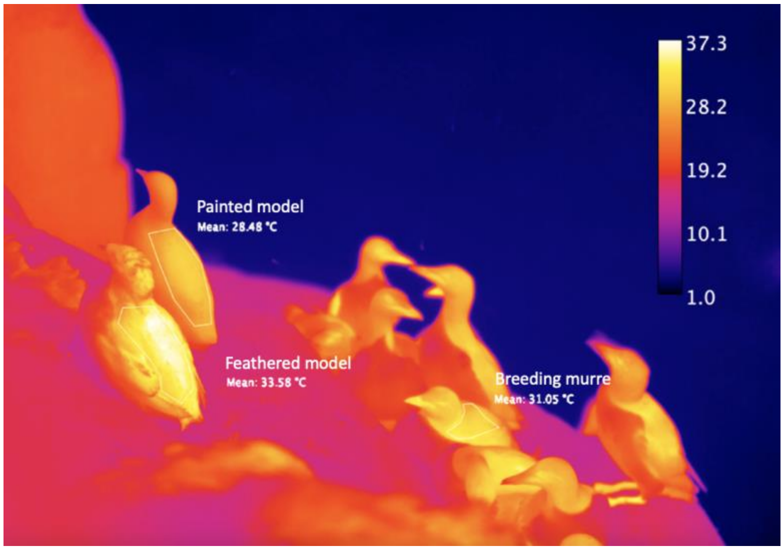


Figure 2.2: Example thermal image of biophysical models and murres in the colony. For each model and murres where at least 1/3 of the back is visible, the back area is indicated by the white perimeter with associated mean back temperature to the right.

We did not obtain data from 14 July to 18 July at one of our colony locations (D blind) as the models were blown into the sea during a storm. Additionally, we did not obtain data from 26 July to 31 July at two colony locations (D blind and T) and from 1 July to 7 July at one colony location (S) due to iButton malfunction.

Measurements of back temperature

We captured infrared images of breeding murres and models using a FLIR T1030sc camera and the telephoto lens with a focal length of 83.4 mm (12°; IFOV of 0.20 mrad.). We captured images regularly but on an opportunistic basis to capture weather variation (every two to five days from 12 July to 27 July 2022). For each image, we recorded ambient temperature (°C), and relative humidity (%) using a Kestrel 0830 portable weather station (Kestrel Meter; Boothwyn, PA). We also estimated reflected temperature (°C) by capturing a thermal image of a crumpled ball of aluminum lying on the colony ground facing the sky (FLIR system, 2010). Due to technical challenges that come with working on sheer cliffs, we estimated, rather than measured, the distance (m) between the camera's lens and the object of the photo. To ensure reproducibility, all distances were estimated by the same person (Playa-Montmany and Tattersall, 2021).

We analyzed all images using ThermImage J functions (Tattersall, 2019) in FIJI (Schindelin et al., 2012). We compared back temperature of feathered and painted models compared to murre's back temperature (N = 44 images). We extracted mean back temperature, where the back area is defined as the area of black feathers starting at the base of the neck to the base of the tail, and delimited on both sides by the

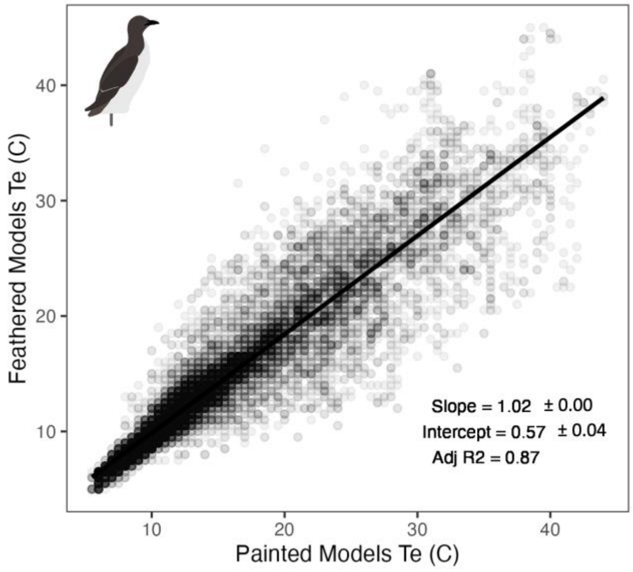


Figure 2.3: Raw operative temperature from painted models compared to feathered models.

wings, excluding upper wing coverts (Figure 2.2). As the painted models do not have a strict body feathers/wing delimitation, we estimated the delimitation while ensuring that only the black area was included. To test for differences in the back reflectance between two model types and the actual murre's plumage, we used a mixed effect model using the *lme4* package (Watson and Francis, 2015) in RStudio 4.2.1 (R Core Team, 2022). We used back temperature as a dependent variable and added model type, cloud cover, ambient temperature (T_a) and reflected temperature (T_r) as fixed effect, with colony location (plot) as a random effect (see eq. 2.1).

$$\text{Back Temp.} = T_a * \text{Cloud Cover} + T_r * \text{Cloud Cover} + \text{Model Type} + (1|\text{Plot}) \qquad (\text{eq. } 2.\mathbf{1})$$

Measurements of operative temperature

We obtained estimates of operative temperature from the biophysical models, where we fitted an iButton inside the body cavity of each model to record temperature at an interval of 10 minutes with a precision of 0.5 °C (models DL1925L-F5 and DL1921G-F5).To validate the use of the painted models compared to the feathered models, we compared operative temperature measurements between them at the six colony locations. We first conducted a two-tailed Welsh t-test on RStudio 4.2.1 (R Core Team, 2022) to test for differences between the models. We then corrected the operative temperature values from the painted model using a linear regression (Figure 2.3) between the two models' operative temperatures:

$$T_{e\text{-}paint\_corr} = T_{e\text{-}paint\_raw} *1.02 +0.57 \quad (\text{eq. } 2.2).$$

where $T_{e\text{-}paint\_corr}$ corresponds to the corrected values on T_e and $T_{e\text{-}paint\_raw}$ corresponds to the raw T_e measured by the painted models.

Evaporative water loss

To estimate evaporative water loss (EWL, in g h^{-1}) in murres at the Coats Island colony, we used equations of EWL as a function of temperature (equation 2.3) published by Choy et al. (2021),

$$EWL = T_e * 0.14 + Mb * 0.00363 - (T_e * M_b * + 0.000126) - 2.4 \qquad \text{if } T > 21.2°\text{C (eq. 2.3)}$$

$$EWL = M_b * 0.0015 + 0.0876 \qquad \text{if } T < 21.2°\text{C (eq. 2.4)}$$

where M_b corresponds to body mass and T corresponds to either operative or ambient temperature. For operative temperature and ambient temperature above or equal to the inflection point of 21.2 °C, we used *equation 2.3* and used *equation 2.4* for all other values of operative temperature (< 21.2 °C). As Choy et al. (2021) reported a significant difference in rate of EWL based on masses below and above 900 g, we calculated EWL for a murre of 800 g, 900 g and 1000 g to capture a wide range of body masses. We also calculated EWL as a proportion of body mass (in %) loss per day murres of 800 g and 1000 g based on the hourly rate of EWL, from midnight to midnight.

