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Assessing the Adaptive Capacity of an Arctic Seabird to Increasing Frequency in Predation Risk from Polar Bears Using Behavioural and Physiological Metrics

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Assessing the adaptive capacity of an Arctic seabird to increasing frequency in predation risk from polar bears using behavioural and physiological metrics

By

Erica Anne Geldart

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Assessing the adaptive capacity of an Arctic seabird to increasing frequency in predation risk from polar bears using behavioural and physiological metrics

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DECLARATION OF CO-AUTHORSHIP

I. Co-Authorship

I hereby declare that this thesis incorporates material that is result of joint research, as follows: I am the sole author of Chapter 1 (General Introduction) and Chapter 4 (General Discussion), and am the primary author of Chapters 2 and 3. Chapter 2 and 3 are co-authored with Dr. Oliver Love, Dr. Andrew Barnas, Dr. H. Grant Gilchrist, Christopher Harris, and Dr. Christina Semeniuk. In regards to both co-authored chapters, the key, primary contributions, study designs, data analysis, interpretation, and writing were performed by the author, and the contribution of co-authors was primarily through the assistance with securing funding, study designs, data analysis, interpretation, logistical support, and editing versions of 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-author(s) to include the above material(s) in my thesis.

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ABSTRACT

Predator-prey dynamics in the Arctic are being altered with changing sea-ice phenology. The increasing frequency of predation on colonial nesting seabird eggs by a rare predator - the polar bear (*Ursus maritimus*), is a consequence of bears shifting to terrestrial food resources through a shortened seal-hunting season. I study a colony of nesting common eiders (*Somateria mollissima*) on Mitivik (East Bay) Island, Nunavut, Canada, that is exposed to established nest predators such as arctic fox (*Vulpes lagopus*), but has recently experienced an increase in polar bear nest predation due to the bears' lost on-ice hunting opportunities. Given eiders' limited eco-evolutionary experience with polar bears, my thesis aimed to determine the capacity of incubating eider hens to perceive and respond to this increasing frequency in predation risk from bears. I used eider heart rate and flight initiation distance (FID) as physiological and behavioural metrics, respectively, to characterize the perceived risk of imminent threat posed by simulated predators that differ in evolved familiarity. I then quantified eider heart rate to examine the capacity of incubating hens to dynamically update their perception of risk across variation in real predation risk by polar bears. My results indicate that eiders were less responsive in terms of heart rate to impending visual cues of polar bears in comparison to that of an evolved egg predator (arctic fox), but responded to all simulated threats with similar FIDs. Eiders exhibited mild tachycardia to bears present closer to their nests, but were insensitive to variation in exposure duration to bears. Taken together, these results suggest eiders do not perceive the full risk that bears pose as egg- and adult predators. This thesis provides insight into the mechanisms governing the ability of eiders to cope with polar bears and subsequent fitness consequences due to indirect effects of anthropogenic climate change.

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CHAPTER 1

General Introduction

Climate-induced changes to predator-prey dynamics

Recent anthropogenic climate change (IPCC 2018) is having complex ecological impacts (reviewed in Hughes 2000, McCarty 2001, Walther et al. 2002). In particular, there is growing evidence of climate-induced phenological shifts in seasonal life history events occurring across terrestrial, freshwater, and marine taxa, with Spring and Summer events generally occurring earlier than they have in the historical past (Thackeray et al. 2010, Johansson et al. 2015). In many of these cases, organisms are responding to climatic effects on landscapes and resource availability by altering the timing of their life history events to take advantage of optimal conditions (e.g., Both 2010, Chisholm et al. 2020). As such, phenological changes can act on predator-prey dynamics by influencing species' potential to occupy the same space at the same time (Guiden et al. 2019), thereby impacting the strength of these biological interactions and creating new matches and mismatches in the activity of predators and prey (Parmesan 2006). Indeed, recent changes in the degree of spatial overlap between predators and their prey have either created novel predator encounters by prey (Guiden et al. 2019) or increased traditionally infrequent interactions (e.g., between newt predators and frog larvae, reviewed in Walther et al. 2002). What is unclear is the extent to which these organisms have the necessary evolved mechanisms to adaptively and successfully respond to this degree of change (Salo et al. 2007, Sih et al. 2011, 2016; Robertson et al. 2013, Sih 2013, Ehlman et al. 2019, Sadoul et al. 2020).

Adaptive responses to evolved predators

In communities where predators and prey have coexisted over evolutionary history, prey have evolved a variety of phenotypically plastic traits (i.e., behavioural, physiological, morphological, and life history traits) that lower their risk of confronting a predator and enhance their likelihood of escape once confronted (Lima and Dill 1990). Prey that have sufficient experience on both evolutionary and ecological timescales with a predator will have the adaptive capacity to discriminate the predator from non-predators, a necessary mechanism that precedes a response (reviewed in Carthey and Blumstein 2018). Equally, prey that have evolved with a community of predators will be primed to recognize a variety of different predator cues and respond accordingly (Blumstein 2006a). Specifically, adaptive mechanisms can include the capacity to discriminate between threatening and non-threatening organisms by recognizing general (i.e., produced by a broad range of predation threats) and/or specific (to one predator species) cues emitted by their evolved predators (reviewed in Carthey and Banks 2014). Once they have detected a predator, prey typically alter their behaviour and underlying physiology in a way that aligns with one of the following two strategies that lower their risk of being detected and captured by predators: 1) passive defense response, whereby prey reduce activity to avoid being detected; or 2) active defense, whereby prey actively attempt to escape predation (Adolphs 2013). Although risk-induced trait responses can improve prey fitness by reducing predation risk, responding to predation risk can also have negative consequences for the fitness of prey via trade-offs between survival and growth or current reproduction (Lima and Dill 1990). According to state-dependent signal detection theory, prey should adjust their cue signal thresholds (i.e., strength of the signal emitted by the predator above which they will respond) according to their internal state, whereby a prey's optimal threshold decreases with their level of reserves (Trimmer et al. 2017). Flexible traits therefore allow prey to optimize their responses to predators in ecological time based on the current risk of predation in its environment and the trade-offs associated with the possible defense strategies.

Anti-predator responses of incubating birds

Nest predation is the largest cause of reproductive failure in birds (Ricklefs 1969). However, some nest predators not only target a bird's clutch of eggs, they can also pose a predation threat to the adult themselves (Lima 2009). Therefore, incubating birds can be faced with conflicting demands (i.e., current reproduction vs survival to invest in future reproductive attempts) which requires a bird to continuously update their response to focus on the more critical demand that maximizes lifetime fitness. An important risk-induced behaviour in breeding birds (especially those that are incubating and tied to an invested clutch of eggs) is the optimal regulation of flight initiation distance (FID). In ground-nesting birds, FID is defined as the distance at which individuals decide to vacate their nest after a predator has been detected (e.g., Blumstein 2006, Tarlow and Blumstein 2007). Despite the obvious benefits of fleeing from a predator, flight can have reproductive and energetic costs (i.e., non-consumptive effects). The 'economics of flight' hypothesis posits that following the detection of a predation threat, prey balance the costs associated with divergent behavioural options (e.g., remaining on the nest or fleeing) to determine at what distance from the predator to flee (Ydenberg and Dill 1986). According to this hypothesis, FID should vary with the level of perceived predation risk, with more risky interactions causing an animal to flee their nests sooner. Both characteristics of the prey and predator influence a prey's perception of risk. For instance, a bird's other defensive tactics (e.g., morphological defenses) can increase their confidence in remaining concealed (e.g., cryptic colouration) or prevent capture (e.g., armour) from predators and therefore influences risk. Prey species that rely on these tactics may defer fleeing and only switch from freezing (i.e., passive defense) to fleeing (i.e., active defense) once a predator reaches a critical distance at which the need to engage outweighs the possibility of evading detection (reviewed in Adolphs 2013). Further, level of risk varies across different predator encounters and even across moments within a single encounter with a predator. For example, different types of predators pose different levels of risk (Tvardíková and Fuchs 2011, Schneider and Griesser 2013) and aside from a predator's distance in relation to prey (e.g., Smith and Edwards 2018), other predator behaviours such as their direction of attention (e.g., gaze, Davidson and Clayton 2016) and speed of attack (Cooper 2006) influence level of risk. Flight initiation distance can therefore be used as a metric to assess an animal's perception of relative risk to predation in the field.

Behaviour interacts reciprocally with inter-related physiological responses to predation risk (Sih et al. 2010). For example, upon detection of a threat, the hypothalamo-pituitary-adrenal (HPA) axis is activated and secretion of circulating glucocorticoids such as corticosterone (CORT; i.e., the primary avian 'stress' hormone, Monaghan 2014) from the adrenal gland initiates physiological mechanisms that sensitize an animal to predators, typically triggering behavioural responses to enhance immediate survival such as inhibition of reproductive behaviour and stimulation of escape behaviour (Sapolsky et al.

2000, Clinchy et al. 2013). Corticosterone responses in birds can be detectable one to two minutes after initial exposure to a stressor (Romero and Reed 2005) and thus comprises only the second wave of the stress response (Cockrem 2007). Modulation of the cardiovascular stress response is a much more immediate physiological response to threat (i.e., less than one second after threat-detection), and is thus involved in the first wave of the stress response (reviewed in Sapolsky et al. 2000). Animals can show flexibility in the relative roles of the sympathetic and parasympathetic branches of the autonomic nervous system in regulating stress-induced changes in heart rate (Löw et al. 2008, Müller et al. 2018). For instance, distinct patterns of autonomic change have been associated with the different defense strategies employed by prey (i.e., active vs passive). An active defense strategy is characterized by a fight-or-flight response (i.e., prepares an animal for danger), and is mediated by the sympathetic nervous system, which releases the catecholamines epinephrine and norepinephrine to accelerate heart rate (i.e., fear tachycardia) (reviewed in Sapolsky et al. 2000). The rest-and-digest response (i.e., promotes self-maintenance processes) is mediated by the parasympathetic nervous system, which releases acetylcholine to decelerate heart rate (i.e., fear bradycardia) and is generally associated with a passive defense strategy to a perceived threat (i.e., linked to freezing behaviour) (Lang et al. 1997, Carravieri et al. 2016). Patterns of use of the different defense strategies within a single predator event has been linked to the proximity (i.e., imminence) of a threat: the first detection of a predator in the distance prompts parasympathetic-mediated bradycardia, and this deceleration in heart rate can grow more intense as a threat gets closer, but once the prey's distance from the predator reaches a critical distance where the threat of attack is perceived as imminent (i.e., when bird assumes they have been detected by the predator), animals switch to a sympathetic-mediated tachycardia preceding flight (e.g., Gabrielsen et al. 1977, 1985; reviewed in Löw et al. 2008). However, there are also reports of birds exclusively displaying a tachycardia (e.g., herring gull *Larus argentatus*, Ball and Amlaner 1979) or bradycardia (e.g., willow grouse *Lagopus lagopus*, Gabrielsen et al. 1977) response to disturbance prior to a flush response. According to Campbell et al. (1997), fear bradycardia is particularly evident in nesting species that rely on concealment (e.g., cover and feather crypsis) to avoid detection by predators, explaining potential interspecific differences in risk-induced heart rate responses. Measuring heart rate responses can thus offer a dynamic understanding of perceived risk by prey in response to approaching predators.

Adaptive capacity to detect and respond to new/rare predators

Prey vary in their capacity to respond to new/rare predators; some animals will have the necessary mechanisms to adaptively respond, while others will exhibit responses that may be maladaptive (Salo et al. 2007, Sih 2013, Sih et al. 2016, Ehlman et al. 2019). Species accumulate experience interacting with predators over both evolutionary and ecological timescales, and their specific (i.e., with focal predator species) and general (i.e., with other predators) eco-evolutionary experience with predators may be applicable in new/rare interactions (Saul and Jeschke 2015). But there exists several hypothesized mechanisms by which prey may be able to still detect and respond adaptively to predators for which they have limited eco-evolutionary experience (reviewed in Carthey and Blumstein 2018). For instance, prey may be more likely to recognize and respond to a predator for which they have no experience, but that 1) are of the same archetype as familiar predators (i.e., show similar morphological and behavioural adaptations in obtaining prey, Cox and Lima 2006); or 2) display features that 'label' them as predatory (e.g., forward facing eyes, Sih et al. 2009). Further, prey with only recent experience coexisting with a predator may be able to respond to an evolutionarily novel predator by rapidly developing appropriate responses via plasticity, learning, and/or rapid evolution (Steindler et al. 2020). Alternatively, prey with insufficient eco-evolutionary experience to recognize and/or adaptively respond to a predator are considered naïve (Cox and Lima 2006, Carthey and Banks 2014). The amount of eco-evolutionary experience prey possess with a predator influences their level of naiveté: either prey do not recognize the predator and thus do not display a response (level 1); prey recognize a predator but display an inappropriate response (level 2; e.g., rely on crypsis to avoid olfactory hunting predators); respond appropriately but ineffectively (level 3); or display a greater response than necessary to reduce risk (level 4; e.g., hide from predator for too long). Understanding the extent to which prey can detect and effectively respond to predators can therefore provide insight on the fitness consequences prey are expected to incur as a result of increasing predation pressure by predators for which prey have limited eco-evolutionary experience.

Arctic predator-prey systems in flux

The effects of climate change are most pervasive in the Arctic (Wassmann et al. 2011), which is experiencing a warming of more than double the global increase (Trenberth et al. 2007). Resultantly, parts of the Canadian Arctic are experiencing earlier sea-ice loss in the Spring and delays in freeze-up in the Fall, altogether creating a lengthened ice-melt season (Stirling et al. 1999, Gagnon and Gough 2005). Ice-associated changes in the abundance and distribution of food resources are affecting the breeding and foraging ecology of most marine birds and mammals (Wrona et al. 2016, Descamps et al. 2017, Frederiksen 2017). Indeed, many Arctic nesting seabirds are advancing their nesting phenology to coincide with optimal sea-ice conditions (e.g., thick-billed murre *Uria lovia*, Gaston et al. 2005; greater snow goose *Chen caerulescens atlantica*, Dickey et al. 2008; common eider *Somateria mollissima*, Love et al. 2010), but this advancement is occurring at a slower rate than advances in sea-ice break-up (e.g., lesser snow goose *Anser caerulescens caerulescens,* Rockwell and Gormezano 2009). This disruption in synchrony is not only creating mismatches between seabirds and other members of their marine food web (e.g., between breeding birds and peak food availability, Gaston et al. 2009), but it is also creating new matches. One of the most dramatic predator-prey overlaps we are seeing involves polar bears (*Ursus maritimus*), a species traditionally dependent on ice as a platform to hunt marine mammals (Thiemann et al. 2008). Bears are now being forced ashore earlier due to a shortened seal-hunting season (Stirling et al. 1999, Stirling and Parkinson 2006), and their time on land is increasingly overlapping with when Arctic nesting birds are breeding (e.g., Rockwell et al. 2011, Iverson et al. 2014). As a result of this new match, we are seeing steady and rapid increases in the occurrences of egg predation in Arctic nesting seabird colonies during the birds' breeding season (e.g., lesser snow goose, Rockwell and Gormezano 2009; snow goose *Chen caerulescens* and thick-billed murre, Smith et al. 2010; common eider, Iverson et al. 2014; barnacle goose *Branta leucopsis* and glaucous gull *Larus hyperboreus*, Prop et al. 2015).

Arctic nesting seabirds experience strong selective pressure on their breeding ecology from their traditional avian and mammalian egg predators (i.e., primarily arctic fox *Vulpes lagopus*, Larson 1960). Anti-predator adaptations that birds have evolved against these predators fail to deter polar bear egg predation. In particular, many seabirds have evolved arctic fox avoidance behaviours by nesting primarily on 1) small islands and after ice-contact with the mainland is lost, or 2) steep mainland cliffs (Larson 1960, Ahlén and Andersson 1970, Mehlum 1991, Mallory and Gilchrist 2003, Hanssen et al. 2013, Maftei et al. 2015). Unlike their traditional mammalian predators, however, polar bears can access islands during the nesting periods of seabirds by swimming (Pagano et al. 2012) and their frequency of visitation at both island and cliff-nesting seabird colonies has increased (Iverson et al. 2014). Second, many Arctic seabirds have evolved to nest in high-density aggregations to reduce the risk of predation by arctic fox and their avian egg predators through a dilution effect or through communal nest defense and predator warning (Schmutz et al. 1983, Mehlum 1991, Oro 1996, Hernández-Matías et al. 2003). Dense colonies make foraging more efficient and profitable for some predators (Ricklefs 1969, Clode 1993, Stokes and Boersma 2000), and this may be the case for polar bears since a single bear can consume hundreds of clutches in a short period of time (Gormezano et al. 2017). Indeed, bears foraging in nesting bird colonies has been shown to be density dependent, with bears preferentially foraging in larger nesting aggregations over solitarily or small aggregations (Iverson et al. 2014). Finally, many Arctic nesting seabirds have evolved high nest attentiveness to reduce exposure of eggs to predation by avian predators (Afton and Paulus 1992), but polar bears can easily displace birds off their nest (Gormezano et al. 2017). Therefore, previously adaptive defenses by nesting seabirds against their traditional egg predators may render some seabird species vulnerable to an evolutionary trap against polar bear egg predators (Schlaepfer et al. 2002).

