Sitting Ducks: The physiological and behavioural responses of incubating common eiders (*Somateria mollissima*) to heat stress in the Canadian Arctic

By

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DECLARATION OF CO-AUTHORSHIP

I. Co-Authorship

I hereby declare that this thesis incorporates material that is the result of joint research, as follows: I am the primary author of Chapters 1 through 4, with supervision and valuable revisions provided by Dr. Oliver Love and Dr. Christina Semeniuk. Chapter 2 is co-authored with Dr. Christina Semeniuk, Dr. Oliver Love, Grant Gilchrist, Shayla Kroeze, Sara Bellefontaine, Erica Geldart, and Hannah ter Hofstede. Chapter 3 is co-authored with Dr. Christina Semeniuk, Dr. Oliver Love, Grant Gilchrist, Shayla Kroeze, Reid Smith, Jacob Peterson-Galema, and Meagan Chorba. In all chapters, the key ideas, contributions, experimental designs, data analyses, and interpretations were performed by the primary author. The contribution of coauthors in Chapters 2 and 3 was primarily through aid in study design, logistical support, data analyses, interpretation, and funding. I am still considering ongoing authors who have contributed to the creation of the long-term data collection used in this thesis for the manuscripts.

I am aware of the University of Windsor Senate Policy on Authorship, and I certify that I have properly acknowledged the contribution of other researchers to my thesis and have obtained written permission from each of the co-authors to include the above materials in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

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ABSTRACT

Rising ambient temperatures driven by climate change can heighten an endotherm's risk of heat stress, eliciting a physiological and behavioural response. Cold-specialist species may be particularly vulnerable to over-heating due to their adaptive ability to retain body heat in cold environments. Moreover, their risk of heat stress may be exaggerated during reproduction, when body temperatures and energetic workloads approach their annual maxima. In this study, I investigated whether a cold-specialist seaduck, the arctic-breeding common eider (*Somateria mollissima*), experiences heat stress during their incubation by examining their heart rate and incubation behaviour at Qikiqtakuluk (East Bay Island), a long-term breeding colony in the Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary, Nunavut. Hens fast for roughly 25 days while incubating their eggs on sun-exposed nests. I used heart-rate data collected from incubating hens using a 3D-printed microphone egg in each nest during the summers of 2019, 2022, and 2023 (N= 62), as well as incubation behaviour recorded via temperature fluctuations from thermal probes in each nest in summers 2018, 2019, 2022, and 2023 (N= 86). Recorded nest-level temperature was also recorded at each nest using hobo temperature pendants, and site-wide ambient temperature and weather factors (e.g. wind) were also measured using heat-stress tracking devices. I found significant temperature thresholds at which eiders begin to increase their heart rate and increase behavioural adjustments on the nest in response to heat stress. However, eiders are not yet experiencing high-enough temperatures in their environment to show statistically significant changes in their heart rate and behaviour. In addition, we found that weather factors contribute to eiders' physiological responses but not behavioural responses to heat stress. Further, hens' heart rates and behavioural adjustments increase later in the breeding season and during later stages of incubation, with later-laying hens also having higher heart rates. We conclude that eiders are not yet significantly heat-stressed during their incubation, but as temperatures continue to rise beyond our found temperature thresholds, incubating eiders may begin to experience significant energetic and behavioural costs of heat stress, particularly later into the season and their incubation, with late-laying hens being especially vulnerable to energetic costs. We show that eiders have the capacity to respond to climate change, but that these responses can interfere with their reproduction. As such, the revealed temperature thresholds and assessment of eiders' vulnerability to heat stress under climate change's warming of arctic summers may aid in informing their timely management and encourage protective policy action in this declining seaduck.

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CHAPTER 1

General introduction

The cost of reproduction

Reproduction is an energetically costly life event for many organisms (Audzijonyte & Richards, 2018). In sexual reproduction, energy must be allocated among several reproductive activities that may include the development and maintenance of reproductive organs (Audzijonyte & Richards, 2018), courtship activities associated with defending a reproductive territory or mate and intrasexual competition (Adkison et al., 2014), and parental care (Stephens et al., 2009). Concurrently, energy must continually be invested into body maintenance (e.g., immunity (Bourgeon et al., 2009; Hanssen et al., 2005), growth (Audzijonyte & Richards, 2018; Zera & Harshman, 2001), and thermoregulation (Rezende & Bacigalupe, 2015). As such, studies suggest that competing energetic demands for reproductive investment and body maintenance can seldom be met by nutrient reserves or gains alone during reproduction, resulting in energetic constraints and, thereafter, a potential trade-off of energy allocated between maintenance and reproduction (Stearns, 1989).

The occurrence of energetic trade-offs between reproduction and other life-history traits suggests that some individuals have the phenotypic flexibility to adaptively alter breeding investment decisions in response to variation in their body condition (Griesser et al., 2017), climatic conditions (Griesser et al., 2017), and resource availability (Stahlschmidt et al., 2013). In fact, studies on model organisms have demonstrated a link between reproductive costs and changes in metabolism, diet, nutrient availability (Harshman & Zera, 2007), and ultimately, breeding success (Nilsson & Svensson, 1996) and lifespan (Hamel et al., 2010; Wiersma et al., 2004). However, the underlying mechanisms that mediate these downstream effects on fitness are not well understood (Harshman & Zera, 2007; Josefson et al., 2024; Zera & Harshman, 2001). Recent studies suggest that the regulation of the endocrine system and intermediary metabolism (i.e., the process of producing and storing metabolic energy from nourishment to then build and break down energy-rich compounds (Veerappa & McClure, 2020) may be primary pathways for mediating reproductive trade-offs (Harshman & Zera, 2007; Williams, 2012a). As a result, how organisms acquire and use energy can greatly impact reproduction or body maintenance, emphasizing the value of understanding resource management strategies when studying reproductive trade-offs (Descamps et al., 2016).

Capital- vs income-based investment strategies

A species' energetic strategy for investment into reproduction is shaped by its life history, as well as when and where resources are available in relation to the spatial (i.e., breeding grounds are a distance away from feeding grounds) and temporal (short window of suitable conditions for their reproduction, typical in polar environments) demands of their reproductive strategy (Williams et al., 2017). For instance, there are two extremes that species may use to fuel the energetic demands of reproduction: income versus capital breeding (Stephens et al., 2009). Income breeders rely solely on energy consumed during the breeding season for immediate investment into reproduction (Stephens et al., 2009). For example, songbirds are typically income breeders during egg production, with energy consumed on the breeding grounds immediately transformed into reproductive machinery (e.g., ovary, oviduct) and reproductive units (e.g., follicles, eggs; Williams, 2012b). Conversely, capital breeders store energy prior to a given breeding stage for later investment into reproduction, a strategy that is advantageous in highly seasonal breeding sites where food availability and weather are unpredictable, coupled with an advantage for early arrival and initiation of breeding, and the ability to store excess energy (Rotics et al., 2018; Sénéchal et al., 2011; Williams et al., 2017). For example, large Arctic-breeding waterfowl, such as swans and geese, arrive on breeding grounds with stores of protein and lipids that they then use to fuel investment into reproductive machinery and eggs at a time when local resources are scarce (Badzinski et al., 2011; Bêty et al., 2004).

Although there are species which rely on purely capital and income breeding investment strategies, the reality for many species is somewhere between the two, often referred to as 'mixed capital-income breeding' when the strategies are differentially applied within or between aspects of reproduction, such as territory defence, egg production, incubation, and offspring-provisioning (Houston et al., 2006; Stephens et al., 2009). For example, large female Weddell seals (*Leptonychotes weddellii*) can alter their capital breeding strategy to an income strategy within their lactation period (an energetically expensive activity) depending on the abundance of prey available to them (Wheatley et al., 2008). Alternatively, female Arctic-breeding common eiders (*Somateria mollissima* -subspecies *borealis* and *sedentaria*) use an income-based or mixed strategy investment to fuel the lipid and protein components of egg production (Sénéchal et al., 2011), but then later rely exclusively on stored (capital) lipids to fuel a fasting incubation period (Bottitta et al., 2003). Indeed, in larger migratory bird species, like the common eider, that occupy seasonally constrained environments, a mixed strategy can be most advantageous to time and energy restrictions of their environment (Williams et al., 2017): an income strategy during egg production reduces weight load during migration (Sénéchal et al., 2011), whereas a capital strategy during incubation shortens incubation length and decreases nest predation. Regardless of whether a mixed-strategy is used within or between pre-breeding, breeding, or post-breeding activities, individuals can benefit from a combination of immediate energetic gain combined with stored energy reserves to capitalize on the most efficient method of resource allocation during their reproduction (Stephens et al., 2009; Williams et al., 2017).

With anthropogenic changes to climate, new energetically expensive pressures can emerge during a species' period(s) of reproductive investment that can disrupt the optimal balance of reproductive investment and energy management for all reproductive strategies (Zera & Harshman, 2001), including increased thermoregulatory costs (Rezende & Bacigalupe, 2015) and a mismatch of timing between energetically costly reproductive activities and peaks in food supply (Williams et al., 2017). In time, the increased energetic costs can negatively impact reproductive success and species' fitness (Jaatinen et al., 2016), highlighting the importance of identifying climate change-induced stressors during reproduction to better inform management policies and mitigation strategies (Culp et al., 2017).

Thermoregulating in a changing Arctic: heat stress during reproduction

In the Arctic, where temperatures are near or at freezing for much of the annual cycle (Førland & Hanssen-Bauer, 2003; Smith et al., 2010), breeding individuals must invest in reproduction while facing potentially high thermoregulatory costs of staying warm (Førland & Hanssen-Bauer, 2003). Endothermic homeotherms, such as birds and mammals, are particularly affected as they must generate their own body heat to maintain a consistent internal body temperature, requiring considerable energetic input when a large thermal gradient exists between the external and internal environment (Dawson & O’Connor, 1996; Hansen, 2009). In fact, endothermic homeotherms can cope with a range of ambient temperatures, known as the thermal neutral zone (TNZ), where little to no additional energy is needed (above basic maintenance costs (e.g., running basal metabolism)) to maintain a constant internal body temperature (Dawson & O’Connor, 1996). However, when temperatures drop below or rise outside the TNZ, individuals are required to increase metabolic energy investment into warming or cooling, respectively to maintain their body temperature (Dawson & O’Connor, 1996). As such, cold-adapted endothermic homeotherms have evolved morphological, physiological, and/or behavioural traits that help produce or retain body heat, thus efficiently warming themselves when Arctic temperatures cool (Clarke, 1991). These morphological cold-adapted traits can include increased density of fur, feathers, or fat to insulate heat in the core (Scholander et al., 1950a); and shorter morphological extremities, both of which reduce external body surface area for heat exchange to the environment (Serrat et al., 2008). In addition, physiological cold adaptations may include shivering and non-shivering thermogenesis (increased metabolism to fuel heat production; Dawson & O’Connor, 1996), and counter-current heat exchangers to retain generated heat within the body core (Ederstrom & Brumleve, 1964). Finally, individuals may also behaviourally respond to the cold by seeking shelter from wind or greater exposure to radiative heat (Glass et al., 2021). The cold adaptations that don’t require significant energetic input, such as insulation and countercurrent heat exchangers, can shift, or extend, a species’ thermal neutral zone towards lower ambient temperatures, buffering the costs of warming at low temperatures until they need to apply more costly warming methods (e.g. shivering; Oswald & Arnold, 2012). Understandably, the range and thresholds of thermal neutral zones will vary between species, seasons and individuals, due to their differing heat dissipation and retention qualities, core body temperatures, and exposure to thermal environments (Speakman & Król, 2010).

Although advantageous in frigid environments (Dawson & O’Connor, 1996), cold adaptations may expectedly become maladaptive under the effects of climate change, as once-cold regions undergo rapid changes and warming (Choy et al., 2021; O'Connor et al., 2021; Oswald & Arnold, 2012). Indeed, climate change is directly impacting arctic ecosystems via increased atmospheric and oceanic temperatures, melting of ice caps, and a decline in sea ice extent (Bennett et al., 2015; Sydeman et al., 2012). According to the Arctic Monitoring and Assessment Program (2021), the Arctic has warmed at three times the rate of the planet between 1971-2019 (AMAP, 2021). Conversely, Rantanen et al., (2022) suggest that the Arctic has warmed nearly four times as fast as the globe during that period (Rantanen et al., 2022). Regardless, the direct and indirect effects of warming have had several studied consequences on arctic breeding species (Oswald & Arnold, 2012). Studies of indirect effects most markedly note increased exposure and susceptibility to disease, accumulated food contaminants and toxins, and changes in predator-prey dynamics and distribution (Sydeman et al., 2012). Less studied are the direct impacts, for example examining how warming ambient temperatures can be a source of heat stress for cold-adapted species, particularly during energetically demanding periods such as reproduction (Choy et al., 2021; O'Connor et al., 2021; Oswald & Arnold, 2012).

Endothermic species with advanced heat-retaining and -producing adaptations may be particularly at risk of over-heating due to their cold adaptations (O'Connor et al., 2021). In fact, endotherms, as a rule, are more forgiving of temperatures below their thermal neutral zone (known as the lower critical limit) than above (known as the upper critical limit; Hansen, 2009). Avian cold specialists may be particularly at risk of overheating due to bird’s already high body temperatures (mammalian average 37 °C, avian average 41 °C; Choy et al., 2021) being fairly close to their lethal limits (most vertebrates' lethal limits do not exceed 47 °C; Freeman et al., 2020). If body temperatures rise to lethal limits, electrolytes and fluids are depleted, proteins denature, and cell membranes become compromised, resulting in death without adequate cooling responses (Hansen, 2009). Even before lethal temperatures are reached, exposing individuals to temperatures above their upper critical limit can negatively impact their health and fitness through physiological or behavioural responses aimed at maintaining their body temperature within a desired range (van Wettere et al., 2021). Such consequences of initiating a thermoregulatory response are expected to be exacerbated in breeding individuals, as they are already undergoing an energetically expensive event, as well as experiencing high thermal pressures (Audzijonyte & Richards, 2018; Speakman & Król, 2010). In fact, recent studies suggest that energetic management during reproduction may be regulated more by the ability to dissipate body heat, rather than limited energetic intake via feeding, known as the heat dissipation limit theory (Nord & Nilsson, 2019; Rogers et al., 2021; Tapper et al., 2020). In other words, the rate of energy turnover in the body is restricted by the rate at which heat can be dissipated from the body

(Sadowska et al., 2016). Regardless of the driving mechanism, a trade-off occurs between investment into reproduction and thermoregulation; and physiology and behaviour are the pathways by which energetic management can be accomplished (Cunningham et al., 2021; Tüzün & Stoks, 2022).

Among arctic-breeding species, birds may be particularly vulnerable to heat stress effects due to low thresholds for heat tolerance. For example, a recent study of heat stress in thick-billed murres (*Uria lomvia*), a cold-adapted seabird, found birds begin using physiological responses to cool themselves at markedly lower temperatures than species breeding in warm or arid climates (Choy et al., 2021). In fact, studies have noted several cases of parent murres dying during their incubation on thermally exposed cliff nests, as suspected, due to overheating (Choy et al., 2021; Gaston & Elliott, 2013). Likewise, recent research in snow buntings (*Plectrophenax nivalis*), a cold-adapted songbird, indicated that they have a limited ability to dissipate heat via physiological mechanisms so that in even mildly warm conditions, they may require behavioural responses to cool down (O'Connor et al., 2021). As such, heat stress in breeding snow buntings during parental care can be harmful to breeding success, as parents are likely forced to behaviourally respond by reducing chick-provisioning (a thermally costly activity) to avoid over-heating themselves (O'Connor et al., 2022). Notably, both thick-billed murres and snow buntings surpassed their upper critical limit at an air temperature of 29.8-29.9 °C, indicating a low heat tolerance when compared to warm-climate species, resulting in an increased metabolic rate to compensate for greater cooling demands (Choy et al., 2021; O'Connor et al., 2021). Accordingly, thermoregulatory costs during reproduction may be particularly detrimental to Arctic species that cannot escape or take short breaks from the effects of increased radiative heat during breeding, such as incubation (Amat & Masero, 2004). Specifically, uniparental species that use capital stores to fuel incubation may risk losing their breeding attempt if they interrupt incubation for even short periods of time, as remaining on the nest not only shortens incubation length but also helps prevent nest predation (Smith et al., 2022). Moreover, while larger individuals under normal temperatures are expected to have greater breeding success due to sufficient fuel reserves (Hanssen et al., 2002), under heat stressed conditions, these same individuals, though slower to take in heat, may also be more likely to have trouble dissipating it (Zagkle et al., 2022). This is because larger bodies have reduced surface area per volume for heat loss, as well as slower heating/cooling rates, and so larger birds are less efficient at physiological cooling mechanisms, requiring them to use active cooling mechanisms at much lower ambient temperatures as compared to smaller birds (Smit et al., 2016). As such, large-bodied, capital and uniparental incubators may be particularly at risk to the detriment of coupled energetic costs of reproduction and heat stress (Viblanc et al., 2014).

Indicators of heat stress in avian populations

The interactive effects of heat stress coupled with reproduction result in notable changes in avian body temperature, energetic use, and behaviour, leading to ultimate outcomes on clutch size (total eggs laid during the breeding attempt), offspring survival (DuRant et al., 2013), and reduced parent body condition, with an expected downstream lowered success of future breeding attempts (Cunningham et al., 2021). As such, avian species may be particularly good models for examining a variety of measurable physiological and behavioural indicators to examine heat stress effects during reproduction (Dawson & O'Connor, 1996). One valuable marker indicative of an individual experiencing heat stress (i.e., it is unable to dissipate body heat at the rate it is being produced), is an increase in body temperature (Chang et al., 2018) above the expected 1-2 °C that naturally occurs for some bird species during reproduction (Guillemette & Pelletier, 2022). On average, body temperatures 6 ˚C above a bird's baseline average can be lethal (Freeman et al., 2022). Another indication of heat stress may be evaporative water loss (Oladokun & Adewole, 2022), typically measured by flow-through respirometry that records the organism's respiration rate in a mask or chamber (O'Connor et al., 2021; Withers, 1977). Evaporative cooling allows greater dissipation of heat via water loss through respiration (Song & Beissinger, 2019). However, this cooling can quickly result in dehydration and a significant heat load to expel, particularly in species with high basal metabolic rates, and thus large body size (Song & Beissinger, 2019) because metabolic heat is produced as a byproduct of cooling, proportional to basal metabolic rate (Oswald & Arnold, 2012). These effects are exacerbated in species without easy access to free water (such as uniparental capital incubators; Lecomte et al., 2009), where metabolizing protein and fat stores may be the most feasible method of freeing water, but comes at the cost of quickly depleting energy stores for incubation (Bourne et al., 2021). Changes in metabolic rate can, therefore, also be an indicator of heat stress (Emami et al., 2020). As such, quantifying an individual's resting or basal metabolic rate can be a valuable baseline for measuring heat stress-related increases in metabolic activity, especially when coupled with measurements of body mass (Dawson & O’Connor, 1996; O'Connor et al., 2021; Speakman & Król, 2010). However, quantifying basal metabolic rate is restricted to studies of at-rest, post-absorptive (i.e., no food in the digestive tract) individuals, which is often challenging to measure in the field (Downs & Brown, 2012). Proxies for metabolic rate, such as heart rate (Green, 2011; Malchaire et al., 2017), can be useful tools to estimate energy expenditure for thermoregulation if validated for the focal study system (Hawkins et al., 2000). Although heart rate and metabolic rate are not interchangeable, heart rate may be used as a proxy (or indicator) of an individual’s metabolic rate (Green, 2011) since heart rate and metabolic rate are intrinsically related through a series of physiological processes that make up “the oxygen cascade” (Green, 2011; Malchaire et al., 2017). In this process, as the body consumes energy (ATP), more energy needs to be produced to replenish the delivery of oxygen to tissues (Dzal et al., 2015). In birds and mammals, the oxygen transport system is fueled by aerobic respiration, meaning that when more energy is required, the respiration rate must be increased to maintain adequate oxygen supply (Green, 2011; Malchaire et al., 2017). However, since blood transports oxygen through the body, an increase in cardiac output (i.e., heart rate) is also needed to maintain a greater oxygen consumption rate (Harris, 1994).

In addition to physiological responses, there are also observable behavioural outcomes to heat stress (Etches et al., 2008; Pattinson et al., 2020). Well-documented in open-ground incubating birds, heat stressed individuals are observed taking frequent incubation breaks or longer nest recesses, leaving nests vulnerable to predation and inconsistent heating (Amat & Masero, 2004; Coe et al., 2015) as parents are driven to seek shade and water (Amat & Masero, 2004). However, even prior to nest departure, parents may display other behavioural indicators that they are thermally strained. For example, in some ground-nesting birds, parents can experience greater heat pressures when a warm boundary layer forms on the ground surface due to radiative heat (Brown & Downs, 2003). In response to over-heating, individuals can then perform nest shading (also known as egg shading) behaviour, in which the parent raises themselves off the nest to escape heat in the boundary layer (Brown & Downs, 2003; Sharpe et al., 2021). Similarly, nesting Heermann’s Gulls (*Larus heermanni*) have been documented holding their wings open and outward when over-heating (Bartholomew & Dawson, 1979). Other thermoregulatory behaviours that can be observed in incubating parents when over-heating include panting (or gular fluttering;

Bartholomew et al., 1968), bathing (Oswald et al., 2008), ruffling feathers (Clauser, 2015), and shifting orientation in relation to the sun (Luskick et al., 1978; Olin et al., 2023), which collectively can be considered unrest (Del Valle et al., 2021; Fernandes et al., 2021) or agitation behaviours (Smith et al., 2022).

To measure heat stress in breeding birds, it is also important to document the source of the stressor: weather conditions experienced at breeding sites. There are several weather variables to consider in heat stress studies, although the most relevant are ambient temperature, radiative temperature (a particularly important variable for heat stress in open-tundra ground nesters; Fortin et al., 2000), humidity, and wind speed (Carroll et al., 2015; Fortin et al., 2000). Though one variable can be most predictive of heat stress risks for a given population, studies show that lead indicators may vary across locations and populations. In fact, recent studies suggest an integrative approach that uses multiple parameters to estimate apparent temperature - the temperature being perceived by the individual - is best (Zhang et al., 2014). In addition, microclimate is a large driver in birds choosing nesting sites, so, when possible, measurements recorded at the nest are favourable over the general area (Fast et al., 2010; Robertson, 2009; With & Webb, 1993). It is important to note that susceptibility to heat stress increases with heat exposure time, making it valuable to examine occurrences of both heat exposure and duration (Oswald & Arnold, 2012).

In summation, heat stress may have detrimental effects on arctic-breeding birds, and these effects are further amplified in species with greater energetic constraints, such as capital incubators under high egg-predation risk (Audzijonyte & Richards, 2018; Speakman & Król, 2010). Indeed, physiological and behavioural outcomes of heat stress are expected to be counter to the goal of preserving limited energetic stores during incubation (Oswald & Arnold, 2012). Thus, even slight increases in thermoregulatory demand may ultimately lead to longer incubation times (due to interrupted incubation consistency), increased chances of clutch abandonment (Bourne et al., 2021; Sharpe et al., 2019), and nest predation (Hand et al., 1981), proximately resulting in lowered within-year reproductive success (Oswald & Arnold, 2012). In the long-term, this could additionally impact lifetime fitness by hindering the individual’s ability to fully invest in future reproductive attempts and survival (Cunningham et al., 2021).

The common eider and Arctic-breeding populations' susceptibility to heat stress

Common eiders (*Somateria mollissima*) are the largest of Northern Hemisphere ducks with a sizeable circumpolar distribution across the Arctic and sub-Arctic regions of North America, Europe, and Asia (Waltho & Coulson, 2015). This species has six subspecies: the Pacific (*Somateria mollissima (hereafter S.m.) nigrum*), northern (*S. m. borealis*), dresser's (*S.m. dresseri*), Hudson's Bay (*S.m. sedentaria*), European (*S.m. mollissima*) and Faeroes (*S.m. faesroeensis*) common eider. However, of these subspecies, only the Hudson's Bay and northern common eider are typically found breeding in the Eastern Canadian Arctic and tundra (Mosbech et al., 2006; Robertson et al., 2001).

Common eiders spend most of their life cycle on water, feeding primarily on low energetic value aquatic invertebrates, with a preference for clams and mussels (Leopold et al., 2001; Varennes et al., 2015). Occupying cold aquatic environments, eiders (particularly arctic populations) are well adapted to withstand the cold by way of physiological, behavioural, and morphological adaptations (Gabrielsen et al., 1991; Jenssen et al., 1989). For example, they have low thermal conduction of the body through an efficient vascular system, constricting blood flow to vessels in the peripheral tissues when cold (Jenssen et al., 1989), as well as highly insulative down properties (D'alba et al., 2017). Although these adaptations minimize their thermoregulatory costs under evolved conditions, in the face of rapid anthropogenic-caused warming, these features may become maladaptive given eiders' potential inability to cope with excess heat. Indeed, eider hens may experience thermal stress, especially during reproduction, when their bodies reach their highest annual temperatures during egg-laying (40.7 °C), strongly suggesting they are most thermally (with regards to warming) constrained during this period (Guillemette & Pelletier, 2022).

Eiders spend most of their annual cycle on water and ice; however, they move inland during reproduction while remaining close to open water sources (Bustnes, 1996; Schamel, 1977) since their young fledge soon after hatching (approx. 24 hours) and move into intertidal waters under their mother's care (Bustnes, 1996; Schamel, 1977). Females lay, on average, 3-6 eggs in a single clutch (Erikstad et al., 1993) per year. Males will accompany females during their nest selection and incubation initiation to ensure paternity, but leave before incubation ends (Schamel, 1977).

Nest characteristics and vegetative cover vary between populations and breeding sites (Fast et al., 2010), but in Arctic populations, female eiders tend to be philopatric colony nesters (McKinnon et al., 2006), nesting on open-ground shallow surface depressions with little cover from the elements, to better view predators from great distances (Fast et al., 2010). This nest site selection may be a source of increased risk of heat stress under climate change as this habitat offers little refuge from heat and radiative exposure (Fortin et al., 2000). Further, it also increases the vulnerability of eggs to predators when females are absent, behaviourally constraining females to maintain a strict incubation consistency (Fast et al., 2010). Collectively, these nesting attributes may cause female eiders significant conflict under heat stress, as high nest attentiveness is counter-productive to heat-avoidant behaviours, such as seeking water to rehydrate (panting is dehydrating) and seeking shade to reduce heat load from the environment (Amat & Masero, 2004). Further, female eiders are uniparental incubators (McKinnon et al., 2006) and as a result of this extreme incubation strategy, females rely entirely on energetic gains collected prior to incubation initiation to fuel this period, fasting for 24-26 days of incubation (Criscuolo et al., 2003). Thus, females do not get recesses from the nest (Tulp & Schekkerman, 2006). Without additional thermoregulatory costs, this incubation strategy has a strict energetic budget, with most females losing 30-45% of their body weight through the incubation period (Gabrielsen et al., 1991). In fact, females may even complete incubation in a near-emaciated state (Criscuolo et al., 2003). Thus, additional thermal costs are expected to increase energetic loss during this period and expose eggs to predators and inconsistent incubation temperatures, at the risk of reduced female health and failed breeding attempts.

As a result, Arctic-breeding female eiders are likely susceptible to negative physiological and behavioural impacts of heat stress during incubation due to their cold adaptations, thermal exposure of their nests, strict incubation strategy, and high risk of egg-predation from nest recesses. These risks of heat stress can negatively impact eider health and fecundity, namely by using more stored body fat and water than is optimal to partially fuel a physiological heat stress response, and behavioural adjustments in an attempt to stay cool and maintain body temperatures below a lethal limit (Lecomte et al., 2009; Nord & Williams, 2015). Notably, Arctic eider populations have experienced several population declines in the last few decades due to overharvesting, avian cholera outbreaks, and climate change-induced exposure to contaminants and novel predators (Barnas et al., 2022; Descamps et al., 2011; Smith et al., 2022; Tjørnløv et al., 2019). Studies have concurrently identified slow population recovery rates (Jónsson et al., 2009; Tjørnløv et al., 2019), highlighting the time-sensitivity of identifying early indicators of new stressors, such as heat stress, to inform timely population management strategies and policy action.

Thesis goal and chapter objectives

In this thesis, I studied the capacity of Arctic incubating common eiders to respond to heat stress as the North undergoes rapid warming and extreme weather events brought on by climate change (Ruuskanen et al., 2021). Specifically, I examined the physiological and behavioural responses of incubating female common eiders to heat stress during the summer months, when environmental temperatures are at their highest, and birds may be most at risk of heat stress due to the physiological and behavioural constraints imposed by their reproductive strategies (capital incubation, in open-nest sites) and cold adaptations.

In **Chapter 1** of the thesis, I provided background information on topics related to the cost of reproduction, cold-adapted species, and the impending risks of heat stress in cold-adapted species during reproduction under a changing climate.

In **Chapter 2**, I explore ambient and nest-level temperatures' impact on incubating female eiders' heart rate, a physiological indicator of a heat stress response. Heart rate's segmented relationships with ambient and nest-level (i.e., radiative) temperature are studied and plotted to visualize an eider hen's heat stress response model, akin to a Scholander-Irving curve or thermal neutral zone (Scholander et al., 1950b). This non-linear model identifies both lower- and upper-critical temperature thresholds at which eiders can be predicted to be undergoing thermal stress conditions, as indicated by a sudden change in heart rate. Though eider cold stress response thresholds have been previously studied, this thesis presents, to our knowledge, the first heat stress response threshold for hens during their reproduction. A heat stress response threshold is a valuable tool in predicting how climate change will impact eiders, and other arctic-breeding populations, in the future as their environment continues to warm (Levesque & Marshall, 2021). In addition, I examine how breeding parameters (sample date, i.e. ordinal date, incubation stage, lay date) and additional weather factors (a heat index and wind and humidity index) linearly influence heart rate, examining how factors apart from temperature play an important role in seabirds' heat stress responses.

In **Chapter 3**, I investigate the behavioural responses of incubating female eiders to heat stress, as eiders predictably experience greater incubation interruptions in response to heat stress when greater thermoregulatory demands occur concurrently with such costly life history events, as is incubation. As such, I examine eiders' daily movements on the nest (agitation) across daily ambient and nest-level temperatures the hens were exposed to, to determine at what temperature thresholds eiders begin exhibiting behavioural indicators of thermal stress, particularly heat stress. By identifying temperature thresholds at which eiders exhibit behavioural responses to heat stress, I can determine how heat stress is impacting their incubation consistency and thus theorize costs to not only hens, but their current breeding attempt. Similar to Chapter 2, I further examine the linear effects of breeding parameters and additional weather factors (a heat index and a humidity index) on eiders' behavioural heat stress responses, as they are expected to play a role in hens' thermal environment and need for thermoregulatory behaviours.

In **Chapter 4**, I provide a general discussion of the wider implications of my results from Chapters 2 & 3 and how, together, the physiological and behavioural responses to heat stress in eiders may translate to fitness costs in this culturally and economically valued species, while predicting their long-term capacity to respond to the direct effects of climate change. Further, I discuss the implications and possible drivers of hens' narrower temperature range for physiological responses to thermal stress as compared to their behavioural response window. Particularly, why a physiological response to heat stress occurs at lower nest-level temperatures than a behavioural response, with possible outcomes for both hens' health and clutch survival. Finally, I discuss the potential limitations of this study and suggestions for future research avenues on this species, as well as how our findings align with current research priorities in the Kivalliq region and address literature gaps needed to better protect common eiders.

References

Adkison, M. D., Ward, M. B., & Quinn, T. P. (2014). Nest site preference and intrasexual competition in female sockeye salmon, Oncorhynchus nerka. *Environmental Biology of Fishes*, *97*(4), 385-399. https://doi.org/10.1007/s10641-013-0159-x

AMAP. (2021). *Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers.*

Amat, J. A., & Masero, J. A. (2004). How Kentish plovers, Charadrius alexandrinus, cope with heat stress during incubation. *Behavioral Ecology and Sociobiology*, *56*(1), 26-33. https://doi.org/10.1007/s00265-004-0758-9

Audzijonyte, A., & Richards, S. A. (2018). The energetic cost of reproduction and its effect on optimal life-history strategies. *The American Naturalist*, *192*(4), E150-E162.

Badzinski, S. S., Kennedy, L., Petrie, S. A., & Schummer, M. L. (2011). Variation in Body Composition and Digestive Organs of Tundra Swans during Migration at Long Point, Lake Erie, Ontario. *Waterbirds*, *34*(4), 468-475, 468. https://doi.org/10.1675/063.034.0409

Barnas, A. F., Geldart, E. A., Love, O. P., Jagielski, P. M., Harris, C. M., Gilchrist, H. G., Hennin, H. L., Richardson, E. S., Dey, C. J., & Semeniuk, C. A. D. (2022). Predatory cue use in flush responses of a colonial nesting seabird during polar bear foraging. *Animal Behaviour*, *193*, 75-90. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.08.009

Bartholomew, G. A., & Dawson, W. R. (1979). Thermoregulatory behavior during incubation in Heermann's Gulls. *Physiological Zoology*, *52*(4), 422-437.

Bartholomew, G. A., Lasiewski, R. C., & Crawford, E. C. (1968). Patterns of Panting and Gular Flutter in Cormorants, Pelicans, Owls, and Doves. *The Condor*, *70*(1), 31-34. https://doi.org/10.2307/1366506

Bennett, J. R., Shaw, J. D., Terauds, A., Smol, J. P., Aerts, R., Bergstrom, D. M., Blais, J. M., Cheung, W. W., Chown, S. L., & Lea, M.-A. (2015). Polar lessons learned: long-term management based on shared threats in Arctic and Antarctic environments. *Frontiers in Ecology and the Environment*, *13*(6), 316-324.

Bêty, J., Giroux, J.-F., & Gauthier, G. (2004). Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (Anser caerulescens atlanticus). *Behavioral Ecology and Sociobiology*, *57*, 1-8.

Bottitta, G. E., Nol, E., & Gilchrist, H. G. (2003). Effects of Experimental Manipulation of Incubation Length on Behavior and Body Mass of Common Eiders in the Canadian Arctic. *Waterbirds*, *26*(1), 100-107, 108. https://doi.org/10.1675/1524-4695(2003)026[0100:EOEMOI]2.0.CO;2

Bourgeon, S., Maho, Y. L., & Raclot, T. (2009). Proximate and ultimate mechanisms underlying immunosuppression during the incubation fast in female eiders: Roles of triiodothyronine and corticosterone. *General and Comparative Endocrinology*, *163*(1), 77-82. https://doi.org/https://doi.org/10.1016/j.ygcen.2008.11.015

Bourne, A. R., Ridley, A. R., McKechnie, A. E., Spottiswoode, C. N., & Cunningham, S. J. (2021). Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the southern pied babbler Turdoides bicolor. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coab043

Brown, M., & Downs, C. T. (2003). The role of shading behaviour in the thermoregulation of breeding crowned plovers (Vanellus coronatus). *Journal of Thermal Biology*, *28*(1), 51-58. https://doi.org/https://doi.org/10.1016/S0306-4565(02)00036-0

Bustnes, J. O. (1996). Is parental care a constraint on the habitat use of Common Eider females? *The Condor*, *98*(1), 22-26.

Carroll, J. M., Davis, C. A., Elmore, R. D., & Fuhlendorf, S. D. (2015). A ground-nesting galliform's response to thermal heterogeneity: implications for ground-dwelling birds. *PLoS One*, *10*(11), e0143676.

Chang, Y., Wang, X. J., Feng, J. H., Zhang, M. H., Diao, H. J., Zhang, S. S., Peng, Q. Q., Zhou, Y., Li, M., & Li, X. (2018). Real-time variations in body temperature of laying hens with increasing ambient temperature at different relative humidity levels. *Poult Sci*, *97*(9), 3119-3125. https://doi.org/10.3382/ps/pey184

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F., & Elliott, K. H. (2021). Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. *Journal of Experimental Biology*, *224*(13), jeb242168.

Clarke, A. (1991). Cold adaptation. *Journal of Zoology*, *225*(4), 691-699. https://doi.org/https://doi.org/10.1111/j.1469-7998.1991.tb04339.x

Clauser, A. J. (2015). *Responses of coastal nesting King Rails (Rallus elegans) to environmental threats of rising water and temperature* East Carolina University].

Coe, B. H., Beck, M. L., Chin, S. Y., Jachowski, C. M., & Hopkins, W. A. (2015). Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. *Journal of Avian Biology*, *46*(4), 385-394.

Criscuolo, F., Chastel, O., Gabrielsen, G. W., Lacroix, A., & Le Maho, Y. (2003). Relationship between nutritional status and prolactin levels in the common eider, a capital incubator. *Antarctic biology in a global context. Backhuys, Leyden*, 193-197.

Culp, L. A., Cohen, E. B., Scarpignato, A. L., Thogmartin, W. E., & Marra, P. P. (2017). Full annual cycle climate change vulnerability assessment for migratory birds. *Ecosphere*, *8*(3), e01565. https://doi.org/https://doi.org/10.1002/ecs2.1565

Cunningham, S. J., Gardner, J. L., & Martin, R. O. (2021). Opportunity costs and the response of birds and mammals to climate warming. *Frontiers in Ecology and the Environment*, *19*(5), 300-307.

D'alba, L., Carlsen, T. H., Ásgeirsson, Á., Shawkey, M. D., & Jónsson, J. E. (2017). Contributions of feather microstructure to eider down insulation properties. *Journal of Avian Biology*, *48*(8), 1150-1157.

Dawson, W. R., & O’Connor, T. P. (1996). Energetic features of avian thermoregulatory responses. *Avian energetics and nutritional ecology*, 85-124.

Del Valle, J. E., Pereira, D. F., Neto, M. M., Gabriel Filho, L. R. A., & Salgado, D. D. A. (2021). Unrest index for estimating thermal comfort of poultry birds (Gallus gallus domesticus) using computer vision techniques. *Biosystems Engineering*, *206*, 123-134.

Descamps, S., Forbes, M. R., Gilchrist, H. G., Love, O. P., & Bêty, J. (2011). Avian cholera, post-hatching survival and selection on hatch characteristics in a long-lived bird, the common eider Somateria mollisima. *Journal of Avian Biology*, *42*(1), 39-48. https://doi.org/https://doi.org/10.1111/j.1600-048X.2010.05196.x

Descamps, S., Gaillard, J. M., Hamel, S., & Yoccoz, N. G. (2016). When relative allocation depends on total resource acquisition: implication for the analysis of trade-offs. *Journal of evolutionary biology*, *29*(9), 1860-1866. https://doi.org/10.1111/jeb.12901

Downs, C. T., & Brown, M. (2012). Is respirometry a standardized technique? A review of measurement of avian resting metabolic rates. *Journal of Thermal Biology*, *37*(7), 531-536. https://doi.org/https://doi.org/10.1016/j.jtherbio.2012.06.004

DuRant, S. E., Hopkins, W. A., Hepp, G. R., & Walters, J. R. (2013). Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biol Rev Camb Philos Soc*, *88*(2), 499-509. https://doi.org/10.1111/brv.12015

Dzal, Y. A., Jenkin, S. E. M., Lague, S. L., Reichert, M. N., York, J. M., & Pamenter, M. E. (2015). Oxygen in demand: How oxygen has shaped vertebrate physiology. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *186*, 4-26. https://doi.org/https://doi.org/10.1016/j.cbpa.2014.10.029

Ederstrom, H., & Brumleve, S. (1964). Temperature gradients in the legs of cold-acclimatized pheasants. *American Journal of Physiology-Legacy Content*, *207*(2), 457-459.

Emami, N. K., Jung, U., Voy, B., & Dridi, S. (2020). Radical response: effects of heat stress-induced oxidative stress on lipid metabolism in the avian liver. *Antioxidants*, *10*(1), 35.

Erikstad, K. E., Bustnes, J. O., & Moum, T. (1993). Clutch-Size Determination in Precocial Birds: A Study of the Common Eider. *The Auk*, *110*(3), 623-628. https://doi.org/10.2307/4088426

Etches, R., John, T., & Gibbins, A. (2008). Behavioural, physiological, neuroendocrine and molecular responses to heat stress. *CABI*, 48–79. https://doi.org/10.1079/9781845932589.0048

Fast, P. L., Gilchrist, H. G., & Clark, R. G. (2010). Nest-site materials affect nest-bowl use by Common Eiders (Somateria mollissima). *Canadian Journal of Zoology*, *88*(2), 214-218.

Fernandes, A. M., de Lucca Sartori, D., de Oliveira Morais, F. J., Salgado, D. D. A., & Pereira, D. F. (2021). Analysis of cluster and unrest behaviors of laying hens housed under different thermal conditions and light wave length. *Animals*, *11*(7), 2017.