Results

Measurements of back temperature

We validated the reflectance of both the feathered and painted model's colouration using infrared thermography. Results from our mixed effect model (Equation 2.1) showed that back temperature was mainly predicted by cloud cover (t_{34}=6.88, p = 0.002), ambient temperature (t_{109}=-3.04, p = 0.003) and an interactive effect between cloud cover and ambient temperature (t_{108}= 3.72 p = 0.0006), and cloud cover and reflected temperature (t_{106}= -3.51, p = 0.0003). Back type (feathered, painted and breeding murre) was not a predictor of back temperature as both feathered (t_{105}= -0.52, p = 0.61) and painted (t_{105}= -1.45, p = 0.15) models' back temperature were comparable to murre's back temperature (Figure 2.4). Reflected temperature on its own was not a strong predictor of back temperature either (t_{109}=1.31, p = 0.19).

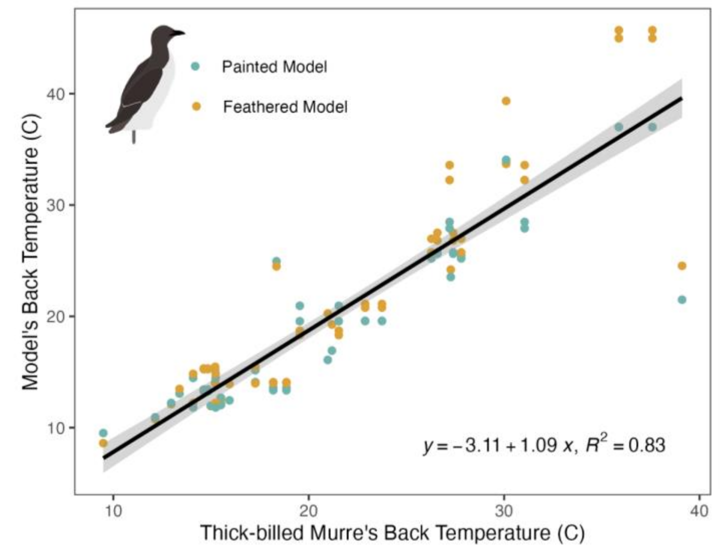


Figure 2.4: Back temperature biophysical models (blue = painted models and tan = feathered models) compared to murres' back temperature.

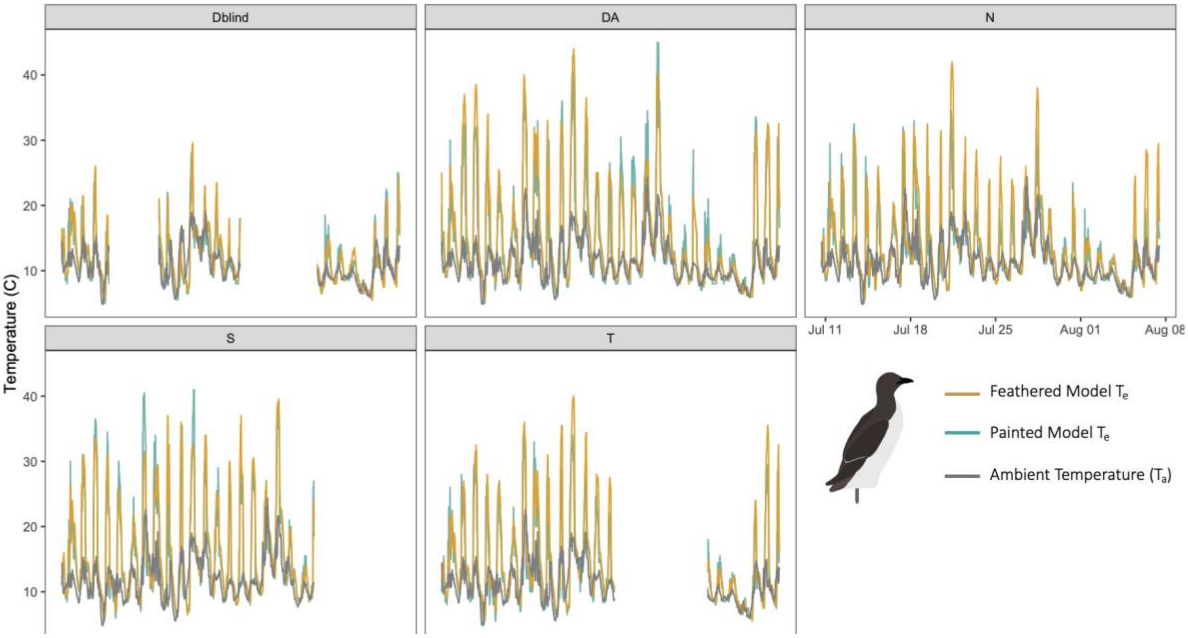
Table 2.1: Minimum, maximum and mean operative temperature, and % of days murres experienced heat stress at different colony locations.

	Min T_e (℃)		Max T_e (℃)		Mean T_e ± SD (℃)		$T_e > 21.2$ ℃ (% Days)
Plot	Day	Night	Day	Night	Day	Night	
D blind	5.5	6.0	29.5	15.4	13.1 ± 4.3	9.25 ± 1.8	0.24
DA	5.5	6.0	46.5	17.0	17.2 ± 8.2	10.1 ± 2.1	0.72
N	5.5	6.0	42.0	17.0	14.9 ± 6.0	10.0 ± 2.0	0.59
S	6.0	6.5	42.4	17.5	17.9 ± 7.7	10.5 ± 2.1	0.86
T	5.5	6.0	40.0	15.4	16.5 ± 7.1	9.7 ± 1.7	0.65
Colony Avg	5.5	6.0	46.5	17.5	16.1 ± 7.1	9.9 ± 2.0	0.612

Operative temperature

We recorded a total of 36 876 measurements of operative temperature between 10 July and 7 August 2022 among five different colony locations (Figure 2.5). Operative temperature ranged between 5.5 °C and 46.5 °C, with an average of 16.1 ± 7.1 °C during the day, and 9.9 ± 2.0 °C at night (Table 2.1). Murres experienced heat stress on average on 61% of the days we recorded operative temperature, but exposure to heat stress varied among colony locations as daily exposition ranged between 24% to 86 % (Table 2.1). We also observed variation in diurnal operative temperature based on different colony locations, with models deployed at D blind never getting warmer than 29.5 °C while all other colony locations recorded temperatures above 40 °C, with a maximum of 46.5 °C recorded at DA (Table 2.1, Figure 2.5).

Figure 2.5: Operative temperature from feathered models (tan) and painted models (blue) compared to ambient temperature (grey) over the length on the model deployment, starting on July 11th to August 8th, where each panel represents a different colony location.