Study system: Common eider

The Hudson Strait is home to internationally significant populations of marine birds, largely comprised of Thick-billed murres and Common eiders. Whereas polar bears are historically a very infrequent and stochastic predator of birds and their eggs (Harrington 1965, Lønø 1970, Russell 1975, Gormezano and Rockwell 2013), both these avian species have experienced a dramatic (sevenfold) increase in polar bear incursions during their breeding period as a consequence of the bear's climate-induced reduced winter diet (Smith *et al.* 2010; Iverson *et al.* 2014). Given a combination of physiological and environmental constraints, Common eiders (hereafter 'eiders'), a long-lived iteroparous sea duck species (Coulson 1984), are highly susceptible to impacts on fitness from polar bear nest predation. First, the threat of polar bear nest predation is increasing at a greater degree for ground nesters such as eiders than for cliff-nesting seabirds because bears do not need to employ intensive feeding techniques (e.g., cliff climbing) when targeting ground-nesters, making them more easily accessible (Iverson et al. 2014, Hamilton et al. 2017). Next, the incubation period is an energetically taxing time for eiders. By using a mixed capital-income reproductive strategy (Sénéchal et al. 2011) females undergo a 25-27 day incubation period in which they forego foraging and spend little time off their nest to minimize the length of the incubation period (Korschgen 1977, Parker and Holm 1990). As a consequence, incubating eider hens are unable to compensate by foraging to buffer energy loss during this extreme incubation fasting, resulting in the loss of 30-45%

of their post-laying body mass (Mehlum 1991). Because of this tight energy budget, any further energy used to respond to new predation risk from polar bears when their own life is not at risk (i.e., where they do not need to flee) could reduce their chances of successfully completing incubation, reducing lifetime fitness. Finally, eider reproductive timing is constrained by sea ice phenology (Love et al. 2010) so disruptive breeding caused by polar bear egg predation during incubation can disrupt ideal timing of hatching ducklings if eiders initiate a replacement clutch, generating additional reproductive fitness deficits (Hanssen and Erikstad 2012). With these combined constraints, eider hens are faced with multiple decisions on how best to optimize their responses to an increase in predation risk by polar bears to maximize their lifetime fitness.

Eiders have evolved various adaptive defenses to their traditional predators, *Larus* gulls and arctic fox, such as nesting primarily on coastal islands (Chaulk et al. 2007) and forming large nesting aggregations (over 1000 nests per hectare, Chaulk et al. 2004). Although advancing Spring ice-melt is expected to reduce predation pressure by foxes (Hanssen et al. 2013), predation risk from polar bears will continue to be exacerbated (Dey et al. 2018). Despite the severe consequences bear presence in eider colonies have shown to have on eider reproductive success (Iverson et al. 2014), Dey et al. (2018) predicted that northern eider population sizes will remain stable over the next 50 years as a result of multiple antagonistic effects of climate change on different vital rates (i.e., increases in polar bear egg predation in combination with increases in breeding propensity and clutch size). However, their results do not imply eider adaptation to changing climatic conditions, such as the adaptive capacity to respond to increases in polar bear predation risk. Moreover, one suggested mechanism that may reduce polar-bear predation in the short term is eider re-nesting to other colonies marked by reduced predation pressure as predicted by Dey and colleagues (2018); however, this has yet to be observed (Dey et al. 2020).

It is suggested that an animal's response to rapid environmental change might depend on the extent to which the new conditions match the conditions in which that species evolved (Sih et al. 2011). Thus, contrasting eiders' responses to the recent predation pressure by an infrequent/rare egg- and adult-predator within the context of their adaptive responses to the threat of arctic fox egg predation can provide insight on eiders capacity to cope with these changes (Sih et al. 2010). Additionally, level of risk within and across predator encounters can vary (as discussed above) and dynamic risk is especially true for female incubating eiders since their cryptic coloration should increase their confidence in remaining concealed from predators (Ydenberg and Dill 1986). Because female incubating eiders are so energetically limited during incubation (Parker and Holm 1990, Gabrielsen 1994), eiders must optimize their responses to predators by assessing risk in their current environment and adjusting their responses accordingly (i.e., dynamic risk assessment, Kleindorfer et al. 2005). Therefore, understanding an eider's perception of polar bear predation risk will also provide insight on their adaptive capacity to respond to this increasing risk. Eiders have been documented displaying various risk-induced trait responses to disturbance, including flushing (Seltmann et al. 2012), hormonal stress (e.g., CORT, Jaatinen et al. 2014), and heart rate responses (Cabanac and Guillemette 2001). Although hormonal responses can be reliable predictors of perceived risk by eiders, blood samples are not always feasible to obtain in free-living birds without interrupting incubation and inducing abandonment. As such, non-invasive metrics such as the monitoring of heart rate during stressful events can be used as real-time physiological measures of perceived risk in the field (e.g., de Villiers et al. 2006, Viblanc et al. 2012), since the magnitude and duration of changes in heart rate can be used to determine an animal's assessment of a stimulus (discussed above). Flight initiation distance and heart rate can therefore be used as non-invasive behavioural and physiological metrics to assess eider perception of risk to polar bears in relation to traditional egg predators and variation in polar bear predation risk.

Thesis objectives

The overall goal of my thesis was to assess the adaptive capacity of common eiders to respond to increasing frequency in predation risk from polar bears, specifically characterizing incubating eiders' risk-induced trait responses in terms of flight response and heart rate to polar bears in relation to traditional egg predators and variation in predation risk by polar bears on Mitivik (East Bay) Island, Nunavut, Canada in 2019.

In **Chapter 2**, ***Heart rate and flight responses to evolutionarily familiar and unfamiliar predators in an Arctic seabird***: My objective was to use a simulated-predator experimental approach to contrast eider perception of and response to imminent risk posed by polar bears and arctic foxes. Due to eiders' limited evolutionary experience with bears and the archetypal differences between polar bears and foxes, I hypothesized that incubating eiders will have a lower perception of risk to polar bears than to their evolved fox predators. I found that eiders had less of an alteration in heart rate to an approaching polar bear stimulus compared to arctic fox and that their heart rate was positively correlated with flight initiation distance, but despite this, eiders did not show differential flight responses to polar bears, arctic foxes, or control. Altogether, eiders have a lower perception of physiological risk to polar bears than to their evolved mammalian egg predators, suggesting their cardiac stress response is restricted to recognize evolutionary-level threats, as oppose to their behavioural escape response that can be modulated to ecological changes in risk.

In **Chapter 3**, ***Arctic colonial-nesting seabird heart rate responses to natural variation in threat of polar bear egg predation***: My objective was to assess eiders' perception of risk to variation in predation risk posed by polar bears. Due to eiders' limited eco-evolutionary experience with polar bears, I hypothesized that eiders would not perceive the full risk posed by polar bears, so do not dynamically update their assessment of risk to variation in risk posed by a bear. I found that eider heart rate changed to various distances to a polar bear, but was unaffected by duration of exposure to a bear, and thus eiders do not realize the full risk bears pose to their eggs and themselves.

In **Chapter 4**, ***General discussion****:* I interpret my findings, then discuss their implications for eider fitness and resultant downstream impacts on eider population dynamics. I discuss my study's limitations and provide suggestions for future research and conservation intervention.

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CHAPTER 2

Heart rate and flight responses to evolutionarily familiar and unfamiliar predators in an Arctic seabird

Introduction

Climate change is predicted to have a variety of ecological consequences from climate-induced species changes, such as impacts on temperature-dependent life history traits (e.g., Robertson 1995), changes in phenology of seasonal life history events (Thackeray et al. 2010), distributional shifts (e.g., Killengreen et al. 2007, Jepsen et al. 2008), and altered species interactions (e.g., Gilg et al. 2009, Hamilton et al. 2017). Indeed, as species respond to climate change by shifting the timing and degree of inter-specific spatial overlap, new interactions may be generated between predators and prey (reviewed in Donnelly et al. 2011); or rare interactions may become more common. In communities where predators and prey coexist, prey have evolved various antipredator adaptations that lower their risk of confronting a predator and enhance their likelihood of escape once confronted (Lima and Dill 1990, Guiden et al. 2019). However, prey vary in their responses to unfamiliar or uncommon predators; some animals will have the necessary mechanisms to adaptively respond, while others will exhibit responses that may be maladaptive (Salo et al. 2007, Sih 2013, Sih et al. 2016, Ehlman et al. 2019). Because effective antipredator responses are dependent on the ability of prey to perceive predators as a threat, threat assessment of a new/rare predator can provide insight into a prey's ability to adapt to the increasing frequency of interactions (Ehlman et al. 2019). Existing literature considers predators 'novel' if they are unfamiliar from a prey's perspective and as such cannot be recognized as dangerous (Cox and Lima 2006, Carthey and Banks

2014, Sih et al. 2016, Ehlman et al. 2019). Prey are more likely to identify a new predator as a threat and respond accordingly should the predator share archetypal similarity to evolved predators - in terms of sensory (e.g., visual, olfactory, acoustic), behavioural (e.g., foraging style, attack mode), and habitat cues (i.e., areas and times that are associated with predator presence). Furthermore, if prey populations have had previous evolutionary encounters with a diversity of predators, populations may retain flexibility in responses to predators (rather than specializations), and therefore also adaptively respond to the new threat (Ehlman et al. 2019). However, if a predator is truly novel, naïve prey can either lack an antipredator response or display an inappropriate one (Carthey and Blumstein 2018, Guiden et al. 2019). Consequently, evolutionarily recent interactions with rare predators can have greater negative effects on prey populations than do traditional predators (Salo et al. 2007).

Identifying metrics that effectively quantify whether prey can recognize and respond to new/rare predators is vital for predicting potential downstream impacts on prey populations (Peacor et al. 2020). Because vertebrates can display neurophysiological responses to stressors in the absence or preceding any behavioural responses (reviewed in Ydenberg and Dill 1986, Weston et al. 2012), certain physiological metrics can be immediately indicative of an animal's awareness of a predator. For example, an animal's cardiac stress response occurs in less than one second of threat-detection, where the sympathetic and parasympathetic nervous system releases circulating catecholamines (i.e., epinephrine and norepinephrine) and acetylcholine (respectively) which have a direct effect on heart rate (reviewed in Lang et al. 1997, Sapolsky et al. 2000, Carravieri et al. 2016). As such, monitoring heart rate during predator events can provide a physiological measure of perceived risk, since the magnitude and duration of changes in heart rate can be used to determine an animal’s assessment of a stimulus (Ydenberg and Dill 1986, Nephew et al. 2003, de Villiers et al. 2006, Viblanc et al. 2015). Further, stress-induced physiological mechanisms - like changes in heart rate, prepare the body for overt action, facilitating subsequent behavioural responses (e.g., predator-avoidance) such as flight (escape) responses (e.g., Gabrielsen et al. 1977). Flight initiation distance (FID) is a common behavioural stress-response metric and is defined as the distance at which individuals can be approached by a perceived threat prior to fleeing (e.g., Blumstein 2006, Tarlow and Blumstein 2007). Because of the energy costs associated with flight behaviour as well as the concomitant downstream survival and reproductive fitness consequences, animals should modulate their flight response according to their perception of risk. Generally, animals tend to flee sooner (i.e., at greater distances) to greater perceived levels of predation risk (Ydenberg and Dill 1986, Cooper and Frederick 2007). Although organisms can coordinate their physiological (i.e., cardiovascular and endocrine) and antipredator behavioural responses to generate an appropriate overall response to stress, stress-induced heart rate and behaviours (e.g., activity level, aggression displays, maintenance) have been shown to maintain independent regulation from one another, meaning organisms can exhibit a heart rate response without observable changes in behaviour and vice versa (e.g., European starling *Sturnus vulgaris*, Nephew et al. 2003). Risk-taking behaviours, such as flight responses, therefore provide further and independent insight on an animal’s perception of threat in addition to heart rate. The evaluation of both physiological and behavioural responses can therefore be used as an effective indicator of a prey's capacity to assess and respond to predation threats in their environment (reviewed in Ydenberg and Dill 1986, Beauchamp 2017).

Here we use responses of common eiders (*Somateria mollissima,* hereafter 'eider') to predators that differ in evolved familiarity (i.e., arctic fox *Alopex lagopus* versus polar bear *Ursus maritimus*) as a useful study system to investigate perception of, and associated responses to, evolutionarily rare and infrequent predators in Arctic nesting seabirds. In particular, nesting eiders in the Arctic are experiencing altered predator regimes from an increasing overlap with polar bears coming ashore from a shortened seal-hunting season (Stirling et al. 2004, Stirling and Parkinson 2006). A consequence of this spatio-temporal overlap is that eiders are now experiencing increasing nest predation pressure by polar bears (Dey et al. 2017, Jagielski et al. 2021a, b). Although polar bear presence in eider nesting colonies had been seldomly reported over the past century (e.g., Lønø 1970), over the past few decades eider encounters with polar bears have steadily increased, and are now associated with persistent and severe consequences for eider nest success in a subset of colonies, an impact far exceeding that caused by their traditional egg predators (Iverson et al. 2014, Prop et al. 2015).

Nesting eiders experience mammalian predatory pressure mainly by arctic foxes, and have evolved several adaptations to reduce predation (Larson 1960). Eiders nest primarily on small islands to avoid land-based arctic foxes (Larson 1960, Ahlén and Andersson 1970). Hens also form high-density nesting aggregations (Chaulk et al. 2007) for communal defense and predator warning (Schmutz et al. 1983, Mehlum 1991); and they exhibit high nest attentiveness and defense (e.g., injury feigning) to reduce exposure of eggs to predation (Larson 1960, Afton and Paulus 1992, Bolduc and Guillemette

2003). While foxes and bears can reach islands by walking over ice during early eider nesting periods, only bears can swim to and from islands when ice begins to break-up (Pagano et al. 2012). Further, bear presence in eider nesting colonies has been positively correlated with nest abundance (Iverson et al. 2014), altogether implying that current eider breeding ecology is not an adaptive strategy to avoid bears (Dey et al. 2017). Polar bears and arctic foxes also differ in several predatory cues, such as size (i.e., bear's bodies are approx. 3.5 times longer and 5 times taller than foxes, worldwildlife.org, Atkinson et al. 1996, Amstrup 2003, Witold et al. 2011) and egg foraging styles (e.g., both predators are active foragers in bird nesting colonies, but bears methodically walk from visible nest to nest, whereas foxes lope towards nests that they locate by scent or flushing birds, and foxes often only cause partial losses to eider clutches by taking a single egg each nest visitation, whereas polar bears typically consume all eggs in a clutch upon visiting the nest, Bahr 1989, Gormezano et al. 2017, Jagielski et al. 2021a, O.P.L. pers. obs.). Despite their differences, both predators can easily displace incubating eiders from their nests to gain access to their eggs, in addition to preying on hens (Bahr 1989, Gormezano et al. 2017); therefore, eiders must modulate their responses to both predators to optimize the impacts of the trade-off between investing in current reproduction and survival/future reproductive success. Eiders across their range have encountered a variety of avian and mammalian egg- and adult-predators (from rats to ursids) in their evolutionary history (reviewed in Waltho and Coulson 2015); as well as a diversity of predators across different stages of their life cycle, such as during migration and overwintering (Cox and Lima 2006). Despite the archetypal differences between polar bears and arctic foxes, and eider's exposure to various predator types, it is still unknown how eiders perceive and respond, both physiologically and behaviourally, to the risk posed by polar bears, and whether these responses differ in relation to arctic foxes.

The aim of the current study was to use a simulated-predator experimental approach to contrast the perception of and response to risk posed by polar bears and arctic foxes. We carried out our study in a large colony of eiders nesting at Mitivik (East Bay) Island, Nunavut, Canada (Jean-Gagnon et al. 2018), that in recent years, has experienced an increase in polar bear nest predation as a consequence of the bear's climate-induced reduced spring diet (Smith et al. 2010, Iverson et al. 2014). From 2005-2018, researchers reported the number of days that arctic foxes were sighted on the island to range from 3 days to 19 days (average 9 days) throughout the eiders' prospecting, laying, and incubation stages (unpublished data). Eiders on Mitivik Island have a relatively consistent, but usually low, encounter rate with foxes on the island, which increases dramatically every few years, whereas eiders are now experiencing a consistently high encounter rate with bears on the island (range 5 days to 31 days, average 17 days, unpublished data). We quantified eider antipredator responses – changes in heart rate and FIDs – to the threat of an approaching predator. Specifically, we tested the hypothesis that due to the difference in evolutionary familiarity between arctic foxes and polar bears, incubating eiders should be naïve and have a lower perception of risk to polar bears. As such, we predicted that female incubating eiders approached by a simulated polar bear would exhibit less of an alteration in their heart rate and concomitantly shorter FIDs when compared to an arctic fox. Since results from this study can provide insight into whether eiders consider polar bears as a functionally novel predator, we discuss implications of the fitness consequences seabirds are expected to face as an indirect effect of anthropogenic climate change.

Materials and Methods

Study species and area

This study was conducted on free-living eiders nesting at Mitivik (East Bay) Island, Nunavut, Canada (64˚02'N, 81˚47'W), located in Southampton Island's Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary (Figure 2.1). Mitivik Island hosts the largest known eider breeding colony in the Canadian Arctic (Inuit Nunangat) and is the only colony within a 100-km radius (Legagneux et al. 2016). Eiders on Mitivik Island initiate laying late June/early July (Jean-Gagnon et al. 2018), and undergo a subsequent 24-day incubation period (Parker and Holm 1990, Bottitta et al. 2003). Due to the increasing rate of polar bear presence on Mitivik Island beginning in July (Smith et al. 2010, Iverson et al. 2014), field work outside the safety of the research compound is limited during this time. We therefore timed our study for the end of June 2019, during eiders' laying/early incubation period.

Heart rate monitoring

From June 24-25, 2019, we deployed heart-rate monitoring equipment on active eider nests (n=11). Each nest was equipped with an artificial-egg heart rate monitor (adapted from Felton et al. 2018). Heart-rate monitors (Figure 2.2) consisted of a 3D-printed plastic eider egg (sub-elliptical, 2.9 in. long x 1.9 in. at the widest point) equipped with two Electret condenser microphones (PUI Audio model AOM-5024L-HD-R), both soldered to and joined by a shielded cable assembly (approx. 72 in. long, 3.5mm stereo plug). The primary microphone was situated at the end of a 3D-printed plastic funnel for amplified sound while the secondary microphone was placed within a hole and flush with the surface of the egg, and used as a back-up in case the eider shifted positions on the egg (i.e., off the primary microphone). Weight was caulked to the bottom half of the egg to ensure the egg maintained a fixed orientation in the nest, with the microphones facing toward the eiders' brood patch. Once equipment was assembled, each half of the 3D-printed egg was glued together, allowing the plug-end of the cable to extend outside of the egg. Finally, the egg was covered by a white balloon membrane for waterproofing. The cable attached to the egg was plugged into the stereo mini jack of a digital recording device (Tascam DR-05X equipped with a 128GB microSD card). To maximize battery life (i.e., approx. 11-12 days of continuous recording), the recorder was attached to an external assembled battery pack (with 24 AA Lithium Ion batteries). See Table A1 for all recorder settings used. The recorder and battery pack were situated within a weatherproof camouflaged storage box (11.4 in. long, 5.4 in. wide, 7.1 in. high).