Førland, E. J., & Hanssen-Bauer, I. (2003). Past and future climate variations in the Norwegian Arctic: overview and novel analyses. *Polar Research*, *22*(2), 113-124. https://doi.org/10.3402/polar.v22i2.6450

Fortin, D., Larochelle, J., & Gauthier, G. (2000). The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. *Journal of Thermal Biology*, *25*(3), 227-238. https://doi.org/https://doi.org/10.1016/S0306-4565(99)00028-5

Freeman, M. T., Czenze, Z. J., Schoeman, K., & McKechnie, A. E. (2020). Extreme hyperthermia tolerance in the world's most abundant wild bird. *Scientific reports*, *10*(1), 13098. https://doi.org/10.1038/s41598-020-69997-7

Freeman, M. T., Czenze, Z. J., Schoeman, K., & McKechnie, A. E. (2022). Adaptive variation in the upper limits of avian body temperature. *Proceedings of the National Academy of Sciences*, *119*(26), e2116645119.

Gabrielsen, G. W., Mehlum, F., Karlsen, H. E., Andresen, Ø., & Parker, H. (1991). Energy cost during incubation and thermoregulation in the female common eider Somateria mollissima. *Norsk Polarinstitutt Skrifter*, *195*, 51-62.

Gaston, A. J., & Elliott, K. H. (2013). Effects of climate-induced changes in parasitism, predation and predator-predator interactions on reproduction and survival of an Arctic marine bird. *Arctic*, 43-51.

Glass, T. W., Breed, G. A., Robards, M. D., Williams, C. T., & Kielland, K. (2021). Trade-off between predation risk and behavioural thermoregulation drives resting behaviour in a cold-adapted mesocarnivore. *Animal Behaviour*, *175*, 163-174.

Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendations. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *158*(3), 287-304.

Griesser, M., Wagner, G. F., Drobniak, S. M., & Ekman, J. (2017). Reproductive trade-offs in a long-lived bird species: condition-dependent reproductive allocation maintains female survival and offspring quality. *Journal of evolutionary biology*, *30*(4), 782-795.

Guillemette, M., & Pelletier, D. (2022). Egg-laying increases body temperature to an annual maximum in a wild bird. *Sci Rep*, *12*(1), 1681. https://doi.org/10.1038/s41598-022-05516-0

Hamel, S., Gaillard, J.-M., Yoccoz, N. G., Loison, A., Bonenfant, C., & Descamps, S. (2010). Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. *Ecology Letters*, *13*(7), 915-935. https://doi.org/https://doi.org/10.1111/j.1461-0248.2010.01478.x

Hand, J. L., Hunt, G. L., Jr., & Warner, M. (1981). Thermal Stress and Predation: Influences on the Structure of a Gull Colony and Possibly on Breeding Distributions. *The Condor*, *83*(3), 193-203. https://doi.org/10.2307/1367307

Hansen, P. J. (2009). Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1534), 3341-3350.

Hanssen, S., Engebretsen, H., & Erikstad, K. (2002). Incubation start and egg size in relation to body reserves in the common eider. *Behavioral Ecology and Sociobiology*, *52*, 282-288.

Hanssen, S. A., Hasselquist, D., Folstad, I., & Erikstad, K. E. (2005). Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1567), 1039-1046. https://doi.org/doi:10.1098/rspb.2005.3057

Harris, D. (1994). The physiology of respiration. *Perfusion*, *9*(3), 159-162. https://doi.org/10.1177/026765919400900302

Harshman, L. G., & Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in ecology & evolution*, *22*(2), 80-86.

Hawkins, P., Butler, P., Woakes, A., & Speakman, J. (2000). Estimation of the rate of oxygen consumption of the common eider duck (Somateria mollissima), with some measurements of heart rate during voluntary dives. *Journal of Experimental Biology*, *203*(18), 2819-2832.

Houston, A. I., Stephens, P. A., Boyd, I. L., Harding, K. C., & McNamara, J. M. (2006). Capital or income breeding? A theoretical model of female reproductive strategies. *Behavioral Ecology*, *18*(1), 241-250. https://doi.org/10.1093/beheco/arl080

Jaatinen, K., Öst, M., & Hobson, K. A. (2016). State-dependent capital and income breeding: a novel approach to evaluating individual strategies with stable isotopes. *Frontiers in zoology*, *13*, 1-8.

Jenssen, B. M., Ekker, M., & Bech, C. (1989). Thermoregulation in winter-acclimatized common eiders (Somateria mollissima) in air and water. *Canadian Journal of Zoology*, *67*(3), 669-673.

Jónsson, J., Gardarsson, A., Gill, J., Petersen, A., & Gunnarsson, T. (2009). Seasonal weather effects on the Common Eider, a subarctic capital breeder, in Iceland over 55 years. *Climate research*, *38*, 237-248. https://doi.org/10.3354/cr00790

Josefson, C. C., Fitzwater, B. M., Beltran, R. S., Costa, D. P., Fornara, J. H., Garland, T., Jr, Harris, B. N., Hinde, K., Hood, W. R., Hunt, E., Kenagy, G. J., Liebl, A. L., Litmer, A. R., Lopes, P. C., Misra, D., Meuti, M., Place, N. J., Powers, L. E., Saltzman, W., & Orr,

T. J. (2024). Balancing Act: An Interdisciplinary Exploration of Trade-offs in Reproducing Females. *Integrative and Comparative Biology, 64*(6), 1734-1756. https://doi.org/10.1093/icb/icae092

Lecomte, N., Gauthier, G., & Giroux, J.-F. (2009). A link between water availability and nesting success mediated by predator–prey interactions in the Arctic. *Ecology, 90*(2), 465-475. https://doi.org/https://doi.org/10.1890/08-0215.1

Leopold, M., Kats, R. K. H., & Ens, B. (2001). Diet (preferences) of common eiders Somateria mollissima. *Wadden Sea Newslett. (2001), 1: 25-31*, *1*.

Levesque, D. L., & Marshall, K. E. (2021). Do endotherms have thermal performance curves? *Journal of Experimental Biology, 224*(3). https://doi.org/10.1242/jeb.141309

Luskick, S., Battersby, B., & Kelty, M. (1978). Behavioral Thermoregulation: Orientation Toward the Sun in Herring Gulls. *Science*, *200*(4337), 81-83. https://doi.org/doi:10.1126/science.635577

Malchaire, J., d, A. A. F. R., & Palella, B. I. (2017). Evaluation of the metabolic rate based on the recording of the heart rate. *Ind Health*, *55*(3), 219-232. https://doi.org/10.2486/indhealth.2016-0177

McKinnon, L., Gilchrist, H. G., & Scribner, K. T. (2006). Genetic evidence for kin-based female social structure in common eiders (Somateria mollissima). *Behavioral Ecology*, *17*(4), 614-621.

Mosbech, A., Gilchrist, G., Merkel, F., Sonne, C., Flagstad, A., & Nyegaard, H. (2006). Year-round movements of northern common eiders Somateria mollissima borealis breeding in Arctic Canada and West Greenland followed by satellite telemetry. *ARDEA-WAGENINGEN-*, *94*(3), 651.

Nilsson, J.-Ǻ., & Svensson, E. (1996). The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 263*(1371), 711-714. https://doi.org/doi:10.1098/rspb.1996.0106

Nord, A., & Nilsson, J. Å. (2019). Heat dissipation rate constrains reproductive investment in a wild bird. *Functional Ecology*, *33*(2), 250-259.

Nord, A., & Williams, J. B. (2015). The energetic costs of incubation. In D. C. Deeming & S. J. Reynolds (Eds.), *Nests, Eggs, and Incubation: New ideas about avian reproduction* (pp. 0). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198718666.003.0013

O'Connor, R. S., Le Pogam, A., Young, K. G., Love, O. P., Cox, C. J., Roy, G., Robitaille, F., Elliott, K. H., Hargreaves, A. L., & Choy, E. S. (2022). Warming in the land of the midnight sun: breeding birds may suffer greater heat stress at high-versus low-Arctic sites. *Proceedings of the Royal Society B, 289*(1981), 20220300.

O'Connor, R. S., Le Pogam, A., Young, K. G., Robitaille, F., Choy, E. S., Love, O. P., Elliott, K. H., Hargreaves, A. L., Berteaux, D., & Tam, A. (2021). Limited heat tolerance in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecology and evolution, 11*(4), 1609-1619.

Oladokun, S., & Adewole, D. I. (2022). Biomarkers of heat stress and mechanism of heat stress response in Avian species: Current insights and future perspectives from poultry science. *Journal of Thermal Biology, 110*, 103332. https://doi.org/https://doi.org/10.1016/j.jtherbio.2022.103332

Olin, A. B., Dück, L., Berglund, P.-A., Karlsson, E., Bohm, M., Olsson, O., & Hentati-Sundberg, J. (2023). Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Marine Ecology Progress Series*.

Oswald, S. A., & Arnold, J. M. (2012). Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. *Integrative Zoology, 7*(2), 121-136.

Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B., & Hamer, K. C. (2008). Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas Catharacta skua. *Journal of Avian Biology, 39*(2), 163-169.

Pattinson, N. B., Thompson, M. L., Griego, M., Russell, G., Mitchell, N. J., Martin, R. O., Wolf, B. O., Smit, B., Cunningham, S. J., McKechnie, A. E., & Hockey, P. A. R. (2020). Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns? *Journal of Avian Biology, 51*(2). https://doi.org/https://doi.org/10.1111/jav.02350

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Rezende, E. L., & Bacigalupe, L. D. (2015). Thermoregulation in endotherms: physiological principles and ecological consequences. *Journal of Comparative Physiology B, 185*(7), 709-727. https://doi.org/10.1007/s00360-015-0909-5

Robertson, B. A. (2009). Nest-Site Selection in a Postfire Landscape: Do Parents Make Tradeoffs Between Microclimate and Predation Risk? *The Auk*, *126*(3), 500-510. https://doi.org/10.1525/auk.2009.08148

Robertson, G. J., Reed, A., & Gilchrist, H. G. (2001). Clutch, egg and body size variation among common eiders breeding in Hudson Bay, Canada. *Polar Research*, *20*(1), 85-94. https://doi.org/https://doi.org/10.1111/j.1751-8369.2001.tb00041.x

Rogers, S. A., Robbins, C. T., Mathewson, P. D., Carnahan, A. M., van Manen, F. T., Haroldson, M. A., Porter, W. P., Rogers, T. R., Soule, T., & Long, R. A. (2021). Thermal constraints on energy balance, behaviour and spatial distribution of grizzly bears. *Functional Ecology*, *35*(2), 398-410. https://doi.org/https://doi.org/10.1111/1365-2435.13727

Rotics, S., Kaatz, M., Turjeman, S., Zurell, D., Wikelski, M., Sapir, N., Eggers, U., Fiedler, W., Jeltsch, F., & Nathan, R. (2018). Early arrival at breeding grounds: Causes, costs and a trade-off with overwintering latitude. *J Anim Ecol*, *87*(6), 1627-1638. https://doi.org/10.1111/1365-2656.12898

Ruuskanen, S., Hsu, B.-Y., & Nord, A. (2021). Endocrinology of thermoregulation in birds in a changing climate. *Molecular and Cellular Endocrinology*, *519*, 111088.

Sadowska, E. T., Król, E., Chrzascik, K. M., Rudolf, A. M., Speakman, J. R., & Koteja, P. (2016). Limits to sustained energy intake. XXIII. Does heat dissipation capacity limit the energy budget of lactating bank voles? *Journal of Experimental Biology*, *219*(6), 805-815. https://doi.org/10.1242/jeb.134437

Schamel, D. (1977). Breeding of the Common Eider (Somateria mollissima) on the Beaufort Sea Coast of Alaska. *The Condor*, *79*(4), 478-485. https://doi.org/10.2307/1367728

Scholander, P., Hock, R., Walters, V., & Irving, L. (1950a). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *The Biological Bulletin*, *99*(2), 259-271.

Scholander, P., Hock, R., Walters, V., Johnson, F., & Irving, L. (1950b). Heat Regulation in Some Arctic and Tropical Mammals and Birds. *Biological Bulletin*, *99*(2), 237-258. https://doi.org/10.2307/1538741

Sénéchal, É., Bêty, J., Gilchrist, H. G., Hobson, K. A., & Jamieson, S. E. (2011). Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. *Oecologia*, *165*, 593-604.

Serrat, M. A., King, D., & Lovejoy, C. O. (2008). Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proceedings of the National Academy of Sciences*, *105*(49), 19348-19353.

Sharpe, L., Cale, B., & Gardner, J. L. (2019). Weighing the cost: the impact of serial heatwaves on body mass in a small Australian passerine. *Journal of Avian Biology*, *50*(11). https://doi.org/https://doi.org/10.1111/jav.02355

Sharpe, L. L., Bayter, C., & Gardner, J. L. (2021). Too hot to handle? Behavioural plasticity during incubation in a small, Australian passerine. *Journal of Thermal Biology*, *98*, 102921. https://doi.org/https://doi.org/10.1016/j.jtherbio.2021.102921

Smit, B., Zietsman, G., Martin, R., Cunningham, S., McKechnie, A., & Hockey, P. (2016). Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Climate Change Responses*, *3*, 1-14.

Smith, R. A., Albonaimi, S. S., Hennin, H. L., Gilchrist, H. G., Fort, J., Parkinson, K. J., Provencher, J. F., & Love, O. P. (2022). Exposure to cumulative stressors affects the laying phenology and incubation behaviour of an Arctic-breeding marine bird. *Science of the Total Environment*, *807*, 150882.

Smith, S. L., Romanovsky, V. E., Lewkowicz, A. G., Burn, C. R., Allard, M., Clow, G. D., Yoshikawa, K., & Throop, J. (2010). Thermal state of permafrost in North America: a contribution to the international polar year. *Permafrost and Periglacial Processes*, *21*(2), 117-135. https://doi.org/https://doi.org/10.1002/ppp.690

Song, S., & Beissinger, S. R. (2019). Environmental determinants of total evaporative water loss in birds at multiple temperatures. *The Auk*, *137*(1). https://doi.org/10.1093/auk/ukz069

Speakman, J. R., & Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, *79*(4), 726-746.

Stahlschmidt, Z. R., Rollinson, N., Acker, M., & Adamo, S. A. (2013). Are all eggs created equal? Food availability and the fitness trade-off between reproduction and immunity. *Functional Ecology*, *27*(3), 800-806. https://doi.org/https://doi.org/10.1111/1365-2435.12071

Stearns, S. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology, 3*(3), 259-268. https://doi.org/10.2307/2389364

Stephens, P. A., Boyd, I. L., McNamara, J. M., & Houston, A. I. (2009). Capital breeding and income breeding: their meaning, measurement, and worth. *Ecology*, *90*(8), 2057-2067.

Sydeman, W. J., Thompson, S. A., & Kitaysky, A. (2012). Seabirds and climate change: roadmap for the future. *Marine Ecology Progress Series*, *454*, 107-117.

Tapper, S., Nocera, J. J., & Burness, G. (2020). Heat dissipation capacity influences reproductive performance in an aerial insectivore. *Journal of Experimental Biology*, *223*(10), jeb222232.

Tjørnløv, R. S., Pradel, R., Choquet, R., Christensen, T. K., & Frederiksen, M. (2019). Consequences of past and present harvest management in a declining flyway population of common eiders Somateria mollissima. *Ecology and evolution*, *9*(22), 12515-12530. https://doi.org/https://doi.org/10.1002/ece3.5707

Tulp, I., & Schekkerman, H. (2006). Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *Journal of Avian Biology*, *37*(3), 207-218.

Tüzün, N., & Stoks, R. (2022). A fast pace-of-life is traded off against a high thermal performance. *Proceedings of the Royal Society B: Biological Sciences*, *289*(1972), 20212414. https://doi.org/doi:10.1098/rspb.2021.2414

van Wettere, W. H., Kind, K. L., Gatford, K. L., Swinbourne, A. M., Leu, S. T., Hayman, P. T., Kelly, J. M., Weaver, A. C., Kleemann, D. O., & Walker, S. K. (2021). Review of the impact of heat stress on reproductive performance of sheep. *Journal of animal science and biotechnology*, *12*, 1-18.

Varennes, E., Hanssen, S. A., Bonardelli, J. C., & Guillemette, M. (2015). A large molluscivore bird (Common Eider, Somateria mollissima) is able to discriminate quality of blue mussels (Mytilus edulis) based on size and provenance. *Canadian Journal of Zoology, 93*(8), 655-663. https://doi.org/10.1139/cjz-2015-0046

Veerappa, S., & McClure, J. (2020). Intermediary metabolism. *Anaesthesia & Intensive Care Medicine*, *21*(3), 162-167. https://doi.org/https://doi.org/10.1016/j.mpaic.2020.01.003

Viblanc, V. A., Saraux, C., Malosse, N., & Groscolas, R. (2014). Energetic adjustments in freely breeding-fasting king penguins: does colony density matter? *Functional Ecology*, *28*(3), 621-631.

Waltho, C., & Coulson, J. (2015). *The common eider* (J. Martin, Ed.). Bloomsbury Publishing.

Wheatley, K. E., Bradshaw, C. J., Harcourt, R. G., & Hindell, M. A. (2008). Feast or famine: evidence for mixed capital-income breeding strategies in Weddell seals. *Oecologia*, *155*(1), 11-20. https://doi.org/10.1007/s00442-007-0888-7

Wiersma, P., Selman, C., Speakman, J. R., & Verhulst, S. (2004). Birds sacrifice oxidative protection for reproduction. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(suppl_5), S360-S363.

Williams, C. T., Klaassen, M., Barnes, B. M., Buck, C. L., Arnold, W., Giroud, S., Vetter, S. G., & Ruf, T. (2017). Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1734), 20160250. https://doi.org/doi:10.1098/rstb.2016.0250

Williams, T. D. (2012a). Hormones, life-history, and phenotypic variation: Opportunities in evolutionary avian endocrinology. *General and Comparative Endocrinology*, *176*(3), 286-295. https://doi.org/https://doi.org/10.1016/j.ygcen.2011.11.028

Williams, T. D. (2012b). *Physiological adaptations for breeding in birds*. Princeton University Press.

With, K. A., & Webb, D. R. (1993). Microclimate of Ground Nests: The Relative Importance of Radiative Cover and Wind Breaks for Three Grassland Species. *The Condor*, *95*(2), 401-413. https://doi.org/10.2307/1369363

Withers, P. C. (1977). Measurement of VO2, VCO2, and evaporative water loss with a flow-through mask. *J Appl Physiol Respir Environ Exerc Physiol*, *42*(1), 120-123. https://doi.org/10.1152/jappl.1977.42.1.120

Zagkle, E., Martinez-Vidal, P. A., Bauchinger, U., & Sadowska, E. T. (2022). Manipulation of Heat Dissipation Capacity Affects Avian Reproductive Performance and Output. *Frontiers in Ecology and Evolution*, *10*. https://doi.org/10.3389/fevo.2022.866182

Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual review of Ecology and Systematics*, *32*(1), 95-126.

Zhang, K., Li, Y., & Schwartz, J. D. (2014). What weather variables are important in predicting heat-related mortality? A new application of statistical learning methods. *Environmental research*, *132*, 350-359.

CHAPTER 2

Introduction

There are a diversity of ways in which species respond to climate change, charismatically referred to as “move, adapt, acclimate, or die” (Beever et al., 2017). For example, these responses can be phenological (Ovaskainen et al., 2013) or range shifts which move the organism further away (temporally or spatially, respectively) from the climatic stressor (Fei et al., 2017), or flexible responses such as behavioural (Buchholz et al., 2019) and physiological changes (Fuller et al., 2010) that enable the organism to remain and endure the stressor. Although these responses can reflect an organism's capacity to cope with environmental change, they can lead to detrimental effects when responses do not match the pace of environmental change (Moritz & Agudo, 2013), or are conflicting with other selective pressures on a given trait (Shaw & Etterson, 2012). Currently, a general lack of mechanistic understanding of physiological responses to climate change is limiting our ability to estimate species' resilience to climate change effects (Fuller et al., 2010). Particularly, knowledge about the upper thermal limits in endothermic organisms is incomplete, despite being a crucial factor in predicting their responses to climate change (Levesque & Marshall, 2021; McKechnie et al., 2017). Moreover, as endotherms' reproductive investment is constrained by the capacity to dissipate heat, exploring thermal limits during this critical life-history event is an important avenue of research (Speakman & Król, 2010). Indeed, as global temperatures rise and extreme weather events become more prevalent and unpredictable (Rantanen et al., 2022), a thorough comprehension of the physiological impacts of climate change-induced warming on energy use in endotherms - specifically, the direct effects of heat stress during breeding (Khaliq et al., 2014; Oswald & Arnold, 2012) - is increasingly vital (Chown et al., 2010; Kronfeld-Schor & Dayan, 2013).

Among endotherms, birds are an increasing focus for studies of physiological responses to climate change (Cooper et al., 2020; Wingfield et al., 2017), given their already high body temperatures and high mass-specific metabolic rates compared to mammals (Gavrilov et al., 2022). Within birds, there is increased concern for heat stress in Arctic-breeding species in particular (Bateman et al., 2020), including arctic seabirds (Choy et al., 2021). The concerns are based on their combination of high-latitude breeding grounds that are experiencing threefold increases in ambient temperature and extreme weather events compared to the rest of the globe (AMAP, 2021; Rantanen et al., 2022), and their cold adaptations resulting in their lower heat tolerance (O'Connor et al., 2021; Oswald & Arnold, 2012). For example, many seabirds feed in cold waters and, as a result, require increased insulative properties to combat the high thermal conductance of these cold feeding grounds (Cook et al., 2020). Though advantageous for limiting heat loss to cold waters, this increased insulation can hinder their ability to dissipate body heat when they move to land to nest on sunny cliffsides (Choy et al., 2021) or open-ground areas (Snell et al., 2024). Indeed, switching to terrestrial habitats can increase exposure to the elements while simultaneously limiting access to fresh water (Alerstam & Högstedt, 1982; Hamer et al., 2001). As such, intense solar radiation can expose birds to operative (e.g., biologically relevant) temperatures far exceeding ambient temperatures without ready water-intensive mechanisms to cool themselves (e.g., evaporative cooling), resulting in birds overheating (Hart et al., 2016; Olin et al., 2023). Thus, increased thermoregulatory costs during the already energetically costly reproductive stage (Reid et al., 2000) may result in energetic trade-offs between reproduction and thermoregulation (Favilla & Costa, 2020). These energetic trade-offs may be particularly acute in species such as Arctic seabirds with additional thermal and reproductive constraints (Grunst et al., 2023), for example, short periods of favourable breeding conditions (Sauser et al., 2021), and variable and short abundance of prime food sources during reproduction (Harding et al., 2011), placing them in a particularly vulnerable state to heat stress (Welman & Pichegru, 2023). However, heat stress in birds in these regions has been greatly understudied (Andreasson et al., 2020; Cook et al., 2020; Snell et al., 2024), despite multiple reports of seabird mortality or failed breeding attempts related to heat, across several species (Choy et al., 2021; Cook et al., 2020; Gaston et al., 2002; Oswald et al., 2008). As such, it is critical to determine which mechanisms might be most capable of enabling Arctic-breeding seabirds to adaptively respond to climate change's direct effects.

When examining the mechanisms available to Arctic seabirds’ capacity to respond to rising ambient temperatures in their current environment, phenotypically flexible responses (e.g., physiology, behaviour) to thermoregulatory challenges may provide the greatest degree of adaptive capacity (Monaco et al., 2017; Visser, 2008; Wingfield et al., 2017). This is because evolutionary changes to traits such as morphology (e.g., insulative plumage; D'alba et al., 2017, large bodies; Waltho & Coulson, 2015) will likely be too slow for population allele changes to be an effective adaptation in a long-lived seabird experiencing rapid environmental change

(Ruuskanen et al., 2021; Visser, 2008). During breeding, incubating (i.e., nest bound) individuals or those raising offspring are expected to be behaviourally constrained to reproductive activities and thus more burdened to absorb the energetic costs of thermoregulating through physiological responses (AlRashidi et al., 2011). For example, although cooling behaviours such as taking a recess to feed in cold waters can help counter the costs of overheating (Cook et al., 2020), they also expose eggs or nest-bound chicks to variable temperatures and greatly increase their risk of predation (Hart et al., 2016). These effects can be particularly detrimental in ground-nesting species where nests are highly accessible to predators, and thus parents have little behavioural flexibility to respond to heat stress without detrimental costs to their young or eggs (Lomas et al., 2014). For example, ground-nesting Arctic skuas (*Stercorarius parasiticus*) faced with predators on their breeding grounds were observed panting at relatively mild temperatures (as low as 9 °C under sunlight) as a symptom of increased energetic demand to cool down, and these responses were detected in the absence of any behavioural responses, such as leaving the nest (Snell et al., 2024). Alternatively, these individuals can employ a diversity of flexible physiological strategies to respond to acute heat stress, all with the goal of trying to avoid overheating to the point where lethal body temperatures are reached (Tattersall et al., 2012). These responses can include allowing their body temperature to rise slightly above normothermic levels, which temporarily reduces the thermal gradient between the body and the environment (Boyles et al., 2011; O'Connor et al., 2024), vasodilating blood vessels for greater blood flow to the skin and hence radiation of excess body heat (Sejian et al., 2018), or using evaporative heat loss mechanisms to cool the body (Ruuskanen et al., 2021). Despite the short-term benefits of these responses to body temperature regulation, each comes with immediate costs of increased water loss and energetic demand (Albright et al., 2017; van de Ven et al., 2019). Moreover, these types of flexible responses to changes in thermoregulatory demands are not without potential longer-term costs since they occur at a time of significant energetic constraint (Stearns, 1989; Zera & Harshman, 2001). As a result, a compromise between investment into current reproduction and self-maintenance often occurs (Stearns, 1989; Zera & Harshman, 2001), as well as with other physiological systems (e.g., immune system; Hanssen et al., 2005), that may impair investment into future reproduction and hence lifetime reproductive success (Stearns, 1989). Given the potential multiple proximate and ultimate costs of using flexible physiological mechanisms to respond to heat stress during reproduction in cold-adapted seabirds, it is critical to determine the biological significance of a given species' heat stress response (Cook et al., 2020). Since direct physiological effects from climate change are suspected to present themselves far sooner than indirect effects, gathering evidence of heat stress effects on arctic-breeding seabirds' physiology is essential to predicting their ongoing vulnerability to climate change (Oswald & Arnold, 2012).

Here we examine the physiological responses of a cold-adapted Arctic-breeding seabird, the common eider (*Somateria mollissima*), to predicted heat stress-inducing conditions caused by rising ambient temperatures and extreme weather events due to climate change. Specifically, we examined the energetic responses of incubating female eiders facing increasingly elevated temperatures during one of the most energetically demanding periods of their life cycle. While studies have examined several indirect effects of climate change on eiders (e.g., changes in breeding propensity; Dey et al., 2018, and exposure to novel predators (polar bears - *Ursus maritimus*) during breeding; Geldart et al., 2023), the direct effects of rising ambient temperature and heat waves on this cold-adapted bird's physiological responses are far less known (see Jenssen et al., 1989). Examining these questions in female Arctic-breeding eiders during their incubation is particularly relevant for several reasons. Firstly, eiders have pre-existing morphological, behavioural and physiological adaptations to the cold that cooperatively work to lower their thermal conductance (retaining body heat; Jenssen et al., 1989), which may now work against birds attempting to resist overheating in the face of increasingly warm conditions (Oswald & Arnold, 2012). Secondly, female eiders use a limited store of body fat to sustain a 24–26 day incubation period under fasting conditions (Bottitta et al., 2003), requiring strict energetic budgeting that hinders their ability to respond to weather conditions without fitness costs (Tulp & Schekkerman, 2006). Thirdly, as uni-parental incubators (McKinnon et al., 2006), females face strong nest predation pressures if they leave the nest and, therefore, must maintain a strict incubation consistency (e.g., 99.8% of the time on the nest; Bottitta et al., 2003) to ensure ducklings hatch (Fast et al., 2007). Fourthly, Arctic-breeding eiders nest in open locations (i.e., without vegetative cover; Fast et al., 2007), meaning they are vulnerable to the impacts of increased temperatures through solar radiation (Choy et al., 2021). Finally, the International Union for Conservation of Nature (IUCN) currently list common eiders as ‘Near Threatened’ (BirdLife International, 2018). Importantly, this most recent assessment communicates that should new information regarding mechanisms behind the declines of *S.m. borealis* subspecies be documented, then the status of the species will be uplisted to a threatened status (BirdLife International, 2018). Thus, addressing the unknown direct effects of climate change on this culturally and ecologically significant subspecies (Henri et al., 2018; Vestbo et al., 2019) may be critical in informing their species' status.

To examine the physiological response of incubating female eiders to heat stress, we used non-invasive techniques to record hens' heart rate responses to changes in temperature as a proxy for their metabolic investment into physiological cooling mechanisms across variable temperatures and environmental conditions (wind, humidity, etc.). We hypothesized that fluctuations in an eider's heart rate in response to increases in temperature and environmental conditions that could induce heat stress indicated energy use towards physiological cooling mechanisms. More specifically, we predicted that when heat stressed, we would see significant increases in heart rate past a specific but unknown temperature threshold indicating birds had begun using physiological cooling mechanisms to avoid overheating. Currently, only the lower critical temperature limits at which eiders show signs of cold stress have been examined (Gabrielsen et al., 1991; Jenssen et al., 1989). Both the temperature threshold and the degree to which eiders respond energetically to heat stress are critical gaps to be filled in our understanding of the thermal tolerances and physiological capacity for eiders, as well as other Arctic-breeding birds, to respond to the direct effects of climate change. More broadly, these results will provide a better understanding of whether arctic breeding birds will be able to keep up with rising temperatures during their breeding seasons, and the mechanisms by which they respond to these environmental changes.

Methods

Study site and system

The incubating common eiders (hereafter eiders) in this study are from an established breeding colony on East Bay Island, Qikiqtakuluk, (64° 02′ N, 81° 47′ W), within the East Bay, Qaqsauqtuuq, Migratory Bird Sanctuary, Nunavut. At the mouth of the Hudson Bay, this flat rocky island (400 X 800 m) is historically the largest breeding colony of eiders in Northern Canada, with up to 9,000 annual breeding pairs (Hennin et al., 2016; Legagneux et al., 2016). However, the colony has declined in recent decades due to human activity and climate change, including novel predators (Iverson et al., 2014) and increased disease exposure, such as avian cholera (Descamps et al., 2012). Eiders in this breeding population migrate from their Western Greenland and

Newfoundland wintering grounds to East Bay Island and surrounding stop-over sites in mid-May to early June (Mosbech et al., 2006). Upon arrival, females begin feeding to replenish energy reserves (Steenweg et al., 2022), much of which will be stored to later fuel the entirety of a ~24-day incubation period, during which time hens do not leave the nest to drink or feed (Bottitta et al., 2003). Pairing and nest selection occur shortly after females' arrival to the breeding grounds, with hens often reusing nest depressions from previous years' eiders to line with new down feathers and moss, for their current breeding attempt (Fast et al., 2010). Females begin laying in mid-June to early July (Steenweg et al., 2022), laying ~one egg per day, with an average clutch size of 2-4 eggs (Descamps et al., 2011a; Love et al., 2010). Incubation initiation begins when the third or fourth egg is laid, depending on the hen’s body condition and clutch size (Hanssen et al., 2002). When broods successfully hatch, ducklings immediately take to the sea with their mothers to begin feeding (Descamps et al., 2011b).

In mid-June, we collected data for East Bay Island’s long-term eider monitoring program, where we caught eiders in mist nets, banded them, nasal-tagged females (unique colour and shape tags on each nostril), and measured their body condition metrics (tarsus length, weight, wing chord, and bill length). Further, we observed eider colony density and breeding behaviour from bird blinds across the island (Hennin et al., 2016), recording colony size, female nesting sites, and breeding behaviour of nasal-tagged females (laying, incubation initiation, nest failure). We deployed our study’s remote nest monitoring equipment (see details below) once females had begun laying and incubating.

Qikiqtakuluk experience nearly 24 hours of sunlight during summer months, with high winds in the bay, and frequent fog early in June (Environment and Climate Change Canada, 2024). When eiders first arrive at the island, ice and snow are still abundant, however, the snow quickly dwindles before hens initiate laying (Love et al., 2010). Surrounding sea ice within the bay typically begins breaking up in late June to early July (Jean-Gagnon et al., 2018), opening the bay for hens and their newly hatched ducklings to make their way to the water (Love et al., 2010). The waters become completely ice-free by early August (Gagnon & Gough, 2005).

Heart rate responses to weather and breeding parameters

To examine the physiological (i.e., heart rate) response of incubating eiders to heat stress, we deployed 3D-printed microphone eggs in 62 nests across three years: 2019 (n=12), 2022 (n=14), and 2023 (n=36) (Figure 2.1), from mid-June to mid-July. We equipped the microphone eggs, previously validated by Geldart and colleagues (Figure 2.2; Geldart et al., 2022), with 128 GB SD cards and two microphones (PUI Audio model AOM-5024L-HD-R) mounted under the egg surface to make contact with the hen's body (Figure 2.3). The microphone wire exited the base of the egg and connected to an audio sound recorder (Tascam DR-05X) placed inside a water-proof ammunition box, powered by a battery pack (24 AA batteries in 2019, 36 in 2022-23). We pre-programmed recorders to record stereo sound at a 44.1k sampling frequency and an input level of 60, before field deployment. In 2019 battery life was ~11.9 days, while in 2022 and 2023 battery life was extended to 19.2 - 19.7 days.

We chose nests for deployment by walking the periphery of the island, or by observation from a blind, to avoid colony disturbance. Females were flushed from their nests to deploy sampling equipment. We collected the first laid egg (when possible) from each nest, as determined by size and colour, to later estimate lay date and days of incubation using candling techniques (details below). Further, by collecting one egg from the nest, we ensured clutch size (i.e., reproductive investment) remained consistent after deploying our microphone egg (Hanssen et al., 2003). We placed the microphone egg in the center of a hen's clutch, and buried the wire under the nest to the ammunition box (Figure 2.3), before securing the microphone egg in place with nails to deter hens from rotating the egg (Kristjánsson & Jónsson, 2011). Finally, the recorder was set to begin recording, a GPS point of the nest was saved, and we covered the clutch with down and debris to help prevent nest predation before the hen's return (Götmark & Åhlund, 1984).

To record environmental parameters faced by incubating females that are indicative of heat stress, we deployed individual HOBO Pendant temperature recorders (Onset Inc., MX2202) at each studied nest to measure fine-scale changes in sun exposure and temperatures that females are experiencing on the nest as they incubate. HOBOs recorded light and temperature readings every two minutes. Further, we deployed 6-8 Kestrel weather meters across the island's breeding colony (Kestrel Inc., 5400) to record the following environmental parameters: ambient temperature, wet bulb temperature, humidity, wind speed, heat index, dew point, and wind chill. Kestrel units recorded environmental conditions every 30 minutes. In 2018 and 2019, Kestrels were placed atop six monitoring-bird blinds, and in 2022 and 2023, Kestrels were placed ~3 feet off the ground in front of five of these blinds, and one weather station within camp confines. Each nest was assigned the Kestrel unit closest to it, as determined by the distance between GPS points in GPS Garmin's Basecamp® software. Finally, trail cameras were also deployed across the island (n=35 in 2019, 2022 and 2023) to account for predator movements and foraging behaviour, as predators are known to impact eider's incubating heart rate (Geldart et al., 2023).

Field teams left the island in early July due to an increased polar bear presence; however, the weather monitoring and nest deployment equipment remained on the island, to later be retrieved by a team helicoptered to the island in mid to late July.

Lay date and incubation stage estimates

We estimated the days of incubation at the time of equipment deployment for each sampled hen by candling the collected first-laid egg from each nest (when possible). Common eiders typically begin incubation before their last egg is laid, however, the incubation initiation date is dependent on an individual's clutch size, with females laying smaller clutches beginning incubation earlier in the laying sequence (Christensen & Balsby, 2020). As such, to remain conservative we considered incubation to begin when the fourth egg was laid. In some cases, the first laid egg was predated before nest deployment; in these cases, if clutch size suggested a later incubation stage than egg age, we relied on clutch size for the days of incubation estimation. Based on candling and clutch size information, we also estimated the lay date of the first-laid egg for each female to determine lay dates for each hen by working back from egg age. We standardized lay dates across years for statistical analyses by subtracting the mean annual ordinal lay date (2019 = 171, 2022 = 170, 2023 = 172) from the female's lay date (Hennin et al., 2016).

Quantifying heart rate

To examine eider heart rate responses to differing thermal conditions, we selected two days within each female’s incubation period corresponding to the highest and lowest peak daily temperature she experienced. We first determined each female's nest duration, which we describe as the day following the female's return to the nest after equipment deployment until nest predation, abandonment, or microphone battery failure. We omitted the first day females returned to the nest, to avoid falsely detecting heart rate responses caused by human disturbance. Using nest duration and HOBO temperature recordings, we then identified the highest daily recorded temperature for each hen’s nest duration. We chose HOBO temperature rather than Kestrel temperature to determine sampling dates and times due to its fine-scale sampling rate (two versus 30 minutes). Further, HOBO units recorded temperatures closest in proximity to a female’s nest, providing a more accurate assessment of the temperatures experienced within the female’s immediate environment while incubating (herein referred to as “nest-level temperature”). We selected two sampling days to record heart rate for each hen: 1) the day with the highest maximum nest-level temperature recorded, and 2) the day with the lowest maximum nest-level temperature recorded within her nest duration. This choice controlled for time-of-day effects, as peak temperatures typically occur between 11:00 and 15:00. For each sampling day, we selected a 30-minute window, 15 minutes before and 15 minutes after the peak temperature had occurred, for heart rate analysis. This window was large enough to minimize bias from acute stressors, while remaining within the available timeframe needed for heart rate analyses. In addition, we excluded heart rate samples taken within several hours of a trail camera’s detection of a polar bear on the island to account for the potential impact of a predator in a hen’s viewshed on her heart rate.

We analyzed audio files from microphone eggs to detect hens' heartbeats within the predetermined 30-minute window of heart rate’s response to temperature using the Avisoft-SASLab Pro (Version 5.3.2) Windows application. We first applied noise reduction and bandpass filters to enhance heartbeat visibility before performing a pulse train analysis to semi-automatically detect and label heartbeats. We then visually verified the detections to remove any false positives and add any missed heartbeats. Due to varying microphone quality, we omitted some heartbeat segments of time (30-second increments) from the 30-minute audio files for certain females. Although we aimed for two sampling days per hen, some females had one day or both removed due to poor audio quality or short nest survival. A single individual, blind to the hen's ID and peak temperature, performed all heartbeat detections to avoid bias. We then converted the heartbeats, along with their dates and times, into heart rates (beats/30 sec) in R Studio Software (Version 4.4.1. 2024-06-14; R Development Core Team, 2024).

Statistical analyses

Quantifying environmental parameters indicative of heat stress

We recorded several environmental parameters as predictors of heat stress: nest-level temperature, ambient temperature, wet bulb temperature, humidity, wind speed, heat index, dew point, and wind chill. We analyzed nest-level temperature and ambient temperature separately as the expected primary drivers of heat stress, but other environmental factors were scaled, centred and rotated into a principal component analysis (PCA). The PCA allowed us to condense the highly correlated parameters into a few meaningful components, to add to our analyses (Forkman et al., 2019). We applied a varimax rotation (Comrey & Lee, 2013) and retained two components with eigenvalues > 1, explaining >10% of the variance. Further, these two components cumulatively explained 93% of variance in the dataset (Table D, Appendix; see details below). The first rotated component, hereafter the 'thermal index', explained 60% of the variance and consisted of heat index, wet bulb temperature, wind chill, and dew point, all with loadings > 0.55, considered to be a valuable loading to the component (Comrey & Lee, 2013). All variables contributing to the thermal index were positively correlated with one another. As such, a high thermal index value was associated with an increased risk of heat stress. The second rotated component, hereafter the 'wind and humidity index', explained 33% of the variance and contained relative humidity and wind speed, each with loadings > 0.55 (Comrey & Lee, 2013), and with a positive correlation between relative humidity and wind speed. As Qikiqtakuluk is a small island within a bay, high winds expectedly carry moisture from surrounding water and thawing ice, which explains why high winds are accompanied by high relative humidity, something that would not be predictably associated to each other at an inland study site. Further, in a cold region, little humidity is needed to saturate air, as compared to a warmer climate. As such, we determine that a high wind and humidity index value decreases an eider's risk of heat stress, as it displaces the heat radiating from hens' bodies with cooler air from the bay, with few effects of humidity on the hens' efficiency of evaporative cooling (i.e., panting).

Effects of environmental parameters and reproductive decisions on heart rate

Of our original 62 deployments in hens' nests, 49 nests produced data that could be used in the statistical analyses (n = 10 in 2019, n = 9 in 2022, and n = 30 in 2023). We used two linear mixed-effects models, one with nest-level temperature and one with ambient temperature, to examine the influence of environmental and reproductive factors on heart rate. The first linear model examined variation in heart rate (continuous, range: 14 – 124 beats/30sec) as the response variable, predicted by nest-level temperature (continuous, range: 5.02 – 43.67 °C), with thermal index (continuous, range: -1.26 – 3.64), wind and humidity index (continuous, range: -1.65 – 1.77), days of incubation (continuous, range: 1 – 19), standardized lay date (continuous, range: -10 to +5), and ordinal date (continuous, range: 172 – 189) as fixed factors, and year (3-factor level: 2019, 2022, and 2023) and nest id (49 levels) as random factors. The second linear model with ambient temperature as the primary response variable included the same covariates and random effects as those in the first model, however excluded the thermal index due to a high variance inflation factor of 28.4 when included in the model (VIF). Indeed, a VIF >10 indicated high collinearity with our ambient temperature.