Evaporative water loss

The rate of EWL (g h^{-1}) experienced by murres at the colony (predicted by estimates of operative temperature) is greater than what ambient temperature predicted (respectively 1.29-2.18 g h^{-1} and 1.29-1.44 g h^{-1}; Figure 2.6; Table 2.2). Murre's average daily maximum EWL rate (g h^{-1}) ranged between 1.32 ± 0.08 g h^{-1} for a small individual at D blind and 1.65 ± 0.06 g h^{-1} for a large individual at Plot S (Table 2.2). Similarly, we found that murres experienced greater maximum and mean daily EWL (% M_b; predicted by estimates of operative temperature) than what ambient temperature predicted (Table 2.2, Figure 2.7). Murre with a smaller body size were more likely to experience greater maximum and mean daily EWL, compared to murres of a larger body size, at all colony sites (Table 2.2). We also observed variation in daily EWL among different sites, where spatial variation in EWL was amplified in individuals with a lower body mass (Table 2.2). Mean daily EWL across sites ranged from 3.88 to 4.07% of M_b for small individuals whereas mean daily EWL only ranged from 3.80 to 3.83% of M_b for larger individuals (Table 2.2).

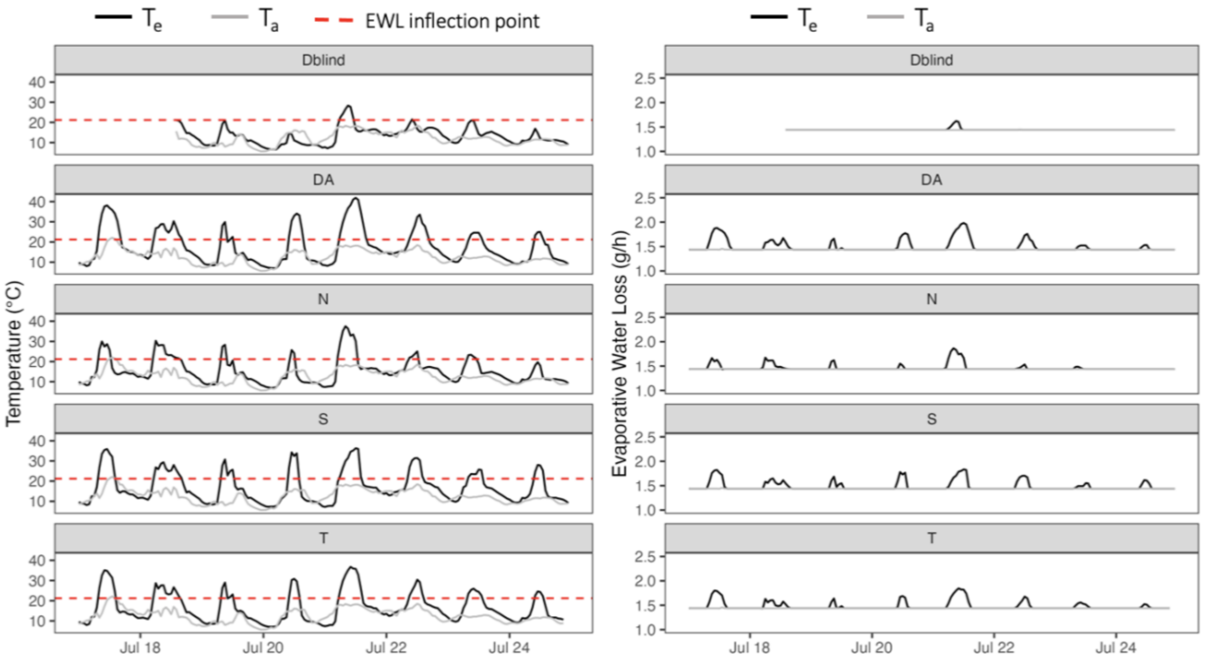


Figure 2.6: Comparison of **a)** operative temperature (T_e; black line) and ambient temperature (T_a ; grey line) where the red dashed line denotes the EWL inflection point for thick-billed murres at 21.2 °C (Choy et al., 2021), and **b)** associated evaporative water loss (EWL) for a murre of 900 g estimated using operative temperature (T_e; black line) and ambient temperature (T_a; grey line) at various colony locations.

Table 2.2: Maximum and average daily maximum EWL rate (g h^{-1}), maximum and mean daily EWL (% M_b), and mean difference in mean daily EWL calculated using operative temperature (T_e) at different colony locations compared to daily EWL calculated from ambient temperature (T_a).

	Max EWL Rate (g h^{-1})		**Avg Daily Max EWL Rate ± SD** (g h^{-1})		**Max Daily EWL** (% M_b)		**Mean Daily EWL ± SD** (% M_b)		**Mean difference $T_e \sim T_a$** (Mean Daily EWL in % M_b (*p-value*))	
Plot	M_b= 800 g	M_b= 1000 g	M_b= 800 g	M_b= 1000 g	M_b = 800g	M_b = 1000g	M_b = 800g	M_b = 1000g	M_b = 800g	M_b = 1000g
D blind	1.62	1.63	1.32 ± 0.08	1.59 ± 0.01	4.02	3.81	3.88 ± 0.04	3.80 ± 0.00	0.01 (p = 0.19)	0.00 (p = 0.08)
DA	2.18	1.83	1.59 ± 0.27	1.64 ± 0.07	4.61	3.94	4.03 ± 0.32	3.83 ± 0.04	0.25 (**p < 0.0001**)	0.02 (**p = 0.02**)
N	1.98	1.76	1.44 ± 0.18	1.61 ± 0.04	4.34	3.89	3.94 ± 0.12	3.81 ± 0.01	0.07 (**p = 0.003**)	0.00 (p = 0.84)
S	2.03	1.77	1.63 ± 0.22	1.65 ± 0.06	4.46	3.87	4.07 ± 0.16	3.83 ± 0.03	0.22 (**p < 0.0001**)	0.02 (**p = 0.01**)
T	1.95	1.75	1.52 ± 0.21	1.62 ± 0.05	4.41	3.90	4.01 ± 0.15	3.82 ± 0.03	0.15 (**p = 0.0004**)	0.01 (p = 0.20)
Colony Avg (T_e)	2.18	1.83	1.51 ± 0.23	1.62 ± 0.06	4.61	3.94	4.00 ± 0.17	3.82 ± 0.03	0.14 (***p < 0.0001***)	0.01 (***p = 0.0007***)
Colony Avg (T_a)	1.44	1.44	1.30 ± 0.03	1.29 ± 0.03	3.89	3.81	3.84 ± 0.14	3.79 ± 0.14	—	—

Discussion

Here, we have shown that in a year of relatively mild conditions (no mortality observed), males sitting on the nest on an exposed site could lose up to 4.07% of their body mass on a hot day. Given that mortality can occur when birds lose 15% of their body mass (25% of body water) due to dehydration (Albright et al., 2017, Conradie et al., 2019), the loss of a third of their body water due to heat stress could have serious consequences on an individual's fitness. Coupled with high water loss due to mosquitoes (Gaston and Elliott 2013), this can explain the high mortality previously reported in warm years (Gaston et al. 2002).