We chose to deploy heart-rate monitoring equipment on nests located on the periphery of the island to limit researcher-induced disturbance from experimental approaches in dense portions of the colony. However, nests selected for the current study did not differ from a group of additional nests monitored across the island (n=38) for another set of projects (e.g., Smith and Love. in prep) in terms of lay date (i.e., range: June 9 to June 24, and June 10 to June 24, respectively) and incubation stage (i.e., age of first laid egg on June 25: average (± SD) of 4 ± 4 days and 4 ± 3 days, respectively). We deployed artificial eggs in nests containing 1-5 eggs at the time of equipment deployment. Study nests were each located an average (± SD) of 288 ± 151 meters (range 37-554 m) apart from each other (Figure 2.3). During deployment, the location of each study nest was marked on a GPS for ease of relocation prior to experimental approaches. The first-laid egg from each study nest was collected for another project (e.g., Smith and Love, in prep) and also used to estimate incubation stage (see *Estimating incubation stage* below). We replaced this egg with the artificial egg. At the time of deployment, we powered the recorder, set date and time accordingly, and started the recording. The storage box was placed approximately one meter outside of the nest, and the box and cable were secured and concealed with the surrounding terrain.

Previous research suggests that incubating artificial-egg heart rate monitors do not affect birds differently compared to incubating their natural eggs (e.g., adélie penguins *Pygoscelis adeliae*, Giese et al. 1999; American oystercatchers *Haematopus palliatus*, Borneman et al. 2014). In our work, no nest abandonment occurred after nest equipment deployment and birds returned within an approximate average of 1.28 hours (0.0001-6.61 hour range). Experiments began approximately 14 hours after the final heart-rate monitor had been deployed.

Predator-simulated experimental protocol

We used a randomized experimental predator-model approach to test the relative responses of birds to a bear, fox and control. Visual predator stimuli consisted of to-scale images of the different predator types (i.e., polar bear and arctic fox) attached to 54-inch diameter grey umbrellas, with an additional plain, grey umbrella to serve as the control (Figure 2.4). Images of a polar bear (approx. 16 in. long and 18 in. wide head, body sizes proportional to head, Figure 2.4A) and arctic fox (approx. 6 in. long and 5 in. wide head, body sizes proportional to head, Figure 2.4B) were sourced on the internet from Creative Common websites. Each umbrella had a round slit covered with dark-coloured mesh so that the experimenter could locate the study hen and monitor their behaviour during an approach without eiders being able to see the experimenter. We randomly assigned the order in which the treatment groups were presented to each study hen prior to the experiment using the RANDBETWEEN function in excel to control for possible habituation or sensitization. Each study eider was approached three times (i.e., once by each predator treatment) at 24-hour intervals from June 26-28, 2019. Every eider was presented with the same within-predator imagery to ensure they were responding to identical visual cues. In preparation for each experimental approach, a single experimenter (E.A.G.), wearing camouflaged and nonreflective gear, crawled into the colony until they reached the location at which they planned to start the approach. Approaches began on average ± SD 22.3 ± 5.26 meters (range 15-33 m) from the study nests (i.e., distances at which the experimenter could spot the nest without disturbing the bird). If focal eiders were absent from their nest prior to an approach, treatments for these individuals were excluded from the experiment (see *Results*). During each approach, a hand-held recording device was used by the experimenter to dictate all necessary data. To start the approach, the experimenter dictated the start time and slowly opened the umbrella, stood up, and began walking towards the study nest concealed behind the umbrella at a consistent pace of approximately 0.5 mps, making sure to keep the predator stimuli upwards and facing the study hen. The experimenter also dictated the time of flush to confirm that the heart-rate interval of 30 seconds prior to flush (see *Heart rate quantification* below) overlapped with when the eider was exposed to the predator stimulus. The experimenter then used a tape measure to measure the distance between the experimenter and the nest as soon as the hen vacated in response to the threat stimuli (i.e., FID). When the experimenter missed flushes by focal hens, we excluded the trial from our analysis of FID (see *Results*). The experimenter recorded clutch size (number of eggs, including the artificial egg) after each approach. When all necessary data were recorded, the experimenter covered the nests with down before departing the area to protect the nest from predation by avian predators and extreme temperature. Neighbouring focal nests were tested sequentially with a minimum of 11 minutes (average ± SD: 22 ± 16 minutes) between approach starting times. Cabanac and Guillemette (2001) observed elevations in eider heart rates to acute stressors subsided after 2-3 minutes only; thus, given both the temporal and spatial distances between nests, we do not believe nearby approaches influenced responses of subsequent focal birds. Due to the topography of the island, all other researchers were out of sight by the focal eider during the period they were undergoing an experimental approach.

Heart rate quantification

A single researcher (E.A.G.) reviewed heart rate recordings of eiders using the sound analysis software Audacity® v2.3.2 (Audacity Team 2019). When reviewing heart rate during the predator-approaches, the researcher collected data on datasheets that did not specify treatment for each sample so that they were blind to the treatment. For measures of heart rate during the simulated-predator approaches, we collected up to three 10-s samples from each eider during each experimental approach (e.g., Figure 2.5). Sampling started 30-s before the hens flushed from the predator stimuli, and heartbeat counts at different sample intervals allowed us to quantify how heart rate varied as the predator stimuli approached the incubating eider and the eider got closer to flushing (i.e., time before flush). Not all study hens had audio files with enough sound quality to accurately determine heart rates for each experimental approach, resulting in different sample sizes for each bird exposed to each predator treatment (i.e., predator stimuli type) (see *Results*). We extracted all of the samples as .wav files and heartbeat sounds were counted aurally at least twice to avoid measurement error and therefore increase accuracy of the counts.

Estimating incubation stage

To estimate incubation stage (i.e., the number of days since an eider laid their first-laid egg) for each focal hen, the first-laid egg from each study nest was collected and eggs were immediately candled (Weller 1956). These methods provided estimates of the age (in days) of the first-laid eggs on the day of heart-rate monitoring equipment deployment, and hence incubation stage on the days of simulated-predator approach.

Eider responses to natural polar bear predation

We also opportunistically estimated focal eider heart rate to actual approaching polar bears on Mitivik Island where possible to confirm responses to our simulated predator were similar to those to actual predators. To find instances where eiders flushed in response to polar bears, we reviewed a combination of the following synchronized remote-monitoring equipment used for another set of projects: 1) footage from Browning trail cameras (model: BTC-5HDPX) dispersed across the island to identify periods when polar bears were present on Mitivik Island (see *Chapter 3* for more details on polar bear monitoring and defining polar bear locations in relation to common eiders); 2) temperature probe data (Tinytag® Plus 2, Smith and Love. in prep) to determine instances when an eider was off her nest; and 3) heart-rate recordings during these times to identify acoustic signs that an eider had indeed vacated their nest (e.g., halt in the sound of incubating eider heartbeats) and a polar bear visited their nest (e.g., sounds of bear eating eggs from focal nest or breathing nearby). We confirmed four instances where focally-recorded eiders flushed in response to a polar bear, one of which had insufficient audio quality to count heartbeats before flush and was therefore excluded. Of the three remaining flushing instances, two hens had bears predate their nests closely after she flushed and we can confirm that bears were within spatial viewing distance to two eiders when they flushed (i.e., were within her viewshed; *Chapter 3*). Additionally, bears arrived at the nest quickly after eiders flushed in all three instances (average ± SD: 9.33 ± 3.25 sec), suggesting eiders flushed in response to bears. We estimated heart rate 30 seconds before eiders flushed in three, 10-second intervals consistent with the sampling of heart rate to simulated-predator approaches (see *Heart rate quantification* section).

Statistical analyses

Nine of our 11 study eiders produced usable heart rate data, five of which had complete data across treatment groups and sampling time. For our FID analysis, three individuals were excluded due to focal hens not being present at their nest at the start of the experimental approach or flushes by focal hens were missed by the experimenter, and of the remaining, three individuals had incomplete data across treatment groups.

We performed all analyses in R v3.5.0 (R Core Team 2018), with an RStudio interface (RStudio Team 2019). All data manipulation was done with packages *dplyr* (Wickham et al. 2019) and *tidyverse* (Wickham 2017). We tested model residuals with visual inspection of diagnostic Q-Q plots (Pinheiro and Bates 2000). We used $\alpha = 0.1$ for all statistical significance tests. We constructed all plots of predicted response variables, calculated under the package *ggeffects* (Lüdecke 2018), under the package *ggplot2* (Wickham 2016).

We analysed both eider heart rate (beats/10s) and flight initiation distance (m) (hereafter, "FID") to simulated-predator approaches separately using linear mixed models (LMMs), with the *lmer4* package (Bates et al. 2015). We modelled heart rate as a function of the fixed effects for predator treatment (categorical with 3 levels: polar bear, arctic fox, control), time before flush (continuous: 0-10s, 10-20s, and 20-30s before flush), and start distance (m) (continuous) and their two-way interactions: predator treatment x time before flush interaction, predator treatment x start distance interaction, and time before flush x start distance interaction. We modelled eider FID as a function of predator treatment (categorical with 3 levels: polar bear, arctic fox, control), heart rate (beats/10s) (continuous) at the 30s interval before flush, start distance (m) (continuous), incubation stage (days) (continuous), clutch size (continuous), and the interaction between predator treatment and heart rate. We chose heart rate at the 30s interval before flush because it had the most complete dataset. We tested incubation stage and clutch size in our model of FID as Forbes et al. (1994) discovered an effect of parental investment on nesting female duck FID. Start distance was included in analysis of FID and heart rate, since results from Blumstein's (2003) study suggest animals respond sooner to a threat as starting distance increases. For both analyses, we included trial day (categorical with 3 levels: June 26, June 27, June 28) and eider ID (categorical: 9 individuals) in our random effect structure to account for habituation or sensitization and any inter-individual variation, respectively. We tested fixed effects using a backward elimination procedure by fitting full models for heart rate and FID with maximum likelihood (ML) estimation (Zuur et al. 2009). Main effects and interaction terms were tested sequentially (beginning with the removal of non-significant interactions) using the backward elimination procedure, leaving in the final model only the fixed effects associated with the outcome, considering a 10% level of significance, being a standard retention criterion for backward elimination (Bursac et al. 2008). The final model with retained fixed effects was refitted using restricted maximum likelihood (REML) estimation, and the effect of any retained categorical variables on both eider heart rate and FID was determined with pairwise comparisons using Tukey's HSD in the *lsmeans* package (Lenth 2016). We reported contributed variance of random factors in our final models. Using the package *MuMIn* (Bartoń 2019)*,* we assessed the variance explained by the fixed effects (i.e., marginal R^2) and the variance explained by the entire model, including both fixed and random effects (i.e., conditional R^2) for both our final heart rate and FID models. We assessed model fit by comparing second-order Akaike Information Criterion (AICc) scores between all competing models in the backward elimination process (ML estimation), as well as an intercept-only model, using the package *MuMIn*.

Results

Heart rate ranged from 3 beats/10s to 39 beats/10s (average 18 beats/10s) to control, 6 beats/10s to 49 beats/10s (average 23 beats/10s) to arctic fox, and 2 beats/10s to 26 beats/10s (average 13 beats/10s) to polar bear. Our model with heart rate as a function of predator treatment and time before flush (marginal $R^2 = 0.063$, conditional $R^2 = 0.901$, Table 2.1) best explained our data according to our backward elimination approach, as well as it had the best model fit according to AICc (Table 2.3). In this model, we detected a statistically significant difference in eider heart rate in response to the predator treatment ($F_{2,50.40} = 15.22$, $P < 0.001$), with eiders displaying a significantly higher heart rate in response to the arctic fox model, than to both the control (Tukey's HSD: $P<0.0027$) and polar bear model ($P<0.0001$; least square [LS] means ± SE heartbeats: control 16.3 ± 4.40; arctic fox 21.2 ± 4.37; polar bear 13.5 ± 4.40). There was no significant difference in heart rate between the polar bear stimulus and the control ($P=0.1265$). Additionally, we detected a statistically significant change in heart rate with time before flush ($F_{1,49.93} = 4.89$, $P < 0.05$): regardless of predator type, eider heart rate decreased the closer to flush (Figure 2.6; Table 2.1). There was no interactive effect of predator treatment and time before flush on heart rate, predator treatment and start distance, or start distance and time before flush. There was also no significant effect of start distance. Within our random effects structure, we detected the most variance for eider ID (Table 2.2), suggesting a large degree of inter-individual variation in heart rate.

FID ranged from 2.95 m to 17.7 m (average 9 m) to control, 3.2 m to 15.1 m (average 7.9 m) to arctic fox, and 1.3 m to 9.3 m (average 6.2 m) to polar bear. Heart rate at the 30s interval before flush ranged from 3 beats/10s to 46 beats/10s (average 20 beats/10s). Incubation stage ranged from 2 days to 16 days (average 6 days) and clutch size ranged from 3 eggs to 5 eggs (average 4 eggs). Our model with FID was best explained as a function of heart rate (marginal $R^2 = 0.139$, conditional $R^2 = 0.764$, Table 2.4). In this model, we detected a marginally significant relationship between FID and heart rate during experimental approaches ($F_{1,18.295} = 3.21$, $P < 0.1$), where higher heart rates predicted larger FIDs (Figure 2.7). There was no significant relationship between FID and predator treatment, clutch size, incubation stage, or start distance, and there was no significant interaction between predator treatment and heart rate. According to AICc, the final model received equal support to the intercept-only model (Table 2.6), in that variation in FID can also be explained by our random effect structure, namely, eider ID (Table 2.5), again suggestive of a large degree of inter-individual variation in behaviour.

Eider heart rate in response to actual polar bears on Mitivik Island (n=3) averaged 12 beats/10s and generally decreased as eiders got closer to flushing: two eiders' heart rate became continuously slower with reduced time before flush (i.e., across 30-10s sample intervals: 12 to 10 to 8 and 11 to 9 to 5 beats/10s), whereas one initially increased their heart rate followed by a decrease right before flush (i.e., 9 to 28 to 12 beats/10s). These heart-rate results help to confirm that eider responses to a simulated polar-bear approach is indicative of a natural response as eiders exhibited a similar pattern of decrease in heart rate and the same magnitude of response.

Discussion

In the current experimental study, incubating female eiders showed differential stress-induced heart rate responses to predator imagery that differ in evolved familiarity (i.e., arctic fox versus polar bear), but birds did not show differential flight initiation distance (FID) responses across predator stimuli. We also found a large degree of inter-eider variation in heart rate and especially FID responses. Overall, these results suggest that female eiders do not recognize polar bears as great of a physiological threat as their evolved mammalian egg predators. Here we discuss what our results might suggest for eiders' capacity to respond to their more recent primary egg predators, and detail possible fitness costs and downstream population effects from this climate-induced increase in polar-bear nest predation.

Differential heart-rate responses to evolved predators

Using an experimental approach, we tested whether female eiders perceive the risk posed by polar bears. Given eiders' limited evolutionary experience with polar-bear egg predators and bears' archetypal differences with eiders' traditional mammalian egg predators, we hypothesized that eiders would exhibit differential alteration in their heart rate to approaching bears and arctic foxes. We found that although all hens eventually flushed to the approaching stimulus regardless of imagery, incubating female eiders responded with higher heart rates when experimentally approached by an arctic-fox stimulus compared to a polar bear (and control). Eiders could have reacted to the experimental predation threat in two opposing ways: 1) by using an active defense strategy associated with the fight-or-flight response, whereby vertebrates increase heart rate, ventilation and skeletal muscle circulation in preparation for flight; or 2) by using a passive defense strategy, whereby in an effort to remain concealed and avoid detection, vertebrates slow their heart rate, which can be associated with a decrease in respiration and metabolic rate that may reduce movements, sounds, and/or scents coming from the body that could be detected by some predators (reviewed in Gabrielsen et al. 1977, Steen et al. 1988, Knight and Temple 1997, Alboni et al. 2008, Löw et al. 2008). We observed that eider heart rates generally decreased immediately prior to flushing regardless of the stimulus. This heart rate response is suggestive of fear bradycardia commonly observed in nesting bird species that use concealment as a predator-avoidance strategy (Campbell et al. 1997) and is therefore not a surprising response given female eiders' cryptic camouflage and nesting strategies. Further, even as eiders went into bradycardia, they still exhibited a comparatively heightened heart rate response to arctic foxes suggesting a stronger evolutionary recognition and response to these mammalian predators. While some avian species respond with an acceleration in heart rate to a looming threat (i.e., tachycardia in conjunction with fight-or-flight; e.g., herring gull *Larus argentatus*, Ball and Amlaner 1979; Yellow-eyed penguin *Megadyptes antipodes*, Ellenberg et al. 2013), other species are known to use both active and passive defense strategies in temporal order and pattern of response (e.g., bradycardia preceded by acceleration of HR; e.g., red deer calves *Cervus elaphus,* Espmark and Langvatn 1979; reviewed in Alboni et al. 2008). Similar to eiders, Gabrielsen et al. (1977) found a small sample of willow ptarmigan (*Lagopus lagopus*) hens examined in their study maintained bradycardia right up until the point of flush, suggesting that both tachy- and bradycardia are likely adequate mechanisms for quick flight.