Identifying temperature thresholds for changes in heart rate

We also performed two segmented regression models to examine nest-level temperature and ambient temperature effects on heart rate, as it can be a valuable tool in identifying thresholds for species' physiological responses to thermal stress (McKechnie et al., 2017; Monaco et al., 2017). While previous studies on eider metabolism and heart rate have suggested there is a critical temperature inflection point at which eiders physiologically respond to cold stress (Gabrielsen et al., 1991; Jenssen et al., 1989; Richman & Lovvorn, 2011), it remains unknown (although it is expected) whether a similar pattern occurs when heat stressed. Our segmented models for nest-level and ambient temperature mirrored the linear models we performed, with the exception that year was treated as a fixed effect (3-factor levels: 2019, 2022, and 2023) due to model complexity issues with iterations of the random effect. For each model, we specified a search for two breakpoints, as we expected a threshold for when eiders become heat stressed and a threshold for when they become cold-stressed during their incubation. However, if both breakpoints were significant, a third breakpoint was searched for to determine if the relationship was further segmented. We did not assess the thermal index and wind and humidity index for segmented relationships with heart rate, as there was no reason to believe they would follow a segmented pattern. However, as with our linear models, we nonetheless included them in the nest-level temperature model as fixed effects, and the humidity and wind index was included in the ambient temperature model as a fixed effect.

We performed all statistical analyses in R studio (Version 4.4.1. 2024-06-14; R Development Core Team, 2024). We used *dplyr* (Wickham et al., 2023) for early data exploration, the *psych* package (Revelle, 2024) for principal component analysis, *lme4* (Bates et al., 2015) for linear mixed effects modelling, *lmerTest* (Kuznetsova et al., 2017) for predictive linear model outputs, and *LIMBARE* (Lee et al., 2024) for segmented modelling. We performed data visuals using *cowplot* (Wilke, 2024), *ggeffects* (Lüdecke, 2018), and *ggplot2* (Wickham, 2016). Lastly, we set $\alpha = 0.05$ as the threshold for statistical significance in all our model analyses.

Results

Linear effects of weather and breeding parameters on heart rate

Our first linear model revealed that variation in heart rate was explained by all fixed effect factors; nest-level temperature ($T = -18.8$, $p < 0.0001$), thermal index ($T = 14.9$, $p < 0.0001$), wind and humidity index ($T = -5.2$, $p < 0.0001$), days of incubation ($T = 14.3$, $p < 0.0001$), standardized lay day ($T = 11.8$, $p < 0.0001$) and ordinal date ($T = -13.9$, $p < 0.0001$) (Table 2.1). Heart rate was positively correlated to thermal index (Figure 2.6), days of incubation (Figure 2.7), and standardized lay date (Figure 2.8). Conversely, heart rate was negatively correlated with nest-level temperature (Figure 2.4), wind and humidity index (Figure 2.9), and ordinal date (Figure 2.10). The greatest degree of variance in our random effects structure was found for nest id (variance= 265.2, SD=16.3), though year also varied (variance = 72.1, SD = 8.5) (Table 2.2).

Similarly, we found that ambient temperature ($T = 2.9$, $p < 0.0001$, Figure 2.5), wind and humidity index ($T = 15.3$, $p < 0.0001$), days of incubation ($T = 12.7$, $p < 0.0001$), standardized lay date ($T = 10.6$, $p < 0.0001$), and ordinal date ($T = -12.2$, $p < 0.0001$) were all significantly related to variation in heart rate (Table 2.3). All variables were positively correlated to heart rate, apart from ordinal date. Further, nest id (variance = 240.8, SD = 15.5) was most variable in our random effects structure, with year (variance = 112.8, SD = 10.6) a source of variance to a lesser extent (Table 2.4).

Segmented effect of temperature on heart rate

We detected a significant effect of nest-level temperature ($T = -15.7$, $p < 0.0001$), thermal index ($T = -2.7$, $p = 0.006$), wind and humidity index ($T = -4.3$, $p < 0.0001$), days of incubation ($T = 16.517$, $p < 0.0001$), standardized lay date ($T = 11.8$, $p < 0.0001$), and ordinal date ($T = -15.3$, $p < 0.0001$) on heart rate in our nest-level temperature's segmented relationship with heart rate (Table 2.5). In fact, only year was not significantly related to variation in heart rate ($p > 0.1$, Table 2.5). Specifically, we detected two significant temperature breakpoints in the model, the first at a nest-level temperature of 19.25 °C ($p < 0.0001$, Table 2.6), and the second at 33.55 °C ($p = 0.0001$, Table 2.6) (Figure 2.11). At temperatures below 19.25 °C, heart rate significantly increased as nest-level temperatures progressively cooled (slope = -1.1, $p = 0.005$, Table 2.7). However, between 19.25 °C and 33.55 °C heart rate remained stable (slope = -0.02, $p > 0.05$, Table 2.7), only marginally increasing at temperatures above 33.55 °C (slope = 0.4, $p > 0.05$, Table 2.7).

In our segmented model of heart rate as a response to ambient temperature, we found that ambient temperature ($T = -4.8$, $p < 0.0001$), wind and humidity index ($T = 3.8$, $p > 0.0002$), days of incubation ($T = 20.0$, $p < 0.0001$), standardized lay day ($T = 14.7$, $p > 0.0001$), ordinal date ($T = -20.7$, $p < 0.0001$) and year (2023 statistically different from 2019, $p = 0.0008$) were all significantly related to variation in heart rate (Table 2.8). Specifically, we detected three significant breakpoints within our model, the first was located at an ambient temperature of 8.7 °C ($p < 0.01$, Table 2.9), the second at 9.0 °C ($p < 0.008$, Table 2.9), and the third at 16.6 °C ($p < 0.0001$, Table 2.9). Breakpoints 8.7 °C and 9 °C are likely a single breakpoint, but due to a lack of heart rate data between the two temperature values (Figure 2.12) they are split into two. A gradual decline in heart rate can be seen as temperatures increase from the lowest recorded temperature of 2.4 °C up to 8.7 °C (slope = -0.5, $p < 0.05$, Table 2.10) before we see a sudden drop in temperature between 8.7- 9 °C (slope = -34.4, $p < 0.01$, Table 2.10). Though not statistically detectable, heart rate then appeared to steadily increase from 9 °C to temperatures of 16.6 °C (slope = 1.7, $p > 0.05$, Table 2.10). Although beyond 16.6 °C heart rate appeared to decline, this slope was not significant (slope = -3.8, $p > 0.05$, Table 2.10), with notably few data in this region (Figure 2.12).

Discussion

We aimed to explore the influence of weather parameters on Arctic breeding and incubating common eiders' changes in heart rate, a physiological signal of heat stress, to determine if they are currently experiencing heat stress in their breeding environment and how this may affect their fixed energetic budget during their incubation. We predicted that heart rate would increase past a nest-level and ambient temperature inflection point, whereby heat-stressed females would then increase energy production towards fueling physiological cooling mechanisms to maintain a stable internal body temperature. Further, we predicted that other weather factors, compiled into a thermal index and a wind and humidity index, would influence hens' heat stress and thus change heart rate. Consistent with our predictions, we found that female incubating eiders are beginning to show signs of heat stress, with nest-level temperature marginally increasing heart rate past an inflection point, and conversely, ambient temperature marginally decreasing heart rate past an inflection point, though heart rate data was scarce beyond the ambient temperature inflection point. Further, we found that heart rate was significantly affected by both the thermal index and wind and humidity index. Below, we examine in further detail the temperature and weather correlations with heart rate, as well as, briefly, interactions with breeding parameters to better understand if eiders are heat stressed and the potential trade-offs occurring between thermoregulation and reproduction in heat-stressed hens. These findings lead us to a better understanding of eider hens' capacity to respond to heat stress, a question of increasing urgency as climate change accelerates in the Arctic, and we still lack evidence on endotherm's physiological mechanisms of response to heat stress, particularly when occurring with other energetically expensive life history events such as reproduction.

Upward trend in heart rate emerges at nest-level temperatures above 33 °C

We predicted that heart rate responses to temperature would follow a similar pattern of a Scholander-Irving curve (Scholander et al., 1950). This curve visualizes how the basal metabolic rate of an endotherm remains stable and low within a range of ambient temperatures, known as the thermal neutral zone, where no or minimal additional energy is needed for thermoregulation. Once temperatures exceed the upper bound, or drop below the lower bound, of the thermal neutral zone, described as the upper and lower critical temperatures (UCT and LCT, respectively), metabolic rate must increase to fuel more active methods of thermoregulating (Dawson & O'Connor, 1996). We found that, as predicted, eiders do increase their heart rate above a temperature inflection point, though only marginally so within our current dataset. Specifically, heart rate began increasing at nest-level temperatures of 33.6 °C, which we suspect to be their UCT in nest-level temperature. This is, to our knowledge, the first estimate of a heat stress response threshold for this species during incubation or, even more generally, in summer-acclimatized eiders. We chose to specifically focus on nest-level temperature in this study, given that recent studies on heat stress have highlighted the importance of moving beyond ambient temperature, and to examine other environmental factors that can have a significant influence on how quickly an individual becomes heat stressed (Liu et al., 2019; Rezende & Bacigalupe, 2015). For example, some studies have evaluated the significance of radiative sunlight and wind with ambient temperature, to focus more on evaluating the operative temperature of a species (Fortin et al., 2000; O'Connor et al., 2022), which describes the temperature of an object with the same size, shape and colour (same radiative properties) as a species whose operative temperature is in question (Dzialowski, 2005). This gives a better idea of the thermal comfort level the species or individual is experiencing in its given environment.

Particularly for seabirds, heat from direct sun has been identified as a significant contributor to heat stress (Choy et al., 2021; Olin et al., 2023; Snell et al., 2024). Indeed, sunlight can be a particularly important feature for heat stress in open-habitat nesting birds (Choy et al., 2021), or ground nesters (With & Webb, 1993). For example, the black back of thick-billed murres (*Uria lomvia*), a cliff-nesting seabird, can register at 46 °C during sun exposure, even when ambient temperatures are as low as 23 °C (Choy et al., 2021). These results are similar to our findings of environmental factors experienced by female incubating eiders, where on sunny days, nest-level temperatures (a metric that contains radiative heat) were far warmer than our recorded ambient temperatures across the island. In fact, our results for nest-level temperatures were precisely the pattern we would expect to see in a species response to warming temperatures outside of their thermal neutral zone, though we saw only a weak effect. We found this marginal increase in heart rate to occur beyond a nest-level temperature threshold of 33.6 °C (which may be equated to 10.2 °C in ambient temperature). Due to our precise sampling rate of nest-level temperature (2-minute intervals), we had a large distribution and sample size of temperatures with heart rate recorded around this threshold, providing further support that though only a marginal increase, this inflection point may hold great ecological significance to eiders perceived heat stress at these nesting temperatures, and the beginning of employing a physiological response to cool themselves.

These marginal increases in heart rate, may be associated to the use of physiological cooling mechanisms, such as panting, though not yet causing any significant changes in metabolic rate (associated to significant changes in heart rate). For example, in the thick-billed murre study (Choy et al., 2021), although resting metabolic rate was determined to significantly increase at ambient temperatures beyond 29.9°C, birds began to steeply increase evaporative water loss at ambient temperatures as low as 21.2°C. So, these birds were likely using active cooling methods, like panting, to maintain a constant internal body temperature, though not yet greatly increasing their metabolic rate to do so. Thick-billed murre parents share incubation duties and thus can take breaks in cool water recesses while feeding (Choy et al., 2021; Ito et al., 2010). However, female common eiders do not have this flexibility, and so, if they are also using these evaporative cooling methods, at what might appear to be relatively mild temperatures, this could result in them quickly becoming dehydrated past this upper boundary we've explored. Dehydration can have negative consequences both for a female's health, and also to her ducklings through increased predation risk if she should choose to leave the nest for water (Bottitta et al., 2003). Further, if a hen chooses to remain on the nest, she will expectedly metabolize more body fat to free water and prevent severe dehydration, but at the cost of depleting incubation energy reserves faster (Bourne et al., 2021). Thus, as we have begun to determine here with nest-level temperature, ambient temperature alone may not be the best indicator of when an individual is becoming heat stressed, and nest-level temperature should be carefully examined as an indicator of heat stress.

In our results of heart rate response to nest-level temperature, we also found a heart rate inflection point at 19.3 °C (associated with an ambient temperature of 5.6 °C), below which, eiders increased their heart rate. We suspect this defines the lower boundary of eiders thermal neutral zone, i.e. the lower critical temperature (LCT), below which hens need to increase energy production towards generating metabolic heat to stay warm. A comparison of the LCTs' found in this study and those previously identified in other eider studies are discussed in more detail in the following section on ambient temperature.

Early signs of a heart rate response emerge at ambient temperatures beyond 16 °C

Most studies examining the thermal neutral zone of a species, or performance curves, use ambient temperature as the primary predictive variable of a response (Choy et al., 2021; Levesque & Marshall, 2021; Scholander et al., 1950), whether that response is a change in heart rate, body temperature, metabolic rate, or even behaviour (Dawson & O'Connor, 1996; Liu et al., 2019; Pereira & Nääs, 2008; Scholander et al., 1950). We found that female incubating eiders showed a marginal response to potential heat stress by decreasing their heart rate at temperatures above an inflection point of 16.6 °C, though we do not believe this threshold accurately depicts the location of a UCT for this species due to data sparsity. A recent critique paper by McKechnie et al., found that a previous study (Khaliq et al., 2014) compiling hundreds of species heat stress response thresholds from the literature (46.2% of which were avian studies), were too close to the edge of provided datasets to be of great statistical, or biological, significance (McKechnie et al., 2017). Though our study's sample size would be adequate for an accurate assessment of a species' heat tolerance during incubation, we particularly lack heart rate data at our highest recorded ambient temperatures and, as such, further data at higher ambient temperatures would be necessary to validate this threshold (McKechnie et al., 2017). Nonetheless, the changes in heart rate at temperatures surrounding 16.6 °C do indicate that hens are starting to respond to higher temperatures and may be approaching a state of heat stress.

Potential decreases in eider heart rate beyond 16.6 °C may indicate that the birds are applying different strategies to respond to heat stress that are less energetic than a heart rate or metabolic response. For example, hens may be allowing their body temperature to rise, a process often referred to as adaptive thermoregulation in endotherms (Boyles et al., 2011). Similarly, hens may be taking advantage of more behavioural thermoregulatory responses to offset physiological costs, such as spreading out their wings for greater surface area of heat loss (Bartholomew & Dawson, 1979). A previous study that recorded winter-acclimatized common eiders' metabolic responses to temperatures as high as 32 °C, found indication of a metabolic heat stress response in three individuals at the upper end of these temperatures (Jenssen et al., 1989). However, despite this increase in metabolic rate at 32 °C, birds were able to increase conductance rates, allowing greater passive heat dissipation, at temperatures as low as 0 °C (Jenssen et al., 1989), which may assist in delaying the need for active cooling methods. As such, our detection of a slight decrease in heart rate may indicate that hens are employing such passive cooling methods to avoid energy loss. In incubating birds, another efficient method of passive heat loss may include increasing heat transfer from their body to their eggs. This is an effective way for parents to increase conductive heat loss, however, highlights the complexity of costs and benefits of heat stress responses. because it may cause changes in the heat tolerance of offspring (Lourens et al., 2005; Morita et al., 2016).

Our results also found a second inflection point at ~9 °C, below which eider heart rate increased with decreasing ambient temperature. We suspect this threshold defines a lower bound of the thermal neutral zone (i.e. LCT) in our incubating hens, where birds need to increase energy production towards generating body heat to stay warm and continue warming their eggs, which we also found in the heart rate relationship with nest-level temperature. In support of our LCT in temperatures relationship with heart rate, an increase in metabolic rate at the lower bound of the thermal neutral zone in eiders has been observed in multiple studies (Gabrielsen et al., 1991; Jenssen et al., 1989), although the specific ambient temperatures of the inflection points, the state of the birds, and the seasonal timing of the work varied across the studies. For example, Gabrielson et al., (1991) measured Resting Metabolic Rate (RMR) in 12 wild, non-incubating eiders during the summer, and reported a LCT of 7 °C. In their measurement of the basal metabolic rate (BMR) of winter acclimated common eiders' across a range of ambient temperatures, Jenssen et al., (1989) reported an LCT of approximately 0 °C, though they detected an increase in BMR as early as 1.5 °C (Jenssen et al., 1989). Thus, our results suggest that, as expected, summer-acclimated, free-living incubating common eiders have an LCT that is shifted to warmer ambient temperatures compared to winter-acclimated birds.

Impact of additional weather factors on eider heart rate

The thermal index had a positively loaded dew point, wet bulb temperature, heat index, and wind chill, and was positively correlated to heart rate. As such, the thermal index may be similar to eiders ‘perceived’ temperature of their environment, closely related to components of a species operative temperature (O'Connor et al., 2022). Studies suggest that operative temperatures are more accurate predictors of heat stress than examination of ambient temperature effect alone (Dzialowski, 2005). Our thermal index results suggest that as eiders perceive a warmer environment, they increase their heart rate, as anticipated if the hens require active thermoregulatory responses to maintain body temperature. Our wind and humidity index was comprised of wind speed, and humidity, both positively loaded, and was negatively associated to heart rate. High winds associated with a lowered heat stress response (i.e. low heart rate) is on par with other studies of heat stress in avian parents, which note wind’s ability to alleviate heat stress effects (Braimoh-Azaki et al., 2023; Cook et al., 2020; Oswald & Arnold, 2012). Heat stress studies also note humidity’s role in increasing the risk of heat stress by inhibiting the effectiveness of evaporative heat loss (e.g. panting) (Gerson et al., 2014; Van Dyk et al., 2019). However, in our study, we found high humidity was also associated with high winds, which had an effect in lowering heart rate, suggesting that wind speed likely has a more prevailing impact on heat stress effects in eiders. This may be a trend in other Arctic-breeding seabirds, as they expectedly experience a similar humidity and wind effect from breeding near large bodies of water. These results highlight the complexity of weather influences on heat stress responses and an organism's susceptibility to heat stress in its environment, indicating the importance of studying heat stress in wild populations in the field.

Impact of reproductive investment and season on heart rate

Although our primary focus was the impact of thermal stress, we also controlled for both the timing of breeding and reproductive investment, as well as the influence of annual and individual variation in heart rate. As expected, standardized lay date, incubation stage, and ordinal date were all related to the heart rate of female common eiders during incubation. As standardized lay date increased, so did heart rate, meaning that females laying earlier had lower heart rates. We suspect that earlier-laying females had lower heart rates because they are of higher quality and likely more experienced mothers. Indeed, early laying female common eiders in our population typically arrive at breeding grounds earlier and heavier than later laying females, and both traits are linked to higher breeding success (Descamps et al., 2011a). Further, earlier laying females tend to be older and more experienced at breeding than late laying hens (Baillie & Milne, 1982). As such, birds laying later in the season may tend to have elevated heart rates because their lack of breeding experience results in greater stress levels and hypervigilance during the breeding period (Angelier et al., 2007; Goutte et al., 2010). Increases in heart rate can be an indicator that the automatic sympathetic nervous system response is being triggered, and so we would suspect a similar heart rate response when they are being impacted by reproductive hypervigilance and stress (Cabanac & Guillemette, 2001). Therefore, inexperienced later laying hens may be more vulnerable to heat stress effects during their incubation (Nord & Nilsson, 2019).

Regarding ordinal date, we may see lower heart rates later in the season due to females depleting more of their fat reserves and needing to conserve energy (Gabrielsen et al., 1991; McNally, 1941) (smaller bodies, lower quality; Williams et al., 2008). However, we have an additional temperature element that may be at play, as generally speaking, ambient and nest-level temperatures are warmer later in the season, meaning that a later ordinal date will generally be associated with greater exposure to high environmental temperatures (MacDonald et al., unpubl data). We found that eiders increase their heart rate, though only marginally so, when exposed to high temperatures, so a decrease in heart rate across ordinal date could possibly be attributed to stressed low-quality hens (that expectedly have higher heart rates; Cabanac & Guillemette, 2001), losing their clutches to predation, or abandonment, earlier on in the season. Alternatively, to these findings, we found that as incubation stage increased, heart rate significantly increased, as well. This is contrary to previous work by Gabrielson et al., in which they found incubating eiders energy expenditure decreases as females lost body mass during their incubation (Gabrielsen et al., 1991). Similarly, previous research on eiders from Qiqiktakuluk found changes in heart rate response decreased as incubation progressed (Geldart et al., 2023). In the context of Geldart et al.'s study, decreased changes in heart rate were associated with a lower response to stimuli (Geldart et al., 2023). However, another recent study found eider heart rate during incubation to be lowest 2 days following the laying of their fourth egg, before increasing steadily throughout the first third of their incubation period (Guillemette & Pelletier, 2022). Despite these results, we suspect that in our common eider hens, an increase in heart rate as incubation progresses is associated with a dire need to access and metabolize body energy reserves (Parker & Holm, 1990), a process that can be mediated by the stress hormone corticosterone (Cherel et al., 1988). Indeed, although corticosterone and heart rate are mediated by different pathways in birds (Nephew et al., 2003), heart rate is correlated to energy expenditure in eiders (Hawkins et al., 2000), which may link the two responses during late stages of incubation. For example, in female incubating wood ducks (*Aix sponsa*) (also a uniparental incubating species) stress-induced circulation of corticosterone in hens can be 105% higher in later stages of incubation, as compared to early stages, and is associated with an increased need to free energy reserves for survival (DuRant et al., 2013). Further, during late stages of incubation, wood duck hens with lower body masses had higher corticosterone (DuRant et al., 2013). As such, we expect to see a similar relationship between corticosterone and incubation stage in eiders, where energy-depleted females in late stages of incubation (Parker & Holm, 1990) need high corticosterone levels to quickly metabolize fat and protein for their survival. As a result, we suggest that eiders increase in heart rate as incubation progresses may be a stress response (Cabanac & Guillemette, 2001) associated with this greater circulation of corticosterone in energy-depleted hens (DuRant et al., 2013).

Given these results, females later into the season (ordinal date), as well as females in later stages of incubation, may be particularly susceptible to heat stress effects due to their incredibly depleted energetic reserves. This underscores that although we did not see statistically significant increases in heart rate in heat-stressed hens, even marginal energetic costs of physiologically responses to heat stress during this time can be detrimental to hen survival or clutch survival. Further, hens may be pushed to abandon their clutch when heat stressed later in the season or later in incubation, as high corticosterone levels are often associated with reduced prolactin levels, a hormone that typically drives parental care (Criscuolo et al., 2005; Shoji et al., 2013).

Significance

Though the Arctic-breeding female eiders we studied here are physiologically responsive to rising temperatures, particularly nest-level temperature, we are not yet seeing high enough temperatures to elicit a statistically significant response in heart rate. In the short term, this may be encouraging news for low Arctic populations of common eiders. However, as the Arctic is predicted to continue to warm, and experience greater extreme weather events in the coming decade, this is a critical avenue to be monitored in arctic cold-adapted species, especially birds (Oswald & Arnold, 2012). Moreover, while low Arctic populations face predictable diel cycles in solar radiation, high Arctic populations can face multiple complete days of strong solar radiation making them more susceptible to thermal stress (O'Connor et al., 2022). Particularly during such an energetically and behaviourally constrained activity, as incubation is for eiders, the health and size of future generations may be severely impacted by effects of heat stress during this period, resulting in higher rates of nest failure.

Species with the ability to use multiple avenues of response may have a larger capacity to respond to a changing environment (Monaco et al., 2017), and as such, it is critical to explore more than physiological responses when trying to determine climate change's direct effects on eiders. One response category well known for offsetting physiological responses to changing environmental conditions and playing a significant role in how responsive an organism can be is behaviour (Abram et al., 2017; Long et al., 2014). As such, to gain a complete picture of eiders' capacity to adaptively respond to heat stress in their environment, we will require an analysis of their physiological and behavioural responses to changes in temperature and environmental conditions.

References

Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. *Biol Rev Camb Philos Soc*, *92*(4), 1859-1876. https://doi.org/10.1111/brv.12312

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O'Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences*, *114*(9), 2283-2288.

Alerstam, T., & Högstedt, G. (1982). Bird Migration and Reproduction in Relation to Habitats for Survival and Breeding. *Ornis Scandinavica (Scandinavian Journal of Ornithology)*, *13*(1), 25-37. https://doi.org/10.2307/3675970

AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C., & Székely, T. (2011). Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Animal Behaviour*, *82*(2), 235-243. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.04.019

AMAP. (2021). *Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers.*

Andreasson, F., Nilsson, J.-Å., & Nord, A. (2020). Avian reproduction in a warming world. *Frontiers in Ecology and Evolution*, *8*, 576331.

Angelier, F., Weimerskirch, H., Dano, S., & Chastel, O. (2007). Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behavioral Ecology and Sociobiology*, *61*(4), 611-621. https://doi.org/10.1007/s00265-006-0290-1

Baillie, S. R., & Milne, H. (1982). The influence of female age on breeding in the Eider Somateria mollissima. *Bird Study*, *29*(1), 55-66. https://doi.org/10.1080/00063658209476738

Bartholomew, G. A., & Dawson, W. R. (1979). Thermoregulatory behavior during incubation in Heermann's Gulls. *Physiological Zoology*, *52*(4), 422-437.

Bateman, B. L., Wilsey, C., Taylor, L., Wu, J., LeBaron, G. S., & Langham, G. (2020). North American birds require mitigation and adaptation to reduce vulnerability to climate change. *Conservation Science and Practice*, *2*(8), e242. https://doi.org/https://doi.org/10.1111/csp2.242

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1), 1-48. https://doi.org/10.18637/jss.v067.i01

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Smith, F. A., & Lawler, J. J. (2017). Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, *15*(6), 299-308.

BirdLife International. (2018). *Somateria mollissima. The IUCN Red List of Threatened Species 2018*.

Bottitta, G. E., Nol, E., & Gilchrist, H. G. (2003). Effects of Experimental Manipulation of Incubation Length on Behavior and Body Mass of Common Eiders in the Canadian Arctic. *Waterbirds*, *26*(1), 100-107, 108. https://doi.org/10.1675/1524-4695(2003)026[0100:EOEMOI]2.0.CO;2

Bourne, A. R., Ridley, A. R., McKechnie, A. E., Spottiswoode, C. N., & Cunningham, S. J. (2021). Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the southern pied babbler Turdoides bicolor. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coab043

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change. *Integrative and Comparative Biology*, *51*(5), 676-690. https://doi.org/10.1093/icb/icr053

Braimoh-Azaki, B. D., Cunningham, S. J., & Cresswell, W. (2023). Incubation scheduling by African Black Oystercatchers: effects of weather, tide phase, and time of day. *Journal of Ornithology*, *164*(1), 139-149.

Buchholz, R., Banusiewicz, J. D., Burgess, S., Crocker-Buta, S., Eveland, L., & Fuller, L. (2019). Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour*, *150*, 127-137. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.005

Cabanac, A., & Guillemette, M. (2001). Temperature and heart rate as stress indicators of handled common eider. *Physiology & Behavior*, *74*(4-5), 475-479.

Cherel, Y., Robin, J. P., Walch, O., Karmann, H., Netchitailo, P., & Le Maho, Y. (1988). Fasting in king penguin. I. Hormonal and metabolic changes during breeding. *American Journal* *of Physiology-Regulatory, Integrative and Comparative Physiology*, *254*(2), R170-R177. https://doi.org/10.1152/ajpregu.1988.254.2.R170

Chown, S. L., Hoffmann, A. A., Kristensen, T. N., Angilletta Jr, M. J., Stenseth, N. C., & Pertoldi, C. (2010). Adapting to climate change: a perspective from evolutionary physiology. *Climate research*, *43*(1-2), 3-15.

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F., & Elliott, K. H. (2021). Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. *Journal of Experimental Biology, 224*(13), jeb242168.

Christensen, T. K., & Balsby, T. J. S. (2020). Condition dependent strategies of egg size variation in the Common Eider Somateria mollissima. *PLoS One, 15*(7), e0226532.

Comrey, A. L., & Lee, H. B. (2013). *A first course in factor analysis*. Psychology press.

Cook, T. R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., Meyer, C., Sparks, E., Underhill, L. G., Ryan, P. G., & Sherley, R. B. (2020). Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conservation Physiology*, *8*(1), coz109.

Cooper, C. E., Hurley, L. L., Deviche, P., & Griffith, S. C. (2020). Physiological responses of wild zebra finches (Taeniopygia guttata) to heatwaves. *Journal of Experimental Biology, 223*(12). https://doi.org/10.1242/jeb.225524

Criscuolo, F., Chastel, O., Bertile, F., Gabrielsen, G. W., Maho, Y. L., & Raclot, T. (2005). Corticosterone alone does not trigger a short term behavioural shift in incubating female common eiders Somateria mollissima, but does modify long term reproductive success. *Journal of Avian Biology, 36*(4), 306-312. https://doi.org/https://doi.org/10.1111/j.0908-8857.2005.03371.x

D'alba, L., Carlsen, T. H., Ásgeirsson, Á., Shawkey, M. D., & Jónsson, J. E. (2017). Contributions of feather microstructure to eider down insulation properties. *Journal of Avian Biology*, *48*(8), 1150-1157.

Dawson, W. R., & O'Connor, T. P. (1996). Energetic features of avian thermoregulatory responses. *Avian energetics and nutritional ecology*, 85-124.

Descamps, S., Bêty, J., Love, O. P., & Gilchrist, H. G. (2011a). Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. *Functional Ecology*, *25*(3), 671-681. https://doi.org/https://doi.org/10.1111/j.1365-2435.2010.01824.x

Descamps, S., Forbes, M. R., Gilchrist, H. G., Love, O. P., & Bêty, J. (2011b). Avian cholera, post-hatching survival and selection on hatch characteristics in a long-lived bird, the common eider Somateria mollisima. *Journal of Avian Biology*, *42*(1), 39-48. https://doi.org/https://doi.org/10.1111/j.1600-048X.2010.05196.x

Descamps, S., Jenouvrier, S., Gilchrist, H. G., & Forbes, M. R. (2012). Avian cholera, a threat to the viability of an Arctic seabird colony? *PLoS One*, *7*(2), e29659.

Dey, C. J., Semeniuk, C. A. D., Iverson, S. A., Richardson, E., McGeachy, D., & Gilchrist, H. G. (2018). Forecasting the outcome of multiple effects of climate change on northern common eiders. *Biological Conservation*, *220*, 94-103. https://doi.org/https://doi.org/10.1016/j.biocon.2018.02.007

DuRant, S. E., Hopkins, W. A., Hepp, G. R., & Romero, L. M. (2013). Energetic constraints and parental care: is corticosterone indicative of energetic costs of incubation in a precocial bird? *Horm Behav*, *63*(2), 385-391. https://doi.org/10.1016/j.yhbeh.2012.12.001

Dzialowski, E. M. (2005). Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, *30*(4), 317-334. https://doi.org/https://doi.org/10.1016/j.jtherbio.2005.01.005

Environment and Climate Change Canada. (2024). *Historical Data.* Government of Canada. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Fast, P. L., Gilchrist, H. G., & Clark, R. G. (2010). Nest-site materials affect nest-bowl use by Common Eiders (Somateria mollissima). *Canadian Journal of Zoology*, *88*(2), 214-218.

Fast, P. L. F., Grant Gilchrist, H., & Clark, R. G. (2007). Experimental evaluation of nest shelter effects on weight loss in incubating common eiders Somateria mollissima. *Journal of Avian Biology*, *38*(2), 205-213. https://doi.org/https://doi.org/10.1111/j.0908-8857.2007.03820.x

Favilla, A. B., & Costa, D. P. (2020). Thermoregulatory strategies of diving air-breathing marine vertebrates: a review. *Frontiers in Ecology and Evolution*, *8*, 555509.

Fei, S., Desprez, J. M., Potter, K. M., Jo, I., Knott, J. A., & Oswalt, C. M. (2017). Divergence of species responses to climate change. *Science Advances*, *3*(5), e1603055. https://doi.org/doi:10.1126/sciadv.1603055

Forkman, J., Josse, J., & Piepho, H.-P. (2019). Hypothesis tests for principal component analysis when variables are standardized. *Journal of Agricultural, Biological and Environmental Statistics*, *24*, 289-308.

Fortin, D., Larochelle, J., & Gauthier, G. (2000). The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. *Journal of Thermal Biology*, *25*(3), 227-238. https://doi.org/https://doi.org/10.1016/S0306-4565(99)00028-5

Fuller, A., Dawson, T., Helmuth, B., Hetem, Robyn S., Mitchell, D., & Maloney, Shane K. (2010). Physiological Mechanisms in Coping with Climate Change. *Physiological and Biochemical Zoology*, *83*(5), 713-720. https://doi.org/10.1086/652242

Gabrielsen, G. W., Mehlum, F., Karlsen, H. E., Andresen, Ø., & Parker, H. (1991). Energy cost during incubation and thermoregulation in the female common eider Somateria mollissima. *Norsk Polarinstitutt Skrifter*, *195*, 51-62.

Gagnon, A. S., & Gough, W. A. (2005). Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic*, 370-382.

Gaston, A. J., Hipfner, J. M., & Campbell, D. (2002). Heat and mosquitoes cause breeding failures and adult mortality in an Arctic-nesting seabird. *Ibis*, *144*(2), 185-191.

Gavrilov, V. M., Golubeva, T. B., Warrack, G., & Bushuev, A. V. (2022). Metabolic Scaling in Birds and Mammals: How Taxon Divergence Time, Phylogeny, and Metabolic Rate Affect the Relationship between Scaling Exponents and Intercepts. *Biology (Basel)*, *11*(7). https://doi.org/10.3390/biology11071067

Geldart, E. A., Barnas, A. F., Semeniuk, C. A., Gilchrist, H. G., Harris, C. M., & Love, O. P. (2022). A colonial-nesting seabird shows no heart-rate response to drone-based population surveys. *Scientific reports*, *12*(1), 1-10.

Geldart, E. A., Love, O. P., Gilchrist, H. G., Barnas, A. F., Harris, C. M., & Semeniuk, C. A. (2023). Heightened heart rate but similar flight responses to evolved versus recent predators in an Arctic seabird. *Avian Conservation and Ecology*, *18*(1).

Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology*, *87*(6), 782-795.

Götmark, F., & Åhlund, M. (1984). Do Field Observers Attract Nest Predators and Influence Nesting Success of Common Eiders? *The Journal of Wildlife Management*, *48*(2), 381-387. https://doi.org/10.2307/3801169

Goutte, A., Antoine, É., Weimerskirch, H., & Chastel, O. (2010). Age and the timing of breeding in a long-lived bird: a role for stress hormones? *Functional Ecology*, *24*(5), 1007-1016. https://doi.org/https://doi.org/10.1111/j.1365-2435.2010.01712.x

Grunst, M. L., Grunst, A. S., Grémillet, D., Kato, A., Gentès, S., & Fort, J. (2023). Keystone seabird may face thermoregulatory challenges in a warming Arctic. *Scientific reports*, *13*(1), 16733. https://doi.org/10.1038/s41598-023-43650-5

Guillemette, M., & Pelletier, D. (2022). Egg-laying increases body temperature to an annual maximum in a wild bird. *Sci Rep*, *12*(1), 1681. https://doi.org/10.1038/s41598-022-05516-0

Hamer, K. C., Schreiber, E., & Burger, J. (2001). Breeding biology, life histories, and life history-environment interactions in seabirds. *Biology of marine birds*, *45*, 217-261.

Hanssen, S. A., Einar Erikstad, K., Johnsen, V., & Jan, O. B. (2003). Differential investment and costs during avian incubation determined by individual quality: an experimental study of the common eider (<i>Somateria mollissima</i>). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1514), 531-537. https://doi.org/doi:10.1098/rspb.2002.2262

Hanssen, S. A., Engebretsen, H., & Erikstad, K. (2002). Incubation start and egg size in relation to body reserves in the common eider. *Behavioral Ecology and Sociobiology*, *52*, 282-288.

Hanssen, S. A., Hasselquist, D., Folstad, I., & Erikstad, K. E. (2005). Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1567), 1039-1046. https://doi.org/doi:10.1098/rspb.2005.3057

Harding, A. M., Welcker, J., Steen, H., Hamer, K. C., Kitaysky, A. S., Fort, J., Talbot, S. L., Cornick, L. A., Karnovsky, N. J., & Gabrielsen, G. W. (2011). Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia*, *167*, 49-59.

Hart, L. A., Downs, C. T., & Brown, M. (2016). Sitting in the sun: Nest microhabitat affects incubation temperatures in seabirds. *Journal of Thermal Biology*, *60*, 149-154. https://doi.org/https://doi.org/10.1016/j.jtherbio.2016.07.001

Hawkins, P., Butler, P., Woakes, A., & Speakman, J. (2000). Estimation of the rate of oxygen consumption of the common eider duck (Somateria mollissima), with some measurements of heart rate during voluntary dives. *Journal of Experimental Biology*, *203*(18), 2819-2832.

Hennin, H. L., Bêty, J., Legagneux, P., Gilchrist, H. G., Williams, T. D., & Love, O. P. (2016). Energetic physiology mediates individual optimization of breeding phenology in a migratory Arctic seabird. *The American Naturalist, 188*(4), 434-445.

Henri, D. A., Jean-Gagnon, F., & Gilchrist, H. G. (2018). Using Inuit traditional ecological knowledge for detecting and monitoring avian cholera among Common Eiders in the eastern Canadian Arctic. *Ecology and Society, 23*(1).

Ito, M., Takahashi, A., Kokubun, N., Kitaysky, A. S., & Watanuki, Y. (2010). Foraging behavior of incubating and chick-rearing thick-billed murres Uria lomvia. *Aquatic Biology*, *8*(3), 279-287.

Iverson, S. A., Gilchrist, H. G., Smith, P. A., Gaston, A. J., & Forbes, M. R. (2014). Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20133128.

Jean-Gagnon, F., Legagneux, P., Gilchrist, G., Bélanger, S., Love, O. P., & Bêty, J. (2018). The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder. *Oecologia*, *186*(1), 1-10. https://doi.org/10.1007/s00442-017-4002-5

Jenssen, B. M., Ekker, M., & Bech, C. (1989). Thermoregulation in winter-acclimatized common eiders (Somateria mollissima) in air and water. *Canadian Journal of Zoology*, *67*(3), 669-673.

Khaliq, I., Hof, C., Prinzinger, R., Böhning-Gaese, K., & Pfenninger, M. (2014). Global variation in thermal tolerances and vulnerability of endotherms to climate change. *Proceedings of the Royal Society B: Biological Sciences, 281*(1789), 20141097. https://doi.org/doi:10.1098/rspb.2014.1097

Kristjánsson, T. Ö., & Jónsson, J. E. (2011). Effects of down collection on incubation temperature, nesting behaviour and hatching success of common eiders (Somateria mollissima) in west Iceland. *Polar Biology*, *34*(7), 985-994. https://doi.org/10.1007/s00300-010-0956-z

Kronfeld-Schor, N., & Dayan, T. (2013). Thermal Ecology, Environments, Communities, and Global Change: Energy Intake and Expenditure in Endotherms. *Annual Review of Ecology, Evolution, and Systematics*, *44*(Volume 44, 2013), 461-480. https://doi.org/https://doi.org/10.1146/annurev-ecolsys-110512-135917

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software, 82*(13), 1-26. https://doi.org/10.18637/jss.v082.i13

Lee, T., Schuman, J. S., Ramos Cadena, M. d. l. A., Zhang, Y., Wollstein, G., & Hu, J. (2024). LIMBARE: An Advanced Linear Mixed-Effects Breakpoint Analysis With Robust Estimation Method With Applications to Longitudinal Ophthalmic Studies. *Translational Vision Science & Technology*, *13*(1), 19-19. https://doi.org/10.1167/tvst.13.1.19

Legagneux, P., Hennin, H. L., Gilchrist, H. G., Williams, T. D., Love, O. P., & Bêty, J. (2016). Unpredictable perturbation reduces breeding propensity regardless of pre-laying reproductive readiness in a partial capital breeder. *Journal of Avian Biology*, *47*(6), 880-886.

Levesque, D. L., & Marshall, K. E. (2021). Do endotherms have thermal performance curves? *Journal of Experimental Biology*, *224*(3). https://doi.org/10.1242/jeb.141309

Liu, J., Li, L., Chen, X., Lu, Y., & Wang, D. (2019). Effects of heat stress on body temperature, milk production, and reproduction in dairy cows: a novel idea for monitoring and evaluation of heat stress — A review. *Asian-Australas J Anim Sci*, *32*(9), 1332-1339. https://doi.org/10.5713/ajas.18.0743

Lomas, S. C., Whisson, D. A., Maguire, G. S., Tan, L. X., Guay, P.-J., & Weston, M. A. (2014). The influence of cover on nesting red-capped plovers: a trade-off between thermoregulation and predation risk? *Victorian Naturalist, The*, *131*(4), 115-127.