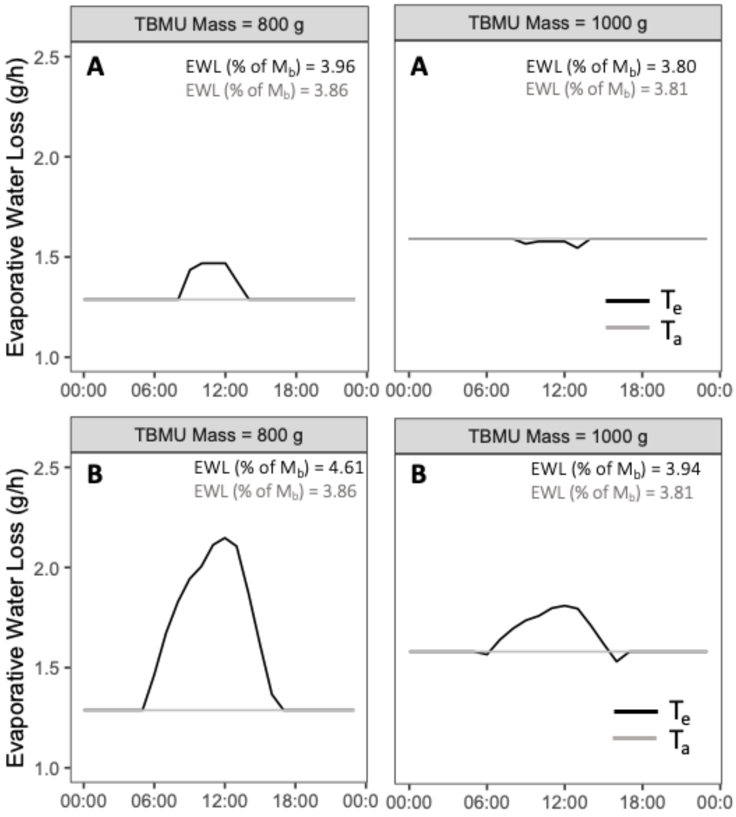


Figure 2.7: Evaporative water loss of murres on a day with A) low maximum operative temperature (T_e max = 24.6 °C) and B) high operative temperature (T_e max = 41.9 °C) calculated using operative temperature (black) and ambient temperature (grey).

Using measurements of operative temperature from our biophysical models, we investigated heat stress experienced by murres at the Coats Island colony during the breeding season. We validated the use of our 3D printed models to measure operative temperature in murres, laying the path for more affordable and easily produced biophysical models for large seabirds. Moreover, thanks to infrared imagery, our paper is the first to validate the use of painted biophysical models in the field for endotherms.

Our measurements of operative temperature highlight the difference between operative temperature and ambient temperature, as operative temperature was consistently higher than ambient temperature (Figure 2.6). Under experimental conditions, where conduction, convection and radiation can be controlled for, ambient temperature often equals operative temperature (Shine and Kearney, 2001), but in the field such assumption does not hold true (Bakken, 1976, O’Connor et al., 2018, O'Connor et al., 2022, Shine and Kearney, 2001). Cliff nesting seabirds such as murres are exposed to radiation from the sun for long periods, with no access to thermal refuge while attending their nest (Gaston and Hipfner, 2020). Under such conditions, our results showed that operative temperature can increase far past ambient temperature, thus, highlighting the importance of considering operative temperature. When investigating heat stress in endotherms, relying on ambient temperature is likely to underestimate the extent of heat stress experienced by Arctic animals.

Exposure to heat stress varies with time of day at the colony, likely leading to differential impacts of heat stress on murre’s population demographics. Murres experienced an increased rate of evaporative water loss during the day, and low rates of evaporative water loss at night. As males attend the nest during the day and females attend at night (Elliott et al., 2010), the direct effects of heat stress are likely to impact males more strongly over time than females as thermal refugia cannot be used while attending the nest. Moreover, it has been shown that older murres are less likely to abandon the nest even when under acute dehydration, resulting in a disproportionate representation of old murre in mortality at the colony (Gaston and Elliott, 2013). As the male exclusively tends the chick at sea for ~37 days post-departure, loss of experienced males may have a disproportionate impact on demography (Gaston and Elliott 2013). At other colonies, where females brood during the day (Elliott et al. 2010), the impact may be less.

In birds, the lethal dehydration limit corresponds to approximately 15% of body mass in desert birds (Albright et al., 2017, Conradie et al., 2019). Although we did not report daily evaporative water loss above or near the lethal dehydration limit (maximum 4.07 % of M_b), sub-lethal effects of dehydration should not be neglected. In bank cormorants (*Phalacrocorax neglectus*), behavioural adjustments at the nest due to heat stress lead to exposure of eggs and chicks to sub-optimal conditions and increased predation risk, ultimately leading to reduction in breeding success (Cook et al., 2020). Conradie et al. (2019) projected greater impacts of sublethal effects of heat than lethal effects on arid African bird conservation even with evaporative water loss as low as ~4% of body mass. Although we reported daily EWL that accounted only for ~1/3 of the known lethal dehydration limit for birds, our estimates did not account for other sources of dehydration. In murres, mortality at the colony has been observed under warm (>18 °C) conditions coupled with high mosquito density (Gaston et al., 2002, Gaston and Elliott, 2013). Necropsies of the deceased individuals clearly reported acute dehydration as the cause of death, likely due to the paired effects of heat stress and mosquito parasitism (Gaston and Elliott, 2013, Gaston et al., 2002).

To conclude, our paper highlighted the physiological challenges faced by Arctic seabirds during the breeding season when faced with a warming climate. Although indirect effects (changing prey base, increased predation and parasitism) are known to impact murre demography, the role of direct heat stress in rapid declines of this species at their southern range limit cannot be ignored. Understanding the thermal physiology and the various factors that influence an individual's capacity to thermoregulate can shed light on the challenges that these individuals face as the climate warms. Despite the fact that we cannot control the increase in ambient temperature, we can consider the various paths of heat exchange that influence operative temperature to develop better conservation plans (i.e., preserving habitats that provide shade to act as thermal refuge (Elmore et al., 2017)). A shift in conservation practices is needed as we could benefit from considering microhabitat in addition to large conservation areas. Nonetheless, the thermal physiology of Arctic species remains vastly understudied, and more research in this field is required to properly assess how Arctic fauna will be impacted directly by climate change.