Similar FID to predators, despite differential recognition

We predicted that eiders would display a shorter FID to polar bears than arctic fox, and therefore a lower perception of risk given limited co-evolutionary time. We found that although eiders may differentially recognize an arctic fox and polar bear as a threat physiologically, eiders did not display a difference in FID between the two predator stimuli. Once a potential predator is detected, animals will often delay their fleeing until the benefits of fleeing equal the costs (Fernández-Juricic et al. 2002). Our results do not support the literature on economics of flight that suggests animals should flush sooner to increasing levels of predation risk (Ydenberg and Dill 1986, Cooper and Frederick 2007) and should therefore display a longer FID to predators that they can recognize as dangerous (reviewed by Guiden et al. 2019). We did, however, detect a link between stress-induced physiology and behaviour in response to threat stimuli; birds in our study that had a higher heart rate to approaching predators were more likely to have longer FIDs. This correlation is consistent with the two response strategies that animals employ when reacting to challenges (i.e., active vs passive defense strategies), whereby eiders that had higher heart rates at 30s prior to flush (and likely relatively higher sympathetic reactivity) may have focused on escape sooner, whereas those that had lower heart rates (and potential higher parasympathetic reactivity) likely focused more on avoiding detection and thus delayed the activation of the flight response (reviewed in Gabrielsen et al. 1977, Steen et al. 1988, Knight et al. 1997, Alboni et al. 2008). Based on this correlation, we would expect eiders to have the longest FID to foxes, for which they displayed the highest heart rate. However, we failed to detect such a behavioural response in the current study. It is possible that while there is an association between heart rate and behaviour, these mechanisms can also be independently regulated, and flight initiation distances may be more of an ecological, immediate response to any approaching threat. Most likely, because of the large degree of inter-eider variation in flight initiation distances, we require a larger sample size to detect this expected effect of predator treatment on FID.

Future directions in studies of seabird responses to predation risk

Eiders have a history of experience interacting with arctic foxes over both evolutionary and ecological timescales (Waltho and Coulson 2015). From an eco-evolutionary perspective, eiders have therefore gained heritable experience within their traditional biotic interactions during breeding (e.g., egg predation by arctic foxes), that, depending on their ecological similarity, may be applicable to new ecological interactions outside their traditional range (e.g., polar bear egg predation on islands). The current study was designed to causally test eiders' ability to discriminate between visual cues of predators that differ in evolved familiarity. From this perspective, our heart rate results suggest visual cues of arctic foxes may be more indicative of a threat than that of a polar bear visual stimulus, indicating that eiders' eco-evolutionary experience with foxes is not fully transferable to their interactions with polar bears. However, our behavioural metric for perceived risk did not add further support to our physiological findings. Nonetheless, there remains many avenues of important future research to build off of these findings. For instance, prey use multiple cues, including sensory and behavioural ones to assess a risk (reviewed in Peers et al. 2018) and the additive effects of these cues can evoke an increased antipredator response (e.g., Eastern grey squirrel *Sciurus carolinensis*, Partan et al. 2009). Our study should therefore be complemented by a correlative study on eider responses to real predators to increase our understanding of individual antipredator responses that would be displayed in natural conditions. Further, whereas eiders have evolutionary experience with arctic foxes, female eiders display high breeding philopatry and nest-site fidelity (Öst et al. 2011), and females nesting on islands further from the mainland may have less ecological experience with foxes than eiders that nest nearer or on the mainland (Birkhead and Nettleship 1995). Thus, as suggested above, eider FID may not be differentially influenced by predator type, as eider hens with fewer arctic-fox encounters may exhibit responses diminished over ecological (reviewed in Carthey and Blumstein 2018) or ontogenetic time (Carrete and Tella 2015) on far-island colonies (such as the Mitivik Island colony). Thus, we predict that eiders that breed on mainland nesting sites and near-shore islands would not only be even more responsive to arctic fox, but also may be more likely to show an FID response to polar bears that differs from controls (i.e., indicative of some level of cue discrimination abilities), assuming eiders' ecological experience with foxes and other mammalian egg predators is transferrable to their responses to polar bears. Future studies can focus on these different eider colonies in the Canadian Arctic to determine if degree of ecological experience with mammalian predators affects eiders' ability to respond to their evolutionarily less familiar egg predator, the polar bear.

In the current study, eiders showed inter-individual variation in heart rate and FID responses to simulated predator approaches. In future work of this type, a larger sample size would allow for repeated predator approaches on each individual using the same models to examine repeatability in eider responses. Repeatability can provide evidence that among-individual variation is caused by factors intrinsic to the individual (Réale et al. 2007), and thus can help determine whether eider FID is a valid personality trait (e.g., Seltmann et al. 2012, 2014), or whether heart rate and FID are phenotypically related to proactive or reactive coping styles in eiders (Koolhaas et al. 1999). These different coping styles offer different adaptive value, and individuals with highly plastic capacities, such as reactive phenotypes, are predicted to perform better to changes in their environment than proactive phenotypes (characterized as being less flexible) (Sadoul et al. 2020). Thus, by understanding the extent to which inter-eider responses are consistent across time and situations, and how these responses relate to coping style, we can make predictions on the adaptive capacity of different groups of individual eiders to respond to changes in predator regimes.

Conclusion

Consequences of novel or increasing frequency of rare predators on prey fitness are challenging to predict (Guiden et al. 2019). The similarities in heart rate response of eiders to bear and control could reflect the limited discriminative ability of eiders to polar bear predation. Our heart rate data suggesting that eiders may not recognize polar bears as great a risk as arctic foxes (but still a risk, nonetheless) provides evidence that eiders may be vulnerable to strong consumptive effects of predation by polar bears (Sih et al. 2009). Although eiders in the current study attempted to escape from all approaching stimuli, our lack of statistical difference in behavioural escape response to polar bears in comparison to other stimuli, coupled with our heart-rate results, reveal eiders do not recognize the serious threat bears pose to their eggs and themselves. Eiders' use of an inappropriate or insensitive heart rate and escape responses can lead to consequences on adult survival or nest success (e.g., eider flushing may cue polar bears to detect their nest, Jagielski et al. 2021a). By collecting experimental data on how animals behave in response to the uncertainty posed by recent predation by rare predators, future research can use optimal decision-making models (e.g., signal detection theory) to determine whether these responses are (mal)adaptive, and thereby estimate fitness outcomes and population persistence (Sih 2013, Trimmer et al. 2017). Data from the current study can therefore be used as a first step to characterizing whether eiders are expected to have the capacity to evolve adaptive responses to increasing polar bear predation.

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Tables

Table 2. 1. Model parameter estimates and standard error for fixed effects used to explain variation in heart rate among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Estimate ± SE**
Intercept	13.276 ± 4.61
Polar bear	-2.758 ± 1.39
Arctic fox	4.917 ± 1.39
Time before flush	0.149 ± 0.07

Reference category = Control treatment

Table 2. 2. Model parameter variance and standard deviation for random effects used to explain variation in heart rate among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Variance ± SD**
Eider ID	155.214 ± 12.46
Trial day	2.847 ± 1.69
Residual	18.681 ± 4.32

Table 2. 3. Predicting common eider (*Somateria mollissima*) heart rate (beats/10s) based on AICc model selection (ML estimation). Models included here were used in a backward stepwise regression until significant effects remained (via ML estimation). AICc weight represents the relative likelihood of a model. Models are sorted by weight from most likely to less likely. The null model is represented by "heart rate ~ 1"

Model	df	AIC_c	ΔAIC_c	w_i
Heart rate ~ predator treatment + time before flush	7	419.7	0.00	0.674
Heart rate ~ predator treatment + time before flush + start distance	8	422.3	2.59	0.184
Heart rate ~ predator treatment + time before flush + start distance + predator treatment*start distance	10	424.0	4.28	0.079
Heart rate ~ predator treatment + time before flush + start distance + predator treatment*start distance + time before flush*start distance	11	424.7	4.99	0.055
Heart rate ~ predator treatment + time before flush + start distance + predator treatment*start distance + time before flush*start distance + predator*time before flush	13	428.7	9.00	0.007
Heart rate ~ 1	4	440.1	20.33	0.000

Table 2. 4. Model parameter estimates and standard error for fixed effects used to explain variation in flight initiation distance among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Estimate ± SE**
Intercept	5.635 ± 2.07
Heart rate	0.141 ± 0.08

Table 2. 5. Model parameter variance and standard deviation for random effects used to explain variation in flight initiation distance among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Variance ± SD**
Eider ID	13.239 ± 3.64
Trial day	0.800 ± 0.89
Residual	5.289 ± 2.30

Table 2. 6. Predicting common eider (*Somateria mollissima*) flight initiation distance (m) (FID) based on AICc model selection (ML estimation). Models included here were used in a backward stepwise regression until significant effects remained (via ML estimation). AICc weight represents the relative likelihood of a model. Models are sorted by weight from most likely to less likely. The null model is represented by "FID ~ 1"

Model	df	AIC_c	ΔAIC_c	w_i
FID ~ 1	4	129.4	0.00	0.437
FID ~ heart rate	5	129.5	0.11	0.414
FID ~ heart rate + clutch size	6	131.9	2.43	0.130
FID ~ heart rate + incubation stage + clutch size	7	135.7	6.27	0.019
FID ~ predator treatment + heart rate + incubation stage + clutch size	9	144.3	14.84	0.000
FID ~ predator treatment + heart rate + start distance + incubation stage + clutch size	10	151.3	21.83	0.000
FID ~ predator treatment + heart rate + start distance + incubation stage + clutch size + predator treatment*heart rate	12	168.5	39.08	0.000

Figures

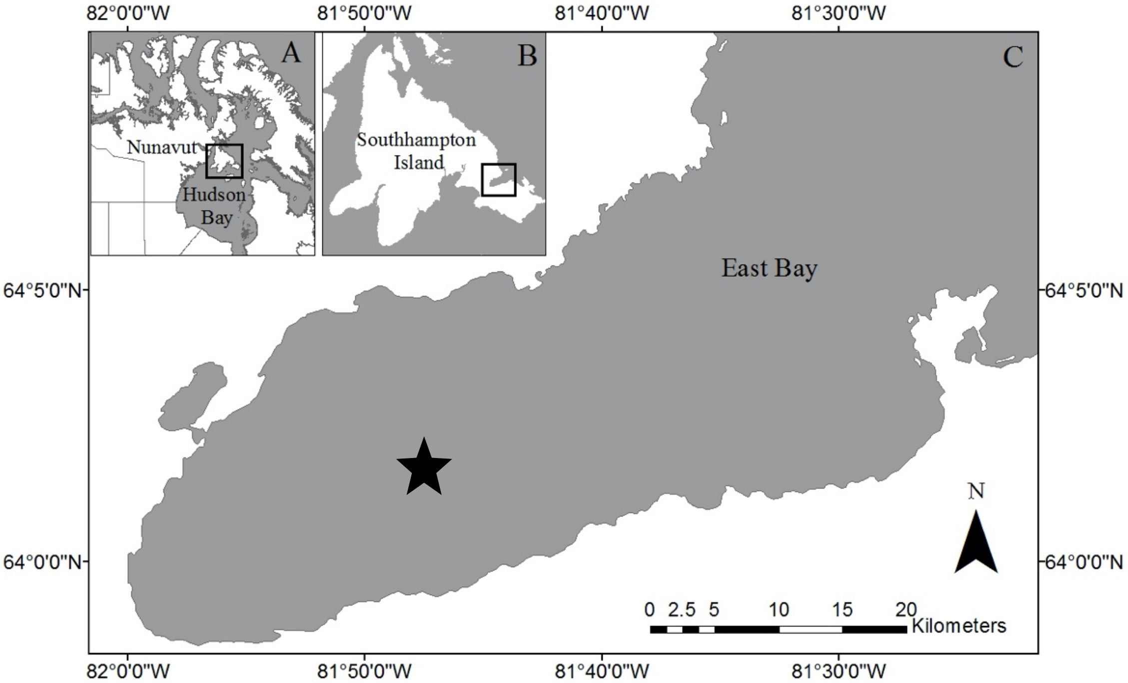

Figure 2. 1. Map of Study Area, displaying our A) general location (Northern Hudson Bay, Nunavut, Canada), B) regional location (Southampton Island, Nunavut, Canada), and C) study site (Mitivik Island, represented by a star) within East Bay, Nunavut, Canada. Canadian Provinces and Territories map layers provided by ESRI online, accessed May 30, 2018

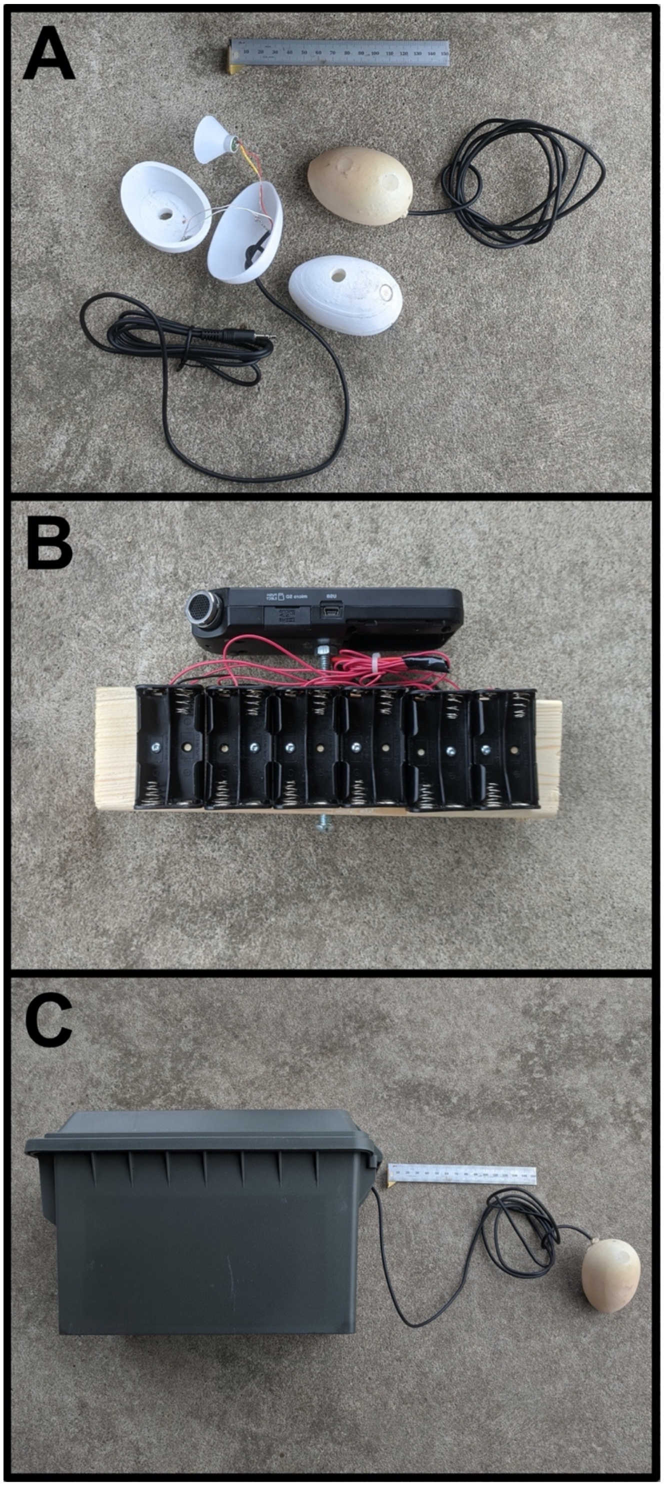

Figure 2. 2. Experimental heart rate recorders, with photographs of A) separate halves of 3D-printed common eider (*Somateria mollissima*) egg, microphones, and funnel (left), two halves of plastic 3D-printed egg assembled (bottom right), artificial eider egg covered with a balloon membrane (top right), B) digital audio recorder (Tascam DR-05X) and external battery pack, and C) storage box and artificial-egg, ready for deployment

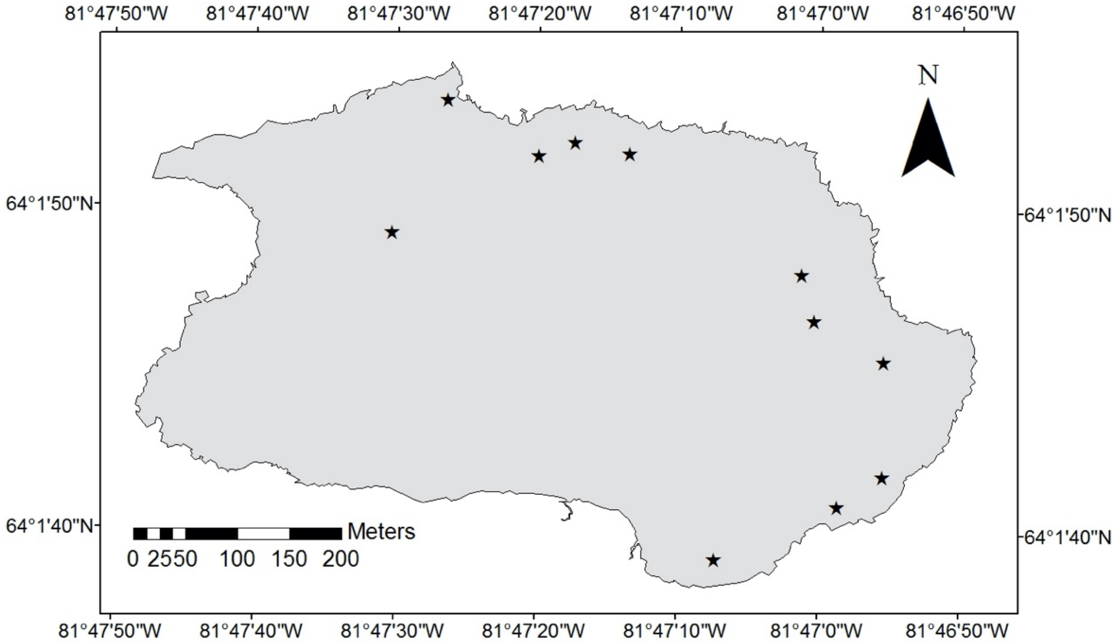

Figure 2. 3. Distribution of focal nests (black stars) across Mitivik Island, Nunavut, Canada. Map layer created using ArcMap v10.6.1 (Esri, Redlands, CA, USA)

Figure 2. 4. Images of our experimental predator stimuli: 54-inch diameter grey umbrellas with to-scale images of A) polar bear, B) arctic fox, and C) plain for control. Images include approximate measurements (width and length) of the animal's head. Images sourced on the internet from Creative Common websites