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., & Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, *84*(3), 513-532. https://doi.org/https://doi.org/10.1890/13-1273.1

Lourens, A., van den Brand, H., Meijerhof, R., & Kemp, B. (2005). Effect of eggshell temperature during incubation on embryo development, hatchability, and posthatch development. *Poultry Science, 84*(6), 914-920. https://doi.org/https://doi.org/10.1093/ps/84.6.914

Love, O. P., Gilchrist, H. G., Descamps, S., Semeniuk, C. A., & Bêty, J. (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia*, *164*, 277-286.

Lüdecke, D. (2018). ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

McKechnie, A. E., Coe, B. H., Gerson, A. R., & Wolf, B. O. (2017). Data quality problems undermine analyses of endotherm upper critical temperatures. *Journal of Biogeography*, *44*(10), 2424-2426. https://doi.org/https://doi.org/10.1111/jbi.12941

McKinnon, L., Gilchrist, H. G., & Scribner, K. T. (2006). Genetic evidence for kin-based female social structure in common eiders (Somateria mollissima). *Behavioral Ecology*, *17*(4), 614-621.

McNally, E. (1941). Heart rate of the domestic fowl. *Poultry Science*, *20*(3), 266-271.

Monaco, C. J., McQuaid, C. D., & Marshall, D. J. (2017). Decoupling of behavioural and physiological thermal performance curves in ectothermic animals: a critical adaptive trait. *Oecologia*, *185*(4), 583-593. https://doi.org/10.1007/s00442-017-3974-5

Morita, V. S., Almeida, V. R., Matos Junior, J. B., Vicentini, T. I., van den Brand, H., & Boleli, I. C. (2016). Incubation temperature alters thermal preference and response to heat stress of broiler chickens along the rearing phase. *Poultry Science*, *95*(8), 1795-1804. https://doi.org/https://doi.org/10.3382/ps/pew071

Moritz, C., & Agudo, R. (2013). The Future of Species Under Climate Change: Resilience or Decline? *Science*, *341*(6145), 504-508. https://doi.org/doi:10.1126/science.1237190

Mosbech, A., Gilchrist, G., Merkel, F., Sonne, C., Flagstad, A., & Nyegaard, H. (2006). Year-round movements of northern common eiders Somateria mollissima borealis breeding in Arctic Canada and West Greenland followed by satellite telemetry. *ARDEA-WAGENINGEN-*, *94*(3), 651.

Nephew, B. C., Kahn, S. A., & Michael Romero, L. (2003). Heart rate and behavior are regulated independently of corticosterone following diverse acute stressors. *General and Comparative Endocrinology*, *133*(2), 173-180. https://doi.org/https://doi.org/10.1016/S0016-6480(03)00165-5

Nord, A., & Nilsson, J.-Å. (2019). Heat dissipation rate constrains reproductive investment in a wild bird. *Functional Ecology*, *33*(2), 250-259. https://www.jstor.org/stable/48582897

O'Connor, R. S., Le Pogam, A., Young, K. G., Love, O. P., Cox, C. J., Roy, G., Robitaille, F., Elliott, K. H., Hargreaves, A. L., & Choy, E. S. (2022). Warming in the land of the midnight sun: breeding birds may suffer greater heat stress at high-versus low-Arctic sites. *Proceedings of the Royal Society B, 289*(1981), 20220300.

O'Connor, R. S., Le Pogam, A., Young, K. G., Robitaille, F., Choy, E. S., Love, O. P., Elliott, K. H., Hargreaves, A. L., Berteaux, D., & Tam, A. (2021). Limited heat tolerance in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecology and evolution*, *11*(4), 1609-1619.

O’Connor, R. S., Love, O. P., Régimbald, L., Le Pogam, A., Gerson, A. R., Elliott, K. H., Hargreaves, A. L., & Vézina, F. (2024). An arctic breeding songbird overheats during intense activity even at low air temperatures. *Scientific reports*, *14*(1), 15193. https://doi.org/10.1038/s41598-024-65208-9

Olin, A. B., Dück, L., Berglund, P.-A., Karlsson, E., Bohm, M., Olsson, O., & Hentati-Sundberg, J. (2023). Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Marine Ecology Progress Series*.

Oswald, S. A., & Arnold, J. M. (2012). Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. *Integrative Zoology*, *7*(2), 121-136.

Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B., & Hamer, K. C. (2008). Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas Catharacta skua. *Journal of Avian Biology*, *39*(2), 163-169.

Ovaskainen, O., Skorokhodova, S., Yakovleva, M., Sukhov, A., Kutenkov, A., Kutenkova, N., Shcherbakov, A., Meyke, E., & Delgado, M. d. M. (2013). Community-level phenological response to climate change. *Proceedings of the National Academy of Sciences*, *110*(33), 13434-13439. https://doi.org/doi:10.1073/pnas.1305533110

Parker, H., & Holm, H. (1990). Patterns of Nutrient and Energy Expenditure in Female Common Eiders Nesting in the High Arctic. *The Auk*, *107*(4), 660-668. https://doi.org/10.2307/4087996

Pereira, D. F., & Nääs, I. A. (2008). Estimating the thermoneutral zone for broiler breeders using behavioral analysis. *Computers and Electronics in Agriculture*, *62*(1), 2-7. https://doi.org/https://doi.org/10.1016/j.compag.2007.09.001

R Development Core Team. (2024). *A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing. https://www.R-project.org/

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Reid, J., Monaghan, P., & Ruxton, G. (2000). Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1438), 37-41.

Revelle, W. (2024). *psych: Procedures for psychological, psychometric, and personality research*. https://CRAN.R-project.org/package=psych

Rezende, E. L., & Bacigalupe, L. D. (2015). Thermoregulation in endotherms: physiological principles and ecological consequences. *Journal of Comparative Physiology B*, *185*(7), 709-727. https://doi.org/10.1007/s00360-015-0909-5

Richman, S. E., & Lovvorn, J. R. (2011). Effects of Air and Water Temperatures on Resting Metabolism of Auklets and Other Diving Birds. *Physiological and Biochemical Zoology: Ecological and Evolutionary Approaches*, *84*(3), 316-332. https://doi.org/10.1086/660008

Ruuskanen, S., Hsu, B.-Y., & Nord, A. (2021). Endocrinology of thermoregulation in birds in a changing climate. *Molecular and Cellular Endocrinology*, *519*, 111088.

Sauser, C., Delord, K., & Barbraud, C. (2021). Sea ice and local weather affect reproductive phenology of a polar seabird with breeding consequences. *Ornithological Applications*, *123*(4). https://doi.org/10.1093/ornithapp/duab032

Scholander, P., Hock, R., Walters, V., Johnson, F., & Irving, L. (1950). Heat Regulation in Some Arctic and Tropical Mammals and Birds. *Biological Bulletin*, *99*(2), 237-258. https://doi.org/10.2307/1538741

Sejian, V., Bhatta, R., Gaughan, J. B., Dunshea, F. R., & Lacetera, N. (2018). Review: Adaptation of animals to heat stress. *animal*, *12*(s2), s431-s444. https://doi.org/10.1017/S1751731118001945

Shaw, R. G., & Etterson, J. R. (2012). Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist*, *195*(4), 752-765. https://doi.org/https://doi.org/10.1111/j.1469-8137.2012.04230.x

Shoji, A., Elliott, K. H., O'Reilly, K. M., & Gaston, A. J. (2013). High corticosterone, not high energy cost, correlates with reproductive success in the burrow-nesting ancient murrelet. *PLoS One*, *8*(12), e84280.

Snell, K. R., Aldará, J., Hammer, S., & Thorup, K. (2024). Thermal stress during incubation in an arctic breeding seabird. *Journal of Thermal Biology*, 103967.

Speakman, J. R., & Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, *79*(4), 726-746.

Stearns, S. (1989). Trade-Offs in Life-History Evolution. *Functional Ecology*, *3*(3), 259-268. https://doi.org/10.2307/2389364

Steenweg, R. J., Crossin, G. T., Hennin, H. L., Gilchrist, H. G., & Love, O. P. (2022). Favorable spring conditions can buffer the impact of winter carryover effects on a key breeding decision in an Arctic-breeding seabird. *Ecology and evolution*, *12*(2), e8588.

Tattersall, G. J., Sinclair, B. J., Withers, P. C., Fields, P. A., Seebacher, F., Cooper, C. E., & Maloney, S. K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperatures. *Compr Physiol*, *2*(3), 2151-2202.

Tulp, I., & Schekkerman, H. (2006). Time allocation between feeding and incubation in uniparental arctic-breeding shorebirds: energy reserves provide leeway in a tight schedule. *Journal of Avian Biology*, *37*(3), 207-218.

van de Ven, T. M. F. N., McKechnie, A. E., & Cunningham, S. J. (2019). The costs of keeping cool: behavioural trade-offs between foraging and thermoregulation are associated with significant mass losses in an arid-zone bird. *Oecologia*, *191*(1), 205-215. https://doi.org/10.1007/s00442-019-04486-x

Van Dyk, M., Noakes, M. J., & McKechnie, A. E. (2019). Interactions between humidity and evaporative heat dissipation in a passerine bird. *Journal of Comparative Physiology B, 189*(2), 299-308.

Vestbo, S., Hindberg, C., Olesen, J. M., & Funch, P. (2019). Eiders as Long Distance Connectors in Arctic Networks. *Cross-cultural research, 53*(3), 252-271. https://doi.org/10.1177/1069397118806820

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 649-659.

Waltho, C., & Coulson, J. (2015). *The common eider* (J. Martin, Ed.). Bloomsbury Publishing.

Welman, S., & Pichegru, L. (2023). Nest microclimate and heat stress in African Penguins Spheniscus demersus breeding on Bird Island, South Africa. *Bird Conservation International*, *33*, e34.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. https://CRAN.R-project.org/package=dplyr

Wilke, C. O. (2024). *cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'*. https://CRAN.R-project.org/package=cowplot

Williams, C. T., Kitaysky, A. S., Kettle, A. B., & Buck, C. L. (2008). Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *Gen Comp Endocrinol*, *158*(1), 29-35. https://doi.org/10.1016/j.ygcen.2008.04.018

Wingfield, J. C., Pérez, J. H., Krause, J. S., Word, K. R., González-Gómez, P. L., Lisovski, S., & Chmura, H. E. (2017). How birds cope physiologically and behaviourally with extreme climatic events. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1723), 20160140. https://doi.org/doi:10.1098/rstb.2016.0140

With, K. A., & Webb, D. R. (1993). Microclimate of Ground Nests: The Relative Importance of Radiative Cover and Wind Breaks for Three Grassland Species. *The Condor, 95*(2), 401-413. https://doi.org/10.2307/1369363

Zera, A. J., & Harshman, L. G. (2001). The physiology of life history trade-offs in animals. *Annual review of Ecology and Systematics*, *32*(1), 95-126.

Tables

Table 2.1 Examination of the impacts of weather conditions and breeding decisions on heart rate during incubation in female common eiders (*Somateria mollissima*) breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A Linear Mixed Effects Model to examine heart rate's response to nest-level temperature, thermal index, wind and humidity index, days of incubation, standardized lay date and ordinal date, with year and nest id as random effects.

Fixed effect	Estimate	Standard Error	T-Value	Pr(>|z|) (p-value)
Intercept	3384.25490	238.41168	14.195	< 2e-16***
Nest-Level Temperature	-0.60503	0.03215	-18.818	< 2e-16***
Thermal Index	3.09309	0.20786	14.880	< 2e-16***
Wind and Humidity Index	-1.69776	0.32767	-5.181	2.31e-07***
Days of Incubation	19.50349	1.36088	14.332	< 2e-16***
Standardized Lay Date	18.34263	1.55434	11.801	< 2e-16***
Ordinal Date	-19.12356	1.37292	-13.929	< 2e-16***

Table 2.2 Determining the impacts of weather conditions and breeding parameters on heart rate in common eider (*Somateria mollissima*) hens breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The random effects structure of Year and Nest ID, which are the random effects included in the model used to examine how heart rate is affected by weather and breeding parameters described in Table 2.1.

Random Effects	Variance	Standard Deviation
Year	72.10	8.491
Nest ID	265.18	16.284
Residuals	69.98	8.366

4197 observations, 3 year groups and 49 nest id groups.

Table 2.3 Examining the effects of weather conditions and breeding parameters on heart rate in female common eiders (*Somateria mollissima*) breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A Linear Mixed Effects Model for exploring heart rate's response to ambient temperature, wind and humidity index, days of incubation, standardized lay date and ordinal date, with year and nest id as random effects.

Fixed effect	Estimate	Standard Error	T-Value	Pr(>|z|) (p-value)
Intercept	3034.31181	245.88565	12.340	< 2e-16 ***
Ambient Temperature	0.14078	0.04903	2.871	0.00411
Wind and Humidity Index	3.72293	0.24286	15.330	< 2e-16 ***
Days of Incubation	17.86325	1.40465	12.717	< 2e-16 ***
Standardized Lay Date	16.59271	1.56920	10.574	< 2e-16 ***
Ordinal Date	-17.21513	1.41628	-12.155	< 2e-16 ***

Table 2.4 Examining how weather conditions and breeding decisions impact heart rate in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The random effects structure of Year and Nest ID, which are the random effects included in the model used to examine how weather and breeding parameters affect heart rate, as described in Table 2.3.

Random Effects	Variance	Standard Deviation
Year	112.79	10.620
Nest ID	240.83	15.519
Residuals	76.13	8.725

4197 observations, 3 year groups and 49 nest id groups.

Table 2.5 Examining weather conditions and breeding parameters effect on common eider (*Somateria mollissima*) hens' heart rate at a breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A segmented model of hens' heart rate with nest-level temperature as the segmented variable. The model examines additional fixed effects correlation to heart rate, including thermal index, wind and humidity index, days of incubation, standardized lay date, ordinal date, and year. Nest id is included as a random effect. We used 95% confidence intervals for all breakpoints.

Variables	Value	Std. Error	Degrees of Freedom	T-Value	P-Value
Intercept	2374.9382	150.70612	3719	15.758738	0.0000
Nest-Level Temperature	-1.9690	0.06987	3719	-15.699003	0.0000
Thermal Index	-0.4352	0.16020	3719	-2.716817	0.0066
Wind and Humidity Index	-0.7959	0.18698	3719	-4.256546	0.0000
Days of Incubation	14.0665	0.85162	3719	16.517283	0.0000
Standardized Lay Date	13.1753	1.11993	45	11.764463	0.0000
Ordinal Date	-13.3454	0.87052	3719	-15.330318	0.0000
Year (2022)	10.4654	6.93920	45	1.508153	0.1385
Year (2023)	9.1498	5.61999	45	1.628082	0.1105
Breakpoint 1	1.0803	0.10166	3719	10.626053	0.0000
Breakpoint 2	0.3932	0.09863	3719	3.986653	0.0001
Breakpoint 1 Confidence Interval	0.0000	0.60636	3719	0.000000	1.0000
Breakpoint 2 Confidence Interval	0.0000	0.96566	3719	0.000000	1.0000

Table 2.6 Examining how weather conditions and breeding parameters impact heart rate in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The estimated temperature breakpoints (°C), standard errors, and p-values of our segmented variable, nest-level temperature, from its segmented model with heart rate (see Table 2.5 for the segmented model summary).

	Estimation	Standard Error	P-Value
Breakpoint 1	19.24857	1.36004	0.0000
Breakpoint 2	33.55000	0.94711	0.0001

Table 2.7 Determining weather conditions and breeding parameters influence on common eider (*Somateria mollissima*) hens' heart rate at a breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The slope estimates, standard errors and confidence intervals (upper and lower bounds) for hens' heart rate's segmented relationship with nest-level temperature (see Table 2.5 for the segmented model summary).

Slope #	Estimate	Standard Error	P-Value	Lower Bound (95%)	Upper Bound (95%)
Slope 1	-1.0969	0.3888	0.0048	-1.8589	-0.3349
Slope 2	-0.0166	0.4908	0.9730	-0.9786	0.9453
Slope 3	0.3765	0.4654	0.4185	-0.5357	1.2890

Table 2.8 Examining the influence of weather conditions and breeding parameters on common eider (*Somateria mollissima*) hens' heart rate at a breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A segmented model of hens' heart rate with ambient temperature as the segmented variable. The model examines additional fixed effects, including, thermal index, wind and humidity index, days of incubation, standardized lay date, ordinal date, and year. Nest id is included as a random effect. We used 95% confidence intervals for all breakpoints.

Variables	Value	Std. Error	Degrees of Freedom	T-Value	P-Value
(Intercept)	3169.577	150.57781	3718	21.049428	0.0000
Ambient Temperature	-0.487	0.10124	3718	-4.806389	0.0000
Wind and Humidity Index	0.699	0.18527	3718	3.771140	0.0002
Days of Incubation	17.186	0.85971	3718	19.990725	0.0000
Standardized Lay Date	16.330	1.10948	45	14.719054	0.0000
Ordinal Date	-17.975	0.86967	3718	-20.668692	0.0000
Year (2022)	10.757	6.74755	45	1.594246	0.1179
Year (2023)	19.638	5.44675	45	3.605466	0.0008
Breakpoint 1	-33.909	13.57663	3718	-2.497575	0.0125
Breakpoint 2	36.045	13.57545	3718	2.655131	0.0080
Breakpoint 3	-5.398	1.34015	3718	-4.027700	0.0001
Breakpoint 1 Confidence Interval	0.000	0.12571	3718	0.000000	1.0000
Breakpoint 2 Confidence Interval	0.000	0.03096	3718	0.000000	1.0000
Breakpoint 3 Confidence Interval	0.000	0.18424	3718	0.000000	1.0000

Table 2.9 Assessing weather conditions and breeding parameters influence on heart rate in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The estimated temperature breakpoints (°C), standard errors, and p-values of our segmented variable, ambient temperature, from its segmented model with heart rate (see Table 2.8 for the segmented model summary).

	Estimation	Standard Error	P-Value
Breakpoint 1	8.697669	0.09581678	0.0125
Breakpoint 2	9.002701	0.08781418	0.0080
Breakpoint 3	16.584902	0.76670515	0.0001

Table 2.10 Determining weather conditions and breeding parameters influence on female common eiders (*Somateria mollissima*) heart rate at a breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The slope estimates, standard errors and confidence intervals (upper and lower bounds) for hens' heart rate's segmented relationship with ambient temperature (see Table 2.8 for the segmented model summary).

Slope #	Estimate	Standard Error	P-Value	Lower Bound (95%)	Upper Bound (95%)
Slope 1	-0.4866082	0.2098767	2.041979e-02	-0.8979665	-0.07524997
Slope 2	-34.3952694	5.9549878	7.655386e-09	-46.0670454	-22.72349338
Slope 3	1.6493223	3.1753610	6.034731e-01	-4.5743852	7.87302985
Slope 4	-3.7484073	3.3694652	2.659389e-01	-10.3525590	2.85574442

Figures

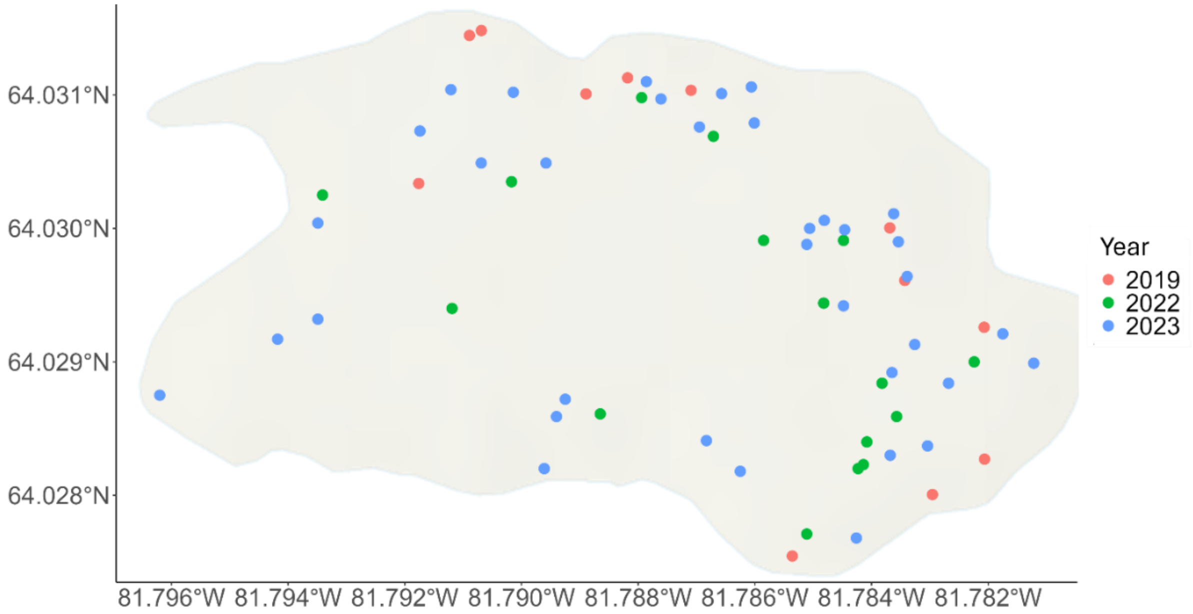


Figure 2.1 Latitude and Longitude coordinates of common eider (*Somateria mollissima*) nests sampled for examining weather and breeding parameters impact on heart rate, an indicator of heat stress, across three years of study (2019, 2022, 2023), underlaid by a map of East Bay Island (Qikiqtakuluk), Nunavut, Canada where the study was conducted.

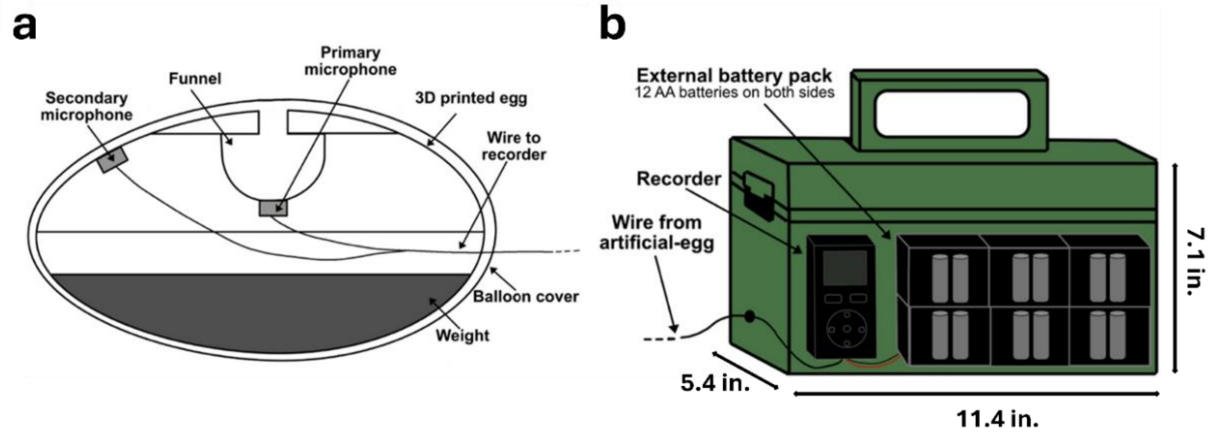


Figure 2.2 Nest deployment equipment used in our study of the impacts of heat stress on female common eider (*Somateria mollissima*) heart rate, at an Arctic-breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. **a)** microphone egg interior anatomy and **b)** interior storage of the external battery pack and Tascam audio recorder (figures by Geldart et al., 2022).

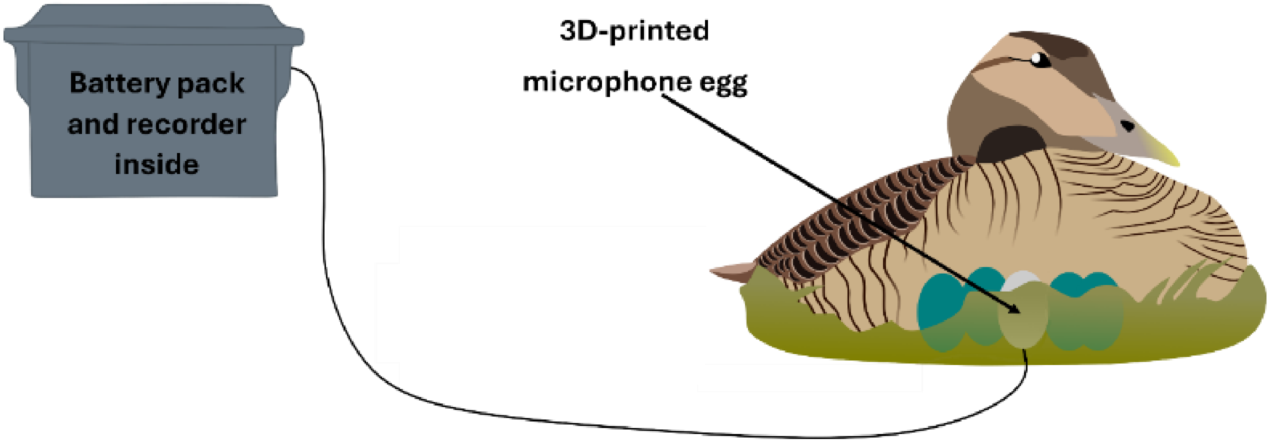


Figure 2.3 Nest deployment of microphone egg and Tascam recorder used in our study of heat stress' impacts on incubating common eiders (*Somateria mollissima*) heart rate at an Arctic-breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada.

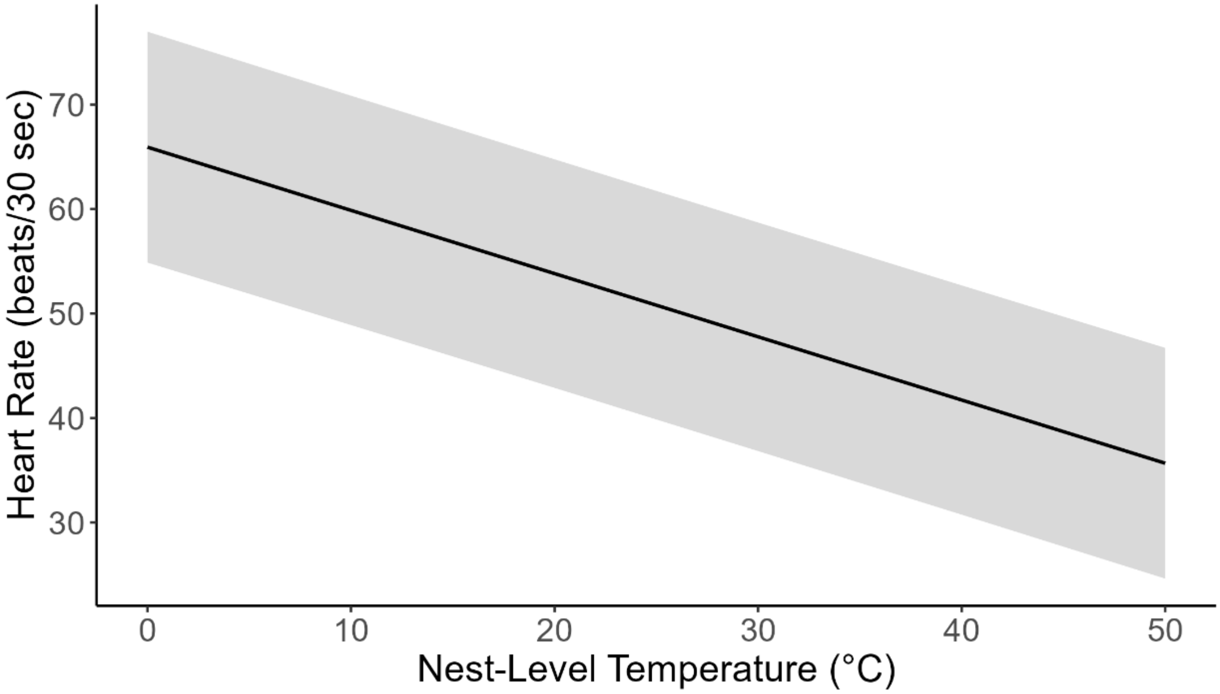


Figure 2.4 Examining the effect of nest-level temperature on heart rate in incubating common eider (*Somateria mollissima*) hens on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between hens' heart rate and nest-level temperature from our nest-level temperature's linear mixed effects model. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values.

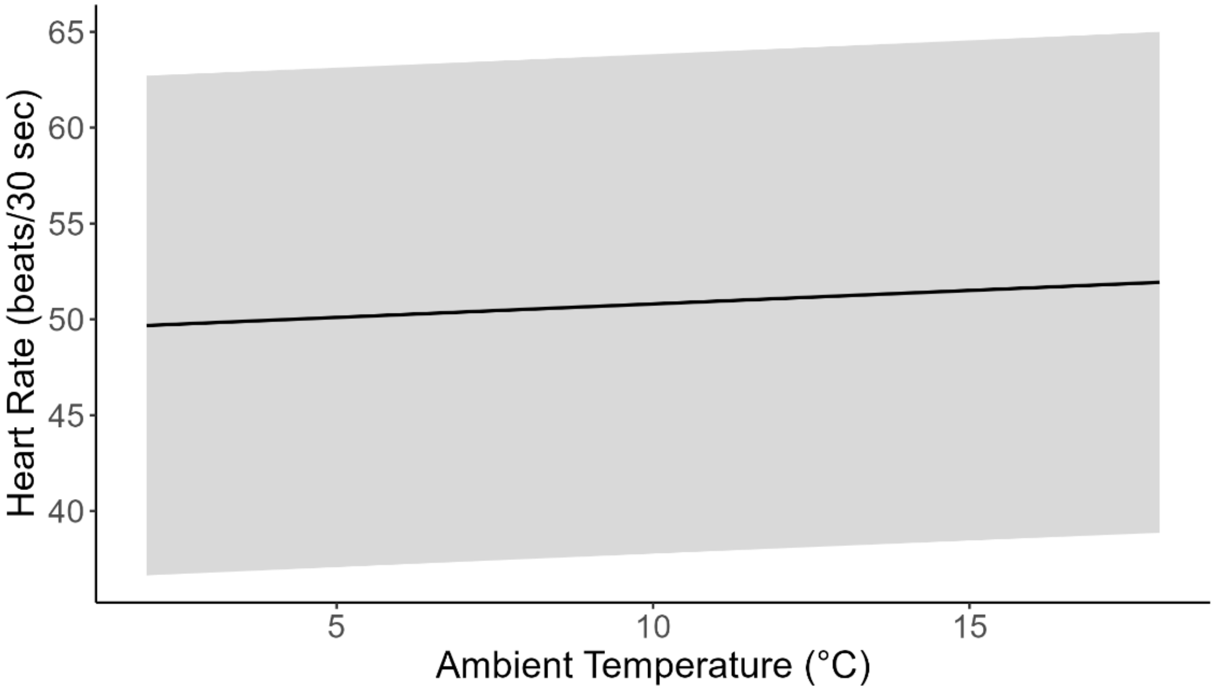


Figure 2.5 Examining the effect of ambient temperature on heart rate in nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between hens' heart rate and ambient temperature from our ambient temperature's linear mixed effects model. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values.

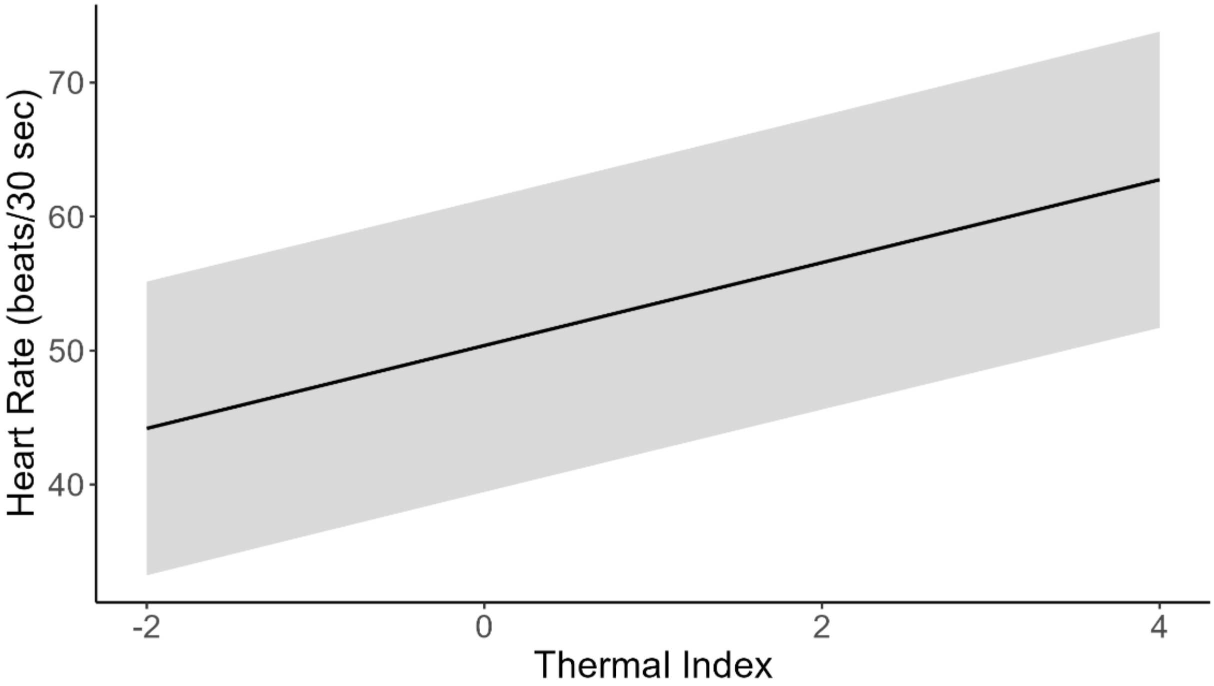


Figure 2.6 Investigating thermal index's impact on heart rate in nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between hens' heart rate and thermal index from our nest-level temperature's linear mixed effects model. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values.

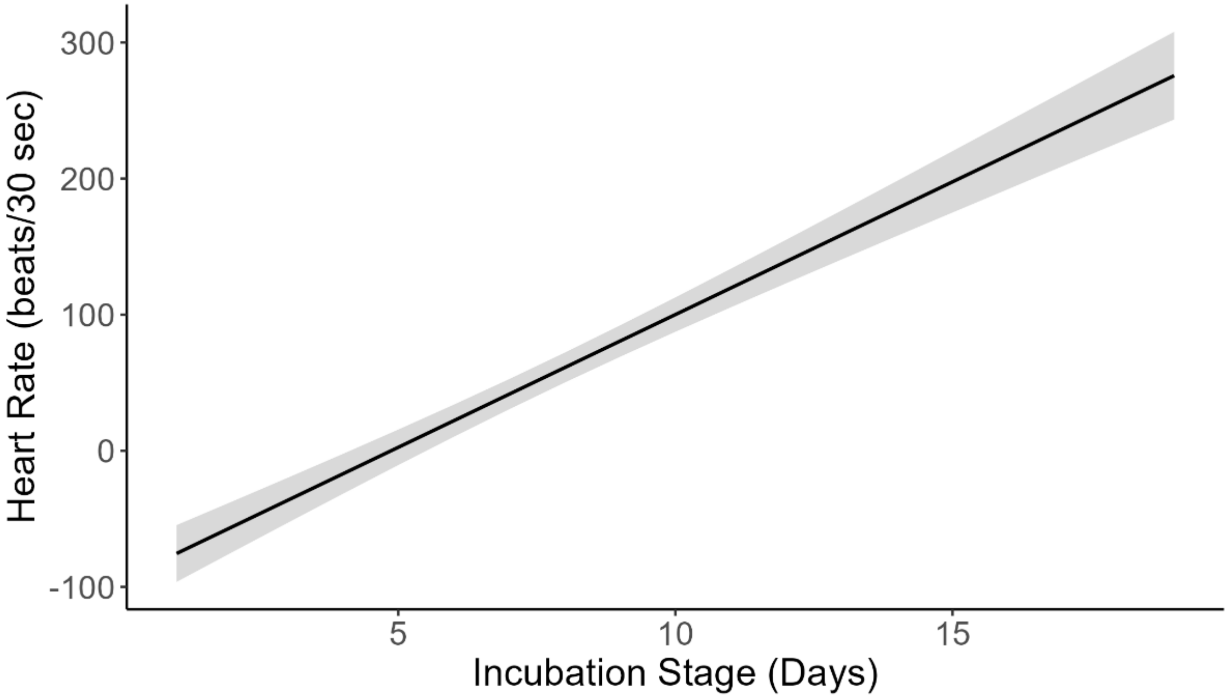


Figure 2.7 Assessing incubation stage's impact on heart rate in nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted is the relationship between heart rate and incubation stage (in days) from the linear mixed effects model of nest-level temperature. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between standardized ordinal date and heart rate in the linear mixed effects model for ambient temperature (Table 2.3).

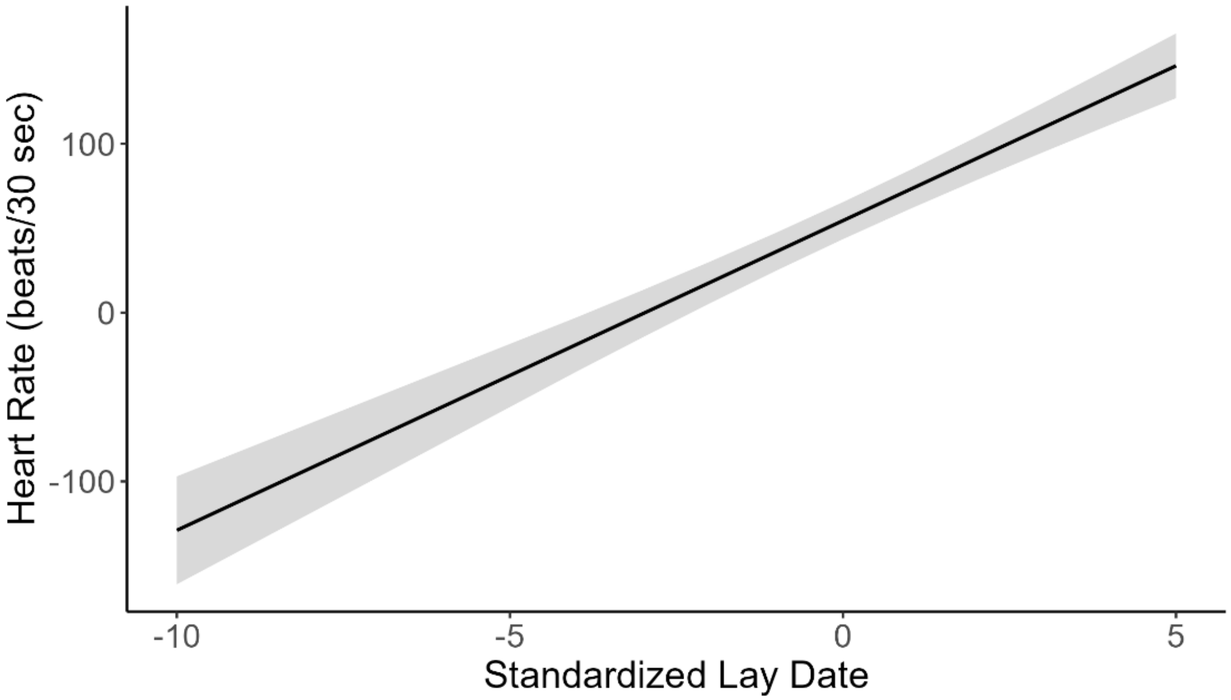


Figure 2.8 Determining breeding parameters impact on heart rate in nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted is the relationship between heart rate and incubation stage (in days) from the linear mixed effects model of nest-level temperature. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between standardized ordinal date and heart rate in the linear mixed effects model for ambient temperature (Table 2.3).

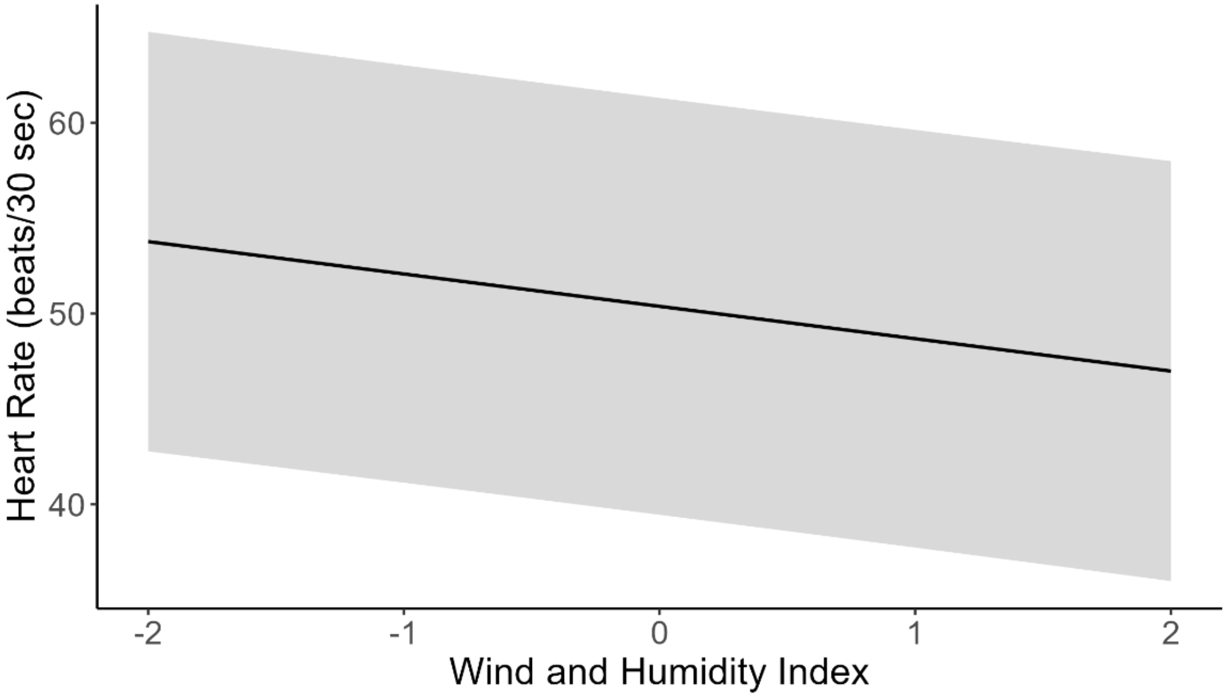


Figure 2.9 Influence of weather parameters on heart rate in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between heart rate and wind and humidity index from the linear mixed effects model of nest-level temperature effects. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between wind and humidity index and heart rate in the linear mixed effects model for ambient temperature (Table 2.3).