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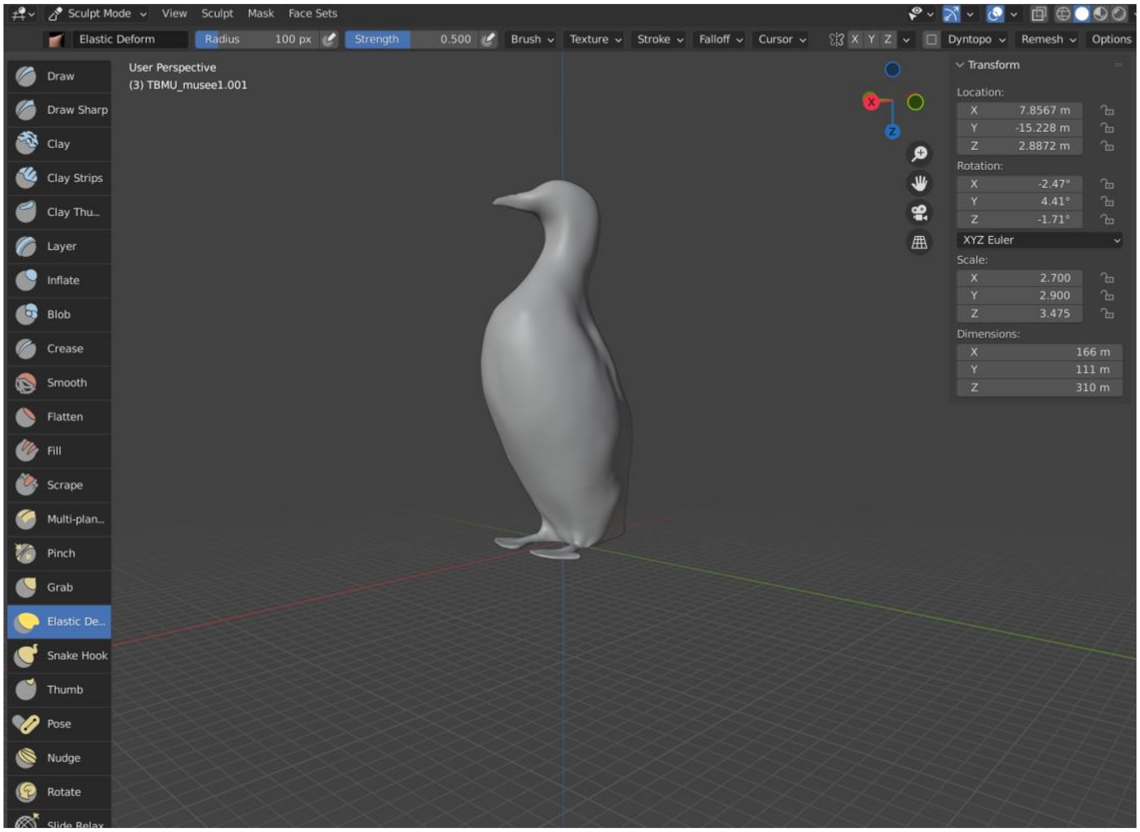
Appendix 1: biophysical model construction

Methods

Model design

To assess operative temperature in thick-billed murres, we used 3D printed biophysical models. To build our model, we first scanned a naturalized murre using the Qlone application (EyeCue Vision Technologies). We then imported the scan as a .stl file into Blender 2.8 (Community, 2018), a free 3D sculpting program to correct any imperfections, and manually add body parts that had not been captured in the original scan such as legs and feet (Figure S2.1). Once shaped properly, we imported the model in Ultimaker Cura (UltiMaker BV 2022), a 3D printing curator, to scale the model properly and slice the 3D model into a prinTable mesh.



Radius 100 px
Strength 0.500

User Perspective
(3) TBMU_musee1.001

Location:
X 7.8567 m
Y -15.228 m
Z 2.8872 m

Rotation:
X -2.47°
Y 4.41°
Z -1.71°
XYZ Euler

Scale:
X 2.700
Y 2.900
Z 3.475

Dimensions:
X 166 m
Y 111 m
Z 310 m

Figure S2.1: Shapefile created on Blender 2.8 used for 3D printing thick-billed murres.

As 3D printed biophysical models of this size have not been reported in the literature to our knowledge, the printing characteristics were unknown. Thus, to select the appropriate printing material and wall thickness, we originally printed four models in acrylonitrile butadiene styrene, (hereafter ABS; black, 1.75 mm ABS filament from OVERTURE, product # 810031292905) with different wall thicknesses (Table S2.1). Although ABS has been used in previous 3D model studies, we also printed two additional models in polyethylene terephthalate glycol (hereafter PETG; black 1.75 mm PETG filaments from DURAMIC 3D, product # 612677937130) with different thicknesses (Table S2.1) as PETG is easier to print, present similar properties than ABS, is less costly and has been found to be much more environmentally friendly than ABS (Kumar et al., 2022). To compare both 3D printing materials (ABS and PETG) to the traditional copper models, we also printed two standard cylinders with exact same dimensions and thickness as a copper cylinder we had on hand.

Table S2.1: Wall thickness of experimental models printed

Material	Thickness
ABS	2.4 mm
ABS	3.2 mm
ABS	4.0 mm
ABS	4.8 mm
PETG	3.2 mm
PETG	4.0 mm

Material testing

To test for model properties, we placed all six murres models and three standard cylinders (see Table S2.1) in a controlled dark chamber and subjected them to changing temperatures (Figure S2.2). All models and cylinders were completely sealed. We recorded the temperature inside the models using two iButtons (model DS1921-F5) placed in the thinnest and thickest part of the model, and one central iButton (model DS1921-F5) inside the standard cylinders. We also placed three additional iButtons suspended in air using small 3D printed supports to record ambient temperature inside the chamber. We then selected the best model based on three criteria: material heat transfer capacity, uniformity of temperature inside the model, and responsiveness to changes in temperature, where the best model has both a uniform temperature and reaches equilibrium with room temperature quickly.