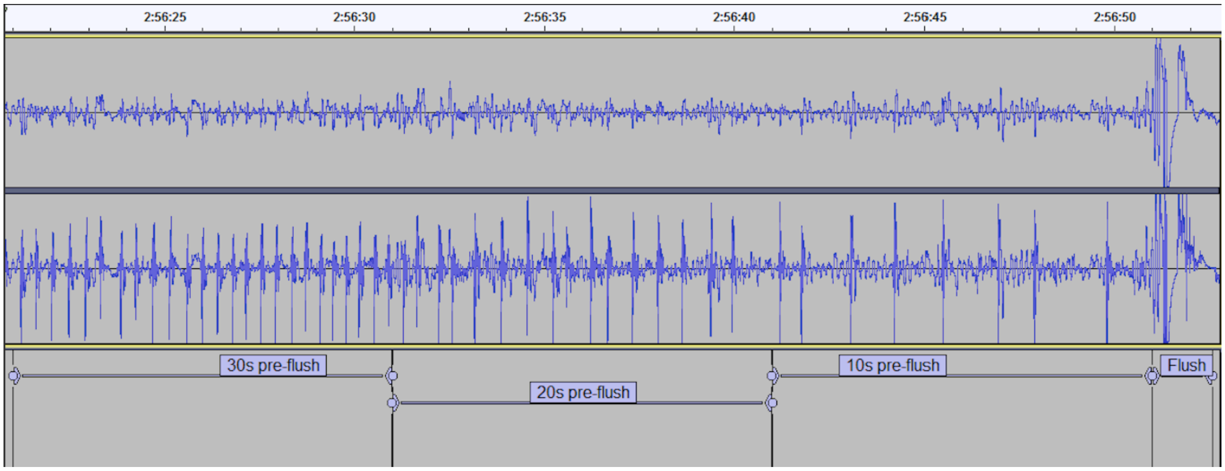

Figure 2. 5. Screenshot of the waveforms from heart sounds produced by an incubating focal common eider (*Somateria mollissima*) in Audacity® v2.3.2 (Audacity Team 2019). At the end, hen flushes, and heart beats were counted for three 10 second intervals before the hen flushed

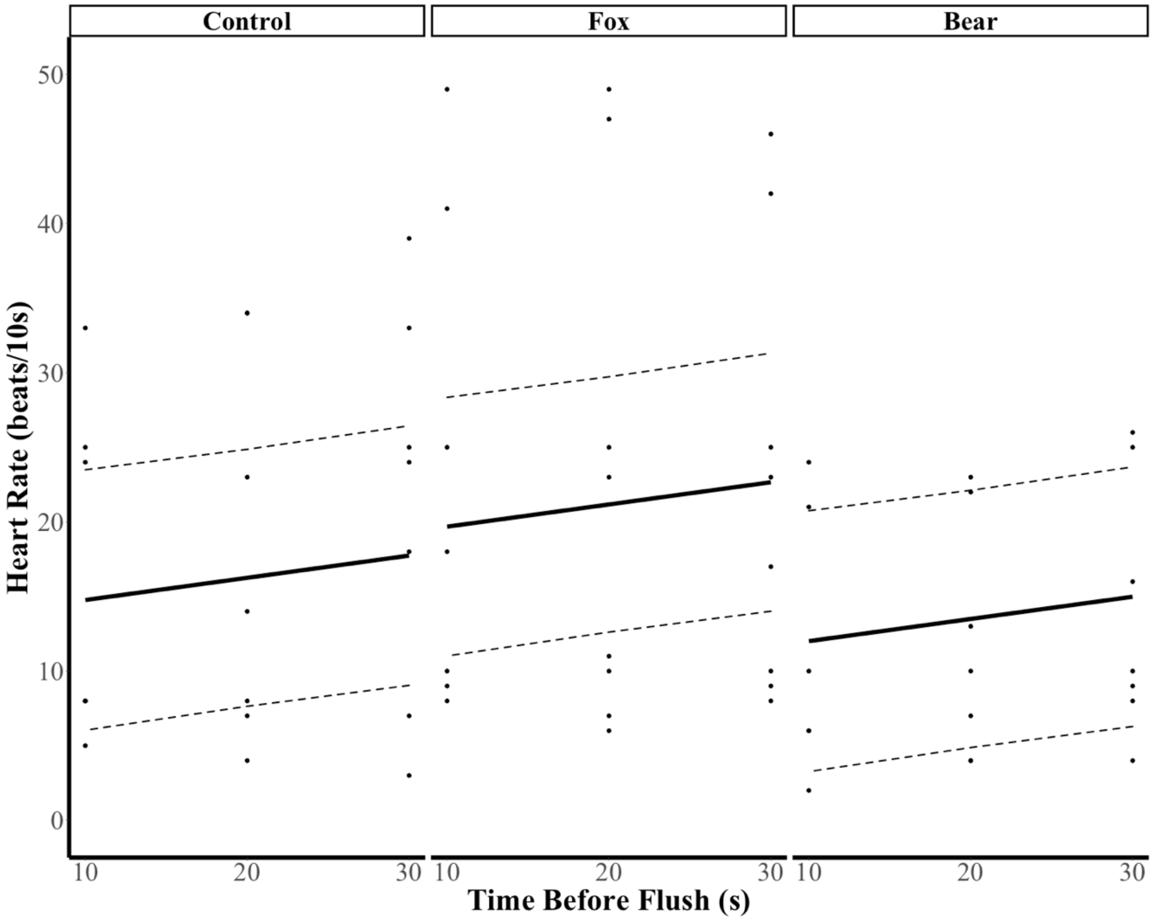

Figure 2. 6. Incubating female common eider (*Somateria mollissima*) heart rate (beats/10s) depending on time before flush (s), for each predator treatment. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

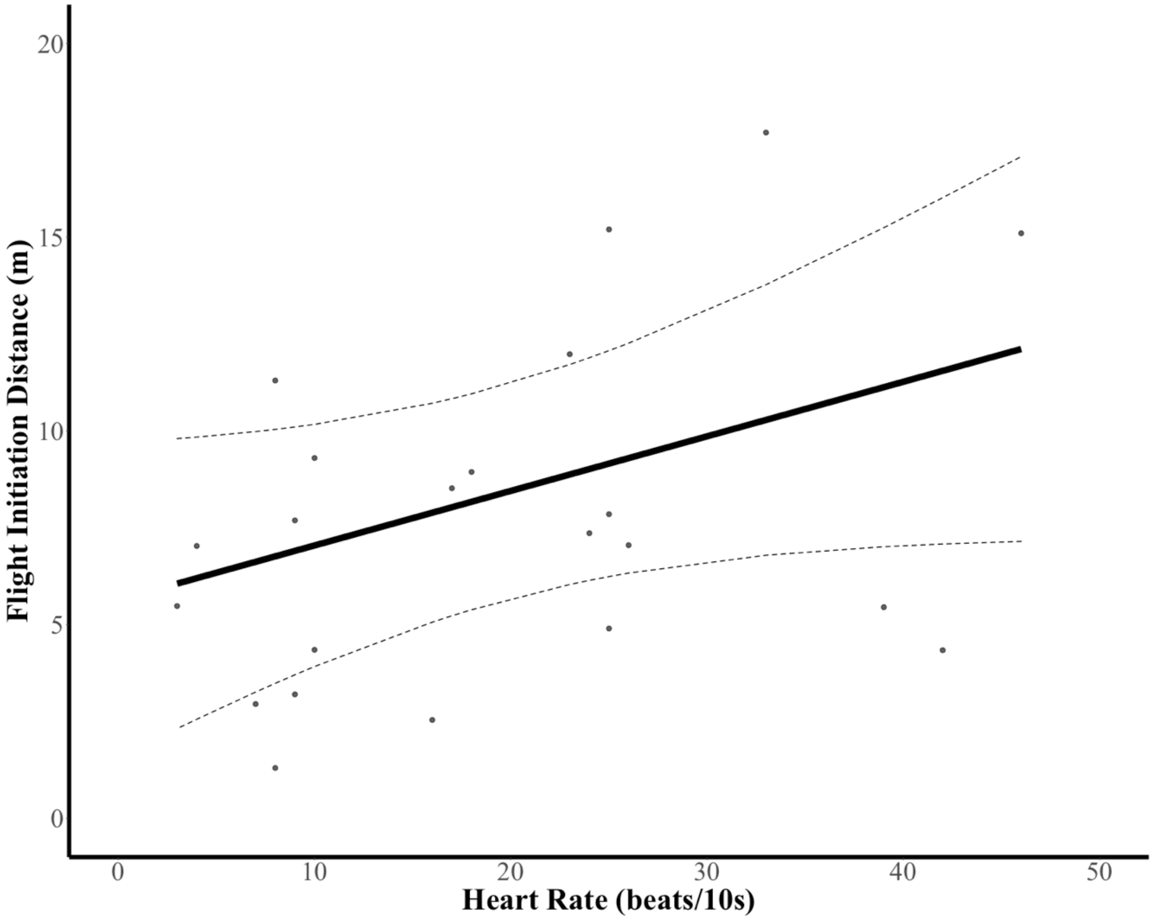

Figure 2. 7. Incubating female common eider (*Somateria mollissima*) flight initiation distance (m, FID) in response to eider heart rate (beats/30s) during experimental approaches by simulated predator. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

CHAPTER 3

Arctic colonial-nesting seabird heart rate responses to natural variation in threat of polar bear egg predation

Introduction

Rapid environmental change is impacting inter-specific relationships across multiple ecosystems worldwide (Tylianakis et al. 2008). Specifically, changes in phenology of seasonal life history events (Parmesan and Yohe 2003, Thackeray et al. 2010) or distribution (Parmesan and Yohe 2003) can create new species relationships or exacerbate existing interactions between antagonistic species, such as between predator and prey (reviewed in Gilman et al. 2010). A prey's experience with a predator on both evolutionary and ecological timescales influences their ability to detect and respond adaptively to the threat posed by the new/historically rare predator (Carthey and Blumstein 2018). Indeed, prey that lack (or have limited) eco-evolutionary experience with a predator are expected to suffer direct (i.e., consumptive) and/or indirect (i.e., non-consumptive) effects associated with their response (Sih et al. 2009). Thus, understanding whether prey can detect and appropriately assess the risk posed by a predator with which they have limited evolutionary and/or ecological experience can provide insight into whether they are expected to suffer fitness costs as a result of increased frequency in interactions.

An animal's ability to respond adaptively to a predation threat depends, in part, on their capacity to recognize the level of predation risk the predator poses and adjust their responses accordingly (i.e., dynamic risk assessment, Kleindorfer et al. 2005). For instance, upon detection of a predation threat, an animal's perception of risk may be further based on characteristics of the interaction such as their distance from and duration of exposure to the predator (e.g., Kleindorfer et al. 2005, Ellenberg et al. 2013). Animals use distance from a threat as a measure of predatory imminence, and regulate their trait responses based on perceived likelihood of detection and capture by the predator (Löw et al. 2008). Prey can exhibit passive defense responses (e.g., freezing and/or vigilance behaviour, and decelerated heart rate) until a threshold distance is reached and predation is perceived as impending, at which point prey typically switch to a fight-or-flight response (e.g., higher vigilance, blood circulation to gross muscles, and accelerated heart rate) (reviewed in Gabrielsen and Smith 1997). An animal's response to the threat of predation can furthermore be influenced by the amount of time prey are in the presence of a predator (i.e., exposure duration). For example, exposure duration of a threat stimulus influences the stress response (e.g., king penguin *Aptenodytes patagonicu*s, Viblanc et al. 2012; yellow-eyed penguin *Megadyptes antipodes*, Ellenberg et al. 2013), where a higher duration of interaction is associated with a greater risk of detection and capture. The magnitude of this exposure time will be further impacted by the availability of visual information – the range at which visual cues are likely to be informative and used by prey to assess threats (Aben et al. 2018). Influenced by the spatial structure of the environment such as topography and cover (Magaña et al. 2010) or environmental conditions (e.g., water turbidity) (Meager et al. 2006), any information deficit resulting from a small spatial visibility range will also play a role in risk perception and affect prey responsiveness. Taken together, the longer amount of time a predator spends within a prey's limited 'area of visibility', the greater the effect on dynamic risk assessment and exacerbated real and perceived risk.

Assessing an animal's perception of (dynamic) predation risk can be accomplished via evaluating antipredator responses (e.g., Löw et al. 2008, Ellenberg et al. 2013, Schneider and Griesser 2013, Lamanna and Martin 2016, Creel et al. 2017, Buitron 2019, Peacor et al. 2020) such as vigilance levels (reviewed in Beauchamp 2017) and escape responses (e.g., the distance at which animals flee from a threat) (reviewed in Ydenberg and Dill 1986). Because both traits are responsive to the degree of predation risk, they are commonly used as behavioural markers of risk perception (e.g., Blumstein 2003, Stankowich and Blumstein 2005, Creel et al. 2017). However, in some cases prey may display a physiological response to threat without exhibiting visually observable signs. In addition, animals may even exhibit signs typically associated with antipredator behaviour (e.g., vigilant posture or fleeing) in the absence of threat (e.g., seemingly vigilant individuals are actually searching for food, Beauchamp 2017). Physiological measures, such as the release of stress hormones and changes in heart rate, provide an alternative objective evaluation of fear in animals (Adolphs 2013, Ellenberg et al. 2013), and are suggested to underly an animal's level of perceived predation risk (reviewed in Hawlena and Schmitz 2010). Modulation of heart rate is considered to be an immediate fear response to the detection of acute predation risk: both sympathetic (i.e., acceleratory influence) and parasympathetic (i.e., deceleratory influence) branches of the autonomic nervous system that mediate heart rate are activated within seconds following the perception of a threat (Löw et al. 2008, Carravieri et al. 2016). Magnitude and duration of change in heart rate from baseline can therefore be used as metrics for perceived level of predation threat across variation in realized predation risk.

Here we assess whether incubating female common eider seaducks (*Somateria* *mollissima*, hereafter ‘eider’) perceive the risk posed by polar bears (*Ursus maritimus*) on a small-island breeding colony in Nunavut, Canada, using non-invasive methods to both measure physiological responses and detect bear presence. Over the past few decades, there has been increasing spatial overlap between incubating colonial-nesting seabirds and polar bears on land as a result of rapidly advancing sea-ice breakup relative to climate-induced advancement in bird nest initiation and hatch (e.g., snow goose *Chen caerulescen*, Rockwell and Gormezano 2009, Rockwell et al. 2011; common eider, Iverson et al. 2014). As a consequence of this recent phenological match, polar-bear egg predation in eider and other Arctic breeding seabird colonies has steadily and rapidly increased in the past few decades (e.g., snow goose and thick-billed murre *Uria lomvia*, Smith et al. 2010; common eider, Iverson et al. 2014; barnacle goose *Branta leucopsis* and glaucous gull *Larus hyperboreus*, Prop et al. 2015) as a substitute to bears’ reduced spring diet (Stirling et al. 2004, Stirling and Parkinson 2006). Colonial island-nesting eiders have evolved several adaptations to reduce predation by their traditional land-based mammalian egg predators (primarily arctic fox *Vulpes lagopus*) by nesting on islands either inaccessible to foxes or attached via ephemeral ice with unpredictable ice breakup making them risky for foxes to visit (Larson 1960, Ahlén and Andersson 1970); and by forming high-density nesting aggregations for communal defense and predator warning (Schmutz et al. 1983, Mehlum 1991). Although eiders have evolutionary experience with some mammalian egg predators, it can be assumed they have limited experience with polar bears since their adaptations do not deter polar bears that can access islands during eider nesting periods (i.e., by inter-island swimming; Pagano et al. 2012), and bear presence in eider nesting colonies has been positively correlated with nest abundance (Iverson et al. 2014). Whether eiders, a long-lived seaduck (Waltho and Coulson 2015), recognize the threat posed by polar bears (Carthey and Blumstein 2018) and thus have the adaptive capacity to keep pace with this rapidly increasing risk of egg predation is unknown. Using a remotely deployed heart-rate monitoring system, we actively monitored female eider heart rate in real time as a metric for perceived predation threat during actual polar bear presence in the colony as detected by an extensive array of trail cameras. Due to eiders' assumed lack of evolutionary experience and rapidly changing ecological experience with polar bear egg predators, we hypothesized that eiders do not perceive the full risk posed by polar bears, and therefore would not dynamically update their assessment of risk. As such, we predicted that eider heart rates would remain unchanged to various distances to a polar bear, and also be unaffected by predator exposure, as measured by the amount of time a bear remained within the eider's viewshed.

Materials and Methods

Study species and area

We conducted work on Mitivik (East Bay) Island (64˚02'N, 81˚47'W), a small (24-ha), low-lying (<8 m elevation) eider nesting colony located within Southampton Island's East Bay, Nunavut, Canada (Figure 3.1). The island experiences almost continuous daylight during the nesting season (Steenweg et al. 2015), and the landscape is flat and is mostly composed of patches of low-lying tundra vegetation, granite rocks, and several small ponds. The island hosts the largest known common eider breeding colony in the Canadian Arctic (Inuit Nunangat; Legagneux et al. 2016) and is the only colony within a

100-km radius (Gaston et al. 1986). Eiders on Mitivik Island initiate laying in late June/early July (Jean-Gagnon et al. 2018), and undergo an approximate 24-day incubation period where they do not feed (Parker and Holm 1990, Bottitta et al. 2003). While the surrounding East Bay area has long been an important migratory route for the Foxe Basin polar bear subpopulation in transit towards summer's last land-fast ice in northern Foxe Basin (H.G.G. pers. obs.), in recent years earlier spring sea-ice breakup and reduced access to seal prey have driven polar bears ashore to Mitivik Island earlier, where bears now overlap with eiders during their laying and incubation periods (Stirling and Derocher 1993, Iverson et al. 2014, Sahanatien et al. 2015).