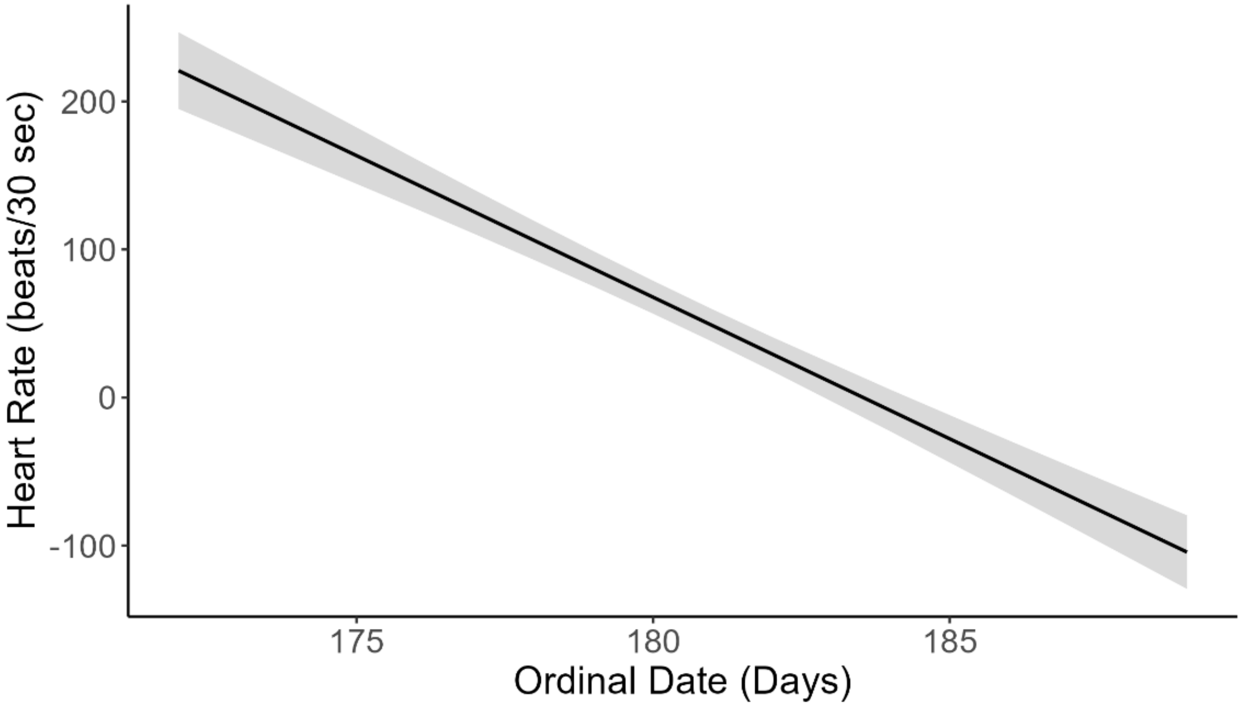


Figure 2.10 Examining the impact of breeding parameters on heart rate in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between heart rate and ordinal date from the linear mixed effects model of nest-level temperature effects. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between ordinal date and heart rate in the linear mixed effects model for ambient temperature (Table 2.3).

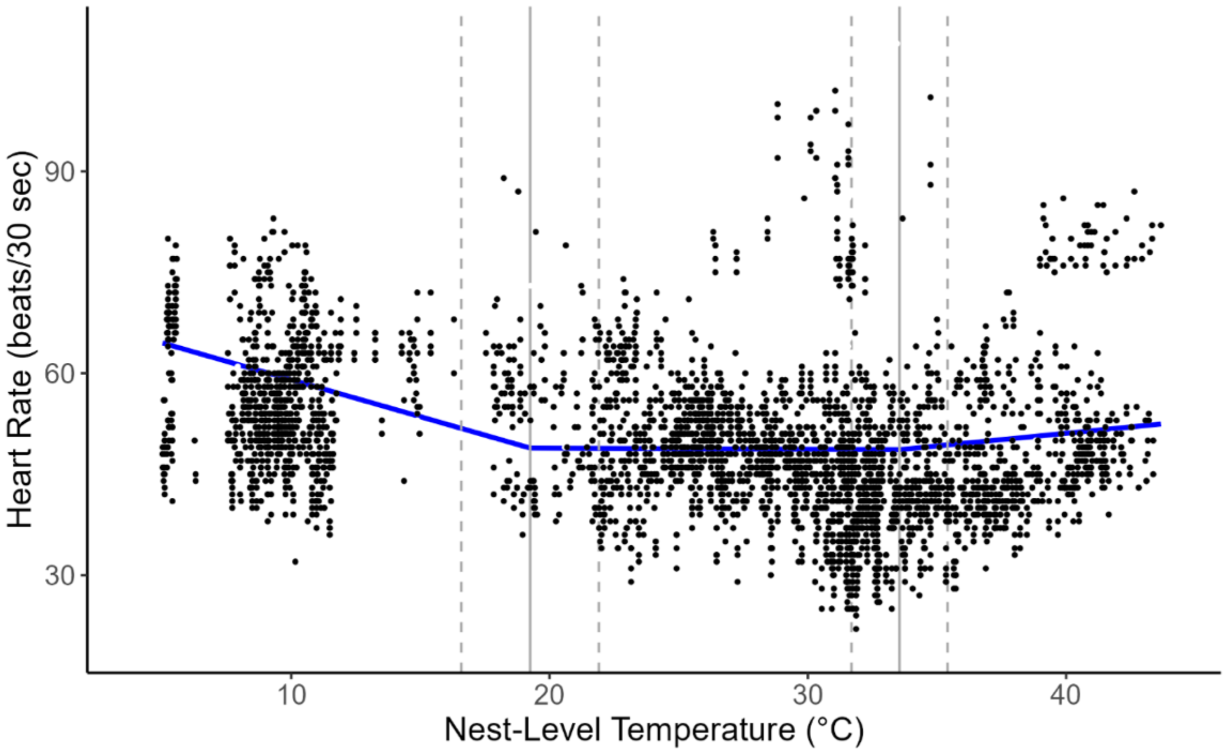


Figure 2.11 Assessing the effects of heat stress on heart rate in common eider (*Somateria mollissima*) hens breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Represented on the plot is nest-level temperature's segmented relationship with hens' heart rate. Grey solid lines indicate the location of breakpoints, with standard errors for each breakpoint indicated by grey dotted lines. Blue solid lines indicate estimated slopes of the relationship, as separated by breakpoints.

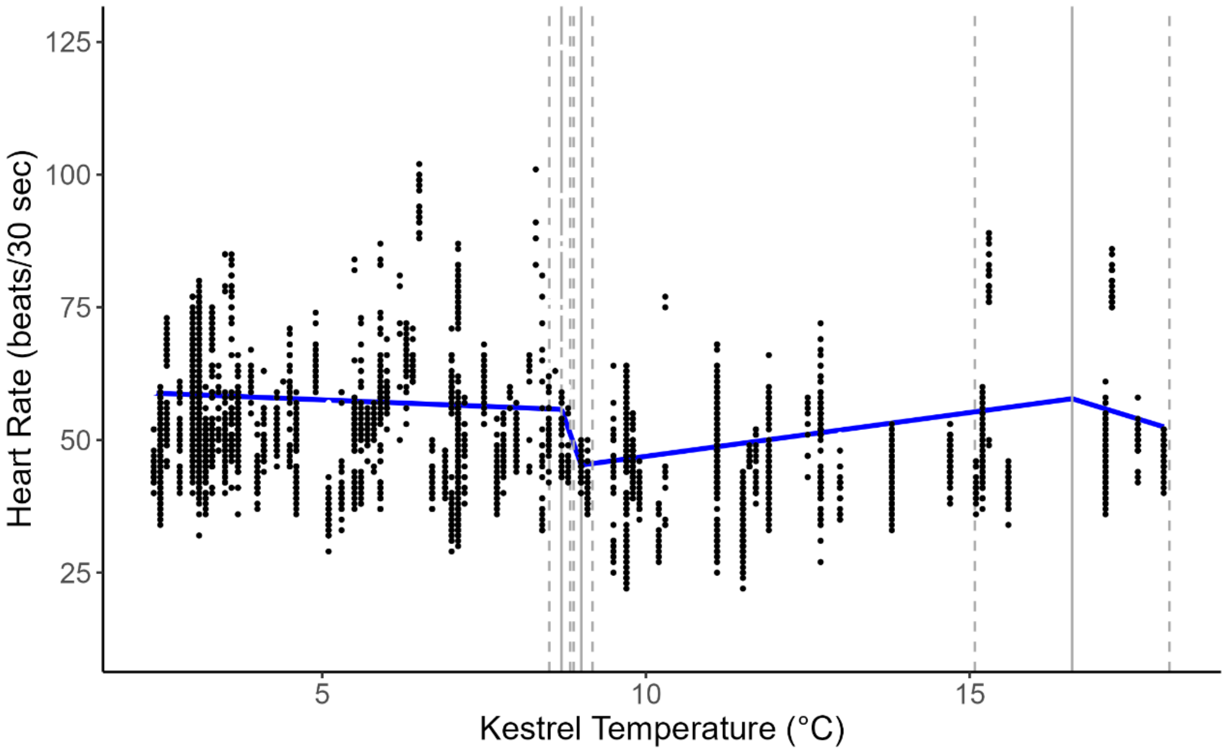


Figure 2.12 Determining the effects of heat stress on heart rate in common eider (*Somateria mollissima*) hens breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Represented on the plot is ambient temperature's segmented relationship with hens' heart rate. Grey solid lines indicate the location of breakpoints, with standard errors for each breakpoint indicated by grey dotted lines. Blue solid lines indicate estimated slopes of the relationship, as separated by breakpoints.

CHAPTER 3

Introduction

The Arctic is undergoing rapid warming as a result of climate change, at a faster rate than the rest of the globe (CAPE-Last Interglacial Project Members, 2006). In fact, some regions of the Arctic are warming at upwards of 4 times the rate (Rantanen et al., 2022). With such rapid warming, it is critical to document how arctic species may be responding, as many terrestrial vertebrates are expected to be unable to adapt to the speed of change without shifting their range distributions (Callaghan et al., 2004). Species' and populations' impacts and responses to indirect effects of climate change in the North are well-researched; including changes in predator-prey dynamics and distribution (Gilg et al., 2009; Renner et al., 2024), changes in migration patterns (Kuletz et al., 2024), impacts of introduced disease and parasitism (Anderson et al., 2021; Kutz et al., 2009; Parkinson et al., 2014), phenological mismatch between predators and prey (Kwon et al., 2019; Lameris et al., 2018), loss of habitat, particularly loss of suitable breeding habitat for birds (Wauchope et al., 2017), and changes in sea ice extent for feeding grounds (Grunst et al., 2023; Laidre et al., 2015). Though important avenues of research (Gunderson et al., 2017), it is equally important to understand how polar species and individuals are impacted by and responding to the direct impacts of climate change, a current and relatively understudied area of research in endothermic species (Oswald & Arnold, 2012).

In the Arctic, direct effects of climate change include rapidly rising ambient temperatures driven by a feedback loop of increased sea-ice melt (arctic amplification) and changes in water vapour and cloud cover (Koenigk et al., 2020). Further, climate change has directly led to more extreme weather events, such as storms and heat waves (Dobricic et al., 2020; Koenigk et al., 2020). These effects have resulted in an increase in reported heat stress in arctic species (Choy et al., 2021; O'Connor et al., 2021). Heat stress can be defined as exposure to temperatures beyond an individual's ability to regulate their internal body temperature by way of passive heat-dissipating mechanisms (Welman et al., 2024), a definition we follow in this work. Arctic breeding species may be particularly vulnerable to heat stress due to their cold adaptations (Choy et al., 2021; Dawson & O'Connor, 1996). Indeed, Arctic species use a variety of cold adaptations that allow them to occupy cold environments with reduced energetic costs of thermoregulation

(Dawson & O’Connor, 1996). For example, many arctic species have thick insulative layers that help retain heat within the core (Scholander et al., 1950). Though energy efficient in a cold environment, this ability may prove less adaptive to a warming environment where these species now need to work harder to lose body heat, increasing their risk of heat stress (Oswald & Arnold, 2012). These effects can pose a severe health risk to cold-adapted populations, highlighted by the fact that several mortality events associated with climate change-induced heat waves have been documented across birds near the poles (Fretwell et al., 2023; Gaston et al., 2002; Olin et al., 2023).

When species face climate-change effects like heat stress in their environment, there are a few ways in which they can attempt to respond, which have been charismatically described as “move, adapt, or die” (Benson & Cummins, 2011; Habary et al., 2017) - with some researchers including “acclimate” in this equation (Beever et al., 2017). In short, species can shift their distributions, adapt to better tolerate heat or heat-avoidant strategies over generations, or they can physiologically or behaviourally respond immediately *in situ*, to avoid death (Beever et al., 2017). For species that cannot change their distribution, an *in situ* behavioural response to heat stress can provide an adaptive response to either avoid or buffer increased thermoregulatory needs (Logan et al., 2019). Particularly, certain behaviours (e.g., shade seeking, orientating the body to dissipate heat) can help mitigate the cost of an energetically demanding physiological response (Angilletta et al., 2010). Behavioural responses to thermal stress have the advantage of being easily observable by researchers and can provide insight into the trade-offs these responses can incur at the expense of other activities during an organism’s life (Cook et al., 2020). One life-history event that can be particularly disrupted by heat stress responses is reproduction, particularly for arctic-breeding birds (Collier et al., 2017; O’Connor et al., 2024). Indeed, many cold-adapted birds migrate to the Arctic during the summer months to breed for a short but seasonally highly productive environment and an abundance of suitable breeding habitats (Fox, 2021). However, due to the time constraints of the reproductive season and the high energetic costs associated with reproduction, increased thermoregulatory behaviours in response to heat stress can disrupt incubation and quickly deplete parental energy reserves (Collier et al., 2017; Cook et al., 2020). Thermoregulatory behaviours commonly observed during incubation in heat-stressed parents can include wing drooping, postural and orientation changes, or standing (sometimes referred to as ‘shading’ where parents hover over the hot boundary layer in their nest while shading eggs from the sun) (Clauser & McRae, 2017; Downs & Ward, 1997; Olin et al., 2023; Smit et al., 2016). Further, many studies note reduced nest attentiveness in heat-stressed parents, with parents taking more frequent or longer breaks from the nest (commonly referred to as ‘off-bouts’) as a means to seek shade or water to cool down (AlRashidi et al., 2011). These breaks may become increasingly necessary as parents need to escape lethal temperatures, but also rehydrate, as exploiting evaporative cooling strategies on the nest (panting, or gular fluttering), can quickly lead to dehydration (Bourne et al., 2021). Unsurprisingly, responding to heat stress by incubation interruptions and increased at-nest activity can have several negative consequences on both parents, eggs, and, ultimately, breeding success (Skutch, 1949; Wang & Beissinger, 2009; Yorio & Boersma, 1994). For example, frequent nest absences can expose eggs to lethal temperatures (Bourne et al., 2021), but also highly variable temperatures, which can reduce egg and chick health (Booth, 1987; Lourens et al., 2005), as well as necessitate that parents expend more energy to rewarm eggs rather than to consistency keep eggs warm (Vleck, 1981). Furthermore, reduced nest attendance can leave eggs exposed to predators (Meyer et al., 2020) and, in some species, increase predation risk indirectly by extending the incubation period and, thus, opportunities for predation attempts (Martin et al., 2015). Additionally, heightened activity by heat-stressed parents on the nest itself can increase nest detection by visual predators (Martin et al., 2000; Skutch, 1949). In the Arctic, this may increase nest detection by polar bears (*Ursus maritimus*) and gulls (*Larus spp.*), effective visual predators that are known to predate on breeding seabirds and their nests (Blanco & Bertellotti, 2002; Jagielski et al., 2021). In conclusion, thermoregulatory behaviours exhibited to mediate heat stress in arctic-breeding species are likely adaptive responses to acute temperatures above an eider's upper critical temperature, but if chronic, can interfere with incubation requirements and lead to greater nest failure.

In this study, we investigated the behavioural responses of incubating common eiders (*Somateria mollissima*), a cold-adapted, Arctic-breeding sea duck, to predict climate change-inducing heat stress conditions in their breeding environment. We focused on the agitation behaviour of hens on their nests as the are exposed to varying environmental conditions and temperatures during one of their most energetically costly and behaviourally constraining life events, incubation. Eiders are large-bodied sea ducks (Waltho & Coulson, 2015), allowing them to maintain a strict capital incubation strategy where they can carry enough body reserves to fuel their entire incubation period, during which time hens fast, refusing to leave the nest to eat or drink for approximately 24 days (Bottitta et al., 2003; Hanssen et al., 2002). In fact, eiders breeding in the Eastern Canadian Arctic have one of the highest recorded incubation consistencies in birds, with hens staying on the nest 99.8% of their incubation period (Bottitta et al., 2003). They choose to breed in open-ground nest cups with little vegetative cover, which much like other ground-nesting species, offers a clear view of approaching predators, but at great risk of clutch predation when hens are absent (Fast et al., 2010; Tertitski et al., 2021). Despite these factors driving hens to remain on the nest, previous studies have noted the indirect effects of climate change on disturbing hens' incubation, including the negative effects of novel predators (Geldart et al., 2023) and contaminant exposure (Smith et al., 2022). Equally important is to document the direct effects of climate change on incubation behaviour, to which recent work has noted high temperatures and low winds associated with contaminant exposure can lead to greater incubation interruption (Smith et al., 2022).

Indeed, with such open nest sites, hens are highly exposed to environmental conditions, including high heat loads from the sun, as well as radiant heat from the earth’s surface beneath their nests (Guthery et al., 2005; Hovick et al., 2014). As the Arctic is undergoing considerable warming in the summer months, this heat load from the sun will likely contribute to heat stress in these birds, as they incubate their eggs during the Arctic summer under nearly 24 hours of sunlight. Further, as a species so well-adapted to the cold (D'alba et al., 2017; Jenssen et al., 1989), eiders are expected to become heat stressed at distinctly lower temperatures compared to lower latitude species, as has been documented in other arctic breeding seabirds (Choy et al., 2021; Oswald et al., 2008). While on the nest, eiders will expectedly respond to heat stress via panting, an effective evaporative cooling method (Song & Beissinger, 2019) which has been previously observed in incubating eiders under high temperatures (Fast et al., 2007). As evaporative cooling works by evaporating water from the body, it can be dehydrating (Albright et al., 2017) and require hens to rehydrate by metabolizing their fat stores to free water uptake (Ma et al., 2020). This heat stress response can deplete energy for incubation and may result in hens reaching a lower critical body mass (previously described as 1,100 g; Korschgen, 1977) before incubation ends, where they may risk abandoning their clutch even temporarily to feed (Criscuolo et al., 2002), or death (Ma et al., 2020). As such, hens may benefit from also exhibiting behavioural responses on the nest to heat stress, which, although it may interrupt incubation consistency, will not lead to significant water loss. However, these responses come with their own set of potential costs: increasing hens' detectability by predators and exposing her eggs to variable incubation temperatures (DuRant et al., 2013; Tertitski et al., 2021).

As such, our goal was to investigate whether eiders exhibit incubation behaviours in response to heat stress during their incubation, and if their response is triggered at a specific threshold temperature. To examine incubating hens' behavioural response to heat stress, we recorded hens' activity on the nest via temperature-sensitive thermal probes placed in the centre of their clutches, which indicated when hens were either agitated, still, or absent from the nest via relative large drops or gains in temperature. We hypothesized that as ambient temperature rose and hens became increasingly heat stressed, they would become more active on the nest, presumably engaging in behavioural responses of cooling, such as standing or shifting (agitation/fidgeting behaviour), to increase body heat loss. Given eider hens’ incredible incubation consistency, we further predicted any increase in movement on the nest would occur only beyond an inflection point in temperature, suggestive of a threshold at which birds are driven to a behavioural heat stress response. The existence of this behavioural-response threshold to heat stress would provide information on whether Arctic-breeding eiders are currently undergoing heat stress during their incubation, whether they are capable of behaviourally responding via behavioural adjustments on the nest, and if so, to what extent does temperature impact their incubation consistency (i.e. are they significantly moving more on the nest when heat stressed?). This information can aid in our understanding of eiders’ capability to behaviourally tolerate warming conditions and can provide insight into temperatures at which they become behaviourally heat stressed, serving as seabird-indicators of arctic ecosystem health (Oswald & Arnold, 2012).

Methods

Study species and site

We studied a northern common eider (hereafter, eider) breeding colony on East Bay Island, Qikiqtakuluk, (64° 02′ N, 81° 47′ W), within the East Bay, Qaqsauqtuuq, Migratory Bird Sanctuary, Nunavut, over four years; 2018 (n=20), 2019 (n=12), 2022 (n=18), and 2023 (n=36), for a total sample size of 86 incubating hens (Figure 3.1). Though historically the largest common eider breeding colony in Canada (Fast et al., 2011), breeding pairs have experienced waves of decline in recent decades due to multiple stressors, including avian cholera outbreaks (Descamps et al., 2012; Love et al., 2010; van Dijk et al., 2021) and exposure to a novel predator (Iverson et al., 2014). Female eiders typically arrive on the flat rocky island (400 m by 800 m), or nearby staging areas, from May to early June to feed and build energy reserves for incubation (Steenweg et al., 2022) before initiating egg laying in mid-June to early July (Love et al., 2010; Steenweg et al., 2022). The deployment of remote nest monitoring equipment for our study took place during egg-laying and early incubation (see details below).

Eiders at Qikiqtakuluk follow a strict capital incubation strategy, with females relying solely on endogenous reserves to fuel approximately 24 days of incubation, during which time they do not leave the nest to feed (Bottitta et al., 2003; Sénéchal et al., 2011). This strategy, supported by their large body size and refuelling at, or nearby, breeding grounds, is particularly effective in cold climates (Jönsson, 1997; Williams et al., 2017). Hens' clutch size at this site averages between 2-4 eggs (Descamps et al., 2011a; Love et al., 2010) and is influenced by a combination of the mother's condition at laying and external environmental conditions (Descamps et al., 2011a). After successful hatching, ducklings quickly head to sea with their mothers, who oversee groups of offspring together to feed (Descamps et al., 2011b). The island receives nearly 24 hours of sunlight during summer, with high winds and frequent fog in June (Environment and Climate Change Canada, 2024). Ice and snow cover is still present when eiders arrive on the island, but snow quickly melts before hens begin laying (Love et al., 2010). Sea ice break-up begins to occur in late June and early July (Jean-Gagnon et al., 2018), opening up the water for eiders and their ducklings after hatching, before being completely ice-free in early August (Gagnon & Gough, 2005).

Incubation interruptions in response to weather and breeding parameters

We located nests for possible equipment deployment by walking the periphery of the island or by observation from bird monitoring blinds (n = 6) to avoid colony disturbance. The location of sampled nests were recorded into a Garmin GPSMAP 64s handheld device (latitude, longitude coordinates). We flushed hens from their nests before deploying our behaviour sampling equipment which consisted of a thermal probe leading from a Tinytag® Plus 2 temperature logger placed into the center of each studied nest. Within the nest, the temperature-sensitive thermistor of the probe was aimed upwards to ideally make contact with the female's brood patch while incubating (Figure 3.2). To help secure the probe into the nest, and prevent females from tampering with it, we buried the probe cord under soil and rock, and the Tinytag logger itself was also buried, to camouflage it within the environment. We preprogrammed Tinytags in the Tinytag explorer software prior to deployment, setting the device to record temperature every minute. Tinytags can be expected to record for approximately 22 and a half days at this rate with their battery life. We deployed units from mid-June to mid-July alongside a 3D-printed egg outfitted with microphones (see Chapter 2 Methods) which replaced a single egg to maintain incubation costs. In 2018, no microphone-based eggs were deployed, only behaviour-monitoring equipment. When possible, we removed the first laid egg from the nest which was later aged (by candling) to help estimate a hen's 'days into incubation' and therefore initial lay date of the first egg. Both incubation days and lay dates were estimated using a combination of egg age and clutch size. Before leaving each nest following equipment deployment, we covered eggs with eider down and nest debris, to prevent egg predation before the female returned to her nest (Götmark & Åhlund, 1984).

We additionally recorded environmental temperatures at the nest and several environmental parameters island-wide to determine conditions conducive to heat stress for incubating hens. Specifically, we deployed a HOBO Pendant temperature and light level recorder (2-minute sampling interval; Onset Inc model MX2202) at each sampled nest to record more fine-scale changes in temperature and radiative heat stress at nest-level (hereafter, nest-level temperature). Additionally, we installed six Kestrel weather meters on six bird-monitoring blinds in 2018 and 2019, and then redeployed these units in 2022 and 2023 to approximately 3 feet off the ground at five of these blinds and one at the EBI weather station. We set Kestrel weather meters to record ambient temperature, wet bulb temperature, humidity, wind speed, heat index, dew point, and wind chill every 30 minutes. We assigned each Kestrel-unit data to the nests it was nearest, as determined by the distance between each nest and the Kestrel unit's GPS point measured in GPS Garmin's Basecamp® software.

Finally, we deployed trail cameras across the island (n=19 in 2018, n=35 in 2019, 2022 and 2023) to record predator movements and foraging behaviours. These data were used to verify if any days used in the study had large predators (primarily polar bears) detected on the island and, if so, whether any of the behavioural data from that date should be omitted from the study. All equipment recorded data remotely, allowing us to continue recording data long after our field team left the island in early July, due to the danger of increased polar bear activity. A retrieval team was then helicoptered onto the island in mid-late July to retrieve remote monitoring and recording devices. Of the 86 nests on which equipment was deployed, 68 nests had behavioural data that could be used for statistical analyses (n= 19 in 2018, n= 9 in 2019, n= 10 in 2022, n= 30 in 2023).

Lay date and incubation stage estimates

We used information from behavioural monitoring and the candling of the first-laid egg collected at nest visits to determine the lay date of that first egg and then the hen's incubation stage (i.e., number of days into incubation at the time of equipment deployment). We additionally used the clutch size for a given bird to help with these estimates when it indicated a later day into incubation than egg age. Lay dates were standardized across years for statistical analyses, and calculated by subtracting the average lay date for the given year (2018 = 177, 2019 = 171, 2022 = 170, 2023 = 172) from the female's lay date (Hennin et al., 2016). We additionally standardized ordinal date, by subtracting ordinal date from a chosen set date for all years of sampling. For this study we chose June 15th, an ordinal date of 166.

Quantifying incubation behaviour

To determine which days to select within the incubation period to examine eider behaviours in response to potential temperature stressors, we identified the maximum daily nest-level temperatures recorded from our HOBO pendant devices at each nest. We first removed the first day females returned to their nest after equipment deployment as human disturbance may impact their behaviour. From the remaining days available, we then selected two sample dates per female (where possible) representing the day with the highest and lowest *maximum* daily nest-level temperature reached, providing us with two days per bird to examine a hen's daily nest movements. For each of those sampling days, we also recorded the maximum daily ambient temperature (from the Kestrel units). Any movements on the nest recorded within 30 minutes before or after a polar bear was detected on the island, via trail cameras, was omitted from the results to avoid misinterpreting a predator response as a heat stress response. In 2022, no bears were detected on the island during the dates incubation behaviour was recorded for our analyses.

We used fine-scale changes of in-nest temperature data from the temperature probe (Tinytag® Plus 2) indicative of a female's movements during incubation as previously validated by our team (Smith et al., 2022). For instance, sudden spikes or drops in temperature detected by the thermistor-based probe indicate incubation interruptions, as females readjust, stand, or leave the nest. We analyzed all temperature recordings in the Tinytag Explorer software, remaining consistent in our visual interpretation of eiders nest movements by examining the temperature traces of all individuals at a resolution of 12 hours (y-axis) and setting the x-axis to a maximum change of 12℃ since temperature variation in nests did not vary more than by this amount. We recorded three behavioural variables for hens: instances of "Movements", periods of "Stationary bouts", and periods of "Absences from the nest". We also recorded the start and end time (by time of day, hh:mm) of each event. We determined a hen's "Movement" on the nest by visually examining the trace of temperature over time for any sudden spike, or drop, in nest temperature greater than 0.25℃. Further, because a hen's movement on her nest can be near-instantaneous to a few minutes long, all movements were classified as events instead of durations for ease of measurement. We documented Stationary bouts as periods between Movements and Absences when females were on the nest. Lastly, we determined Absences from the nest by a sudden drop in temperature of more than 4℃. We verified all possible nest absences for 2019, 2022, and 2023 by listening to audio recordings from the microphone-equipped 3D-printed egg to determine if the hen's heartbeats or digestive sounds could be heard, indicating that she is on the nest. We recorded no absences in any females in 2018. In the behavioural monitoring of 68 incubating hens in this study, we only detected 21 instances of nest absences in 9 females, and two of those absences were determined to be clutch abandonment events. Of the nest recesses (not including the two nest abandonments), absences accounted for only 9 hours and 46 minutes of 3,192 hours of sampled incubation behaviour, representing a 99.7 % incubation consistency as supported by previous work in eiders (Bottitta et al., 2003). Due to the low sample size of hen absences, we did not explore this behaviour further.

Statistical analyses

Quantifying environmental parameters indicative of heat stress

We rotated, centred and scaled the Kestrel weather parameters prior to being used in a principal component analysis (PCA) to reduce redundancy while producing meaningful associations between variables (Forkman et al., 2019). Weather parameters included heat index, wet bulb temperature, wind chill, dew point, wind speed and humidity. A varimax rotation was applied (Comrey & Lee, 2013), and two components with eigenvalues > 1 and explaining >10% variance were retained. Additionally, the two rotated components cumulatively explained 85% of the variance in the dataset (Table F, Appendix; see details below). Maximum daily ambient temperature and maximum daily nest-level temperatures were not included in the PCA as these were the primary variables of interest that we expected would be most likely to directly impact incubation behaviour. Rotated component 1, referred to hereafter as thermal index, explained 66% of the variance and consisted of heat index, wet bulb temperature, wind chill, dew point, and wind speed, with individual loadings all > 0.55 (Comrey & Lee, 2013). All but one variable were positively correlated to one another, with wind speed being negatively correlated. Thus, a high thermal index is associated with an increased risk of heat stress in eiders, as a low wind speed, but a high wind chill value (not to be mistaken with wind chill 'effect'), dewpoint, heat index and wet bulb temperature, should increase the perceived temperature of their thermal environment. The second rotated component, referred to hereafter as humidity, explained 19% of the variance and consisted entirely of relative humidity and was positively loaded. Relative humidity is expected to be negatively associated with risk of heat stress in polar regions. In a warm environment, relative humidity is expected to inhibit evaporative cooling efficiency, increasing the risk of heat stress; however, in a colder environment, high humidity is typically accompanied by a colder air mass. Indeed, cold, dense air requires less moisture than warm, buoyant air to be fully saturated (i.e., have a high relative humidity). As such, given the climate of our field site, high relative humidity is expected to occur most often due to moist cold air coming in from the bay by strong winds, and thus will expectedly have an effect of relieving heat stress.

Effects of reproductive decisions and environmental parameters on incubation consistency

To examine which reproductive and weather metrics were impacting interruptions to incubation behaviour, we analyzed eider daily nest movement counts using two generalized linear mixed models with a Poisson distribution. Maximum daily nest-level temperature and maximum daily ambient temperature were analyzed separately, one in each model, as they were both of primary interest to us as predictive variables, and we wanted to be able to examine their individual and unique influence on eider daily nest movements. Our model of incubation behaviour (response variable, count data, range: 1 – 75 movements) incorporated the following predictor: maximum daily nest-level temperature (continuous, range: 9.18 – 44.61 °C), and the following additional fixed effects: thermal index (continuous, range: -1.96 – 2.30), humidity (continuous, range: -5.04 – 1.36), days of incubation (continuous, range: 0 – 19), relative lay date (continuous, range: -10 – 15.9) and standardized ordinal date (continuous, range: 6 – 23). Year (4-factor level: 2018, 2019, 2022, and 2023) and nest id (68 levels) were included as random effects. The second GLMM model of incubation behaviour explored maximum daily ambient temperature (continuous, range: 3 – 19.8 °C) as the main predictor, and similarly included the covariates and random effects described above, except for the thermal index. When included in the model, the thermal index had a variance inflation factor (VIF) of 19.0. However, since a VIF > 10 indicates a variable is exhibiting high collinearity with other variables in the model we excluded thermal index from this particular model. Our generalized linear mixed model residuals were further assessed for overdispersion and goodness of fit by way of Kolmogorov–Smirnov tests (Hartig, 2022).

Identifying temperature thresholds for alterations in incubation behaviour

To assess for expected temperature threshold effects on interruptions to incubation behaviour, we performed two segmented regression models of the effect of maximum daily nest-level temperature and maximum daily ambient temperature on changes in incubation behaviour. We used the LIMBARE package in R to run the segmented analyses (Lee et al., 2024) searching for two breakpoints, predicting there would be a change in behavioural response when cold stressed, and again a response when heat stressed. Thermal index and humidity were not assessed for threshold effects as there was no *a priori* expectation the effect of thermal index and humidity on behaviour would follow a segmented pattern. The maximum daily nest-level temperature model contained the same fixed-effect structures as described above, with the addition of year as an additional fixed effect (categorical, four levels) since the segmented analysis could only incorporate a single random effect. The maximum daily ambient temperature model also included a similar fixed and random effect structure, excluding the thermal index due to a high VIF value detected in the previous generalized linear mixed model for maximum daily ambient temperature.

Because LIMBARE does not accept non-gaussian family distributions, we performed a square root transformation on the behavioural count data that resulted in a more normal distribution for analysis. However, in the maximum daily nest-level temperature model we experienced convergence- and singularity issues with our random-effects structure that was nevertheless necessary to retain (i.e., nest id). Therefore, we performed a segmented regression using non-transformed behavioural data in the maximum daily nest-level temperature model; and this revision further allowed us to identify two breakpoints (i.e., the package prevented the transformed variable from running in the model when searching for more than one breakpoint). Nevertheless, the location of the first breakpoint found in the transformed and un-transformed behaviour models for maximum daily nest-level temperature were similar (17.3°C and 19.2 °C, respectively), and the significance of the breakpoints were similar ($p=0.0004$ vs $p=0.0006$), providing reassurance that breakpoints did not largely differ in the untransformed vs transformed models. As such, we felt confident evaluating the second breakpoint using the non-transformed count data for the nest-level temperature model.

Although we searched for two breakpoints, if a breakpoint was not statistically significant, we lowered the search to one breakpoint; and if two breakpoints were significant, a third breakpoint was explored. In some cases, when a breakpoint was marginally significant, it was still explored as a possible behavioural response threshold. We set $\alpha = 0.05$ as the threshold for statistical significance in all our model analyses. All manipulations and data analyses were performed in R Studio (Version 4.4.1. 2024-06-14; R Development Core Team, 2024), using *dplyr* (Wickham et al., 2023) and *car* package (Fox & Weisberg, 2019) for data manipulation and exploration, D*HARMa* package (Hartig, 2022) for model residual diagnostics, *psych* package (Revelle, 2024) for principal component analysis, and *glmmTMB* package (Brooks et al., 2017) to create general linear models. Additionally, we used the *LIMBARE* package (Lee et al., 2024), to perform a linear mixed-effects breakpoint analysis that builds off of the *segmented* package (Muggeo, 2008) in R Studio, but allows for greater inclusion of random factors and estimation of multiple breakpoints. Lastly, *ggplot2* (Wickham, 2016), *cowplot* (Wilke, 2024), or, *ggeffects* (Lüdecke, 2018) were used to create data visuals and model predictions. Coefficients ± standard errors (SE) for all model outputs are included in the results.

Results

Linear effects of breeding and weather parameters on incubation interruptions

In exploring the effect of maximum daily nest-level temperature on hen daily nest movements, we found a significant effect of days of incubation, with females moving less as days of incubation progressed (Z = -3.1, p < 0.002, Figure 3.4, Table 3.1). In contrast, daily nest movements significantly increased with ordinal date (Z = 2.0, p = 0.04, Figure 3.5 Table 3.1), but not with lay date (Z = -0.8, p > 0.05), Table 3.1). Year (variance = 0.1, SD = 0.3, Table 3.2) and nest ID (variance = 0.2, SD = 0.4, Table 3.2) contributed little variance to the overall model. No significant statistical effects of maximum daily nest-level temperature (Z = 1.277), thermal index (Z = 1.8), and humidity (Z = -0.2) were found (all p > 0.05, Table 3.1) in the Poisson regression models.

We observed a significant effect of maximum daily ambient temperature on hen's daily nest movements, with hens moving more as maximum daily ambient temperatures increase (Z = 5.0, p < 0.0001, Figure 3.3, Table 3.3). In addition, hens significantly decreased movement on the nest as the number of days into incubation progressed (Z = -3.5, p < 0.001, Table 3.3). Further, daily nest movements significantly increased with ordinal date (Z = 2.3, p = 0.02, Table 3.3), but there was no significant relationship with lay date (Z = -1.0, p > 0.05, Table 3.3). Similarly, humidity did not significantly influence daily nest movement, either (Z = -0.2, p > 0.05, Table 3.3). Year (variance = 0.1, SD = 0.3, Table 3.4) and nest ID (variance = 0.2, SD = 0.4, Table 3.4) contributed minimal variance to the overall model.

Segmented effect of temperature on incubation interruptions

In our segmented model of daily nest movements as a response to maximum daily nest-level temperature, we found significant effects temperature ($T = 2.3$, $p = 0.005$, Table 3.5), thermal index ($T = 4.0$, $p < 0.001$, Table 3.5) and year on daily nest movements, with 2022 being statistically different from our 2018 reference year. However, humidity ($T = -0.5$), days of incubation ($T = -0.8$), standardized ordinal date ($T = -0.3$), and standardized lay date ($T = -0.2$) did not significantly affect daily nest movement in the model (all *p-values* > 0.05, Table 3.5). Further, two nest-level temperature breakpoints in nest movements were found: one significant breakpoint at 19.12°C ($p < 0.001$, Table 3.6) and a second marginally significant breakpoint at 38.62°C ($p = 0.07$, Table 3.6) (Figure 3.6). As maximum daily nest-level temperatures rose from the lower bound of temperatures to the first breakpoint at 19.12 °C, we see a significant increase in daily nest movements by hens (slope = 1.3, $p = 0.0004$, Table 3.7). In temperatures ranging from 19.12 °C to 38.62 °C we see a slight decrease in daily nest movements though not significant (slope = -0.7, $p = 0.3$, Table 3.7). For the max daily temperatures above 38.62 °C, we see what appears to be an upward trend in daily nest movements, though not significantly so (slope = 0.8, $p = 0.7$, Table 3.7) (Figure 3.6).

In our maximum daily ambient temperature's segmented model with daily nest movements, we found significant effects of temperature ($T = 2.6$, $p = 0.01$, Table 3.8) and year on daily nest movements, with nest movements in 2022 being statistically distinct from our referenced year of 2018. However, no significant effects of humidity ($T = -0.7$), days of incubation ($T = -1.1$), standardized lay date ($T = -0.1$) and standardized ordinal date ($T = -0.4$) (all *p-values* > 0.05, Table 3.6). Two significant ambient-temperature breakpoints were also found with daily nest movements, one at 5.9 °C ($p = 0.01$, Table 3.9, Figure 3.7) and the other at 17.2 °C ($p = 0.04$, Table 3.9, Figure 3.7). On days where maximum ambient temperatures were less than 5.9 °C, eiders significantly increased their activity on the nest as temperatures increased (slope = 0.6, $p = 0.01$, Table 3.10). Movements then plateaued between 5.9 °C and 17.2 °C (slope= -0.03, $p > 0.05$, Table 3.10). Then, from 17.2 °C to the upper bound of the temperature dataset, hens again further increased their daily nest movements as temperatures rose, though not significantly so (slope = 0.5, $p > 0.05$, Table 3.10).