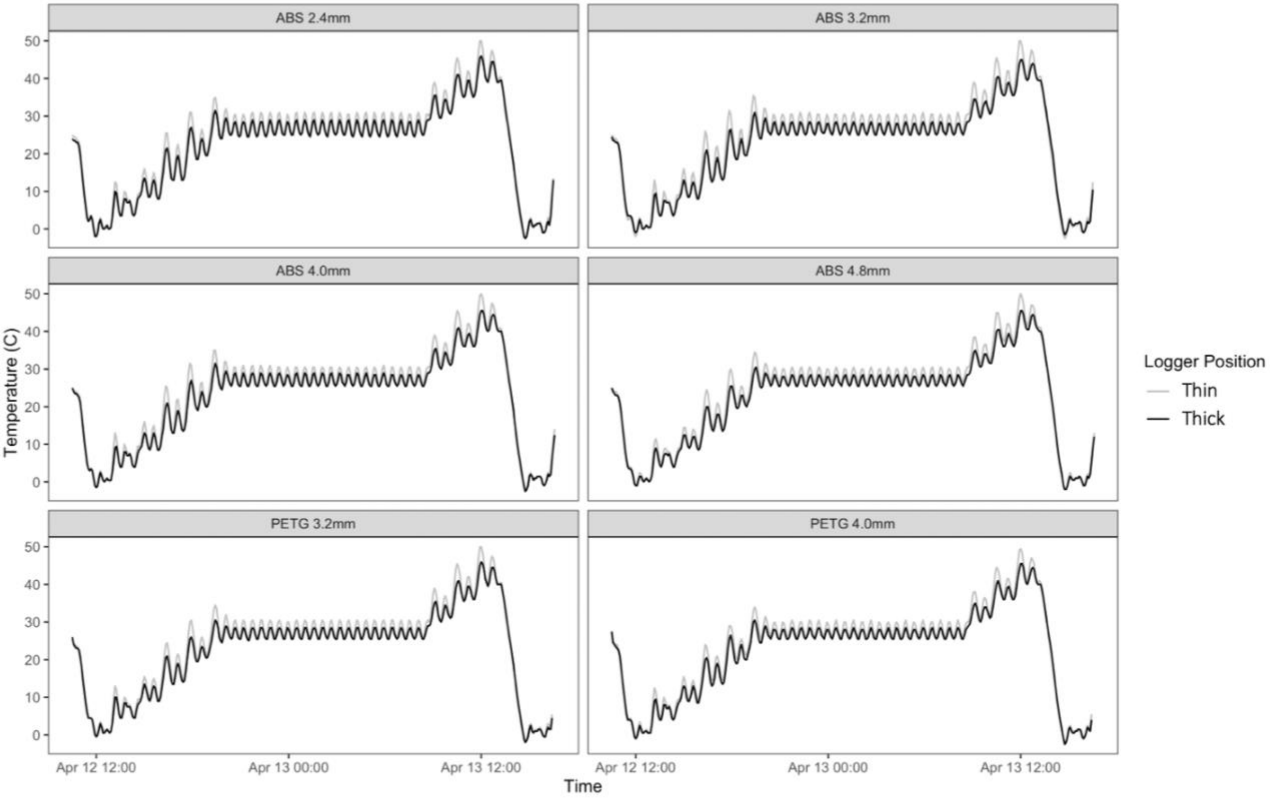


Figure S2.2: Temperature changes recorded by the iButtons inside the various 3D printed models while inside the controlled dark chamber. The two lines in each panel represent the high button positioned inside the thin part of the model (grey) and thicker part of the model (black).

To test for material heat transfer capacities, we placed all three standard cylinders (Copper, ABS and PETG) inside a controlled dark chamber and subjected them to changing temperatures. Even though the use of ABS to construct 3D printed biophysical model has already been validated (Watson and Francis, 2015, O'Connor et al., 2018), we conducted a paired t-test to compare PETG to copper and ABS to copper. To test for model uniformity, we extracted temperature from the logger inside the models (placed at a low and high point inside the model) and conducted a paired t-test between the two loggers. To test for responsiveness, we modelled our model's average temperature against average room temperature and compared slope and adjusted R^2. We conducted all analyses mentioned above in RStudio 4.2.1 (R Core Team, 2022).

Model colouration

To represent murre colouration as accurately as possible, we painted the models based on our measurements of the spectral reflectance of the murre plumage. Using a freshly naturalized murre, we measured the spectral reflectance of the white plumage (ventral plumage) and of the black plumage (dorsal plumage, head feathers, and wing coverts) using a hand-held photo spectrometer. We used the Benjamin Moore outdoor paint in colours HC-190 and AC- 195 as their light reflectance values (LVR = 2.48 and LVR = 52.76 respectively) matched the black and the white feathers' reflectance (r = 1.52 ± 1.24 % and r = 47.49 ± 9.60% respectively; Figure S2.3).

To compare against the painted models, we also fitted a subset of models with thick-billed murre skin and feathers from murres shot by hunters as part of a subsistence hunt in Newfoundland, and which were provided by the Canadian Wildlife Service. We mounted the murre skin over the models in a way that only the bill, legs and bottom surface of the models were not covered (Figure S2.3).

Figure S2.3: Final models, with the feathered models in the front on the left and the back row.

Results

Material testing

The PETG cylinder performed similarly to the ABS and the copper cylinder. Under dark conditions in a controlled chamber, all three cylinders responded closely to changes in ambient temperature, with the copper cylinder responding the least with a slope of 0.98 ± 0.01, followed by the ABS cylinder with a slope of 0.99 ± 0.02 and the PETG cylinder with a slope of 1.00 ± 0.01 (Figure S2.4). Statistically, we found that the PETG cylinder performed differently than the copper cylinder ($t(358) = -13.16$, $p < 0.0001$) with a sample mean difference of - 0.51 °C, and so did the ABS ($t(358) = 9.28$, $p < 0.0001$) with a sample mean difference of 0.77 °C,. However, we did not reject the use of PETG as the use of ABS has been validated already, and the sample mean difference between the PETG and copper cylinder is smaller than the difference between the ABS and the copper cylinder.

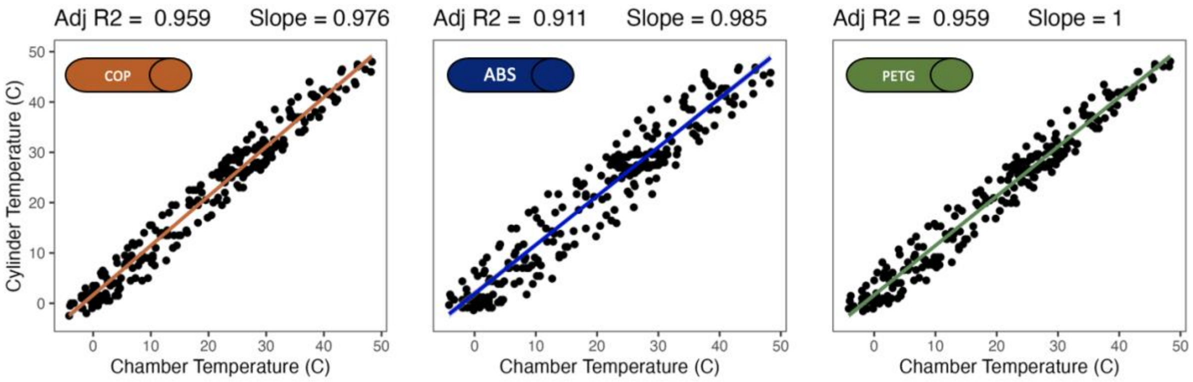


Figure S2.4: Internal temperature of the cylinders based on chamber temperature under dark conditions.

Model uniformity

Sample mean difference in temperature between the loggers within a model ranged between 1.27 °C in the 2.4mm ABS model, and 1.47 °C in the 4.8mm ABS model, with the PETG models falling in between the ABS models with a sample mean difference of 1.30 °C and 1.31 °C for the 3.2mm and 4.0 mm respectively (Figure S2.2). As the difference between the models' sample mean difference is lower than the iButtons' resolution (0.5 °C), we did not accept nor reject a model based on uniformity.

Model responsiveness

Models responded highly to changes in room temperature, with slope ranging from 0.96 ± 0.02 for the 4.8mm ABS model, to 0.99 ± 0.02 for the 3.2mm PETG model (Figure S2.5). As model responsiveness was highest in the 3.2mm PETG model (Figure S2.5), and its model uniformity was good (second most uniform model), we selected this model for the continuity of our experiment.