Heart rate monitoring

The heart rate of actively incubating eiders was recorded using an artificial-egg heart-rate monitor added to the clutch. Artificial-egg heart-rate monitors have been used previously on other bird species throughout the length of their incubation and they have been shown to be minimally invasive (e.g., American oystercatcher *Haematous palliates*, Borneman et al. 2014). We adapted our methods from these studies to create artificial eider-egg heart-rate monitors for our system. Full details on the construction of heart-rate monitors can be found in *Chapter 2*, but briefly, we constructed heart-rate monitors by embedding Electret condenser microphones (PUI Audio model AOM-5024L-HD-R) in a plastic eider egg (sub-elliptical, 2.9 in. long x 1.9 in. at the widest point). Each artificial-egg was wired to a digital audio recorder (Tascam DR-05X) in a weatherproof camouflaged storage box (11.4 in. long, 5.4 in. wide, 7.1 in. high). The recorders continuously recorded for 11-12 days powered by 24 AA Lithium-Ion batteries allowing us to collect continuous audio recordings of the incubating eiders' heart rate during their laying/incubation period. We deployed artificial-egg heart-rate monitors at active eider nests (n=11) on June 24, 25 and 28, 2019, with 1-5 eggs at time of visit (i.e., clutch size during laying or incubation). Heart rate monitors at focal nests were coupled with a ground-based trail camera for polar bear monitoring (see *Polar bear monitoring* below). The location of each focal nest was recorded using a GPS (Garmin GPSMAP 64s) (i.e., labeled Ground-based (Focal Nests) Trail Cameras in Figure 3.1C). During deployment, we replaced the first-laid egg from each study nest, collected for another project (Smith and Love, in prep) and used to estimate incubation stage (see *Eider incubation stage* below), with the artificial egg. Artificial eggs were constructed so that the side of the egg with microphones continuously remained facing upwards in the nest against the eider's brood patch (i.e., by caulking weight to the bottom half inside the egg to prevent egg rolling). The recorder was powered upon deployment and the storage box was placed approximately one meter away from the nest, and both the wire and box were secured and concealed with the surrounding terrain. In the current study, birds returned to their nest approximately 1.19 hours (i.e., average, 0.00139-6.607 hours range) after equipment was deployed on their nest.

Heart rate quantification

A single researcher (E.A.G.) reviewed heart-rate recordings of eiders using the sound analysis software Audacity® v2.3.2 (Audacity Team 2019). We synchronized heart-rate monitors and trail cameras used to define bear locations (see *Defining polar bear locations in relation to eiders* below) to the nearest minute from the clock of a single device. We estimated baseline (i.e., resting) heart rate by collecting heart-rate samples when the island is most quiet (12-2am) on June 29, 2019. These low-disturbance time periods were further confirmed by reviewing i) trail camera footage from ground-based trail cameras on focal nests (i.e., no nearby disturbances for our focal eiders by gulls, geese, or conspecifics), and ii) other cameras included in our remote trail camera system (i.e., no polar bears present on the island, see *Polar bear monitoring* below). To confirm that baseline heart rate is relatively stable during this period, we collected 10-s samples of heart rate every ten minutes during this two-hour period when possible and determined that the SDs of baseline heart rates for each individual ranged from 0.79 beats/10s to 2.79 beats/10s (average 1.72 beats/10s). We then collected a 120-sec sample (i.e., further broken down into twelve 10-s intervals) of 'clean' baseline heart rate from each eider to calculate average baseline for each female for statistical analysis (see below). To quantify eider heart rate in response to polar bears, we similarly collected a 120-sec sample (i.e., twelve 10-s intervals) around the midpoint of a period when a polar bear was observed within an eider's viewshed for a series of consecutive minutes (see *Estimating eider exposure to bears given their viewsheds* below). Multiple heart-rate samples were collected within a bear event (when possible; see *Results*), spaced at least one minute-apart. The opportunistic nature of our sampling-method generated different sample sizes for number of eider exposures to bears (i.e., bear events) and number of heart-rate samples within (see *Results*). We extracted all of the sample intervals as .wav files and heartbeats were counted aurally at least twice to avoid measurement error and therefore increase accuracy of the counts. We excluded sample intervals from analysis for which the sound quality was so poor that heart rates could not be accurately determined. Note that no researchers were present on the island when heart-rate samples were collected in response to polar bears.

For statistical analysis of heart rate as our response variable, we calculated the magnitude of change in heart rate response to polar bears (as beats/10s) by subtracting the average baseline for a female from each sample interval for that bird (collected during polar bear presence). Average baseline heart rate (beats/10s) for each bird comprised the mean of the twelve baseline 10-sec sample intervals.

Polar bear monitoring

A large array (n=84) of GPS-marked remote trail cameras (Browning inc. model: BTC-5HDPX) were distributed across the small island (Figure 3.1C) to define approximate locations of polar bears in relation to focal eiders. A portion of the trail cameras (n=35, set to motion-triggered 30-s videos, equipped with a 128GB SD card) were mounted approximately 6-feet Above Ground Level (AGL) on wooden posts or fixed bird observation blinds (Figure 3.2A, 3.2B, deployed on June 11-14, and 28), while the remaining (n=49, set to 2-min videos once triggered, equipped with a 256GB SD card) were deployed on the ground, approximately one meter from active eider nests (Figure 3.2C, deployed on June 18, 24-25 and 28, 2019). At time of deployment, we powered the camera, selected our desired settings (Table 3.1), set date and time accordingly, and recorded the camera's GPS location and cardinal direction. All cameras collected data from the time of their deployment up to July 19th at the latest (i.e., collected data for 22-39 days (mounted cameras) and 2-26 days (ground-based cameras), start and end date inclusive). A subset of the ground-based trail cameras (n=11, labeled Ground-based

(Focal Nests) Trail Cameras in Figure 3.1C) were coupled with a heart-rate monitor. A companion study by Barnas and Semeniuk (in prep), estimates a high likelihood that the majority of bears present on the island were captured by our trail camera array given the number of cameras deployed, the camera range, coupled with the small size of the island (a conservative estimate of 85% 'probability of capture', using a spatially explicit simulation model).

Defining polar bear locations in relation to eiders

For safety purposes, polar-bear presence on Mitivik Island was discouraged by the eider research team during the daytime from late-May to June 29. However, researchers were absent from the island from June 30 to July 19, and bears were able to forage freely during this time. To identify trail-camera footage with bear(s) present, two observers reviewed all of the videos from the 35 mounted trail cameras, and one observer reviewed footage from the 49 ground-based trail cameras. All videos (n=293) from June 24 to July 10 (i.e., range of eider heart rate monitoring period) with a polar bear(s) present were used to locate bears on a georeferenced, true colour, 3cm Ground Sampling Distance (GSD) orthomosaic map of Mitivik Island in June 2019. ArcMap v10.6.1 (Esri Inc, Redlands, CA) was used to plot locations of bears on the island mosaic. A single observer (E.A.G.) matched patterns of rock, vegetation outcrops, and other landscape features (e.g., infrastructure and pond edges) between the trail camera videos and the island mosaic; bear locations at every 15-sec intervals in the videos (i.e., at video timestamp 0:00, 0:15, 0:30, etc.) were marked on the island mosaic using the *Point* tool. We created buffers of either 1-, 5-, or 10-meter radiuses around each bear location point using the

Buffer tool, based on the observer's level of certainty that they were able to accurately define the bear's exact location on the island mosaic to acquire a conservative estimate of bear location. Only 3.57% of our samples had bear location points with 10-meter buffers, whereas 28.57% and 67.86% had location points associated with 5- and 1-meter buffers, respectively. Importantly, all bear location points involved in our closest bear location points had associated buffers within 5-meters, with the majority having 1-meter buffers. When multiple bears were detected on the island at the same time (e.g., multiple bears in a video or bears present simultaneously on two or more cameras with different detection zones), bear IDs were differentiated based on their different morphometric features (e.g., body size and markings on its fur). Despite the presence of multiple bears, there were no instances of more than one bear detected within a focal eider's viewshed at the same time.

Estimating eider exposure to bears given their viewsheds

To calculate the amount of time polar bears were within viewing distance to an eider, we first estimated the areal size of a focal eider's viewshed given the island's topography. We performed a viewshed analysis of the entire island for each focal eider nest location using ArcMap's *Viewshed* tool. We performed our viewshed analysis on a 3cm GSD Digital Surface Model (DSM) of Mitivik Island (raster grid) in June 2019. We then estimated viewshed for each eider by including a 14 cm vertical offset to account for the approximate eye level of nesting eiders (i.e., observer point; measured using a sitting male eider decoy, Figure 3.3) and a 1.5 m offset to account for the approximate average height of a polar bear standing on all fours (i.e., the z-value being considered for visibility; Amstrup 2003). We then used the *Raster to Polygon* tool to convert each viewshed raster to a polygon layer. We manually clipped out a polygon of Mitivik Island using the *Polygon* tool, and we used ArcMap's *Clip geoprocessing* tool to clip each of our viewshed polygons (i.e., input feature) within our island polygon (i.e., clip feature). Finally, we extracted the area (in m^2) of the clipped polygon layers, representing each focal eider's area of potential polar-bear visibility on Mitivik Island.

Estimating eider distances and exposure durations to polar bears

We estimated the distance (in m) between a nesting focal eider and polar bears observed within their viewshed using ArcMap's *Measure* tool. To do so, we collected distance measurements for all bear observation points included in each heart-rate sampling period (i.e., consisting of bear points observed at every 15-second interval from trail camera footage and located within an eiders' viewshed for a series of consecutive minutes), and calculated the average distance for each heart-rate sample. We estimated eider's exposure duration to polar bears (in minutes) by calculating the length of a bear event within the eider's viewshed, and we assigned these durations to any heart-rate samples within their respective bear event. A bear event is the period of time when a polar bear was observed to be within an eider's viewshed. A bear event was considered new when there was a gap of more than five minutes when the bear was not observed within the eider's viewshed.

Eider incubation stage

To account for additional covariates that may also dynamically influence heart rate, we quantified incubation stage (i.e., stage of embryo development) for each focal hen. To do so, the first-laid egg from each study nest was immediately candled (Weller 1956). These methods provided estimates of the number of days the first-laid egg had been incubated on the day of heart-rate monitoring equipment deployment, and hence incubation stage was updated and matched to the days of bear events.

Air temperature and wind speed

To examine meteorological conditions for each focal hen during heart-rate sampling to polar bear presence, we collected measurements of air temperature (in degrees Celsius) and wind speed (m/s) from Kestrel weather meters (Kestrel® 5500) deployed at multiple locations within the colony. Kestrels were set to log weather parameter estimates at every 30-minute interval. For each eider, we sampled weather from the Kestrel that was collecting data nearest to the focal nest and we sampled these measurements at the closest 30-minute interval to our heart rate sampling times to bears.

Statistical analyses

We used a general linear mixed model (LMM) using the *lmer4* package (Bates et al. 2015) to analyse magnitude of change of eider heart rates to polar bears. Fixed effects included distance to the bear, exposure duration to the bear (with duration corrected for size of viewshed), time of day, incubation stage, air temperature, wind speed, and the interaction between distance and exposure duration. We tested incubation stage in our model since Viblanc et al. (2015) discovered an effect of breeding stage on king penguin magnitude of change in heart rate. We tested air temperature and wind speed since they have both been found to influence rate of oxygen consumption (positively related to heart rate) in adélie penguins (*Pygoscelis adeliae*) and blue-eyed shags (*Phalacrocorax atriceps*) (Chappell et al. 1989). Our nested random effect structure comprised of heart-rate sample number nested within bear event and bear event nested within eider ID. We also included eider ID as a random effect to account for inter-individual differences among hens. We tested fixed effects using a backward elimination procedure by fitting the full model for magnitude of change in heart rate with maximum likelihood (ML) estimation (Zuur et al. 2009). Main effects and our interaction term were tested sequentially using the backward elimination procedure, leaving in the final model only the fixed effects associated with the outcome, considering a 10% level of significance (i.e., a standard retention criterion for backward elimination, Bursac et al. 2008). The final model with retained fixed effects was refitted using restricted maximum likelihood (REML) estimation. We assessed the variance explained by the fixed effects (i.e., marginal R^2) and the variance explained by the entire model, including both fixed and random effects (i.e., conditional R^2) for our model, using the package *MuMIn* (Bartoń 2019). We assessed model fit by comparison of second-order Akaike Information Criterion (AICc) scores between all competing models in the backward elimination process, as well as an intercept-only model, all fit with maximum likelihood (ML) estimation (Zuur et al. 2009), using the package *MuMIn* (Bartoń 2019).

All analyses were performed in R v3.5.0 (R Core Team 2018), with an RStudio interface (RStudio Team 2019). All data manipulation was done with packages *dplyr* (Wickham et al. 2019) and *tidyverse* (Wickham 2017). We checked variance inflation factors (VIF) (i.e., multicollinearity) for all predictor variables using the *car* package (Fox and Weisberg 2019); and model residuals were assessed by visual inspection of Q-Q plots. For all statistical significance tests, we used $\alpha = 0.1$. All plots of predicted response variables, calculated under the package *ggeffects* (Lüdecke 2018), were constructed under the package *ggplot2* (Wickham 2016).

Results

We collected 28 heart-rate samples within 21 bear events from our 8 focal eiders. We estimated that ten individual bears were involved in our bear events and were all independent ages (i.e., subadult and/or adult) and of average to good body condition (i.e., no thin, skinny, or obese appearance; polarbearinternational.org). For most individual eiders, we were able to collect multiple heart-rate samples from each eider, although three birds either did not have a bear present in its viewshed during the study period, the bird was not on her nest when a bear was present, or we were unable to collect a sample of sufficient audio quality. Magnitude of change of eider heart rates ranged from -20 beats/10s to 39 beats/10s (average 1.39 beats/10s). Distances to bears ranged from 12 meters to 286.67 meters (average 110.81 m) and exposure duration to bear ranged from 1 minute to 14 minutes (average 4.05 min). Areal size of eider viewshed ranged from 5730 m^2 to 33,231 m^2 (average 18,897 m^2). Incubation stage ranged from 4 days to 19 days (average 11 days). Air temperature ranged from 1.1˚C to 9˚C (average 3.53˚C), and wind speed ranged from 0 m/s to 8.3 m/s (average 4.53 m/s). Our model with magnitude of change in heart rate as a function of distance to polar bear, incubation stage, air temperature and wind speed best explained our data according to our backward elimination approach (Table 3.2). In this model, we detected a marginally significant relationship between magnitude of change of eider heart rates and distance ($F_{1,12.78}$ =

4.49, P = 0.054), where eiders had a greater positive increase in heart rate to closer bears (Figure 3.4). Magnitude of change in heart rate was also significantly negatively related to incubation stage ($F_{1,7.87}$ = 5.45, P = 0.048, Figure 3.5), air temperature ($F_{1,15.92}$ = 11.92, P = 0.003, Figure 3.6), and wind speed ($F_{1,15.14}$ = 4.62, P = 0.048, Figure 3.7), where changes in heart rate over baseline decreased as incubation stage progressed, and temperature and wind speed increased. Based on model parameter estimates, eider heart rate was estimated to be influenced by incubation stage, air temperature, and wind speed more than distance to polar bear (Table 3.2). There was no significant relationship between magnitude of change in heart rate and exposure duration to polar bears or time of day, and there was no significant interaction between distance and exposure duration to polar bears. Much of our variance was explained by our final model (including random effects; condition R^2 = 0.8847) versus our fixed effects-only model (marginal R^2 = 0.3727). According to AICc, the final model received equal support to the intercept-only model (Table 3.4), in that variation in magnitude of change in heart rate was also driven by our random effect structure, namely, eider ID (Table 3.3), suggesting a large degree of inter-individual variation in magnitude of change in eider heart rate. We did not detect collinearity in any fixed effects within each model based on estimated VIFs < 5.

Discussion

Using non-invasive, observational, and spatially explicit approaches, our goal was to monitor eider heart rate in response to variation in real predation risk to assess eiders' capacity to perceive changes in the degree of threat posed by a predator for which eiders have limited eco-evolutionary experience. Results from our study show mild support for dynamic risk assessment of polar-bear threat, in contrast to our predictions. Eiders in the current study exhibited (albeit to a marginal extent) risk-induced trait responses (i.e., birds modulated their heart rate) to varying levels of risk based on distance from foraging polar bears, but not to varying exposure durations. Additionally, increase in heart rate to decreasing distance from bears was mild in comparison to alteration in heart rate to some of the additional covariates assessed in this study. These results suggest that although eiders perceive the risk of polar bears as adult- and egg predators, they do not perceive their full risk (Carthey and Banks 2014). Historically, birds and bird eggs were a rare occurrence in polar bear diets (Harrington 1965, Lønø 1970, Russell 1975, Gormezano and Rockwell 2013), and bear presence in bird colonies was seldomly reported during birds' nesting season (Lønø 1970, Russell 1975) as polar bears focused on hunting seals, their preferred diet item, from the sea ice during this time (Russell 1975). Eiders in this Arctic system therefore have limited evolutionary experience with polar bears during incubation and have instead evolved antipredator adaptations to avoid predation by their primary arctic fox nest predators (see *Introduction*; Larson 1960, Ahlén and Andersson 1970, Schmutz et al. 1983, Mehlum 1991). Polar bears differ from arctic foxes in their egg foraging styles: arctic fox rely heavily on scent (Bahr 1989), whereas polar bears are highly visual (Jagielski et al. 2021). Arctic fox often cause partial losses to eider clutches by taking a single egg to cache during each nest visitation (Bahr 1989), whereas polar bears typically consume all eggs in a clutch upon visiting the nest (Jagielski et al. 2021). These differences in predation behaviour likely require different antipredator adaptations by eider prey. However, eiders are a long-lived species (Waltho and Coulson 2015) and are thus unlikely to have adapted to polar bears by way of rapid evolution (Carthey and

Blumstein 2018). Instead, eiders may have learned to recognize polar bears through experience with bears over ontogenetic time (reviewed in Carthey and Blumstein 2018; e.g., burrowing bettongs *Bettongia lesueur*, Steindler et al. 2020). We discuss the consumptive and non-consumptive effects eiders are expected to endure based on our results in the following discussion after considering possible sources of inter- and intra-eider variation in heart rate responses to bears.