Discussion

In our study of eider hen incubation, we expected nest movements, which we equate to agitation behaviour, to increase in frequency on days when eiders were exposed to temperatures and environmental conditions past a critical inflection point indicative of heat stress. Additionally, we predicted that other weather factors, comprised of a thermal index and humidity, would fluctuate with eiders nest movements due to their presumed link to the thermal environment eiders experience. In addition, we examined the effects of reproductive parameters, individual variation, and year, as these factors can also affect incubation behaviour. Our findings revealed that agitation behaviour varies across temperature conditions with predicted inflection points, supporting our initial hypothesis. However, the increases in agitation behaviour beyond the high-temperature inflection points were not statistically significant. We also found that agitation behaviour did not fluctuate with weather factors, rejecting our initial hypothesis. We further noted that hens move less frequently on the nest as incubation progresses, but that hens sampled later in the season indicated greater agitation behaviour. In our work, we identified a potentially critical temperature threshold at which heat stress may begin to interrupt incubation consistency and deplete energy reserves in hens.

Incubation behaviour's nest-level temperature response

We found hens decreased agitation behaviours below a lower nest-level temperature threshold (19.12 °C) as a response to cold stress, with eiders remaining relatively more still at nest-level temperatures from 19.12 °C to 38.62 °C. We suspect this threshold indicates a cold-response threshold for hens. Indeed, hens reducing activity on the nest (Baerends, 1959), and tucking their bill and limbs into the shelter of their highly insulative plumage (D'alba et al., 2017) can be an energetically low-cost strategy to reduce convective heat loss during incubation (Cook et al., 2020), as these extremities are primary sites of heat exchange in many duck species (Guillemette et al., 2017). We also found the expected increase in agitation behaviours beyond a marginally significant upper nest-level temperature threshold of 38.62 °C in response to heat stress, though the increase in behaviour was not statistically significant. Nest-level temperatures were recorded at values that well-exceeded those of ambient temperature at our site; for example, our maximum ambient temperature recorded was 19.8°C, whereas our maximum nest-level temperature was 44.61°C. As a reminder, nest-level temperature is the measure of air temperatures under sun exposure, whereas ambient temperature is the measure of air temperature in the shade. As such, the fact that nest-level temperatures recorded at each hen's nest are substantially higher than the ambient temperatures recorded around our site shows that eider nests are exposed to substantial heat in their nest environment from direct solar rays. If eiders are absorbing this radiative heat from the sun, it may suggest ambient temperature alone may not be the best predictor of when hens are heat stressed (Hart et al., 2016). For example, in a study on bank cormorants nesting on sunny cliff sides, the effects of sun and wind with temperature were found to be better predictors of heat stress in incubating parents than ambient temperature alone (Cook et al., 2020). Several other studies on cliff-nesting and ground-nesting species that nest in sun-exposed nest sites found heat from solar rays to be a significant contributor to heat stress (Choy et al., 2021; Oswald et al., 2008; Welman & Pichegru, 2023). In arctic-breeding seabirds such as thick-billed murres (*Uria lomvia*), common murres (*Uria aalge*) and Arctic skuas (*Stercorarius parasiticus*), sun exposure plays a significant role in parents' expression of heat stress during their incubation (Choy et al., 2021; Olin et al., 2023; Snell et al., 2024). As such, we suspect eiders that nest in open-nest sites (Fast et al., 2010) under the lengthy arctic sun (O'Connor et al., 2022), may also be vulnerable to the effects of sun on heat stress during incubation.

When nesting parents are exposed to direct sun and high ambient temperatures causing them to overheat, many will interrupt their incubation by leaving the nest to participate in thermoregulatory behaviours, such as bathing and drinking water (Hand et al., 1981; Olin et al., 2023; Oswald et al., 2008). However, in our study, we found only marginal increases in interruptions to hens' incubation at nest-level temperatures above 38.62 °C, and these behaviours were constrained to movements on the nest. These results may suggest that hens are not yet significantly heat-stressed, or dehydrated, from evaporative cooling methods that might cause them to leave their nest for cool-down behaviours. Alternatively, these results may highlight just how dedicated eiders are to remaining on their nest during their incubation period (Bottitta et al., 2003). In fact, in Arctic skua parents, heat stress was not found to significantly impact incubation consistency, despite parents physiologically responding to heat stress at markedly low temperatures, which researchers suggested may indicate a maladaptive drive to maintain high incubation consistency at an energetic cost to parents when heat stressed (Snell et al., 2024). As uniparental capital incubators (Sénéchal et al., 2011), eider hens may similarly restrain from leaving the nest when heat stressed in order to maintain their extremely high incubation consistency (Bottitta et al., 2003), and only employ the use of on-nest agitation behaviours when necessary to offset the energy and water costs of physiological responses. Unfortunately, eiders breeding on Qikiqtakuluk have several nest predators, including gulls, arctic foxes and polar bears (Barnas et al., 2022; Reed et al., 2007). Thus, increased agitation behaviour on the nest may increase their visibility to predators and risk of clutch predation (Cresswell et al., 2003; Martin et al., 2000), posing a breeding cost of thermoregulatory behaviour to hens.

Incubation behaviour's ambient temperature response

Similar to our nest-level temperature results, in our ambient temperature recordings we saw that movement on the nest significantly decreased below a lower temperature threshold (5.9 °C). Studies on passerines and waterfowl alike have observed this pattern in which incubation consistency is negatively correlated to ambient temperature (Batt et al., 1992; Haftorn, 1988; White & Kinney, 1974), particularly in open-nesting birds, where presence of snow, rain and fog contribute to an increase in nest attentiveness (Baerends, 1959; Batt et al., 1992; Oscar, 1957; Skutch, 1962). Alternatively, when exposed to temperatures beyond a significant upper ambient temperature boundary, which we found to be 17.2 °C, we observed marginally the predicted increase in movement on the nest. Increased movement, by way of adjusting body position, standing, and increased egg rotation on the nest can be an indication of discomfort, stress, and agitation in birds (Chatwin et al., 2013; Sieving et al., 2024), but also a means to dissipate excess body heat (Cook et al., 2020). In fact, standing with legs exposed to the external environment while on the nest may be an effective method of passive heat dissipation (Cook et al., 2020). Many cold-adapted birds have specialized blood vessel networks in their legs for countercurrent heat exchange, effectively recycling heat within the body to conserve energy in the cold (Guillemette et al., 2017). However, for birds that can control blood flow in this region, they may also be able to advantageously dilate the warm blood vessels when over-heating to increase convective heat loss (Guillemette et al., 2017). For example, Southern African breeding bank cormorants (*Phalacrocorax neglectus*) will behaviourally respond to heat stress on the nest by adjusting their posture and standing on the nest as a suspected means to offset the need for an active physiological cooling response (gular fluttering) (Cook et al., 2020). Such behavioural movements allowed parents to decrease gular fluttering by up to 30%, indicating that a behavioural response may adaptively lower energy costs for parents of this species, but at a thermoregulatory cost to eggs (Cook et al., 2020).

Impact of additional weather factors on eider incubation behaviour

Contrary to our predictions, weather factors, particularly a thermal index and humidity, did not significantly affect eider movement on the nest. This was unexpected, as studies highlight the influence of weather factors, like wind, on heat stress behaviours in other breeding birds (Braimoh-Azaki et al., 2023; Cook et al., 2020). Further, weather factors like wind speed, heat index, and humidity are frequently used in equations of species operative temperature in heat stress analysis studies, as a measure of an organism's perceived environment (Bourne et al., 2021), usually based on their size, colour and shape (Dzialowski, 2005). However, many of these studies focus on operative temperature's relationship to energetics (Bakken, 1980), evaporative cooling and water loss (Bakken et al., 1991; Van Dyk et al., 2019). Thus, weather factors like our thermal index and humidity may play a more direct role in physiological responses due to their interactions with the effectiveness of evaporative cooling methods and water loss (Gerson et al., 2014). Again, this supposition is further supported by our Chapter 2 result, where we found significant effects of a thermal index and wind and humidity index on eider heart rate.

Impact of reproductive investment and season on incubation behaviour

Standardized ordinal date and incubation stage were found to significantly influence eider incubation behaviour, whereas standardized lay date did not. We found that as incubation stage progressed, hen movement on the nest significantly decreased. Smith et al. (2022) similarly found eiders breeding on Qikiqtakuluk to be more active on the nest during the early stages of incubation, when temperatures were warm (Smith et al., 2022). They suspected such a response to be the result of low nest investment in the early days of incubation, and so when exposed to warm temperatures during this period, they may have been prioritizing their heat dissipation over incubation consistency (Smith et al., 2022). In our case, increased activity in the early stages of incubation was significant irrespective of temperature, yet this could still be driven by low initial incubation investment as hens may be weighing current versus future reproductive effort (Martin, 2002). Decreased activity in later stages of incubation is not surprising, as common eider hens can benefit from decreasing activity when energetic reserves become alarmingly low and need to be strategically used (Bottitta et al., 2003). Further, increased investment in the form of consistent incubation leads to healthy egg development and future offspring fitness (DuRant et al., 2013). Indeed, Bolduc and Guillemette (2003) found that as incubation stages progressed for female eiders breeding in Denmark, their nest attendance also increased (Bolduc & Guillemette, 2003). Alternatively, breeding eiders in the central Baltic do not change their frequency of nest absences throughout their incubation; however, the duration of nest absences (or recesses) for some hens is marginally shortened towards later stages of incubation (Garbus et al., 2018).

At Qikiqtakuluk, breeding common eiders have some of the highest incubation consistency in birds (99.8%) (Bottitta et al., 2003). For example, Icelandic eiders leave the nest on average 1.3-1.8 times per day during incubation, depending on their nesting material (Kristjánsson & Jónsson, 2011), whereas Qikiqtakuluk eiders have been recorded to only take nest recesses every second day, on average, during the last four days of incubation when more frequent nest absences occur as females become dehydrated and deplete their fat reserves (Bottitta et al., 2003). It is important to note that although incubation consistency may increase as incubation progresses, if energy and water reserves are depleted before eggs hatch parents may leave the nest more frequently to refuel (Bottitta et al., 2003). However, this may come at great risk of clutch predation (Barnas et al., 2022; Reed et al., 2007), as mentioned above. In our study, sampled females' incubation stages ranged from 0-19 days (average = day 8), and as eiders typically complete incubation on days 24-26, this may explain why we did not detect the increase in female absences or incubation interruptions that occur in the last days before incubation completion.

Contrary to incubation stage, we observed that as standardized ordinal date advances (the date at which a behaviour sample was taken), the number of daily hen movements on the nest also increases. Because hens in our study did not initiate breeding all at the same time, during the later seasonal period, there were hens still in the beginning stages of incubation. Furthermore, because females in poorer condition tend to delay (or forfeit) breeding, higher stress levels may also result in reduced incubation consistency, as other studies note that stressed avian parents are more absent due to prematurely depleted energy reserves, forcing parents to increase nest absences for water, or altogether nest abandonment (DuRant et al., 2013). This absence may be preceded by increased movement on the nest, as those observed in this study. For example, fasting king penguin (*Aptenodytes patagonicus*) parents that abandon their clutches or chicks due to depleted energetic reserves can be seen using ‘comfort behaviours’ prior to abandonment, such as wing flapping and calling (Groscolas et al., 2008).

Females' incubation behaviour was not significantly correlated to lay date, though one might suspect that late layers would experience greater incubation interruptions, as late breeders in a given year are typically of lower quality than early breeders (Descamps et al., 2011a). However, the effects of lay date may be more directly linked to another phenotypic pathway, such as physiology, rather than behaviour in this species, supported by the fact that we see a significant correlation between heart rate and lay date in Chapter 2.

Significance and concluding remarks

We found the predicted pattern of eider hen behaviour where movement on the nest decreased below thresholds of a cold-stress response and increased when hens were exposed to temperatures beyond heat stress-inducing thresholds. However, hens are not yet exposed to temperatures in their environment that induce behavioural responses of statistical significance to heat stress beyond these (significant) thresholds. Eiders' behavioural responses during reproduction can negatively interact with their reproductive success (Carroll et al., 2018), depending on their decision to use physiological versus behavioural responses to their thermal environment (Monaco et al., 2017). For instance, if eiders deplete their energetic budget for incubation in attempts to physiologically thermoregulate, they may choose to replenish energetic reserves by abandoning their clutch (Bottitta et al., 2003; Gabrielsen et al., 1991) or chicks (Bustnes & Erikstad, 1991; Gabrielsen et al., 1991). Alternatively, if they offset physiological thermoregulation with increased behavioural movement on the nest, they risk increasing clutch predation by making themselves more detectable to predators (Smith et al., 2012), as well as risk diminishing embryo health by exposing eggs to frequent, or large, temperature fluctuations (Booth, 1987; Lourens et al., 2005).

Given the potential negative costs of increased agitation movement on nest success, we suggest future studies focus on establishing the outcomes of behavioural responses to heat stress during incubation. While in our study we examined the heat stress responses of hens during incubation, we did not determine if these responses impacted nest outcome (e.g. eggs hatched, nest predated, hen abandoned). Specific studies could relate the degree of hen agitation with the likelihood of clutches being depredated and/or embryo health impacted. These analyses would provide evidence of whether or not eiders' heat stress responses on the nest impact their current reproductive success (Amat & Masero, 2004) and, thus, the effect of heat stress on arctic-breeding eiders population health. Further, future studies should explore other behavioural strategies eiders may exploit to offset thermoregulatory costs on the nest, such as nest-site selection (Carroll et al., 2018; Robertson, 2009). For example, as hens' breeding environment is now experiencing higher environmental temperatures, they may be selecting the quality of their nest sites based on different attributes, such as low solar variability or selecting nests within closer distances to water (Wright et al., unpubl data). In summary, we find that eiders have the capacity to behaviourally respond to heat stress, but future studies should examine how these behavioural responses influence their breeding success and explore other breeding decisions eiders may be making in response to heat stress.

References

Albright, T. P., Mutiibwa, D., Gerson, A. R., Smith, E. K., Talbot, W. A., O’Neill, J. J., McKechnie, A. E., & Wolf, B. O. (2017). Mapping evaporative water loss in desert passerines reveals an expanding threat of lethal dehydration. *Proceedings of the National Academy of Sciences, 114*(9), 2283-2288.

AlRashidi, M., Kosztolányi, A., Shobrak, M., Küpper, C., & Székely, T. (2011). Parental cooperation in an extreme hot environment: natural behaviour and experimental evidence. *Animal Behaviour*, *82*(2), 235-243. https://doi.org/https://doi.org/10.1016/j.anbehav.2011.04.019

Amat, J. A., & Masero, J. A. (2004). How Kentish plovers, Charadrius alexandrinus, cope with heat stress during incubation. *Behavioral Ecology and Sociobiology*, *56*(1), 26-33. https://doi.org/10.1007/s00265-004-0758-9

Anderson, D. M., Fachon, E., Pickart, R. S., Lin, P., Fischer, A. D., Richlen, M. L., Uva, V., Brosnahan, M. L., McRaven, L., & Bahr, F. (2021). Evidence for massive and recurrent toxic blooms of Alexandrium catenella in the Alaskan Arctic. *Proceedings of the National Academy of Sciences*, *118*(41), e2107387118.

Angilletta, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2010). The evolution of thermal physiology in endotherms. *Frontiers in Bioscience E, 2*, 861-881.

Baerends, G. (1959). The ethological analysis of incubation behaviour. *Ibis*, *101*(3-4), 357-368.

Bakken, G. S. (1980). The Use of Standard Operative Temperature in the Study of the Thermal Energetics of Birds. *Physiological Zoology*, *53*(1), 108-119. http://www.jstor.org.ledproxy2.uwindsor.ca/stable/30155779

Bakken, G. S., Murphy, M. T., & Erskine, D. J. (1991). The Effect of Wind and Air Temperature on Metabolism and Evaporative Water Loss Rates of Dark-Eyed Juncos, Junco hyemalis: A Standard Operative Temperature Scale. *Physiological Zoology*, *64*(4), 1023-1049. http://www.jstor.org.ledproxy2.uwindsor.ca/stable/30157955

Barnas, A. F., Geldart, E. A., Love, O. P., Jagielski, P. M., Harris, C. M., Gilchrist, H. G., Hennin, H. L., Richardson, E. S., Dey, C. J., & Semeniuk, C. A. D. (2022). Predatory cue use in flush responses of a colonial nesting seabird during polar bear foraging. *Animal Behaviour*, *193*, 75-90. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.08.009

Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A., & Krapu, G. L. (1992). Incubation and Brood Care. In *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press.

Beever, E. A., Hall, L. E., Varner, J., Loosen, A. E., Dunham, J. B., Gahl, M. K., Smith, F. A., & Lawler, J. J. (2017). Behavioral flexibility as a mechanism for coping with climate change. *Frontiers in Ecology and the Environment*, *15*(6), 299-308.

Benson, D., & Cummins, M. (2011). Move, adapt, or die: Lagopus leucura changes in distribution, habitat, and number at Glacier National Park, Montana. *Gyrfalcons and Ptarmigan in a Changing World*, *1*, 237-246.

Blanco, G., & Bertellotti, M. (2002). Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. *Biological Journal of the Linnean Society*, *75*(2), 137-146. https://doi.org/10.1046/j.1095-8312.2002.00026.x

Bolduc, F., & Guillemette, M. (2003). Incubation constancy and mass loss in the common eider Somateria mollissima. *Ibis*, *145*(2), 329-332.

Booth, D. T. (1987). Effect of temperature on development of mallee fowl Leipoa ocellata eggs. *Physiological Zoology*, *60*(4), 437-445.

Bottitta, G. E., Nol, E., & Gilchrist, H. G. (2003). Effects of Experimental Manipulation of Incubation Length on Behavior and Body Mass of Common Eiders in the Canadian Arctic. *Waterbirds*, *26*(1), 100-107, 108. https://doi.org/10.1675/1524-4695(2003)026[0100:EOEMOI]2.0.CO;2

Bourne, A. R., Ridley, A. R., McKechnie, A. E., Spottiswoode, C. N., & Cunningham, S. J. (2021). Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the southern pied babbler Turdoides bicolor. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coab043

Braimoh-Azaki, B. D., Cunningham, S. J., & Cresswell, W. (2023). Incubation scheduling by African Black Oystercatchers: effects of weather, tide phase, and time of day. *Journal of Ornithology*, *164*(1), 139-149.

Brooks, M. E., Kristensen, K., Benthem, K. J. v., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M., & Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, *9*, 378-400, Article 2. https://doi.org/10.32614/RJ-2017-066

Bustnes, J. O., & Erikstad, K. E. (1991). Parental care in the common eider (Somateria mollissima): factors affecting abandonment and adoption of young. *Canadian Journal of Zoology*, *69*(6), 1538-1545.

Callaghan, T. V., Björn, L. O., Chernov, Y., Chapin, T., Christensen, T. R., Huntley, B., Ims, R. A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., Oechel, W., Shaver, G., Elster, J., Henttonen, H., Laine, K., Taulavuori, K., Taulavuori, E., & Zöckler, C. (2004). Biodiversity, Distributions and Adaptations of Arctic Species in the Context of Environmental Change. *AMBIO: A Journal of the Human Environment*, *33*(7), 404-417, 414. https://doi.org/10.1579/0044-7447-33.7.404

CAPE-Last Interglacial Project Members. (2006). Last Interglacial Arctic warmth confirms polar amplification of climate change. *Quaternary Science Reviews*, *25*(13), 1383-1400. https://doi.org/https://doi.org/10.1016/j.quascirev.2006.01.033

Carroll, R. L., Davis, C. A., Fuhlendorf, S. D., Elmore, R. D., DuRant, S. E., & Carroll, J. M. (2018). Avian parental behavior and nest success influenced by temperature fluctuations. *Journal of Thermal Biology*, *74*, 140-148. https://doi.org/https://doi.org/10.1016/j.jtherbio.2018.03.020

Chatwin, T. A., Joy, R., & Burger, A. E. (2013). Set-Back Distances to Protect Nesting and Roosting Seabirds Off Vancouver Island from Boat Disturbance. *Waterbirds*, *36*(1), 43-52, 10. https://doi.org/10.1675/063.036.0108

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F., & Elliott, K. H. (2021). Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. *Journal of Experimental Biology*, *224*(13), jeb242168.

Clauser, A. J., & McRae, S. B. (2017). Plasticity in incubation behavior and shading by king rails Rallus elegans in response to temperature. *Journal of Avian Biology*, *48*(4), 479-488.

Collier, R., Renquist, B., & Xiao, Y. (2017). A 100-Year Review: Stress physiology including heat stress. *Journal of dairy science*, *100*(12), 10367-10380.

Comrey, A. L., & Lee, H. B. (2013). *A first course in factor analysis*. Psychology press.

Cook, T. R., Martin, R., Roberts, J., Häkkinen, H., Botha, P., Meyer, C., Sparks, E., Underhill, L. G., Ryan, P. G., & Sherley, R. B. (2020). Parenting in a warming world: thermoregulatory responses to heat stress in an endangered seabird. *Conservation Physiology*, *8*(1), coz109.

Cresswell, W., Holt, S., Reid, J., Whitfield, D., & Mellanby, R. (2003). Do energetic demands constrain incubation scheduling in a biparental species? *Behavioral Ecology*, *14*(1), 97-102.

Criscuolo, F., Gabrielsen, G. W., Gendner, J.-P., & Le Maho, Y. (2002). Body mass regulation during incubation in female common eiders Somateria mollissima. *Journal of Avian Biology*, *33*(1), 83-88. https://doi.org/https://doi.org/10.1034/j.1600-048X.2002.330113.x

D'alba, L., Carlsen, T. H., Ásgeirsson, Á., Shawkey, M. D., & Jónsson, J. E. (2017). Contributions of feather microstructure to eider down insulation properties. *Journal of Avian Biology*, *48*(8), 1150-1157.

Dawson, W. R., & O'Connor, T. P. (1996). Energetic features of avian thermoregulatory responses. *Avian energetics and nutritional ecology*, 85-124.

Descamps, S., Bêty, J., Love, O. P., & Gilchrist, H. G. (2011a). Individual optimization of reproduction in a long-lived migratory bird: a test of the condition-dependent model of laying date and clutch size. *Functional Ecology*, *25*(3), 671-681. https://doi.org/https://doi.org/10.1111/j.1365-2435.2010.01824.x

Descamps, S., Forbes, M. R., Gilchrist, H. G., Love, O. P., & Bêty, J. (2011b). Avian cholera, post-hatching survival and selection on hatch characteristics in a long-lived bird, the common eider Somateria mollisima. *Journal of Avian Biology*, *42*(1), 39-48. https://doi.org/https://doi.org/10.1111/j.1600-048X.2010.05196.x

Descamps, S., Jenouvrier, S., Gilchrist, H. G., & Forbes, M. R. (2012). Avian cholera, a threat to the viability of an Arctic seabird colony? *PLoS One*, *7*(2), e29659.

Dobricic, S., Russo, S., Pozzoli, L., Wilson, J., & Vignati, E. (2020). Increasing occurrence of heat waves in the terrestrial Arctic. *Environmental Research Letters*, *15*(2), 024022.

Downs, C. T., & Ward, D. (1997). Does shading behavior of incubating shorebirds in hot environments cool the eggs or the adults? *The Auk*, *114*(4), 717-724.

DuRant, S. E., Hopkins, W. A., Hepp, G. R., & Walters, J. R. (2013). Ecological, evolutionary, and conservation implications of incubation temperature-dependent phenotypes in birds. *Biol Rev Camb Philos Soc*, *88*(2), 499-509. https://doi.org/10.1111/brv.12015

Dzialowski, E. M. (2005). Use of operative temperature and standard operative temperature models in thermal biology. *Journal of Thermal Biology*, *30*(4), 317-334. https://doi.org/https://doi.org/10.1016/j.jtherbio.2005.01.005

Environment and Climate Change Canada. (2024). *Historical Data*. Government of Canada. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Fast, P. L., Fast, M., Mosbech, A., Sonne, C., Gilchrist, H. G., & Descamps, S. (2011). Effects of implanted satellite transmitters on behavior and survival of female common eiders. *The Journal of Wildlife Management*, *75*(7), 1553-1557.

Fast, P. L., Gilchrist, H. G., & Clark, R. G. (2010). Nest-site materials affect nest-bowl use by Common Eiders (Somateria mollissima). *Canadian Journal of Zoology*, *88*(2), 214-218.

Fast, P. L. F., Grant Gilchrist, H., & Clark, R. G. (2007). Experimental evaluation of nest shelter effects on weight loss in incubating common eiders Somateria mollissima. *Journal of Avian Biology*, *38*(2), 205-213. https://doi.org/https://doi.org/10.1111/j.0908-8857.2007.03820.x

Forkman, J., Josse, J., & Piepho, H.-P. (2019). Hypothesis tests for principal component analysis when variables are standardized. *Journal of Agricultural, Biological and Environmental Statistics*, *24*, 289-308.

Fox, A. D. (2021). Ecology of Arctic Birds. In *Arctic Ecology* (pp. 385-408). https://doi.org/https://doi.org/10.1002/9781118846582.ch14

Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (Third Edition ed.). Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Fretwell, P. T., Boutet, A., & Ratcliffe, N. (2023). Record low 2022 Antarctic sea ice led to catastrophic breeding failure of emperor penguins. *Communications Earth & Environment*, *4*(1), 273. https://doi.org/10.1038/s43247-023-00927-x

Gabrielsen, G. W., Mehlum, F., Karlsen, H. E., Andresen, Ø., & Parker, H. (1991). Energy cost during incubation and thermoregulation in the female common eider Somateria mollissima. *Norsk Polarinstitutt Skrifter*, *195*, 51-62.

Gagnon, A. S., & Gough, W. A. (2005). Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. *Arctic*, 370-382.

Garbus, S.-E., Lyngs, P., Garbus, M., Garbus, P., Eulaers, I., Mosbech, A., Dietz, R., Gilchrist, H. G., Huusmann, R., & Christensen, J. P. (2018). Incubation Behaviour of Common Eiders in the Central Baltic: Nest Attendance and Loss in Body Mass. *Acrocephalus*, *39*(178-179), 91-100.

Gaston, A. J., Hipfner, J. M., & Campbell, D. (2002). Heat and mosquitoes cause breeding failures and adult mortality in an Arctic-nesting seabird. *Ibis*, *144*(2), 185-191.

Geldart, E. A., Love, O. P., Gilchrist, H. G., Barnas, A. F., Harris, C. M., & Semeniuk, C. A. (2023). Heightened heart rate but similar flight responses to evolved versus recent predators in an Arctic seabird. *Avian Conservation and Ecology*, *18*(1).

Gerson, A. R., Smith, E. K., Smit, B., McKechnie, A. E., & Wolf, B. O. (2014). The impact of humidity on evaporative cooling in small desert birds exposed to high air temperatures. *Physiological and Biochemical Zoology*, *87*(6), 782-795.

Gilg, O., Sittler, B., & Hanski, I. (2009). Climate change and cyclic predator–prey population dynamics in the high Arctic. *Global Change Biology*, *15*(11), 2634-2652. https://doi.org/https://doi.org/10.1111/j.1365-2486.2009.01927.x

Götmark, F., & Åhlund, M. (1984). Do Field Observers Attract Nest Predators and Influence Nesting Success of Common Eiders? *The Journal of Wildlife Management*, *48*(2), 381-387. https://doi.org/10.2307/3801169

Groscolas, R., Lacroix, A., & Robin, J.-P. (2008). Spontaneous egg or chick abandonment in energy-depleted king penguins: A role for corticosterone and prolactin? *Hormones and Behavior*, *53*(1), 51-60. https://doi.org/https://doi.org/10.1016/j.yhbeh.2007.08.010

Grunst, M. L., Grunst, A. S., Grémillet, D., Kato, A., Gentès, S., & Fort, J. (2023). Keystone seabird may face thermoregulatory challenges in a warming Arctic. *Scientific reports*, *13*(1), 16733. https://doi.org/10.1038/s41598-023-43650-5

Guillemette, M., Polymeropoulos, E. T., Portugal, S. J., & Pelletier, D. (2017). It Takes Time to Be Cool: On the Relationship between Hyperthermia and Body Cooling in a Migrating Seaduck. *Frontiers in physiology*, *8*, 532-532. https://doi.org/10.3389/fphys.2017.00532

Gunderson, A. R., Tsukimura, B., & Stillman, J. H. (2017). Indirect Effects of Global Change: From Physiological and Behavioral Mechanisms to Ecological Consequences. *Integrative and Comparative Biology*, *57*(1), 48-54. https://doi.org/10.1093/icb/icx056

Guthery, F. S., Rybak, A. R., Fuhlendorf, S. D., Hiller, T. L., Smith, S. G., Puckett Jr, W. H., & Baker, R. A. (2005). Aspects of the thermal ecology of bobwhites in north Texas. *Wildlife Monographs*, *159*(1), 1-36.

Habary, A., Johansen, J. L., Nay, T. J., Steffensen, J. F., & Rummer, J. L. (2017). Adapt, move or die – how will tropical coral reef fishes cope with ocean warming? *Global Change Biology, 23*(2), 566-577. https://doi.org/https://doi.org/10.1111/gcb.13488

Haftorn, S. (1988). Incubating Female Passerines Do Not Let the Egg Temperature Fall below the 'Physiological Zero Temperature' during Their Absences from the Nest. *Ornis Scandinavica (Scandinavian Journal of Ornithology), 19*(2), 97-110. https://doi.org/10.2307/3676458

Hand, J. L., Hunt, G. L., Jr., & Warner, M. (1981). Thermal Stress and Predation: Influences on the Structure of a Gull Colony and Possibly on Breeding Distributions. *The Condor, 83*(3), 193-203. https://doi.org/10.2307/1367307

Hanssen, S. A., Engebretsen, H., & Erikstad, K. (2002). Incubation start and egg size in relation to body reserves in the common eider. *Behavioral Ecology and Sociobiology, 52*, 282-288.

Hart, L. A., Downs, C. T., & Brown, M. (2016). Sitting in the sun: Nest microhabitat affects incubation temperatures in seabirds. *Journal of Thermal Biology, 60*, 149-154. https://doi.org/https://doi.org/10.1016/j.jtherbio.2016.07.001

Hartig, F. (2022). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. https://CRAN.R-project.org/package=DHARMa

Hennin, H. L., Bêty, J., Legagneux, P., Gilchrist, H. G., Williams, T. D., & Love, O. P. (2016). Energetic physiology mediates individual optimization of breeding phenology in a migratory Arctic seabird. *The American Naturalist, 188*(4), 434-445.

Hovick, T. J., Elmore, R. D., Allred, B. W., Fuhlendorf, S. D., & Dahlgren, D. K. (2014). Landscapes as a moderator of thermal extremes: a case study from an imperiled grouse. *Ecosphere, 5*(3), art35. https://doi.org/https://doi.org/10.1890/ES13-00340.1

Iverson, S. A., Gilchrist, H. G., Smith, P. A., Gaston, A. J., & Forbes, M. R. (2014). Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceedings of the Royal Society B: Biological Sciences, 281*(1779), 20133128.

Jagielski, P. M., Dey, C. J., Gilchrist, H. G., Richardson, E. S., Love, O. P., & Semeniuk, C. A. (2021). Polar bears are inefficient predators of seabird eggs. *Royal Society Open Science, 8*(4), 210391.

Jean-Gagnon, F., Legagneux, P., Gilchrist, G., Bélanger, S., Love, O. P., & Bêty, J. (2018). The impact of sea ice conditions on breeding decisions is modulated by body condition in an arctic partial capital breeder. *Oecologia*, *186*(1), 1-10. https://doi.org/10.1007/s00442-017-4002-5

Jenssen, B. M., Ekker, M., & Bech, C. (1989). Thermoregulation in winter-acclimatized common eiders (Somateria mollissima) in air and water. *Canadian Journal of Zoology*, *67*(3), 669-673.

Jönsson, K. I. (1997). Capital and Income Breeding as Alternative Tactics of Resource Use in Reproduction. *Oikos*, *78*(1), 57-66. https://doi.org/10.2307/3545800

Koenigk, T., Key, J., & Vihma, T. (2020). Climate Change in the Arctic. In A. Kokhanovsky & C. Tomasi (Eds.), *Physics and Chemistry of the Arctic Atmosphere* (pp. 673-705). Springer International Publishing. https://doi.org/10.1007/978-3-030-33566-3_11

Korschgen, C. E. (1977). Breeding stress of female eiders in Maine. *The Journal of Wildlife Management*, 360-373.

Kristjánsson, T. Ö., & Jónsson, J. E. (2011). Effects of down collection on incubation temperature, nesting behaviour and hatching success of common eiders (Somateria mollissima) in west Iceland. *Polar Biology*, *34*(7), 985-994. https://doi.org/10.1007/s00300-010-0956-z

Kuletz, K. J., Ferguson, S. H., Frederiksen, M., Gallagher, C. P., Hauser, D. D., Hop, H., Kovacs, K. M., Lydersen, C., Mosbech, A., & Seitz, A. C. (2024). A review of climate change impacts on migration patterns of marine vertebrates in Arctic and Subarctic ecosystems. *Frontiers in Environmental Science*, *12*, 1434549.

Kutz, S. J., Jenkins, E. J., Veitch, A. M., Ducrocq, J., Polley, L., Elkin, B., & Lair, S. (2009). The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. *Veterinary Parasitology*, *163*(3), 217-228. https://doi.org/https://doi.org/10.1016/j.vetpar.2009.06.008

Kwon, E., Weiser, E. L., Lanctot, R. B., Brown, S. C., Gates, H. R., Gilchrist, G., Kendall, S. J., Lank, D. B., Liebezeit, J. R., McKinnon, L., Nol, E., Payer, D. C., Rausch, J., Rinella, D. J., Saalfeld, S. T., Senner, N. R., Smith, P. A., Ward, D., Wisseman, R. W., & Sandercock, B. K. (2019). Geographic variation in the intensity of warming and phenological mismatch between Arctic shorebirds and invertebrates. *Ecological Monographs*, *89*(4), e01383. https://doi.org/https://doi.org/10.1002/ecm.1383

Laidre, K. L., Stern, H., Kovacs, K. M., Lowry, L., Moore, S. E., Regehr, E. V., Ferguson, S. H., Wiig, Ø., Boveng, P., Angliss, R. P., Born, E. W., Litovka, D., Quakenbush, L., Lydersen, C., Vongraven, D., & Ugarte, F. (2015). Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conservation Biology*, *29*(3), 724-737. https://doi.org/https://doi.org/10.1111/cobi.12474

Lameris, T. K., van der Jeugd, H. P., Eichhorn, G., Dokter, A. M., Bouten, W., Boom, M. P., Litvin, K. E., Ens, B. J., & Nolet, B. A. (2018). Arctic geese tune migration to a warming climate but still suffer from a phenological mismatch. *Current Biology*, *28*(15), 2467-2473. e2464.

Lee, T., Schuman, J. S., Ramos Cadena, M. d. l. A., Zhang, Y., Wollstein, G., & Hu, J. (2024). LIMBARE: An Advanced Linear Mixed-Effects Breakpoint Analysis With Robust Estimation Method With Applications to Longitudinal Ophthalmic Studies. *Translational Vision Science & Technology*, *13*(1), 19-19. https://doi.org/10.1167/tvst.13.1.19

Logan, M. L., van Berkel, J., & Clusella-Trullas, S. (2019). The Bogert Effect and environmental heterogeneity. *Oecologia*, *191*(4), 817-827. https://doi.org/10.1007/s00442-019-04541-7

Lourens, A., van den Brand, H., Meijerhof, R., & Kemp, B. (2005). Effect of eggshell temperature during incubation on embryo development, hatchability, and posthatch development. *Poultry Science*, *84*(6), 914-920. https://doi.org/https://doi.org/10.1093/ps/84.6.914

Love, O. P., Gilchrist, H. G., Descamps, S., Semeniuk, C. A., & Bêty, J. (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia*, *164*, 277-286.

Lüdecke, D. (2018). ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *Journal of Open Source Software*, *3*(26), 772. https://doi.org/10.21105/joss.00772

Ma, N. L., Hansen, M., Roland Therkildsen, O., Kjær Christensen, T., Skjold Tjørnløv, R., Garbus, S.-E., Lyngs, P., Peng, W., Lam, S. S., Kirstine Havnsøe Krogh, A., Andersen-Ranberg, E., Søndergaard, J., Rigét, F. F., Dietz, R., & Sonne, C. (2020). Body mass, mercury exposure, biochemistry and untargeted metabolomics of incubating common eiders (Somateria mollissima) in three Baltic colonies. *Environment International*, *142*, 105866. https://doi.org/https://doi.org/10.1016/j.envint.2020.105866

Martin, T. E. (2002). A new view of avian life-history evolution tested on an incubation paradox. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *269*(1488), 309-316. https://doi.org/doi:10.1098/rspb.2001.1879

Martin, T. E., Oteyza, J. C., Boyce, A. J., Lloyd, P., & Ton, R. (2015). Adult Mortality Probability and Nest Predation Rates Explain Parental Effort in Warming Eggs with Consequences for Embryonic Development Time. *The American Naturalist*, *186*(2), 223-236. https://doi.org/10.1086/681986

Martin, T. E., Scott, J., & Menge, C. (2000). Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1459), 2287-2293. https://doi.org/doi:10.1098/rspb.2000.1281

Meyer, N., Bollache, L., Dechaume-Moncharmont, F.-X., Moreau, J., Afonso, E., Angerbjörn, A., Bêty, J., Ehrich, D., Gilg, V., Giroux, M.-A., Hansen, J., Lanctot, R. B., Lang, J., Lecomte, N., McKinnon, L., Reneerkens, J., Saalfeld, S. T., Sabard, B., Schmidt, N. M., . . . Gilg, O. (2020). Nest attentiveness drives nest predation in arctic sandpipers. *Oikos*, *129*(10), 1481-1492. https://doi.org/https://doi.org/10.1111/oik.07311

Monaco, C. J., McQuaid, C. D., & Marshall, D. J. (2017). Decoupling of behavioural and physiological thermal performance curves in ectothermic animals: a critical adaptive trait. *Oecologia*, *185*(4), 583-593. https://doi.org/10.1007/s00442-017-3974-5

Muggeo, V. M. (2008). Segmented: an R package to fit regression models with broken-line relationships. *R news*, *8*(1), 20-25.

O'Connor, R. S., Le Pogam, A., Young, K. G., Love, O. P., Cox, C. J., Roy, G., Robitaille, F., Elliott, K. H., Hargreaves, A. L., & Choy, E. S. (2022). Warming in the land of the midnight sun: breeding birds may suffer greater heat stress at high-versus low-Arctic sites. *Proceedings of the Royal Society B*, *289*(1981), 20220300.

O'Connor, R. S., Le Pogam, A., Young, K. G., Robitaille, F., Choy, E. S., Love, O. P., Elliott, K. H., Hargreaves, A. L., Berteaux, D., & Tam, A. (2021). Limited heat tolerance in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecology and evolution*, *11*(4), 1609-1619.

O'Connor, R. S., Love, O. P., Régimbald, L., Le Pogam, A., Gerson, A. R., Elliott, K. H., Hargreaves, A. L., & Vézina, F. (2024). An arctic breeding songbird overheats during intense activity even at low air temperatures. *Scientific reports*, *14*(1), 15193. https://doi.org/10.1038/s41598-024-65208-9

Olin, A. B., Dück, L., Berglund, P.-A., Karlsson, E., Bohm, M., Olsson, O., & Hentati-Sundberg, J. (2023). Breeding failures and reduced nest attendance in response to heat stress in a high-latitude seabird. *Marine Ecology Progress Series*.

Oscar, H. (1957). Ecology of a Breeding Population of Arctic Terns. *Bird-Banding*, *28*(2), 57-92. https://doi.org/10.2307/4510623

Oswald, S. A., & Arnold, J. M. (2012). Direct impacts of climatic warming on heat stress in endothermic species: seabirds as bioindicators of changing thermoregulatory constraints. *Integrative Zoology*, *7*(2), 121-136.

Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B., & Hamer, K. C. (2008). Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas Catharacta skua. *Journal of Avian Biology*, *39*(2), 163-169.

Parkinson, A. J., Evengard, B., Semenza, J. C., Ogden, N., Børresen, M. L., Berner, J., Brubaker, M., Sjöstedt, A., Evander, M., & Hondula, D. M. (2014). Climate change and infectious diseases in the Arctic: establishment of a circumpolar working group. *International journal of circumpolar health*, *73*(1), 25163.

R Development Core Team. (2024). *A Language and Environment for Statistical Computing*. In R Foundation for Statistical Computing. https://www.R-project.org/

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Reed, J. A., Lacroix, D. L., & Flint, P. L. (2007). Depredation of common eider, Somateria mollissima, nests on a central Beaufort Sea barrier Island: A case where no one wins. *The Canadian Field-Naturalist*, *121*(3), 308-312.