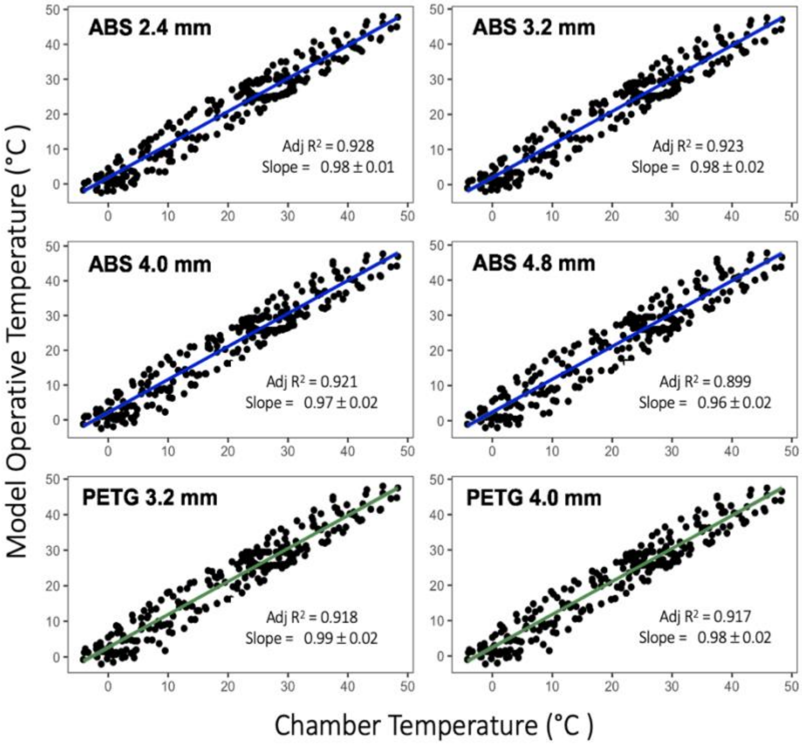


Figure S2.5: Plot of various models' operative temperature based on chamber temperature where models varied both in thicknesses (2.4 mm, 3.2 mm, 4.0 mm and 4.8 mm) and printing materials (ABS in blue and PETG in green).

General discussion

The aim of this thesis was to advance knowledge on physiological costs of climate change on Arctic seabirds. Using two species with different natural histories, I showed that kittiwakes and murres are likely to be significantly impacted by climate change.

In the first chapter, I showed that kittiwake energetic expenditure can be predicted by their activity budget, and obtained activity-specific metabolic rates for five important behavioural classes. We showed that flapping flight is the costliest behaviour, likely providing a mechanistic explanation as to why kittiwakes tend to do poorly in warm years, when they forage at greater distances (Osborne et al. 2020).

In the second chapter, we investigated the incidence of heat stress in thick-billed murres and showed that murres experienced heat stress frequently (mean = 61%), but that exposure to heat stress was not uniform across the colony. On top of showing evidence of heat stress, we created a biophysical model for murres, opening the possibility for future studies on heat stress at various microclimates, and potentially in other auk species as well.

In this general discussion, I will discuss more in depth the challenges faced in both of the chapters as this was not addressed in the individual papers. I will also address the relevance of both studies more broadly and the importance of reducing invasiveness when studying physiology, as well as future avenues for studies in the field of conservation physiology.

Challenges and Caveats

Chapter 1

Kittiwakes' energy expenditure was best predicted by time-activity budgets. Thus, using our five behavioural classes, I obtained activity-specific metabolic rates for each behaviour. The goal of using broad behavioural classes was to ensure that the classification remained fairly simple to remove the analytical challenge that often comes with using accelerometry data. On the other hand, I also ensured that identified behaviours were not too broad so that they still had high enough explanatory power to obtain the most accurate estimate of energy expenditure. Although I succeeded at obtaining five behavioural categories that are broad enough yet explained most of the variation in energy expenditure, I acknowledge that my classification used three types of data, namely GPS, accelerometry and bathymetry data. This methodological choice was the results of analytical challenges faced when analyzing behavioural data from a plunge-diving species with high variability in its flying behaviour, where using metrics of accelerometry yielded poor results. I recognize that this adds a level of complexity as some of our behavioural classes may not be obtainable by using solely one type of data (i.e., resting on land vs. resting on water).

Chapter 2

In my second chapter, I developed a 3D printed biophysical model to measure operative temperature of murres at various microclimates inside the colony. Although the biophysical model construction is not discussed much in the main manuscript, and most of the details pertaining to its construction are in the Appendix 1, developing our model was the greatest challenge of this project. In the literature, very little information is available on the construction of 3D printed models. The few papers I found addressed with insufficient details how they created their models, and how they selected their material and print settings (O'Connor et al., 2018, O'Connor et al., 2022). As biophysical models vary based on species, and the rationale behind how to construct a proper biophysical model was simply not available, I had to start from 'scratch' and conduct basic material test myself, often removing myself from the limits of biology and moving more towards engineering and physics. Thus, I created this model in the most rigorous way I could, to the limit of my abilities. I acknowledge that our biophysical model may not experience exactly the same conditions as a real murre. Nonetheless, I believe that my models provide the best available estimate. To prevent other researchers from having the same challenges and "reinventing the wheel", I plan on fully publishing my methodology.

Methods in physiology

As highlighted above, studying physiology can be challenging, especially when developing novel techniques. Physiology is a key field in biology, and as I have shown in my two chapters, it can answer important questions about a species' biology, but also its conservation. However, the methods to study physiology have a tendency to be quite invasive, often including blood sampling, surgical implantation and/or long handling time (Butler et al., 2004). Thus, sometimes posing a limit as to what we can do and with which species we can work with (but see: Cook et al., 2020). In both of the chapters presented above, we developed novel methods to study different aspects of physiology using less invasive techniques than traditionally used.

In the first chapter, we obtained activity-specific metabolic rates for five behavioural categories. Although activity-specific metabolic rates were already available for black-legged kittiwakes (Jodice et al., 2003), the behavioural classes were not suitable for biologging data. Indeed, the behavioural classes used in that study were classified using behavioural observations of kittiwakes detected via radio telemetry, and were likely inaccurate. With the advancement of biologging technologies, obtaining time-activity budget based on behavioural observation is no longer necessary. However, the challenge of analyzing complex data such as accelerometry data limits the resolution at which we can classify behaviour; thus broad behavioural classes are more appropriate. Using our DLW-movement calibration, we can now look at energy expenditure of kittiwakes without using invasive methods such as doubly-labelled water, using both novel and historical data.