Heart rate responses to various distances to polar bears

Eiders exhibited a marginal increase in heart rate response from baseline to bears the closer bears were observed to their nest. Such increased responsiveness (e.g., via heart rate) to predator distance has also been reported in other nesting species (e.g., wandering albatross *Diomedea exulans*, Weimerskirch et al. 2002; warblers *Acrocephalus sp*, Kleindorfer et al. 2005). Bears in the current study were observed at distances from eiders (i.e., 12 to 18.5 m) within the range eiders have been reported flushing to disturbance (e.g., 0-20 m to human approaches, Seltmann et al. 2014; 3-15 m and 3-18 m to approaching arctic fox and control models, respectively, see *Chapter 2*), but also above the range at which eiders have been reported to flush from visual polar bear stimuli (i.e., 1-9 m, see *Chapter 2*). Because neurophysiological responses typically precede any behavioural responses (reviewed in Ydenberg and Dill 1986, Weston et al. 2012), the mounted heart rate response of eiders when bears were observed closer to their nests suggests the use of active defense (i.e., fight-or-flight response), a strategy commonly exhibited by animals and associated with an increase in heart rate and mobilization of energy for quick flight (Bandler et al. 2000). Thus, the regulation of heart rate by eiders to varying distance from bears in the current study suggests female eiders dynamically updated their assessment of risk to bears and thus perceived risk posed by polar bears.

Heart rate responses to various exposure durations to polar bears

Eider heart rate remained unaffected by exposure duration to visible polar bears. From the perspective of the bear, a bear could technically see an eider at any location within the eider's viewshed (Aben et al. 2018). Thus, the longer that a bear is within an eider's viewshed, the greater chance of the bear detecting and targeting the eider and their nest. Similarly, bystander king penguins displayed heightened heart rates the longer the duration of a nearby agnostic encounter since longer conflicts can increase risk of redirected aggression for bystanders (Viblanc et al. 2012). Further, an eider's 'area of visibility' should represent their 'ratio of risk', in that eiders with a narrower, and therefore limited spatial visibility range should perceive a polar bear detected within their viewshed as a greater risk than an eider with a larger viewshed where risk is diluted. Additionally, incubating birds have been shown to compensate for information deficits upon detection of a threat cue by behavioural risk assessment mechanisms such as increasing vigilance (e.g., incubating brown thornbill *Acanthiza pusilla* to predator calls, Schneider and Griesser 2013); and heart rate responses have been positively linked to vigilance following the detection of a threat in several species of birds (reviewed in Beauchamp 2017). Thus, our finding that eiders did not vary their heart rate response across variation in large (i.e., exposed to a bear for a long duration in a small viewshed) and small (i.e., exposed to a bear for a short duration in a large viewshed) exposure durations suggest eiders do not perceive the full risk posed by polar bears.

Intra- and inter-individual variation in physiological responses

In the current study, we also discovered intra-eider and inter-individual variation in the magnitude of change in heart rate (from baseline heart rate). Some of this variation was accounted for via incubation stage and meteorological conditions. Specifically, the heart-rate responses of eiders lessened the further into incubation. Heart-rate responses associated with flight may be reduced with incubation investment (e.g., incubation stage and clutch size) due to parents focusing their energy on reproduction over survival (e.g., common eider, Jaatinen et al. 2014), or in attempts to save energy as they become more energetically limited (Criscuolo et al. 2002, Cyr et al. 2008). Heart-rate responses also increased with decreasing temperature and wind speeds. One way in which endothermic animals maintain high body temperature is by increasing metabolic heat production in low ambient temperatures (Heinrich 1977). Metabolic heat production requires an increase in cardiac output and thus increased heart rate (reviewed in Price and Dzialowski 2018). Gabrielsen et al. (1991) studied eider thermoregulation in a field-laboratory setting and found that female eider metabolism increased as ambient temperature decreased below eiders' lower critical temperature of 7˚C. Indeed, in most cases, eiders in the present study were exposed to temperatures below this lower critical temperature which explains increasing heart rates with decreasing temperature. This relationship may be further exacerbated during incubation as incubating birds must compensate for the reduced efficiency of heat transfer to their eggs with decreasing ambient temperature (reviewed in Tazawa and Causey 2000). In one study, eiders protected (with artificial shelter) from extreme temperatures (and presumably wind) saved more energy than birds in exposed nests (Fast et al. 2007). Interestingly however, our observed negative influence of wind speed on eider heart rate is surprising since wind can dissipate body heat by disrupting plumage and reducing the bird's thermal insulation (Weimerskirch et al. 2002). Indeed, wind speed has been positively associated with energy expenditure in incubating eiders (i.e., positive correlate of heart rate, Hilde et al. 2016) and incubating adélie penguins *Pygoscelis adeliae* (Culik et al. 1989). It is possible postural changes where birds may be altering their overall height on the nest to reduce exposure to wind, and/or the use of plumage compression to avoid deleterious cooling effects of the wind (Taylor 1986) could both result in decreased energetic expenditure and hence lowered heart-rate responses. More research is needed to explain these results.

The remaining inter-specific variation in heart rates can be driven by intrinsic and extrinsic factors not already accounted for in our system. For instance, female body condition (i.e., mass) and breeding experience (i.e., age) can influence the degree of risk perception, manifested in terms of stress-induced physiology (e.g., circulating corticosterone) and antipredator behaviour (e.g., flight initiation distance) (reviewed in Wingfield and Sapolsky 2003; e.g., common eider, Seltmann et al. 2012). To the best of our knowledge, no studies have related predator-induced heart rate to body condition, although basal and average heart rates have been positively correlated with mass of incubating birds (e.g., wandering albatross, Weimerskirch et al. 2002). Further, incubating birds have been shown to have differential stress-induced heart rate responses based on experience with predators. For example, Snares penguins (*Eudyptes robustus*) previously exposed to human activities in the preceding breeding season showed stronger heart rate responses to human approaches than birds without experience (Ellenberg et al. 2012). Although it was not logistically possible to determine eider hen age or condition, these two factors can credibly contribute to the variation seen between individuals in our system.

Lastly, variation in eider heart rates may be attributable to individual characteristics of the bears. To assess risk, eiders use a complex set of overt and subtle predatory cues that provide information on a predator's likely future actions. Direct and rapid predator approaches, and those where the predator's head and gaze directly face the focal prey, are perceived as a greater risk than tangential and slower approaches or when the predator's head and gaze are averted (Burger and Gochfeld 1981, Bateman and Fleming 2011, Lee et al. 2013, Davidson and Clayton 2016). In the current study, we were unable to quantify possible predator cues such as whether bears were mobile, their speed, and their direction of attention (i.e., body, head, and gaze) in relation to focal eiders. Current work is being conducted to assess flushing responses of eiders to multiple subtle cues by foraging polar bears (Barnas et al. in prep), but similar work assessing eider heart rate to these cues is needed to better characterize eiders' ability to perceive risk from polar bears. In future work of this type, a larger sample size would also allow us to control for some of these intra- and inter-individual differences in factors that may be affecting individual eider heart rate responses to natural variation in polar bear predation risk.

Conclusion

Our findings on incubating common eiders reveal novel insights on the adaptive capacity for eiders to perceive variation in risk posed by their increasing interaction with polar bear egg predators. To the best of our knowledge, this is the first quantitative examination of avian physiology in response to polar bears. We assume a fitness-driven role for dynamic risk assessment in birds since heart rate responses can affect individual fitness via its associated energetic costs (e.g., European starlings *Sturnus vulgaris*, Cyr et al. 2008). Our finding that eiders updated their responses to one of the conspicuous indicators of risk (distance) examined in the current study suggests eiders are able to recognize polar bears as threatening, but their lack of physiological response to exposure duration by bears indicates eiders cannot fully recognize when polar bears pose a greater risk and are thus less likely to avoid capture/nest predation. Thus, compared to responses to evolved predators, eiders are expected to endure more consumptive effects and a slightly reduced level of non-consumptive (i.e., energetic) effects from the increasing frequency in interactions with polar bears (Sih et al. 2009). Although population modelling suggests eider's population growth rate is mainly determined by variations in adult survival, survival rates have been relatively stable over time, whereas fluctuations in eider's population size has been driven primarily by variations in annual productivity (Coulson 2010, Wilson et al. 2012). Bears have been observed in 30% of eider colonies in the Hudson Strait (Iverson et al. 2014). The effect of polar-bear predation on the reproductive fitness value of hens can be dramatic, and therefore our findings of a weak anti-predator response to polar bears have implications for eider population persistence in these colonies.

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Tables

Table 3. 1. Trail camera (Browning Inc. model BTC-5HDPX) settings selected to record polar bear (*Ursus maritimus*) movement behaviour on Mitivik Island, Nunavut Canada

Settings	Selected Setting		
	Mounted	Ground-based	Ground-based (Focal Nests)
Capture Mode (Mode)	Video	Video	Video
Capture Delay	1s	5s	5s
Multishot Modes (Multishot)	Off	Off	Off
Video Resolution (Video Quality)	High	Ultra	Ultra
Video Length	30s	2min	2min
Smart IR Video (Smart IR)	Off	Off	Off
Adjustable IR Flash (Night Exp)	Long Range	Power Save	Power Save
Temperature Units (Temp)	C	C	C
Info Strip	On	On	On
SD Card Management	Off	Off	Off

Table 3. 2. Model parameter estimates and standard error for fixed effects used to explain variation in magnitude of change in heart rate among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Estimate ± SE**
Intercept	51.216 ± 16.07
Distance	-0.049 ± 0.02
Incubation stage	-1.953 ± 0.84
Air temperature	-3.418 ± 1.00
Wind speed	-2.107 ± 0.98

Table 3. 3. Model parameter variance and standard deviation for random effects used to explain variation in magnitude of change in heart rate among nesting common eiders (*Somateria mollissima*) on Mitivik Island

Model Parameter	**Variance ± SD**
Sample number[Bear event]	2.86 ± 1.69
Bear event[Eider ID]	31.67 ± 5.63
Eider ID	116.50 ± 10.79
Residual	34.01 ± 5.83

Table 3. 4. Predicting the magnitude of change in heart rate (i.e., "delta heart rate", beats/10s) in female incubating common eiders (*Somateria mollissima*) in response to polar bears (*Ursus maritimus*) based on AICc model selection (ML estimation). Models included here were used in a backward stepwise regression until significant effects remained (via ML estimation). AICc weight represents the relative likelihood of a model. Models are sorted by weight from most likely to less likely. The null model is represented by "magnitude of change in heart rate ~ 1"

Model	df	AIC_c	ΔAIC_c	w_i
Delta heart rate ~ distance + incubation stage + air temperature + wind speed	9	1843.4	0.00	0.428
Delta heart rate ~ 1	5	1844.1	0.70	0.302
Delta heart rate ~ distance + time of day + incubation stage + air temperature + wind speed	10	1845.2	1.78	0.176
Delta heart rate ~ distance + exposure duration + time of day + incubation stage + air temperature + wind speed	11	1847.4	3.94	0.060
Delta heart rate ~ distance + exposure duration + time of day + incubation stage + air temperature + wind speed + distance*exposure duration	12	1848.5	5.03	0.035

Figures

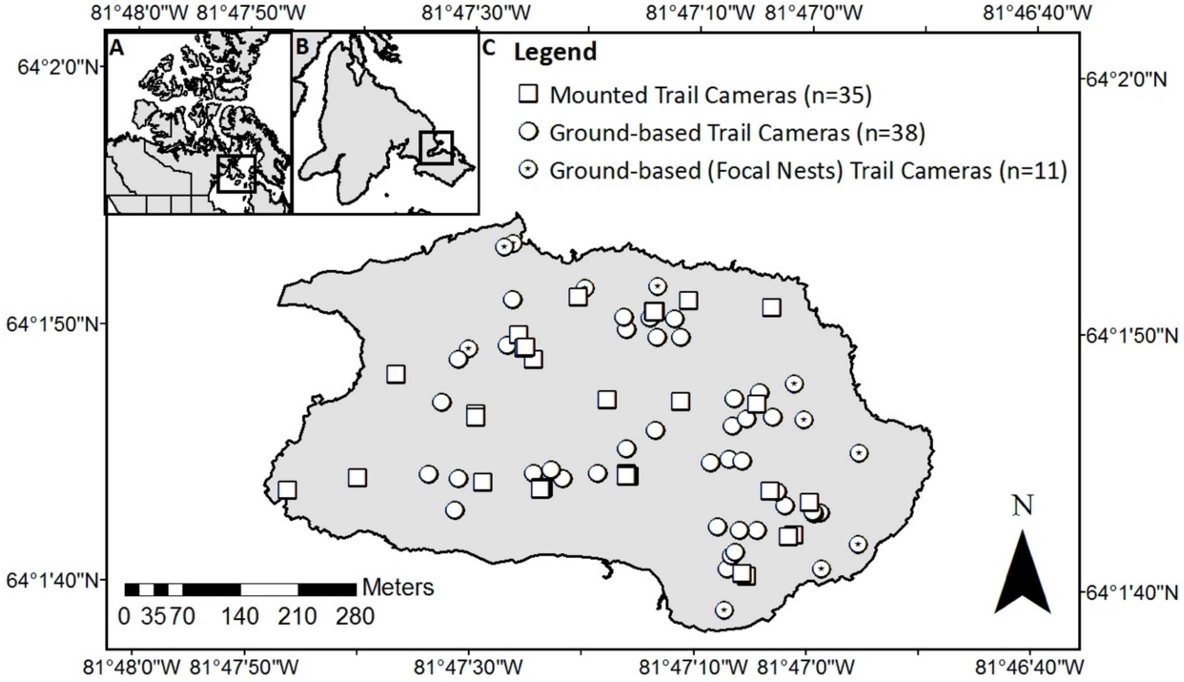

Figure 3. 1. Map of the study area, displaying our A) general location (Northern Hudson Bay, Nunavut, Canada), B) regional location (Southampton Island, Nunavut, Canada), and C) study site (Mitivik Island, Nunavut, Canada) with the distribution of trail cameras. Canadian Provinces and Territories map layers provided by ESRI online, accessed May 30, 2018

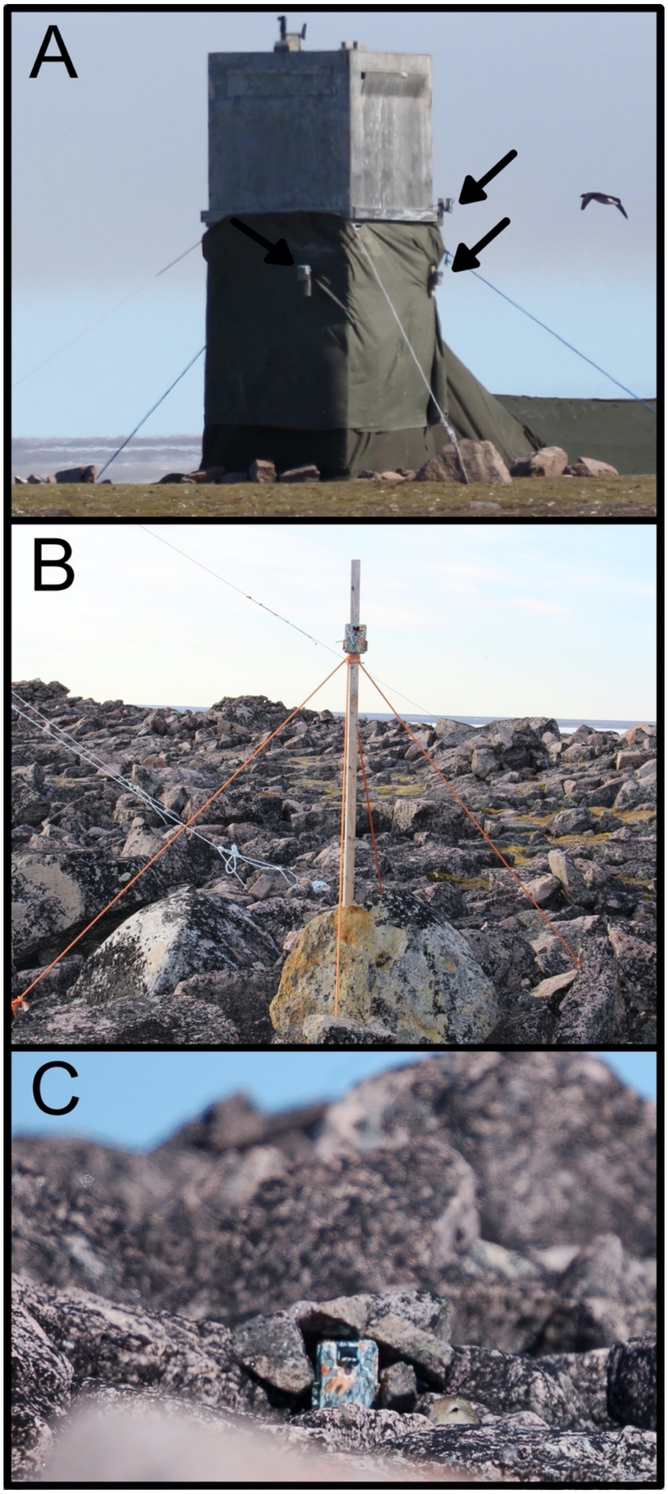

Figure 3. 2. Photographs of trail cameras (Browning Inc. model BTC-5HDPX) on Mitivik Island, Nunavut, Canada: A) mounted on a bird observation blind (arrows point to cameras), B) mounted on a wooden post (photo credit to Erica Geldart), and C) on the ground, next to an active common eider (*Somateria mollissima*) nest (photo credit to Russell Turner)

Figure 3. 3. Estimated vertical offset for a common eider's (*Somateria mollissima*) eye level above ground using a sitting male common eider decoy