Renner, H. M., Piatt, J. F., Renner, M., Drummond, B. A., Laufenberg, J. S., & Parrish, J. K. (2024). Catastrophic and persistent loss of common murres after a marine heatwave. *Science*, *386*(6727), 1272-1276. https://doi.org/doi:10.1126/science.adq4330

Revelle, W. (2024). *psych: Procedures for psychological, psychometric, and personality research*. https://CRAN.R-project.org/package=psych

Robertson, B. A. (2009). Nest-Site Selection in a Postfire Landscape: Do Parents Make Tradeoffs Between Microclimate and Predation Risk? *The Auk*, *126*(3), 500-510. https://doi.org/10.1525/auk.2009.08148

Scholander, P., Hock, R., Walters, V., & Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *The Biological Bulletin*, *99*(2), 259-271.

Sénéchal, É., Bêty, J., Gilchrist, H. G., Hobson, K. A., & Jamieson, S. E. (2011). Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. *Oecologia*, *165*, 593-604.

Sieving, K. E., Liu, Y., & Maurelli, O. V. (2024). Intermittent and chronic noise impacts on hatching success and incubation behavior of Eastern Bluebirds (Sialia sialis). *Avian Conservation and Ecology*, *19*(1).

Skutch, A. F. (1949). Do tropical birds rear as many young as they can nourish? *Ibis*, *91*(3), 430-455.

Skutch, A. F. (1962). The Constancy of Incubation. *The Wilson Bulletin*, *74*(2), 115-152. http://www.jstor.org/stable/4159040

Smit, B., Zietsman, G., Martin, R., Cunningham, S., McKechnie, A., & Hockey, P. (2016). Behavioural responses to heat in desert birds: implications for predicting vulnerability to climate warming. *Climate Change Responses*, *3*, 1-14.

Smith, P. A., Tulp, I., Schekkerman, H., Gilchrist, H. G., & Forbes, M. R. (2012). Shorebird incubation behaviour and its influence on the risk of nest predation. *Animal Behaviour*, *84*(4), 835-842. https://doi.org/https://doi.org/10.1016/j.anbehav.2012.07.004

Smith, R. A., Albonaimi, S. S., Hennin, H. L., Gilchrist, H. G., Fort, J., Parkinson, K. J., Provencher, J. F., & Love, O. P. (2022). Exposure to cumulative stressors affects the laying phenology and incubation behaviour of an Arctic-breeding marine bird. *Science of the Total Environment*, *807*, 150882.

Snell, K. R., Aldará, J., Hammer, S., & Thorup, K. (2024). Thermal stress during incubation in an arctic breeding seabird. *Journal of Thermal Biology*, 103967.

Song, S., & Beissinger, S. R. (2019). Environmental determinants of total evaporative water loss in birds at multiple temperatures. *The Auk*, *137*(1). https://doi.org/10.1093/auk/ukz069

Steenweg, R. J., Crossin, G. T., Hennin, H. L., Gilchrist, H. G., & Love, O. P. (2022). Favorable spring conditions can buffer the impact of winter carryover effects on a key breeding decision in an Arctic-breeding seabird. *Ecology and evolution*, *12*(2), e8588.

Tertitski, G. M., Semashko, E. V., Cherenkov, A. E., & Semashko, V. Y. (2021). Studies of the time budget and daily activity of Common Eider Somateria mollissima during incubation. *Marine Ornithology*, *49*, 151-158.

van Dijk, J. G., Iverson, S. A., Gilchrist, H. G., Harms, N. J., Hennin, H. L., Love, O. P., Buttler, E. I., Lesceu, S., Foster, J. T., & Forbes, M. R. (2021). Herd immunity drives the epidemic fadeout of avian cholera in Arctic-nesting seabirds. *Scientific reports*, *11*(1), 1046.

Van Dyk, M., Noakes, M. J., & McKechnie, A. E. (2019). Interactions between humidity and evaporative heat dissipation in a passerine bird. *Journal of Comparative Physiology B*, *189*(2), 299-308.

Vleck, C. M. (1981). Energetic Cost of Incubation in the Zebra Finch. *The Condor*, *83*(3), 229-237. https://doi.org/10.2307/1367313

Waltho, C., & Coulson, J. (2015). *The common eider* (J. Martin, Ed.). Bloomsbury Publishing.

Wang, J. M., & Beissinger, S. R. (2009). Variation in the onset of incubation and its influence on avian hatching success and asynchrony. *Animal Behaviour*, *78*(3), 601-613. https://doi.org/https://doi.org/10.1016/j.anbehav.2009.05.022

Wauchope, H. S., Shaw, J. D., Varpe, Ø., Lappo, E. G., Boertmann, D., Lanctot, R. B., & Fuller, R. A. (2017). Rapid climate-driven loss of breeding habitat for Arctic migratory birds. *Global Change Biology*, *23*(3), 1085-1094. https://doi.org/https://doi.org/10.1111/gcb.13404

Welman, S., Green, J. A., Ryan, P. G., Parsons, N. J., & Pichegru, L. (2024). Body temperature and thermoregulatory behaviour in the Endangered African Penguin Spheniscus demersus. *Bird Conservation International*, *34*, e29, Article e29. https://doi.org/10.1017/S095927092400025X

Welman, S., & Pichegru, L. (2023). Nest microclimate and heat stress in African Penguins Spheniscus demersus breeding on Bird Island, South Africa. *Bird Conservation International*, *33*, e34.

White, F. N., & Kinney, J. L. (1974). Avian Incubation. *Science*, *186*(4159), 107-115. https://doi.org/doi:10.1126/science.186.4159.107

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Wickham, H., François, R., Henry, L., Müller, K., & Vaughan, D. (2023). *dplyr: A Grammar of Data Manipulation*. https://CRAN.R-project.org/package=dplyr

Wilke, C. O. (2024). *cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'*. https://CRAN.R-project.org/package=cowplot

Williams, C. T., Klaassen, M., Barnes, B. M., Buck, C. L., Arnold, W., Giroud, S., Vetter, S. G., & Ruf, T. (2017). Seasonal reproductive tactics: annual timing and the capital-to-income breeder continuum. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1734), 20160250. https://doi.org/doi:10.1098/rstb.2016.0250

Yorio, P., & Boersma, P. D. (1994). Consequences of Nest Desertion and Inattendance for Magellanic Penguin Hatching Success. *The Auk*, *111*(1), 215-218. https://doi.org/10.2307/4088528

Tables

Table 3.1 Examination of the impacts of weather conditions and breeding decisions on incubation interruptions in female common eiders (*Somateria mollissima*) breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A Generalized Linear Mixed Model with a Poisson distribution was used to examine how daily nest movements were affected by variation in maximum daily nest-level temperature, thermal index, humidity, days of incubation, standardized lay date and standardized ordinal date, with year and nest id as random effects.

Fixed effect	Estimate	Standard Error	Z-Value	Pr(>|z|) (p-value)
Intercept	2.614	0.346	7.563	3.95e-14 ***
Maximum Daily Nest-Level Temperature	0.005	0.004	1.277	0.202
Thermal Index	0.075	0.041	1.818	0.069
Humidity	-0.005	0.030	-0.168	0.867
Days of Incubation	-0.052	0.017	-3.139	0.002 **
Standardized Lay Date	-0.009	0.011	-0.768	0.443
Standardized Ordinal Date	0.044	0.022	2.040	0.041 *

Table 3.2 The random effects structure, Year and Nest ID, of the Poisson regression examining effects of nest-level temperature, thermal index, humidity, days of incubation, standardized lay date and standardized ordinal date on daily nest movements of incubating common eider hens (*Somateria mollissima*) breeding on East Bay Island, Qikiqtakuluk.

Random Effects	Variance	Standard Deviation
Year	0.101	0.318
Nest Id	0.182	0.426

133 observations, 4-year groups and 68 nests in groups.

Table 3.3 Determining the impacts of weather conditions and breeding decisions on incubation interruptions in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The Generalized Linear Mixed Model with a Poisson distribution for examining hens' daily nest movements in response to maximum daily ambient temperature, humidity, days of incubation, standardized lay date and standardized ordinal date, with year and nest id as random effects.

Fixed effect	Estimate	Standard Error	Z-Value	Pr(>|z|) (P-Value)
Intercept	2.427	0.350	6.935	4.06e-12 ***
Maximum Daily Ambient Temperature	0.024	0.005	5.012	5.40e-07 ***
Humidity	-0.005	0.027	-0.175	0.861
Days of Incubation	-0.058	0.017	-3.452	0.0006 ***
Standardized Lay Date	-0.012	0.011	-1.030	0.303
Standardized Ordinal Date	0.051	0.022	2.279	0.023 *

Table 3.4 The random effects structure, Year and Nest ID, of the Poisson regression examining effects of ambient temperature, humidity, days of incubation, standardized lay date and standardized ordinal date on daily nest movements of incubating common eider hens (*Somateria mollissima*) breeding on East Bay Island, Qikiqtakuluk.

Random Factor (grouping factor)	Variance	Standard Deviation
Year	0.108	0.329
Nest Id	0.185	0.430

133 observations, 4 year groups and 68 nest id groups.

Table 3.5 Determining the impacts of weather conditions and breeding decisions on incubation interruptions in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. A segmented model of hens' daily nest movements with maximum daily nest-level temperature as the segmented variable. The model examines additional fixed effects impact on daily nest movements, including, thermal index, humidity, days of incubation, standardized lay date, standardized ordinal date, and year. Nest id is included as a random effect. We used 95% confidence intervals for all breakpoints.

Variables	Value	Std. Error	Degrees of Freedom	T-Value	P-Value
Intercept	6.084	9.595	60	0.634	0.528
Maximum Daily Nest-Level Temperature	1.346	0.454	45	2.962	0.005
Thermal Index	4.570	1.144	45	3.995	0.0002
Humidity	-0.346	0.642	45	-0.539	0.593
Days of Incubation	-0.279	0.365	45	-0.765	0.448
Standardized Lay Date	-0.078	0.255	45	-0.305	0.762
Standardized Ordinal Date	-0.099	0.472	45	-0.210	0.835
Year (2019)	0.993	4.323	60	0.230	0.819
Year (2022)	12.210	4.932	60	2.476	0.016
Year (2023)	-0.125	3.479	60	-0.036	0.972
Breakpoint 1	-2.021	0.550	45	-3.677	0.0006
Breakpoint 2	1.463	0.801	45	1.826	0.075
Breakpoint 1 Confidence Interval	0.0000	2.051	45	0.0000	1.000
Breakpoint 2 Confidence Interval	0.0000	1.783	45	0.0000	1.000

Table 3.6 Examining how weather conditions and breeding decisions impact incubation consistency in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The estimated temperature breakpoints (^{o}C), standard errors, and p-values of our segmented variable, maximum daily nest-level temperature, from its segmented model with daily nest movements (see Table 3.5 for the segmented model summary).

	Estimation	Standard Error	P-Value
Breakpoint 1	19.119	1.979	0.0006
Breakpoint 2	38.617	1.229	0.075

Table 3.7 Examining the influence of weather conditions and breeding decisions on common eider (*Somateria mollissima*) hens incubation interruptions at a breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The slope estimates, standard errors and confidence intervals (upper and lower bounds) for hens' daily nest movements segmented relationship with maximum daily nest-level temperature (see Table 3.5 for the segmented model summary).

Slope #	Estimate	Standard Error	P-Value	Lower Bound (95%)	Upper Bound (95%)
Slope 1	1.346	0.383	0.0004	0.595	2.096
Slope 2	-0.675	0.623	0.278	-1.897	0.546
Slope 3	0.787	1.810	0.664	-2.760	4.335

Table 3.8 Investigating the influence of weather conditions and weather conditions on incubation interruptions in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Daily nest movements segmented model summary with maximum daily ambient temperature. The model includes additional fixed effects: humidity, days of incubation, standardized lay date, standardized ordinal date, and year. Nest id is included as a random effect. We used 95% confidence intervals for all breakpoints.

Variables	Value	Std. Error	Degrees of Freedom	T-Value	P-Value
Intercept	1.146	1.472	62	0.779	0.439
Maximum Daily Ambient Temperature	0.579	0.222	44	2.612	0.012
Humidity	-0.054	0.076	44	-0.706	0.484
Days of Incubation	-0.051	0.045	44	-1.137	0.262
Standardized Lay Date	-0.004	0.032	44	-0.113	0.910
Standardized Ordinal Date	0.021	0.056	44	0.371	0.713
Year (2019)	0.964	0.532	62	1.810	0.075
Year (2022)	1.346	0.573	62	2.349	0.022
Year (2023)	-0.339	0.410	62	-0.828	0.411
Breakpoint 1	-0.604	0.225	44	-2.686	0.010
Breakpoint 2	0.518	0.245	44	2.113	0.040
Breakpoint 1 Confidence Interval	0.0000	0.593	44	0.0000	1.000
Breakpoint 2 Confidence Interval	0.0000	0.875	44	0.0000	1.000

Table 3.9 Examining the effects of weather conditions and weather conditions on incubation consistency in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The estimated temperature breakpoints (^{o}C), standard errors, and p-values of our segmented variable, maximum daily ambient temperature, from its segmented model with daily nest movements (see Table 3.8 for the segmented model summary).

	Estimation	Standard Error	P-Value
Breakpoint 1	5.900	0.412	0.010
Breakpoint 2	17.200	0.708	0.040

Table 3.10 Analysis of how weather conditions and weather conditions influence incubation interruptions in common eider (*Somateria mollissima*) hens nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. The slope estimates, standard errors and confidence intervals (upper and lower bounds) for hens' daily nest movements segmented relationship with maximum daily ambient temperature (see Table 3.8 for the segmented model summary).

Slope #	Estimate	Standard Error	P-Value	Lower Bound (95%)	Upper Bound (95%)
Slope 1	0.579	0.225	0.010	0.138	1.019
Slope 2	-0.025	0.233	0.914	-0.482	0.432
Slope 3	0.492	0.739	0.505	-0.955	1.940

Figures

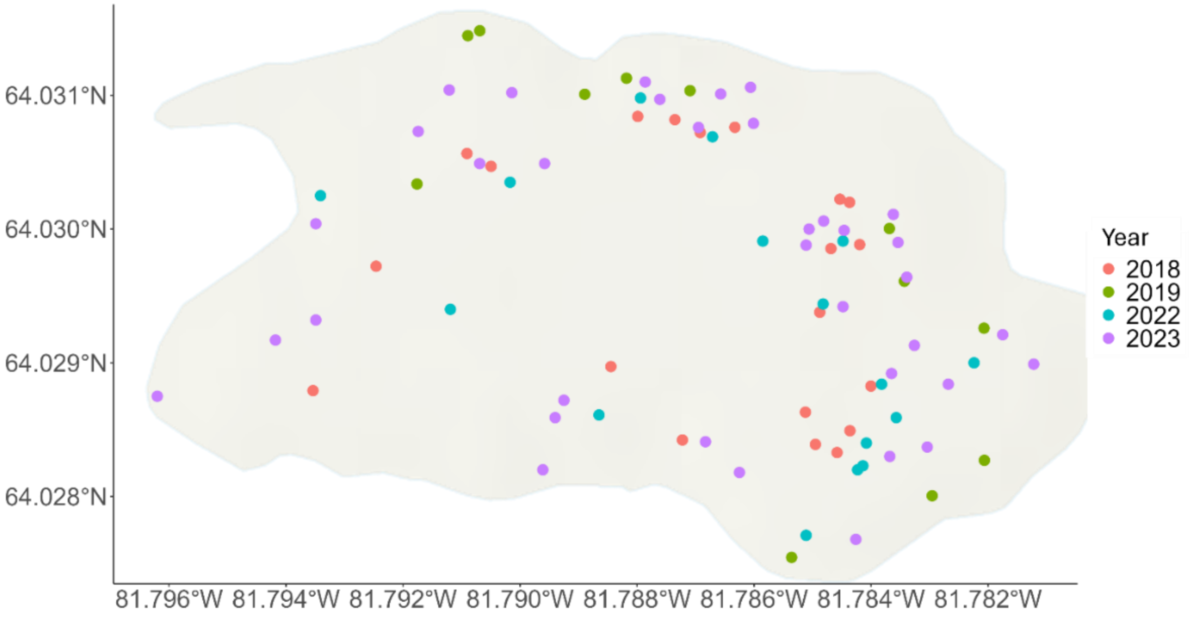


Figure 3.1 Latitude and Longitude coordinates of common eider (*Somateria mollissima*) nests sampled for examining the heat stress effects of weather and breeding parameters on incubation interruptions across four years of study (2018, 2019, 2022, 2023), underlaid by a map of East Bay Island (Qikiqtakuluk), Nunavut, Canada where the study was conducted.

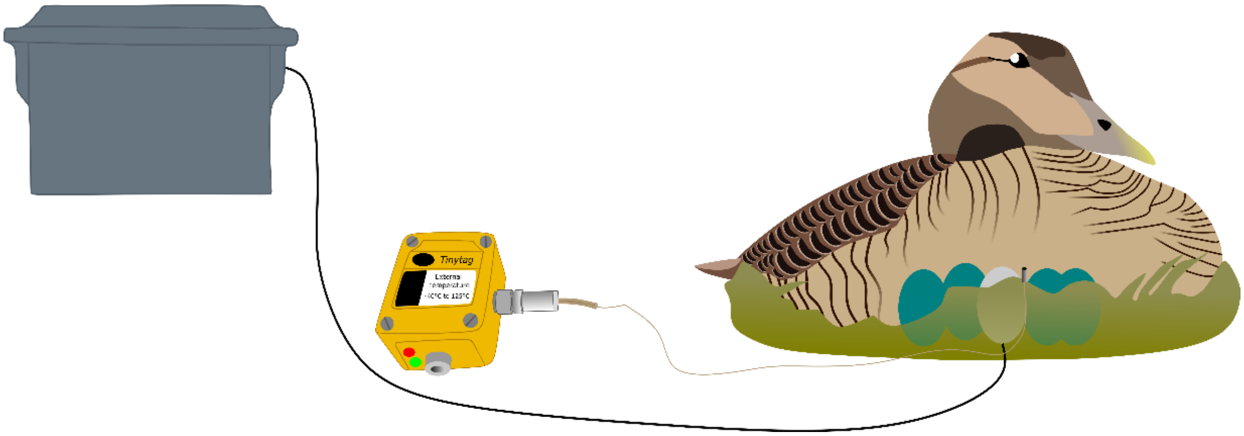


Figure 3.2 Nest deployment set up for our study of the impacts of heat stress on female common eider (*Somateria mollissima*) incubation interruptions, at an Arctic-breeding colony on East Bay Island, Qikiqtakuluk, Nunavut, Canada.

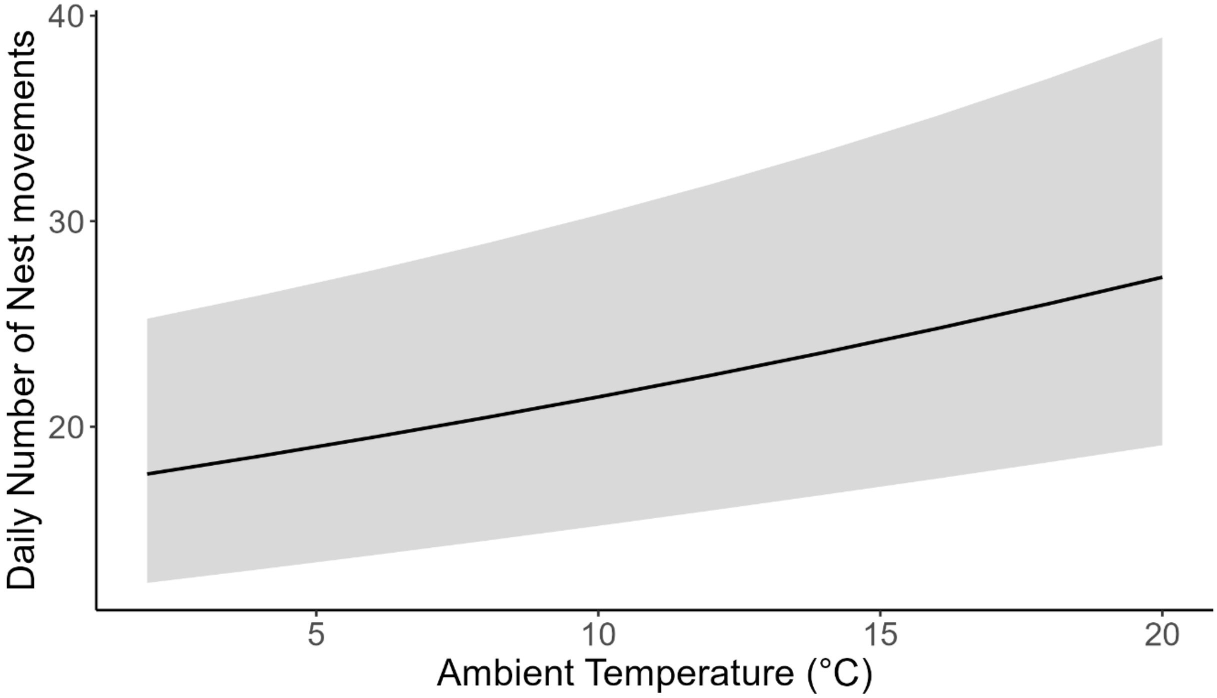


Figure 3.3 Examining the effect of ambient temperature on the incubation consistency of nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between hen daily nest movements and maximum daily ambient temperature from our ambient temperature's generalized linear mixed model. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values.

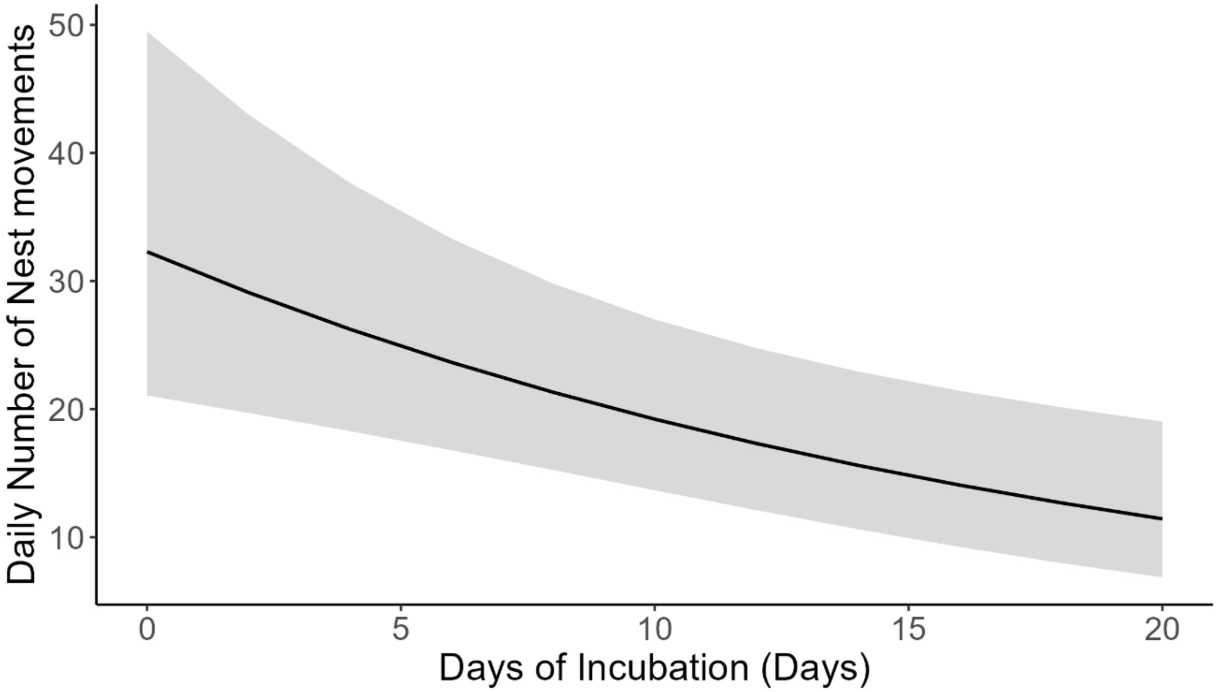


Figure 3.4 Influence of incubation stage on incubation interruptions in female common eiders (*Somateria mollissima*) nesting on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted here is the relationship between hen daily nest movements and incubation stage (i.e., days of incubation) from the generalized linear mixed model of nest-level temperature effects. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between days of incubation and daily nest movements in the generalized linear mixed model for maximum daily ambient temperature (Table 3.3).

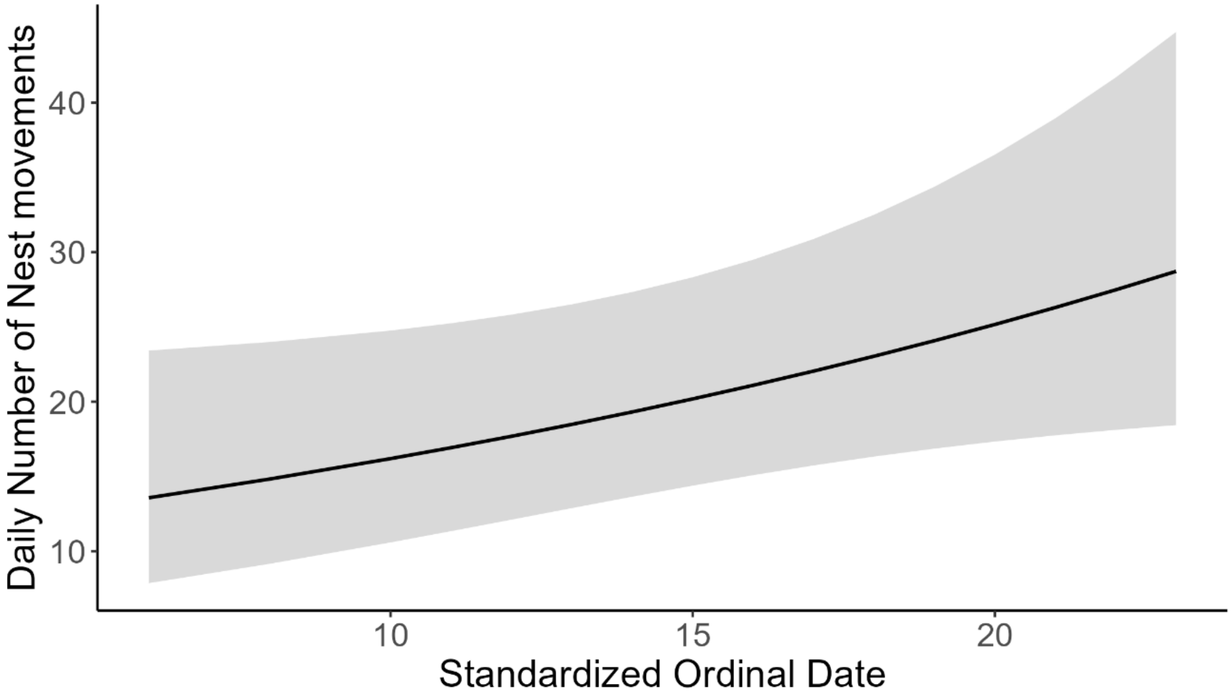


Figure 3.5 Assessing the impacts of ordinal date (i.e., progression of the season) on the incubation consistency of nesting female common eiders (*Somateria mollissima*) on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted is the relationship between hen daily nest movement and standardized ordinal date from the generalized linear mixed model of nest-level temperature. The trendline is denoted by a black line, and the shaded region surrounding the trendline indicates the confidence interval of the predicted values. A similar significant relationship was found between standardized ordinal date and daily nest movements in the generalized linear mixed model for maximum daily ambient temperature (Table 3.3).

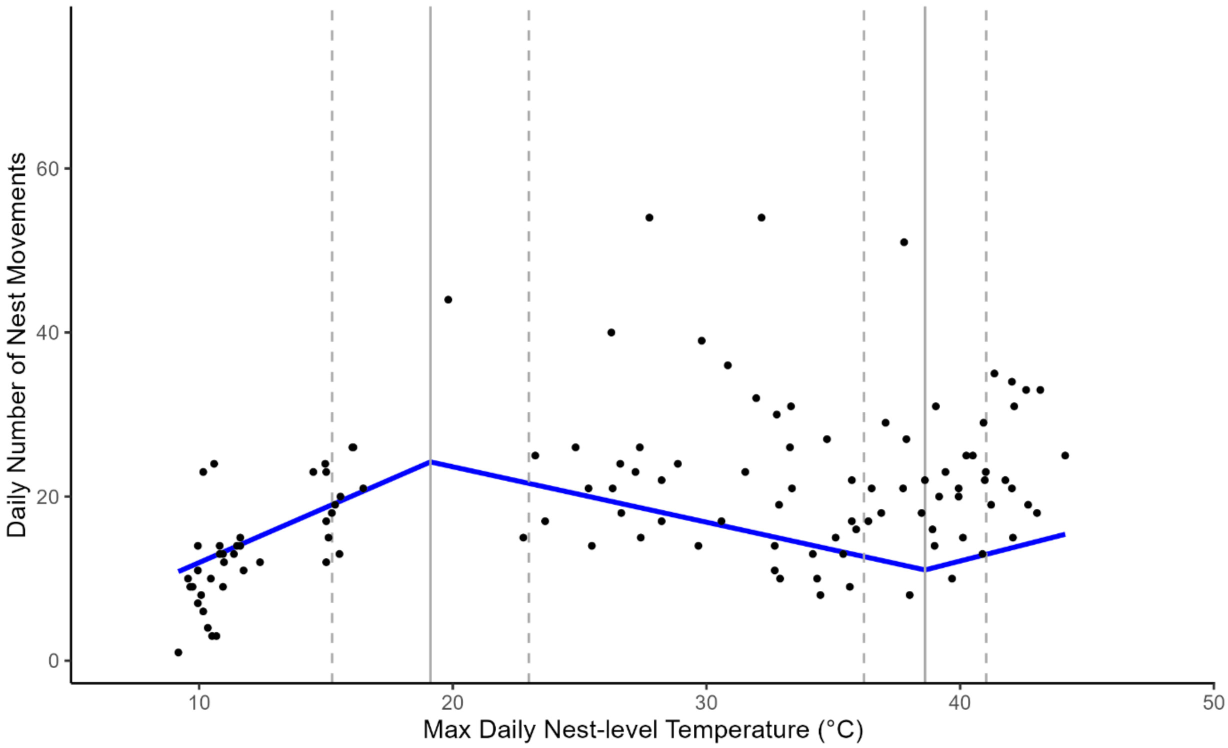


Figure 3.6 Determining the effects of heat stress on incubation consistency in common eider (*Somateria mollissima*) hens breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Represented on the plot is maximum daily nest-level temperature's segmented relationship with daily nest movements for hens. Grey solid lines indicate the location of breakpoints, with standard errors for each breakpoint indicated by grey dotted lines. Blue solid lines indicate estimated slopes of the relationship, as separated by breakpoints.

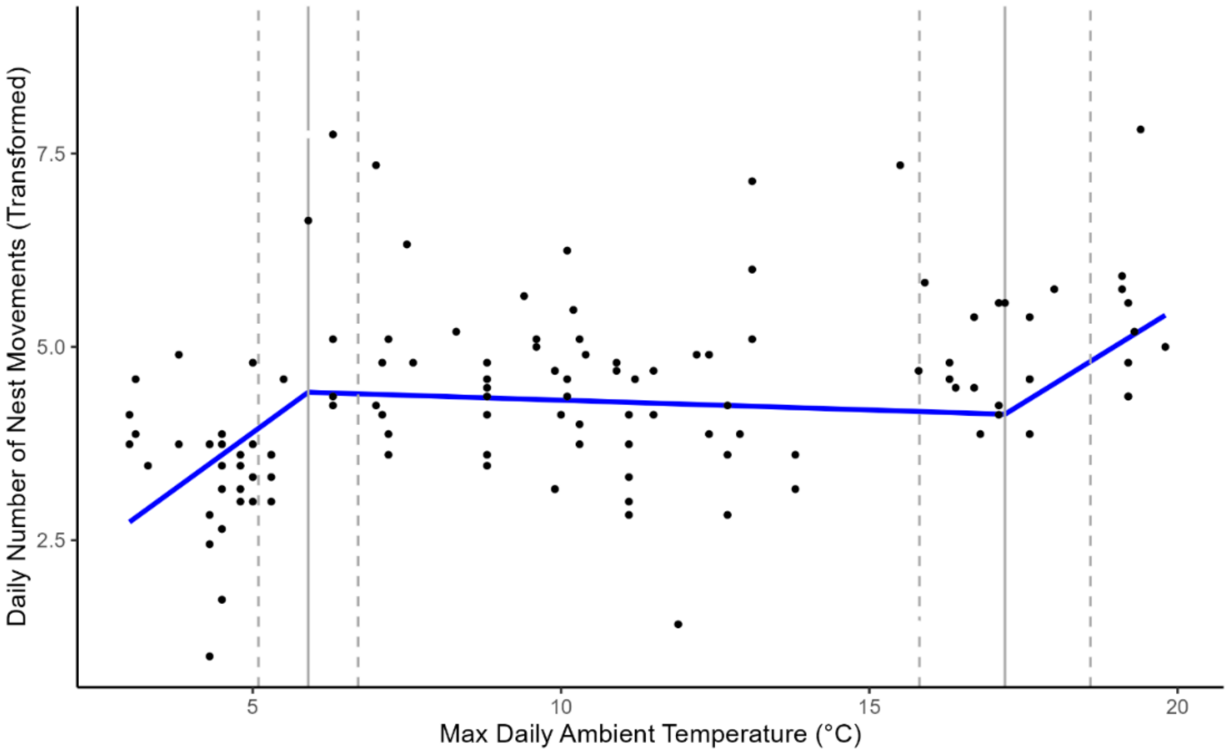


Figure 3.7 Examining heat stress' effects on incubation consistency in common eider (*Somateria mollissima*) hens breeding on East Bay Island, Qikiqtakuluk, Nunavut, Canada. Plotted is maximum daily ambient temperature's segmented relationship with daily nest movements (transformed) for hens. Grey solid lines indicate the location of breakpoints, with standard errors for each breakpoint indicated by grey dotted lines. Thick blue solid lines indicate estimated slopes of the relationship, as separated by breakpoints.

CHAPTER 4

General discussion

The Arctic is undergoing accelerated warming (Rantanen et al., 2022) accompanied by more frequent and extreme weather events (AMAP, 2021), such as floods (Walsh et al., 2020), and heat waves (Walsh et al., 2018). For some high-latitude species, rising temperatures may actually improve overall fitness (Peck et al., 2006) as their environments tend to be far below their thermal limits (Sørensen et al., 2024). However, these effects will likely only be positive in the short term (Peck et al., 2006) and do not account for the negative effects of greater temperature fluctuations and extreme weather events that accompany climate warming (Vasseur et al., 2014). Thus, examining species' responses to acute thermal conditions is critical in determining their capacity to respond to these changes and how they will be impacted by climate change (Buckley & Huey, 2016b). Currently, a lack of understanding of the mechanisms of heat stress responses in endotherms inhibits our understanding of the adaptiveness of these responses (Boyles et al., 2011; Long et al., 2014) and the potential trade-offs between thermoregulatory responses and other energetic activities, like reproduction (Brown & Downs, 2003). Nonetheless, studies note that many endotherms can integrate multiple response mechanisms to heat stress, such as offsetting energetic physiological responses with behavioural adjustments (Logan et al., 2019; Long et al., 2014), but that these responses can negatively interact with reproductive activities (Hansen, 2009). These negative effects have appeared in multiple arctic-breeding birds (Choy et al., 2021; Oswald et al., 2008). Therefore, species' use of multiple response mechanisms (Monaco et al., 2017) and how they interplay with reproduction is expected to reveal their capacity to cope with heat stress in the face of climate change (Brown & Downs, 2003; Monaco et al., 2017).

Incubating common eiders breeding in the Arctic provide an ideal study species and framework for examining Arctic species' physiological and behavioural responses to heat stress due to their combined cold adaptations, exposed nest sites, and capital incubation strategy. Indeed, eiders are incredibly well-insulated birds (D'alba et al., 2017) that use physiological, behavioural and morphological adaptations to stay warm in their cold environment (Gabrielsen et al., 1991; Jenssen et al., 1989). As a result, these adaptations may hinder their tolerance to heat (Schou et al., 2022). Further, hens nest in open-ground nest cups (Fast et al., 2010), where they are exposed to nearly 24 hours of Arctic sun during their breeding period (Steenweg et al., 2015). These nesting sites can expose hens to a high radiative heat load from solar rays (Fortin et al., 2000) at a time when hens are already thermally constrained (Guillemette & Pelletier, 2022). In addition to their vulnerability to heat stress, hens may be limited in their ability to energetically or behaviourally respond to heat stress during reproduction due to their reproductive tactics. Female eiders solely incubate their eggs for ~24 days (McKinnon et al., 2006), during which time they completely fast (Bottitta et al., 2003; Criscuolo et al., 2003), depleting through as much as 30-45% of body fat (Gabrielsen et al., 1991). Thus, a depleted fixed energetic budget could restrict their ability to respond to greater thermoregulatory demands during this time. Further, hens are driven to maintain a high incubation consistency due to the high risk of clutch predation at their breeding sites (Amat & Masero, 2004; Fast et al., 2010), inhibiting them from leaving the nest to refuel or rehydrate without reproductive consequence (Swennen et al., 1993). Therefore, hens' health and fecundity may be particularly at risk of behavioural or physiological thermoregulatory responses that deplete through energy or water and increase their predator visibility (Lecomte et al., 2009; Nord & Williams, 2015).

Incubating eiders physiological and behavioural responses to temperature, with interactions of weather and breeding parameters

We are excited to present, to our knowledge, the first measures of significant temperature thresholds for both heart rate and behavioural adjustments in response to heat stress in common eiders. Establishing significant temperature-response thresholds for populations or species can be a valuable tool for understanding their distributions (Peck et al., 2009) and how they respond to temperature extremes and fluctuations in their environment (Buckley & Huey, 2016a). As a result, these thresholds can provide insight into their adaptive capacity to climate change (Debnath, 2024). Further, establishing these clear response thresholds of eiders to high environmental temperatures can be a valuable management tool to track threat severity for these birds, and determine when to involve management strategies (Ingram et al., 2021).

We found that incubating female eiders can respond to rising temperatures in their environment over significant temperature thresholds, but are not yet exposed to high enough temperatures to cause large changes in their heart rate or behavioural adjustments. This is positive news for hens, as it indicates that they can continue their incubation activities and maintain their energetic budgets with little impact from heat stress in their current breeding environment. However, the mild upward trend in heart rate and nest movements do suggest a need to monitor temperatures that incubating eiders are exposed to in the future as the Arctic continues to warm, and these trends could become more significant at exposure to higher temperatures. Indeed, if eiders continue to breed at Qikiqtakuluk when temperatures largely exceed our found temperature thresholds, we suspect that they will be exposed to higher energetic and reproductive costs of thermoregulatory responses, as has been documented in other Arctic species (Choy et al., 2021; O'Connor et al., 2021; Snell et al., 2024).

Alternatively, our results may indicate that hens are employing other strategies to cope with heat stress, that were not recorded in our study. For example, hens could be taking advantage of facultative hyperthermia, which is when an organism allows their body temperature to rise slightly above normal levels in response to environmental temperatures above their thermal neutral zone (Boyles et al., 2011; Gerson et al., 2019). Similar to behavioural responses, facultative hyperthermia can be an energy-efficient and water-saving thermoregulatory strategy, as it reduces the temperature gradient between the body and the environment, thus delaying the need for energetic evaporative cooling methods (Beaman et al., 2024; Boyles et al., 2011; McKechnie et al., 2016; Tapper et al., 2020). This strategy would not have been detected in our study as we did not measure hens’ body temperatures (for example, via implanted passive integrated transponder (PIT) tags; Andreasson et al., 2023) that could aid in their balance of heart rate and behavioural responses (McKechnie et al., 2016). It is important to note that although energetically efficient and water-saving, facultative hyperthermia may be associated with variable costs on parent health and reproduction (Speakman & Król, 2010; Tapper et al., 2020).

In our assessment of temperature effects on heart rate and incubation behaviour, we also found that heat load from solar rays played a significant role in the detectability of eiders' suspected thermal neutral zone (i.e., Scholander-Irving curve). Indeed, our heart rate’s nest-level temperature model (as a reminder to the reader, nest-level temperature is air temperature under sun exposure) mirrored that of a Scholander-Irving curve, where energy use remains stable within a range of air temperatures, but increases beyond an upper and lower critical temperature boundary (Scholander et al., 1950). In fact, our heart rate model with nest-level temperature more closely followed a Scholander-Irving curve than our heart rate model with ambient temperature, which is the temperature metric normally used to build these curves (McNab, 1992; Scholander et al., 1950). It is important to note that we had a lower sampling rate for ambient temperature and a lack of high ambient temperatures recorded beyond its threshold. Nonetheless, our nest-level temperature model presents a clear pattern where heart rate remains stable within a range of nest-level temperatures and only increases beyond the boundaries of this range. Thus, we propose that sun-sensitive temperature metrics may be more valuable in detecting physiological heat stress in arctic-breeding eider populations, than ambient temperature alone. In addition to sun effects, we found that weather variables, particularly a thermal index and wind and humidity index, also contributed to hens' heart rate response on the nest. Indeed, heart rate increases with increasing thermal index and decreases with increasing wind and humidity. Interestingly, however, these variables didn’t significantly affect hen behaviour. Further, we found eiders' thermal stress responses, in both heart rate and behavioural adjustments, interact with their breeding decisions and metrics. Firstly, we found heart rates to be generally higher and hens to move more on the nest, in measurements that were recorded later into the season. Secondly, we found that as incubation progressed, hens’ heart rates increased, but they reduced physical activity on the nest. Lastly, heart rate was significantly higher in hens that laid eggs later into the breeding season. As such, hens may be most vulnerable to heat stress effects later in the season, later into their incubation, and when they are inexperienced or of low quality, as assessed by their lay date. As such, it is important to account for these interactions in heat stress studies in natural environments and during reproduction. Therefore, our results of temperature effects and interactions of weather and breeding parameters on heat stress in eiders contribute to the literature on our understanding of arctic seabirds' thermal limits and how hens' breeding decisions and stages are influenced by these thermal constraints (Braschler et al., 2021).