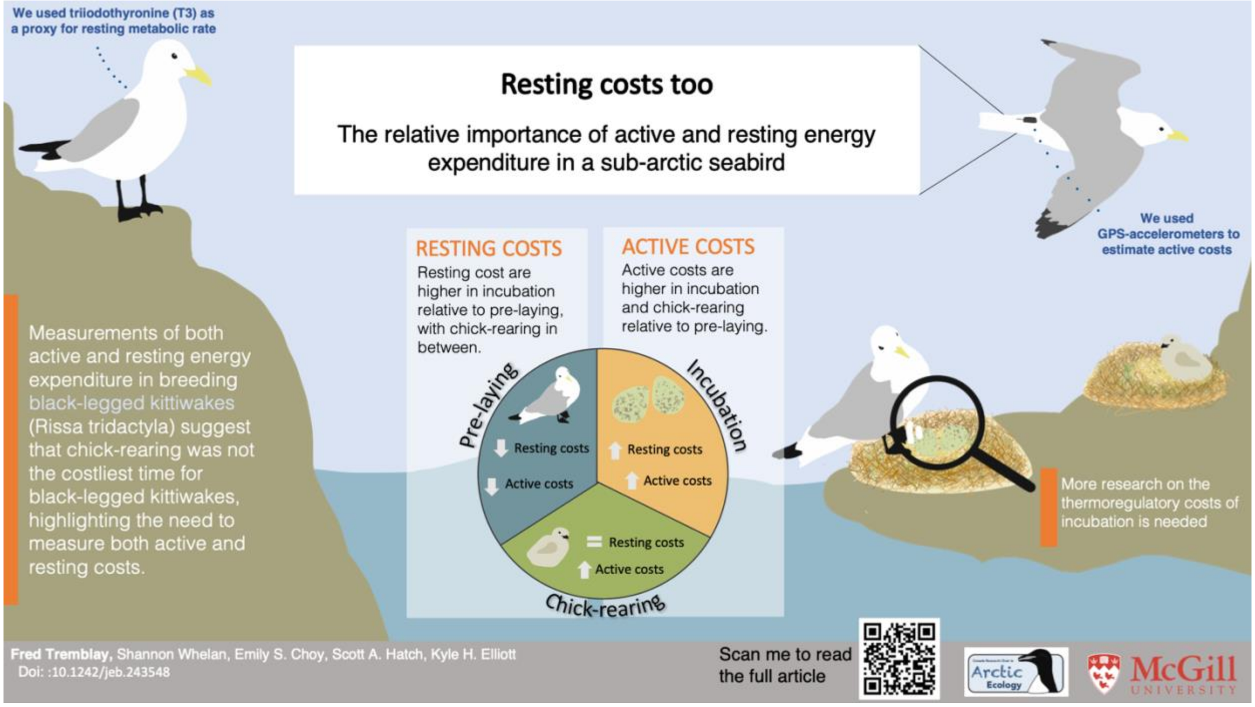
In the second chapter, I developed a biophysical model that enabled me to measure operative temperature of murres. I would like to highlight the value of those models as they enable us to gain valuable insight on seabirds' physiology using a minimally invasive method. Remote sensing methods, including infrared imagery, biophysical models and other technologies such as drone surveys allow us to gain critical information on a species and broaden the range of possibilities, especially when working with cryptic or endangered species (Cook et al., 2020). A study by Cook et al. (2020) used simplified biophysical models to show that the endangered bank cormorant (*Phalacrocorax neglectus)* behaviourally adjusts to better tolerate heat. Yet, they suggest that this thermoregulatory trade-off could result in a negative impact on their reproductive success over time (Cook et al., 2020). This study is a great example of the value of remote sensing when studying endangered and/or highly sensitive species. More specifically, biophysical models can be used as a window to animal physiology. I hope that the model I developed will be used in future studies to investigate the effects of heat stress in murres at various latitudes.

Using a passive biophysical model (non-heated), I highlighted the variability of environmental conditions that murres perceive based on varying environmental conditions and microhabitat use. Although it has been suggested that a heated biophysical model may be more appropriate to study endotherms, the value of passive biophysical models has been highlighted in the literature for a few endothermic species, namely snow buntings (*Plectrophenax nivalis*; (O'Connor et al., 2022)) and rufous-cheeked nightjars (*Caprimulgus rufigena;* (O’Connor et al., 2018)). Nonetheless, comparing our passive model to a heated model would be the next logical step.

Future avenues of research

In this thesis, I investigated the different factors that can impact the physiology of a species in the broad context of climate change. Yet, many questions remain unanswered. In the first chapter, I showed that activity predicted energy expenditure fairly accurately, whereas in the second chapter, I showed that factors other than activity can have an impact on an individual’s physiological state. Thus, an open question is how to incorporate both the cost of activity and the metabolic cost not associated with activity (i.e., breeding stage and heat stress).

As demonstrated in my previous article (see infographic below), the cost of resting can drive total energy expenditure up or down depending on the breeding stage (Tremblay et al., 2022). Measurements of triiodothyronine, a thyroid hormone used as a proxy for resting metabolic rate, showed that kittiwakes’ resting metabolic rates increased significantly during incubation (Tremblay et al., 2022). This was likely due to increased heat exchange with the environment through the brood patch. As a future research avenue, I suggest investigating the link between heat stress and energy expenditure, looking more specifically at the influence of resting metabolic rate on daily energy expenditure.



Resting costs too

The relative importance of active and resting energy expenditure in a sub-arctic seabird

We used triiodothyronine (T3) as a proxy for resting metabolic rate

Measurements of both active and resting energy expenditure in breeding black-legged kittiwakes (Rissa tridactyla) suggest that chick-rearing was not the costliest time for black-legged kittiwakes, highlighting the need to measure both active and resting costs.

RESTING COSTS

Resting cost are higher in incubation relative to pre-laying, with chick-rearing in between.

ACTIVE COSTS

Active costs are higher in incubation and chick-rearing relative to pre-laying.

We used GPS-accelerometers to estimate active costs

More research on the thermoregulatory costs of incubation is needed

Fred Tremblay, Shannon Whelan, Emily S. Choy, Scott A. Hatch, Kyle H. Elliott

Doi: :10.1242/jeb.243548

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General conclusion

As ambient temperature keeps increasing, Arctic wildlife will suffer from both the indirect and direct effects of climate change. Seabirds are highly sensitive to changes in their environment and sample large areas daily, making them ideal indicator species to study the effects of climate change. In this thesis, I suggest that physiology can shed light on how both direct and indirect effects are likely to impact on seabirds. I developed two novel methods; 1) a DLW- movement calibration for black-legged kittiwakes, and 2) a biophysical model to measure operative temperature in thick-billed murres. Using physiology as a tool for conservation, I provided two potential mechanistic explanations of how climate change is likely to impact on seabird species with different life history traits. Within seabirds, different species can be impacted differentially because drivers of energy expenditure can differ taxonomically (surface foragers vs divers), temporally (pre-breeding vs breeding conditions) and spatially (among and within colony variation). With that in mind, next steps should try to incorporate multiple factors that can influence physiology, including the cost of activity paired with the influence of breeding stage and environmental conditions on metabolic costs to obtain a more holistic view of the challenges faced by seabirds and Arctic wildlife in general .

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