Decoupling of physiological and behavioural responses to temperature

In addition to our findings of thresholds for eiders' behavioural and physiological responses to their thermal environments, we made another fascinating discovery: that thresholds for physiological and behavioural responses can deviate from one another under differing thermal conditions. Indeed, in our *ambient* temperature models, we found that eiders exhibit physiological and behavioral responses to heat stress at similar temperature thresholds (16.6 °C and 17.2 °C, respectively), but respond to cold stress at different temperature thresholds (8.9 °C and 5.9 °C, respectively). Alternatively, in our *nest-level* temperature models for physiology and behaviour, cold-stress responses occurred at similar thresholds, but in this instance, heat-stress responses differed by approximately 5 °C (33.6 °C for a physiological response and 38.6 °C for a behavioural response). This divergence between physiology and behaviour with regard to performance curves has been previously described in individuals undergoing thermal or physiological constraints (Monaco et al., 2017). For example, ectotherms from arid environments limit movement at high temperatures to slow desiccation- the extensive drying of their bodies, resulting in the reach of behavioural performance limits before physiological limits, effectively decoupling the two. At eiders ambient temperature thresholds for cold stress, we see behaviour and physiology are decoupled with eiders initiating physiological responses to cold stress first. Given eiders' strict energetic budgets during incubation (Gabrielsen et al., 1991; Sénéchal et al., 2011), we would expect hens to reduce nest movements first in response to cold before energetic physiological responses (Tullett & Deeming, 1987). Specifically, reduced nest activity should work in harmony with breeding constraints, as it lends to a high incubation consistency, promoting a shorter and energetically efficient incubation period (Bottitta et al., 2003; Hanssen et al., 2022). However, some degree of egg rotation is important for egg viability and thus may impose a constraint on hens' ability to reduce activity on the nest altogether at cold temperatures, which could explain why we found that eiders illicit a physiological response first. In fact, eiders have been recorded to rotate their eggs on average 13.9 times a day in more insulative nests, and 15.3 per day in less insulative nests (Kristjánsson & Jónsson, 2011), so egg rotation may be particularly critical in the cold. At the heat stress response threshold, we see responses to heat stress decoupled in nest-level temperatures, where once again, a physiological response to heat stress is initiated before a behavioural response. Thus, as a whole, our results suggest hens are behaviourally constrained to the nest by a hormonal drive to diligently incubate their eggs (Mohring et al., 2024), and therefore, may resist behavioural responses until energetic (Conway & Martin, 2000) or water costs (Bourne et al., 2021) of physiological responses become too encumbering. This information provides valuable insight into how hens may balance their energetic needs with their behavioural constraints, and the trade-off’s that may emerge from these decisions (Mathot et al., 2019).

Conservation implications and research priorities

Our findings show that incubating eiders at Qikiqtakuluk are not currently at serious risk of heat stress in their environment. Indeed, as previously mentioned, warming can alleviate the energetic costs of thermoregulating for eiders in the short term (Peck et al., 2006). Hens will not as often be exposed to environmental temperatures below their thermal neutral zone (TNZ) (Sørensen et al., 2024), and instead spend more time within the TNZ where they do not need to actively regulate their body temperature (Dawson & O'Connor, 1996). Further, warming during the incubation period can reduce the amount of heat eiders need to generate to warm their eggs, which is typically a large cost of incubation for birds in cold environments (Nord & Williams, 2015). Further, hens dissipating heat to their eggs may provide a buffer to heat stress as hens approach their upper critical (Grant, 1982). Despite this short-term benefit, our results suggest that eiders will begin to experience significant energetic costs and behavioural disturbances to their incubation in the future if nest-level temperatures greatly exceed 33.55 °C throughout their incubation. Particularly because arctic-breeding eiders are extremely well adapted to the cold (Jenssen et al., 1989) and have occupied these climates since the Pleistocene (Tiedemann et al., 2004), and therefore it remains unknown how their cold environment-selected traits will cope with a warmer climate (Boonstra, 2004).

Indeed, the Arctic has experienced dramatic warming as a result of human-induced climate change, with one of the most extreme warming events recorded in summer 2023 (Ballinger et al., 2023). This warming is only expected to continue into the end of the century, with detrimental effects on warming oceans and reducing sea ice coverage (Crawford et al., 2021; Mohammadzadeh Khani et al., 2022). As Qikiqtakuluk holds the largest known breeding colony of common eider in the Canadian Arctic (Love et al., 2010), monitoring their exposure to high nest-level temperatures in the future will be critical in informing the health of arctic-breeding populations, and of common eiders as a species. The International Union for Conservation of Natures' (IUCN) 2018 assessment report of common eiders noted that evidence of declines in the *borealis* subspecies (our population of eiders) would warrant uplisting the species status to a threatened status from its current listing as 'Near Threatened' (BirdLife International, 2018). Indeed, eiders meet nearly all markers for this uplisting, and declines in the *borealis* subspecies would provide the final confirmation that this species needs greater conservation efforts (BirdLife International, 2018). As such, finding evidence to uplist their status could provide greater momentum for eider conservation, as the IUCN Red List of Threatened Species has the power to generate policy-making towards species protection, design effective management strategies and increase funding towards a species conservation (Betts et al., 2020). For example, uplisting common eiders to a more vulnerable species status could provide the momentum needed for the development of Marine Protected Areas (MPAs) in the ocean waters surrounding eider breeding grounds (Lalonde et al., 2022). Indeed, Arctic waters have experienced a substantial increase in boating activity in recent decades due to climate change-induced reduction of sea ice, opening waters up for increased oil and gas exploration, fishing vessels, cargo transportation and boating tourism (Lemelin & Dawson, 2014). Thus, an MPA would provide a particularly effective conservation strategy, especially as it targets the protection of ecosystems as a whole (Wenzel et al., 2016).

In addition, our research is performed in the Kivalliq region of the Inuit Nunangat. Every three years, the Nunavut Wildlife Management Board visits with representatives from this region to discuss local issues in wildlife management and create a list of regional wildlife research and management priorities (Nunavut Wildlife Management Board, 2023a). The goal of this list is to ensure that wildlife and the environment are conserved and managed in a way that benefits wildlife and Nunavut's residents, in accordance with the Nunavut Agreement (Nunavut Wildlife Management Board, 2023b). As such, we hope that our research will contribute to this goal and address Kivalliq Regional Wildlife Priorities (2023-2025) priority #6C: "Understand the impacts of climate change on ecosystems and wildlife" (Nunavut Wildlife Management Board, 2023a). Eiders hold great cultural significance to Inuit communities (Henri et al., 2018), harvested for warm materials and food (Gilliland et al., 2009; Vestbo et al., 2019) with further ecological significance to Arctic communities (Vestbo et al., 2019), so we hope our findings will inform management strategies that profit Inuit and the local ecosystem.

Future directions

Based on our findings and gaps in the literature, we believe future research should focus on extending our understanding of heat tolerances across endothermic species in field settings by examining individual variations in responses and effects of temperature fluctuations and length on heat stress. Further, a better understanding of species' behavioural responses to heat stress will be needed to examine species' full capacity to respond to temperature changes and trade-offs with reproduction. Lastly, heat response strategies should be explored beyond heart rate and movement on the nest to provide further insight into eiders' and other arctic breeding birds' capacity to respond to climate change.

We suggest that to develop more biologically significant estimates of wild species' thermal capacities, future studies should focus on quantifying thermal limits in natural environments as opposed to laboratory settings (Phoenix & Lee, 2004). Many studies establishing upper and lower critical temperatures of species have done so in controlled chambers, whether on wild or captive populations (Scholander et al., 1950; Terblanche et al., 2007; Thonis et al., 2020). Though these studies provide valuable, repeatable thresholds for physiological response limits to temperature, they often do not reflect the true conditions experienced by populations in their natural habitat (Hoffmann & Sgro, 2018) and thus lack conservation applications (Braschler et al., 2021). Further, laboratory studies can lack the context of organisms' states and conditions in their environment that can influence their response thresholds and mechanisms of response (Steyn et al., 2022). In this context, an important avenue to explore is individual variation in trait-based responses (Zhang et al., 2023). For example, studies note that an individual's body size and body condition can influence decision-making tactics when heat-stressed (Buchholz et al., 2019). In addition, individuals in populations can show large inter-individual variation in physiological parameters, like cardiac output (Zhang et al., 2023). Further, the length of exposure to high temperatures, and fluctuation of temperature exposure, can influence susceptibility to heat stress (Ørsted et al., 2022; Sadeghi et al., 2021), so monitoring high temperatures as well as duration of exposure to said temperatures can provide a more robust understanding of a populations' risk of heat stress (Cook et al., 2024; Sadeghi et al., 2021). More broadly, when examining endothermic species responses to climate change and how these responses interact with reproduction, we need more studies testing for behavioural responses to heat stress (Buchholz et al., 2019). Indeed, although we have a solid foundation of endotherms' physiological responses to heat stress, few studies examine their behavioural responses (Buchholz et al., 2019). Nonetheless, behavioural responses to heat stress can significantly buffer more energetic responses (Huey et al., 2012), with variable outcomes on reproductive activities (Gudka et al., 2019; Verzuh et al., 2023). As a result, exploring the combined effects of physiological and behavioural responses is critical in assessing species resilience to climate change (Buchholz et al., 2019).

As discussed previously, eiders and other endothermic organisms may use several mechanisms of response to heat stress, beyond changes in heart rate and behavioural adjustments on the nest. For example, we discussed that facultative hyperthermia can be an energetically favourable response to heat stress in eiders that buffers a more energetic response (Boyles et al., 2011; Gerson et al., 2019). However, as hens are confined to their nests during incubation, another useful strategy may be changes in breeding decisions before incubation commences, such as nest-site selection (Kauffman et al., 2021). For example, eiders may change the parameters by which they assess nest-site quality to choose nests that provide more protection from heat and sun. Previous studies have found that breeding birds selecting nest sites sheltered from heat or sun can be a valuable tool for parents to reduce their thermoregulatory costs (Robertson, 2009) and increase breeding success in hot or fluctuating temperature environments (Carroll et al., 2018). In fact, recent work on nest-site selection in arctic-breeding eiders suggests hens select for nest sites exposed to lower solar variability and closer to bodies of water irrespective of changes in climate over the past 20 years (Wright et al., unpubl data), indicating their insensitivity to climate change as of yet. Instead, at Qikiqtakuluk, eider nest site selection may now be driven by their need to detect approaching predators from large distances (Fast et al., 2010), which may impose a trade-off between selecting a thermally favourable and predator-detectable nest site (Robertson, 2009).

Indeed, common eiders at Qikiqtakuluk have a number of terrestrial and aerial nest predators (Barnas et al., 2022; Reed et al., 2007). In fact, nest predation has become so prevalent at this site, that it challenged our ability to observe heat stress impacts on incubation success and chick hatching. Therefore, we believe future studies on heat stress responses in incubating hens should be carried out at other breeding colonies with fewer predators to examine if there are any heat stress effects linked to the success of a given breeding attempt (e.g., the number of eggs hatched, clutch abandonment, chick abandonment). Further, as our study site only experienced marginal heat stress-inducing temperatures, we suggest that future studies examine the heat stress of eiders at warmer or more sun-exposed sites to determine just how significant the energetic and behavioural responses are at these sites.

Concluding words

In conclusion, we find that eiders may be vulnerable to significant heat stress in the coming future, and that their physiological and behavioural responses to heat stress will require trade-offs with energy use and incubation consistency during their breeding period. As such, we suggest that heat stress-inducing temperatures should continue to be monitored in this arctic-breeding eider population to help inform future assessments of their health and contribute to the management of eiders within the Kivalliq region. Further, we suggest this study should be extended to warmer breeding sites with fewer predators to study the effects of heat stress on not only physiology and behaviour, but the success of breeding attempts. More generally, to develop our understanding of heat stress across Arctic populations, future studies will need to quantify heat stress response thresholds across more diverse taxa and in field-setting experiments (Braschler et al., 2021) exploring more how external conditions and inter-individual variation alter vulnerability to heat stress (Cook et al., 2024; Steyn et al., 2022; Zhang et al., 2023). Lastly, researchers will want to focus on building an understanding of both physiological and behavioural responses to heat stress, together, to better understand their influence on reproduction (Buchholz et al., 2019).

References

AMAP. (2021). *Arctic Climate Change Update 2021: Key Trends and Impacts. Summary for Policy-makers.*

Amat, J. A., & Masero, J. A. (2004). How Kentish plovers, Charadrius alexandrinus, cope with heat stress during incubation. *Behavioral Ecology and Sociobiology*, *56*(1), 26-33. https://doi.org/10.1007/s00265-004-0758-9

Andreasson, F., Rostedt, E., & Nord, A. (2023). Measuring body temperature in birds - the effects of sensor type and placement on estimated temperature and metabolic rate. *J Exp Biol*, *226*(24). https://doi.org/10.1242/jeb.246321

Ballinger, T., Bigalke, S., Walsh, J., Brettschneider, B., Thoman, R., Bhatt, U., Hanna, E., Hanssen-Bauer, I., Kim, S.-J., & Overland, J. (2023). NOAA Arctic Report Card 2023: Surface Air Temperature.

Barnas, A. F., Geldart, E. A., Love, O. P., Jagielski, P. M., Harris, C. M., Gilchrist, H. G., Hennin, H. L., Richardson, E. S., Dey, C. J., & Semeniuk, C. A. D. (2022). Predatory cue use in flush responses of a colonial nesting seabird during polar bear foraging. *Animal Behaviour*, *193*, 75-90. https://doi.org/https://doi.org/10.1016/j.anbehav.2022.08.009

Beaman, J. E., White, C. R., Clairbaux, M., Perret, S., Fort, J., & Grémillet, D. (2024). Cold adaptation does not handicap warm tolerance in the most abundant Arctic seabird. *Proceedings of the Royal Society B: Biological Sciences*, *291*(2015), 20231887. https://doi.org/doi:10.1098/rspb.2023.1887

Betts, J., Young, R. P., Hilton-Taylor, C., Hoffmann, M., Rodríguez, J. P., Stuart, S. N., & Milner-Gulland, E. J. (2020). A framework for evaluating the impact of the IUCN Red List of threatened species. *Conservation Biology*, *34*(3), 632-643. https://doi.org/https://doi.org/10.1111/cobi.13454

BirdLife International. (2018). *Somateria mollissima. The IUCN Red List of Threatened Species 2018.*

Boonstra, R. (2004). Coping with changing northern environments: the role of the stress axis in birds and mammals. *Integrative and Comparative Biology*, *44*(2), 95-108.

Bottitta, G. E., Nol, E., & Gilchrist, H. G. (2003). Effects of Experimental Manipulation of Incubation Length on Behavior and Body Mass of Common Eiders in the Canadian

Arctic. *Waterbirds*, *26*(1), 100-107, 108. https://doi.org/10.1675/1524-4695(2003)026[0100:EOEMOI]2.0.CO;2

Bourne, A. R., Ridley, A. R., McKechnie, A. E., Spottiswoode, C. N., & Cunningham, S. J. (2021). Dehydration risk is associated with reduced nest attendance and hatching success in a cooperatively breeding bird, the southern pied babbler Turdoides bicolor. *Conservation Physiology*, *9*(1). https://doi.org/10.1093/conphys/coab043

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive Thermoregulation in Endotherms May Alter Responses to Climate Change. *Integrative and Comparative Biology*, *51*(5), 676-690. https://doi.org/10.1093/icb/icr053

Braschler, B., Chown, S. L., & Duffy, G. A. (2021). Sub-critical limits are viable alternatives to critical thermal limits. *Journal of Thermal Biology*, *101*, 103106. https://doi.org/https://doi.org/10.1016/j.jtherbio.2021.103106

Brown, M., & Downs, C. T. (2003). The role of shading behaviour in the thermoregulation of breeding crowned plovers (Vanellus coronatus). *Journal of Thermal Biology*, *28*(1), 51-58. https://doi.org/https://doi.org/10.1016/S0306-4565(02)00036-0

Buchholz, R., Banusiewicz, J. D., Burgess, S., Crocker-Buta, S., Eveland, L., & Fuller, L. (2019). Behavioural research priorities for the study of animal response to climate change. *Animal Behaviour*, *150*, 127-137. https://doi.org/https://doi.org/10.1016/j.anbehav.2019.02.005

Buckley, L. B., & Huey, R. B. (2016a). How Extreme Temperatures Impact Organisms and the Evolution of their Thermal Tolerance. *Integrative and Comparative Biology*, *56*(1), 98-109. https://doi.org/10.1093/icb/icw004

Buckley, L. B., & Huey, R. B. (2016b). Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities. *Global Change Biology*, *22*(12), 3829-3842. https://doi.org/https://doi.org/10.1111/gcb.13313

Carroll, R. L., Davis, C. A., Fuhlendorf, S. D., Elmore, R. D., DuRant, S. E., & Carroll, J. M. (2018). Avian parental behavior and nest success influenced by temperature fluctuations. *Journal of Thermal Biology*, *74*, 140-148. https://doi.org/https://doi.org/10.1016/j.jtherbio.2018.03.020

Choy, E. S., O'Connor, R. S., Gilchrist, H. G., Hargreaves, A. L., Love, O. P., Vézina, F., & Elliott, K. H. (2021). Limited heat tolerance in a cold-adapted seabird: implications of a warming Arctic. *Journal of Experimental Biology*, *224*(13), jeb242168.

Conway, C. J., & Martin, T. E. (2000). Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology, 11*(2), 178-188. https://doi.org/10.1093/beheco/11.2.178

Cook, A. M., Rezende, E. L., Petrou, K., & Leigh, A. (2024). Beyond a single temperature threshold: Applying a cumulative thermal stress framework to plant heat tolerance. *Ecology Letters*, *27*(3), e14416. https://doi.org/https://doi.org/10.1111/ele.14416

Crawford, A., Stroeve, J., Smith, A., & Jahn, A. (2021). Arctic open-water periods are projected to lengthen dramatically by 2100. *Communications Earth & Environment*, *2*(1), 109. https://doi.org/10.1038/s43247-021-00183-x

Criscuolo, F., Chastel, O., Gabrielsen, G. W., Lacroix, A., & Le Maho, Y. (2003). Relationship between nutritional status and prolactin levels in the common eider, a capital incubator. *Antarctic biology in a global context. Backhuys, Leyden*, 193-197.

D'alba, L., Carlsen, T. H., Ásgeirsson, Á., Shawkey, M. D., & Jónsson, J. E. (2017). Contributions of feather microstructure to eider down insulation properties. *Journal of Avian Biology*, *48*(8), 1150-1157.

Dawson, W. R., & O'Connor, T. P. (1996). Energetic features of avian thermoregulatory responses. *Avian energetics and nutritional ecology*, 85-124.

Debnath, C. (2024). Assessing the thermal limits and metabolic profiles of small indigenous fish species: Informing conservation and aquaculture in a changing climate. *Aquaculture Reports*, *39*, 102396. https://doi.org/https://doi.org/10.1016/j.aqrep.2024.102396

Fast, P. L., Gilchrist, H. G., & Clark, R. G. (2010). Nest-site materials affect nest-bowl use by Common Eiders (Somateria mollissima). *Canadian Journal of Zoology*, *88*(2), 214-218.

Fortin, D., Larochelle, J., & Gauthier, G. (2000). The effect of wind, radiation and body orientation on the thermal environment of Greater Snow goose goslings. *Journal of Thermal Biology*, *25*(3), 227-238. https://doi.org/https://doi.org/10.1016/S0306-4565(99)00028-5

Gabrielsen, G. W., Mehlum, F., Karlsen, H. E., Andresen, Ø., & Parker, H. (1991). Energy cost during incubation and thermoregulation in the female common eider Somateria mollissima. *Norsk Polarinstitutt Skrifter*, *195*, 51-62.

Gerson, A. R., McKechnie, A. E., Smit, B., Whitfield, M. C., Smith, E. K., Talbot, W. A., McWhorter, T. J., & Wolf, B. O. (2019). The functional significance of facultative hyperthermia varies with body size and phylogeny in birds. *Functional Ecology*, *33*(4), 597-607. https://doi.org/https://doi.org/10.1111/1365-2435.13274

Gilliland, S. G., Grant Gilchrist, H., Rockwell, R. F., Robertson, G. J., Savard, J.-P. L., Merkel, F., & Mosbech, A. (2009). Evaluating the Sustainability of Harvest Among Northern Common Eiders Somateria Mollissima Borealis in Greenland and Canada. *Wildlife Biology*, *15*(1), 24-36. https://doi.org/https://doi.org/10.2981/07-005

Grant, G. S. (1982). Avian Incubation: Egg Temperature, Nest Humidity, and Behavioral Thermoregulation in a Hot Environment. *Ornithological Monographs*(30), iii-75. https://doi.org/10.2307/40166669

Gudka, M., Santos, C. D., Dolman, P. M., Abad-Gómez, J. M., & Silva, J. P. (2019). Feeling the heat: Elevated temperature affects male display activity of a lekking grassland bird. *PLoS One*, *14*(9), e0221999.

Guillemette, M., & Pelletier, D. (2022). Egg-laying increases body temperature to an annual maximum in a wild bird. *Sci Rep*, *12*(1), 1681. https://doi.org/10.1038/s41598-022-05516-0

Hansen, P. J. (2009). Effects of heat stress on mammalian reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1534), 3341-3350.

Hanssen, S., Erikstad, K. E., Sandvik, H., Tveraa, T., & Bustnes, J. O. (2022). Eyes on the future: buffering increased costs of incubation by abandoning offspring. *Behavioral Ecology*, *34*(2), 189-196. https://doi.org/10.1093/beheco/arac116

Henri, D. A., Jean-Gagnon, F., & Gilchrist, H. G. (2018). Using Inuit traditional ecological knowledge for detecting and monitoring avian cholera among Common Eiders in the eastern Canadian Arctic. *Ecology and Society*, *23*(1).

Hoffmann, A. A., & Sgro, C. M. (2018). Comparative studies of critical physiological limits and vulnerability to environmental extremes in small ectotherms: How much environmental control is needed? *Integrative Zoology*, *13*(4), 355-371. https://doi.org/https://doi.org/10.1111/1749-4877.12297

Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1596), 1665-1679. https://doi.org/doi:10.1098/rstb.2012.0005

Ingram, D. J., Ferreira, G. B., Jones, K. E., & Mace, G. M. (2021). Targeting Conservation Actions at Species Threat Response Thresholds. *Trends in ecology & evolution*, *36*(3), 216-226. https://doi.org/https://doi.org/10.1016/j.tree.2020.11.004

Jenssen, B. M., Ekker, M., & Bech, C. (1989). Thermoregulation in winter-acclimatized common eiders (Somateria mollissima) in air and water. *Canadian Journal of Zoology*, *67*(3), 669-673.

Kauffman, K. L., Elmore, R. D., Davis, C. A., Fuhlendorf, S. D., Goodman, L. E., Hagen, C. A., & Tanner, E. P. (2021). Role of the thermal environment in scaled quail (Callipepla squamata) nest site selection and survival. *Journal of Thermal Biology*, *95*, 102791. https://doi.org/https://doi.org/10.1016/j.jtherbio.2020.102791

Kristjánsson, T. Ö., & Jónsson, J. E. (2011). Effects of down collection on incubation temperature, nesting behaviour and hatching success of common eiders (Somateria mollissima) in west Iceland. *Polar Biology*, *34*(7), 985-994. https://doi.org/10.1007/s00300-010-0956-z

Lalonde, S., Abashidze, A., & Solntsev, A. (2022). Marine Protected Areas and Other Effective Area-based Conservation Measures. *Arctic Review on Law and Politics*, *13*, 312-337.

Lecomte, N., Gauthier, G., & Giroux, J.-F. (2009). A link between water availability and nesting success mediated by predator–prey interactions in the Arctic. *Ecology*, *90*(2), 465-475. https://doi.org/https://doi.org/10.1890/08-0215.1

Lemelin, R. H., & Dawson, J. (2014). Great expectations: Examining the designation effect of marine protected areas in coastal Arctic and sub-Arctic communities in Canada. *Canadian Geographies / Géographies canadiennes*, *58*(2), 217-232. https://doi.org/https://doi.org/10.1111/j.1541-0064.2013.12059.x

Logan, M. L., van Berkel, J., & Clusella-Trullas, S. (2019). The Bogert Effect and environmental heterogeneity. *Oecologia*, *191*(4), 817-827. https://doi.org/10.1007/s00442-019-04541-7

Long, R. A., Bowyer, R. T., Porter, W. P., Mathewson, P., Monteith, K. L., & Kie, J. G. (2014). Behavior and nutritional condition buffer a large-bodied endotherm against direct and indirect effects of climate. *Ecological Monographs*, *84*(3), 513-532. https://doi.org/https://doi.org/10.1890/13-1273.1

Love, O. P., Gilchrist, H. G., Descamps, S., Semeniuk, C. A., & Bêty, J. (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia*, *164*, 277-286.

Mathot, K. J., Dingemanse, N. J., & Nakagawa, S. (2019). The covariance between metabolic rate and behaviour varies across behaviours and thermal types: meta-analytic insights. *Biological Reviews*, *94*(3), 1056-1074.

McKechnie, A. E., Whitfield, M. C., Smit, B., Gerson, A. R., Smith, E. K., Talbot, W. A., McWhorter, T. J., & Wolf, B. O. (2016). Avian thermoregulation in the heat: efficient evaporative cooling allows for extreme heat tolerance in four southern hemisphere columbids. *Journal of Experimental Biology, 219*(14), 2145-2155.

McKinnon, L., Gilchrist, H. G., & Scribner, K. T. (2006). Genetic evidence for kin-based female social structure in common eiders (Somateria mollissima). *Behavioral Ecology*, *17*(4), 614-621.

McNab, B. K. (1992). Energy Expenditure: A Short History. In T. Tomasi & T. TH Horton (Eds.), *Mammalian Energetics: Interdisciplinary Views of Metabolism and Reproduction* (pp. 1–15). Cornell University Press.

Mohammadzadeh Khani, H., Kinnard, C., & Lévesque, E. (2022). Historical Trends and Projections of Snow Cover over the High Arctic: A Review. *Water (Basel)*, *14*(4), 587. https://doi.org/10.3390/w14040587

Mohring, B., Öst, M., Jaatinen, K., Parenteau, C., Pallud, M., & Angelier, F. (2024). Parenting in a changing environment: A long-term study of prolactin, parental effort and reproductive success in common eiders. *General and Comparative Endocrinology*, *357*, 114574. https://doi.org/https://doi.org/10.1016/j.ygcen.2024.114574

Monaco, C. J., McQuaid, C. D., & Marshall, D. J. (2017). Decoupling of behavioural and physiological thermal performance curves in ectothermic animals: a critical adaptive trait. *Oecologia*, *185*(4), 583-593. https://doi.org/10.1007/s00442-017-3974-5

Nord, A., & Williams, J. B. (2015). The energetic costs of incubation. In D. C. Deeming & S. J. Reynolds (Eds.), *Nests, Eggs, and Incubation: New ideas about avian reproduction* (pp. 0). Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198718666.003.0013

Nunavut Wildlife Management Board. (2023a). *Kivalliq Regional Wildlife Priorities (2023-2025), ᑭᕙᓪᓕᖅᒥ ᐆᒪᔪᑦ ᓯᕗᓪᓕᐅᑎᖁᔭᑦ (2023-2025).*

https://www.nwmb.com/en/conservation-education/list-all-documents/funding-guides/priorities/6784-kivalliq-regional-wildlife-priorities-list-bilingual/file

Nunavut Wildlife Management Board. (2023b). *Research Priorities*. Retrieved December 27 from https://www.nwmb.com/en/funding/priorities#

O'Connor, R. S., Le Pogam, A., Young, K. G., Robitaille, F., Choy, E. S., Love, O. P., Elliott, K. H., Hargreaves, A. L., Berteaux, D., & Tam, A. (2021). Limited heat tolerance in an Arctic passerine: Thermoregulatory implications for cold-specialized birds in a rapidly warming world. *Ecology and evolution*, *11*(4), 1609-1619.

Ørsted, M., Jørgensen, L. B., & Overgaard, J. (2022). Finding the right thermal limit: a framework to reconcile ecological, physiological and methodological aspects of CTmax in ectotherms. *Journal of Experimental Biology*, *225*(19), jeb244514.

Oswald, S. A., Bearhop, S., Furness, R. W., Huntley, B., & Hamer, K. C. (2008). Heat stress in a high-latitude seabird: effects of temperature and food supply on bathing and nest attendance of great skuas Catharacta skua. *Journal of Avian Biology*, *39*(2), 163-169.

Peck, L. S., Clark, M. S., Morley, S. A., Massey, A., & Rossetti, H. (2009). Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology*, *23*(2), 248-256. https://doi.org/https://doi.org/10.1111/j.1365-2435.2008.01537.x

Peck, L. S., Convey, P., & Barnes, D. K. A. (2006). Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biological Reviews*, *81*(1), 75-109. https://doi.org/10.1017/S1464793105006871

Phoenix, G. K., & Lee, J. A. (2004). Predicting impacts of Arctic climate change: past lessons and future challenges. *Ecological Research*, *19*, 65-74.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., & Laaksonen, A. (2022). The Arctic has warmed nearly four times faster than the globe since 1979. *Communications Earth & Environment*, *3*(1), 168. https://doi.org/10.1038/s43247-022-00498-3

Reed, J. A., Lacroix, D. L., & Flint, P. L. (2007). Depredation of common eider, Somateria mollissima, nests on a central Beaufort Sea barrier Island: A case where no one wins. *The Canadian Field-Naturalist*, *121*(3), 308-312.

Robertson, B. A. (2009). Nest-Site Selection in a Postfire Landscape: Do Parents Make Tradeoffs Between Microclimate and Predation Risk? *The Auk*, *126*(3), 500-510. https://doi.org/10.1525/auk.2009.08148

Sadeghi, M., de Dear, R., Morgan, G., Santamouris, M., & Jalaludin, B. (2021). Development of a heat stress exposure metric – Impact of intensity and duration of exposure to heat on physiological thermal regulation. *Building and Environment*, *200*, 107947. https://doi.org/https://doi.org/10.1016/j.buildenv.2021.107947

Scholander, P., Hock, R., Walters, V., Johnson, F., & Irving, L. (1950). Heat Regulation in Some Arctic and Tropical Mammals and Birds. *Biological Bulletin*, *99*(2), 237-258. https://doi.org/10.2307/1538741

Schou, M. F., Engelbrecht, A., Brand, Z., Svensson, E. I., Cloete, S., & Cornwallis, C. K. (2022). Evolutionary trade-offs between heat and cold tolerance limit responses to fluctuating climates. *Science Advances*, *8*(21), eabn9580.

Sénéchal, É., Bêty, J., Gilchrist, H. G., Hobson, K. A., & Jamieson, S. E. (2011). Do purely capital layers exist among flying birds? Evidence of exogenous contribution to arctic-nesting common eider eggs. *Oecologia*, *165*, 593-604.

Snell, K. R., Aldará, J., Hammer, S., & Thorup, K. (2024). Thermal stress during incubation in an arctic breeding seabird. *Journal of Thermal Biology*, 103967.

Sørensen, J. G., Noer, N. K., Kristensen, T. N., & Bahrndorff, S. (2024). Acclimation to moderate temperatures can have strong negative impacts on heat tolerance of arctic arthropods. *Functional Ecology*, *38*(7), 1549-1561. https://doi.org/https://doi.org/10.1111/1365-2435.14573

Speakman, J. R., & Król, E. (2010). Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *Journal of Animal Ecology*, *79*(4), 726-746.

Steenweg, R. J., Hennin, H. L., Bêty, J., Gilchrist, H. G., Williams, T. D., Crossin, G. T., & Love, O. P. (2015). Sources of diel variation in energetic physiology in an Arctic-breeding, diving seaduck. *General and Comparative Endocrinology*, *216*, 39-45. https://doi.org/https://doi.org/10.1016/j.ygcen.2015.04.012

Steyn, V. M., Mitchell, K. A., Nyamukondiwa, C., & Terblanche, J. S. (2022). Understanding costs and benefits of thermal plasticity for pest management: insights from the integration of laboratory, semi-field and field assessments of Ceratitis capitata (Diptera: Tephritidae). *Bulletin of Entomological Research*, *112*(4), 458-468. https://doi.org/10.1017/S0007485321000389

Swennen, C., Ursem, J., & Duiven, P. (1993). Determinate laying and egg attendance in common eiders. *Ornis Scandinavica*, 48-52.

Tapper, S., Nocera, J. J., & Burness, G. (2020). Experimental evidence that hyperthermia limits offspring provisioning in a temperate-breeding bird. *Royal Society Open Science*, *7*(10), 201589. https://doi.org/doi:10.1098/rsos.201589

Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits depend on methodological context. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1628), 2935-2943.

Thonis, A., Ceballos, R. M., Tuen, A. A., Lovegrove, B. G., & Levesque, D. L. (2020). Small Tropical Mammals Can Take the Heat: High Upper Limits of Thermoneutrality in a Bornean Treeshrew. *Physiological and Biochemical Zoology*, *93*(3), 199-209. https://doi.org/10.1086/708467

Tiedemann, R., Paulus, K. B., Scheer, M., Von Kistowski, K. G., Skírnisson, K., Bloch, D., & Dam, M. (2004). Mitochondrial DNA and microsatellite variation in the eider duck (Somateria mollissima) indicate stepwise postglacial colonization of Europe and limited current long-distance dispersal. *Molecular Ecology*, *13*(6), 1481-1494. https://doi.org/https://doi.org/10.1111/j.1365-294X.2004.02168.x

Tullett, S., & Deeming, D. (1987). Failure to turn eggs during incubation: effects on embryo weight, development of the chorioallantois and absorption of albumen. *British Poultry Science*, *28*(2), 239-243.

Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D., & O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20132612. https://doi.org/doi:10.1098/rspb.2013.2612

Verzuh, T. L., Rogers, S. A., Mathewson, P. D., May, A., Porter, W. P., Class, C., Knox, L., Cufaude, T., Hall, L. E., Long, R. A., & Monteith, K. L. (2023). Behavioural responses of a large, heat-sensitive mammal to climatic variation at multiple spatial scales. *Journal of Animal Ecology*, *92*(3), 619-634. https://doi.org/https://doi.org/10.1111/1365-2656.13873

Vestbo, S., Hindberg, C., Olesen, J. M., & Funch, P. (2019). Eiders as Long Distance Connectors in Arctic Networks. *Cross-cultural research*, *53*(3), 252-271. https://doi.org/10.1177/1069397118806820

Walsh, J. E., Ballinger, T. J., Euskirchen, E. S., Hanna, E., Mård, J., Overland, J. E., Tangen, H., & Vihma, T. (2020). Extreme weather and climate events in northern areas: A review. *Earth-Science Reviews*, *209*, 103324. https://doi.org/https://doi.org/10.1016/j.earscirev.2020.103324

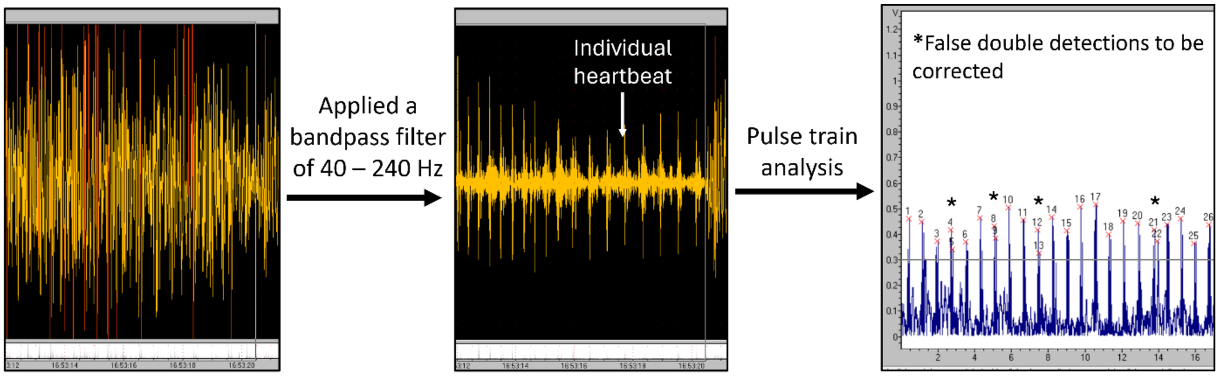
Walsh, J. E., Thoman, R. L., Bhatt, U. S., Bieniek, P. A., Brettschneider, B., Brubaker, M., Danielson, S., Lader, R., Fetterer, F., & Holderied, K. (2018). The high latitude marine heat wave of 2016 and its impacts on Alaska. *Bull. Am. Meteorol. Soc*, *99*(1), S39-S43.

Wenzel, L., Gilbert, N., Goldsworthy, L., Tesar, C., Mcconnell, M., & Okter, M. (2016). Polar opposites? Marine conservation tools and experiences in the changing Arctic and Antarctic. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *26*(S2), 61-84. https://doi.org/https://doi.org/10.1002/aqc.2649

Zhang, L., Zhang, Y.-Y., Ma, L.-X., & Dong, Y.-W. (2023). Evaluation of species thermal sensitivity with individual-based physiological performance. *Marine Environmental Research*, *192*, 106212. https://doi.org/https://doi.org/10.1016/j.marenvres.2023.106212

APPENDICES

Appendix A. Methodology for detecting heart beats in the raw audio files from microphone eggs deployed in incubating common eider (*Somateria mollissima*) nests at Qikiqtakuluk (East Bay Island), Nunavut. Avisoft audio filtering and heartbeat detection process.



raw audio

Filtered audio

Detected heartbeats of filtered audio, with numbered label markers.

Appendix B. Settings for programming Tinytag temperature recording loggers deployed in common eider (*Somateria mollissima*) nests at Qikiqtakuluk (East Bay Island), Nunavut.

Categories	Chosen settings for the given category
Description:	Tiny tag name (TT#)
Logging interval:	Taking a measurement every 1 minute
Start options:	Starting immediately
Measurements:	Measuring temperature
Stop options:	Stop when full
Alarms:	No alarms enabled

Appendix C. Eigenvalues of principal components and percent variance (%) associated to each component of the principal component analysis for environmental parameters used in the heart rate analysis of incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6
Eigenvalues	4.366	1.225	0.404	0.004	0.001	0.0002
Cumulative Variance (%)	72.76	93.18	99.91	99.98	99.99	100

Appendix D. Cumulative variance for our two retained and rotated components of our original principal component analysis of environmental parameters. The principal component analysis was performed for environmental parameters used in the heart rate component of our heat stress study on incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

	Rotated component 1	Rotated component 2
Sum of Squared Loadings	3.59	2.00
Cumulative Variance (%)	60.00	93.00

Appendix E. Variables' loadings into each of our rotated components (rotated components 1 and 2) that were retained from our original principal component analysis. The principal component analysis was performed for environmental parameters used in the heart rate component of our heat stress study on incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

Variables	Rotated component 1	Rotated component 2
Wet Bulb Temperature	0.955	-0.267
Relative Humidity		0.974
Wind Speed	-0.575	0.601
Heat Index	0.860	-0.481
Dew Point	0.987	0.155
Wind Chill	0.798	-0.600

Appendix F. Eigenvalues of principal components and percent variance (%) associated to each component of the principal component analysis for environmental parameters used in the behavioural analysis of incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

	Comp 1	Comp 2	Comp 3	Comp 4	Comp 5	Comp 6
Eigenvalues	3.988	1.096	0.742	0.150	0.021	0.003
Cumulative Variance (%)	66.47	84.74	97.10	99.60	99.95	100

Appendix G. Cumulative variance for our two retained and rotated components of our original principal component analysis of environmental parameters. The principal component analysis was performed for environmental parameters used in the behavioural component of our heat stress study on incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

	Rotated component 1	Rotated component 2
Sum of Squared Loadings	3.97	1.11
Cumulative Variance (%)	66.00	85.00

Appendix H. Variables' loadings into each of our rotated components (rotated components 1 and 2) that were retained from our original principal component analysis. The principal component analysis was performed for environmental parameters used in the behavioural component of our heat stress study on incubating common eiders (*Somateria mollissima*) at Qikiqtakuluk (East Bay Island), Nunavut.

Variables	Rotated component 1	Rotated component 2
Wet Bulb Temperature	0.978	
Relative Humidity	0.130	0.889
Wind Speed	-0.573	0.530
Heat Index	0.982	
Dew Point	0.887	0.154
Wind Chill	0.960	

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