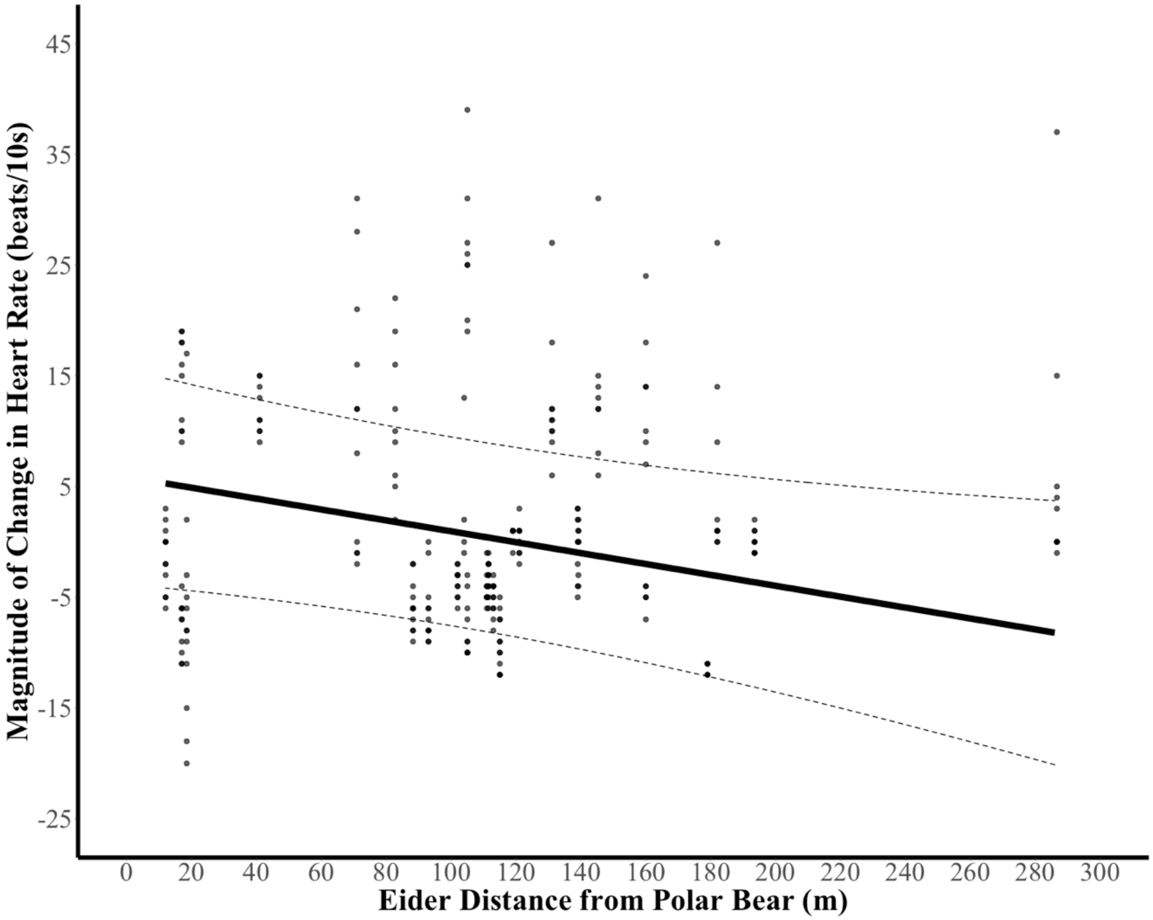

Figure 3. 4. Magnitude of change in common eider (*Somateria mollissima*) heart rate (beats/10s) depending on their distance (m) from a polar bear on Mitivik Island. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

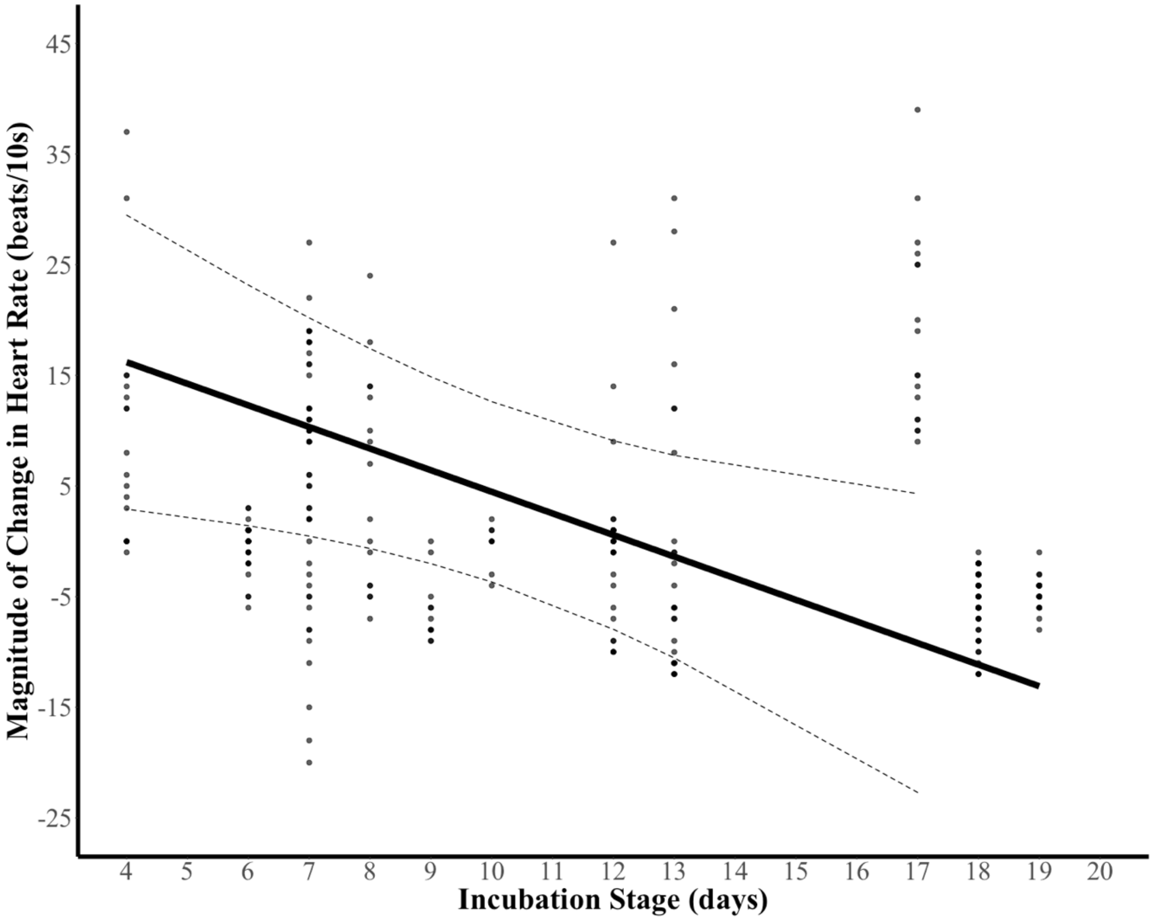

Figure 3. 5. Magnitude of change in common eider (*Somateria mollissima*) heart rate (beats/10s) depending on eider incubation stage (days). Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

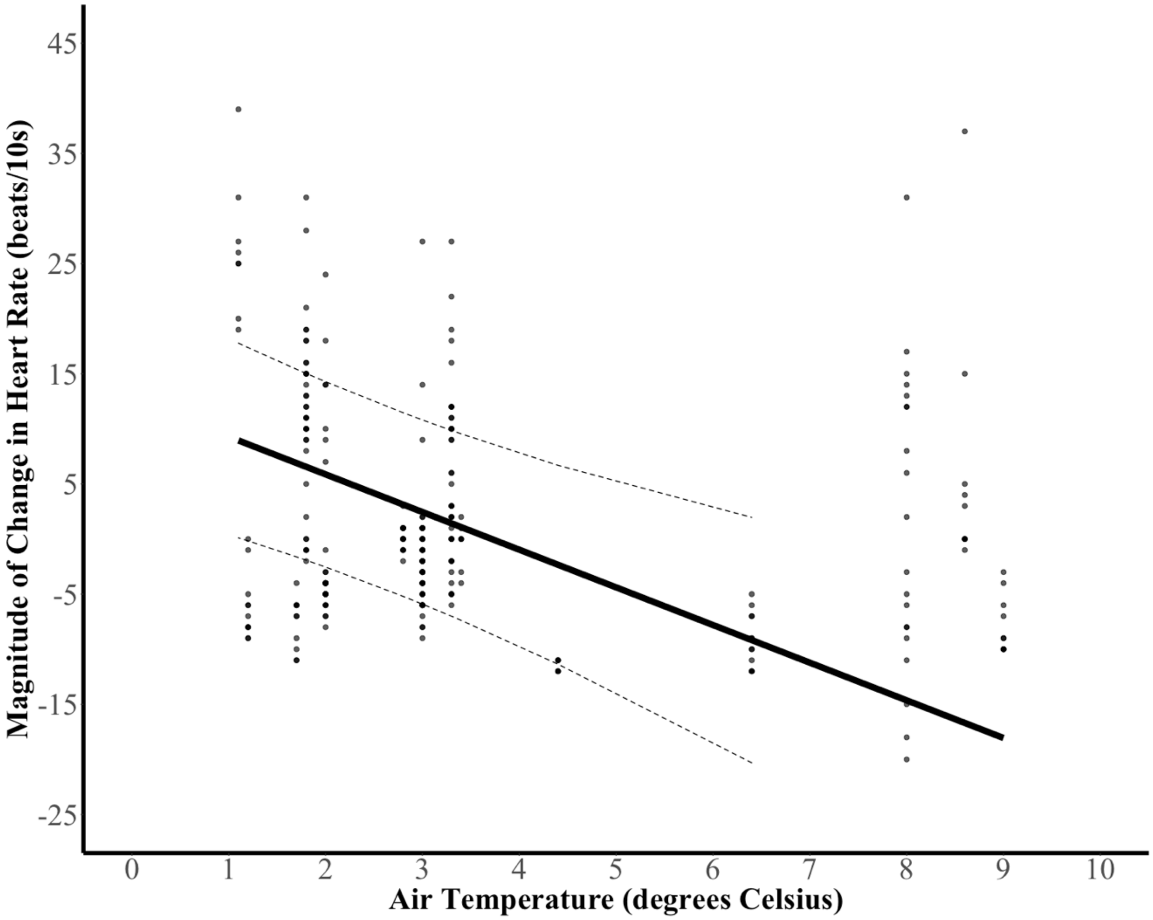

Figure 3. 6. Magnitude of change in common eider (*Somateria mollissima*) heart rate (beats/10s) depending on air temperature (degrees Celsius) on Mitivik Island. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

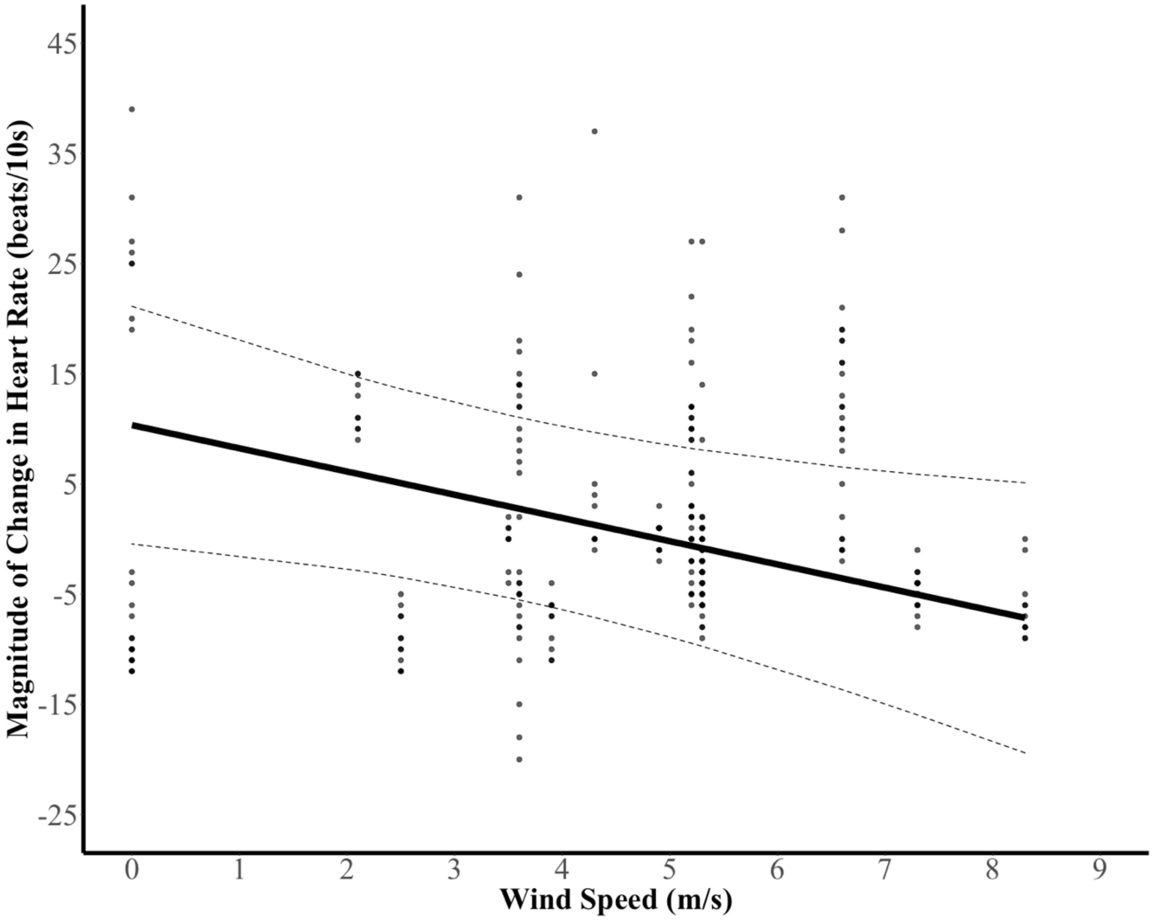

Figure 3. 7 Magnitude of change in common eider (*Somateria mollissima*) heart rate (beats/10s) depending on wind speed (m/s) on Mitivik Island. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively

CHAPTER 4

General Discussion

Recent climate-driven matches between polar bears (*Ursus maritimus*) and Arctic nesting seabirds could have dramatic impacts on local bird populations. We know that recent increases in polar bear presence in common eider (*Somateria mollissima*, hereafter 'eider') breeding colonies is a major cause of reproductive failure for these birds (Iverson et al. 2014, Dey et al. 2017). Eider hens are predicted to increase their lay date due to earlier access to food resources from warming springs (and hence reduce their temporal overlap with arriving bears), and to relocate to other nesting areas after successive failed nesting attempts (Love et al. 2010, Öst et al. 2011, Chaulk and Mahoney 2012). Eiders have not yet responded predictably to increasing polar bear nest predation with large-scale relocation (Dey et al. 2017, 2020); and their ability to reduce overlap and/or avoid nest predation and capture from polar bears may depend on their capacity to recognize polar bears as egg and adult predators (Guiden et al. 2019). The aim of my thesis was to assess whether eider behavioural and physiological responses to predators may provide them with the adaptive capacity to respond to increasing frequency in predation risk from polar bears. Overall, my results suggest eiders do not perceive the full risk posed by polar bears and are thus expected to suffer negative fitness consequences from this interaction.

Animals can only respond to the risks that they perceive, and these responses will be selected for only if perceived risk accurately reflects the true risk of predation (Creel et al. 2017). Interestingly, changes in sea-ice phenology are not only exacerbating predation risk from polar bears, but also reducing predation risk from arctic fox (*Vulpes lagopus*) due to reduced sea ice making islands inaccessible to them (Hanssen et al. 2013, Iverson et al. 2014). Further, bear presence in eider colonies has a greater realized negative impact on nest success than fox presence (Iverson et al. 2014). However, the strength of eiders' physiological response to different mammalian egg predators in *Chapter 2* (i.e., greater response to the fox than bear) does not reflect recent patterns of actual egg predation by polar bears and arctic fox in eider colonies. Thus, our heart rate results from *Chapter* 2 suggest that because eiders are responding to predators at an evolutionary level they may not be able to physiologically respond to the ecological changes in risk currently being posed by bears. Our findings in *Chapter 3* suggesting that eiders perceive polar bears as a predation risk, but do not perceive their full risk, indicates eiders have insufficient experience to develop an appropriate response. Indeed, their failing to mediate their heart rate response across risk of predation by bears (i.e., exposure duration) could indicate that eiders do not perceive the full consequence that bears pose to their eggs and are therefore expected to suffer long-term fitness costs from reduced reproductive success. Across both chapters then, eiders' limited physiological and behavioural responses to bears suggests eiders are to some extent naïve to polar bears as egg predators (and potentially as adult predators as well), and are thus at risk of suffering marked consumptive impacts from their increasing interaction with them (Sih et al. 2009). A consequence of this weak recognition and ineffective response may place eider populations at risk of population decline (Carthey and Banks 2014, Carthey and Blumstein 2018) should polar bear–eider interactions occur on a larger spatial scale.

Whether eiders can recognize polar bears as sufficiently dangerous and respond accordingly depends then on whether their ecological experience with bears is enough (in terms of frequency and intensity of encounters, McLean et al. 2000, Griffin et al. 2001, Sih et al. 2011, Sih 2013) for rapid change via evolution, learning, and/or plasticity (Carthey and Blumstein 2018). Eiders must first learn to assess the risk that bears pose to their clutch and/or undergo selection for individuals that display plasticity in their responses to predation risk from bears for eiders to have the adaptive capacity to cope with increasing frequency in polar bear egg predation. Eiders therefore still require more experience to develop an adaptive response to bears and may require conservation intervention to aid in their management. These ideas are further explored below.

Predator discrimination via rapid change

According to the literature, naïve prey that do not rapidly go extinct following a new interaction will not remain eternally naïve to predators (Sih et al. 2011, Saul and Jeschke 2015, Carthey and Banks 2016). Naïve prey can rapidly develop cue discrimination and adaptive antipredator behaviour by adaptation or learning, and/or may be able to respond accordingly to unfamiliar predators by being flexible in their responses. Since eiders are a long-lived species, they are unlikely to have developed predator recognition abilities via rapid molecular evolution given that their slow life histories may cause them to go extinct before they have had time to adapt (via selection) to change in predation risk from polar bears (Kokko and Sutherland 2001, Ofori et al. 2017, Thurman et al. 2020). Alternatively, several animals have shown the ability to recognize and develop antipredator responses within their lifetime via learning through experience (i.e., learned recognition hypothesis, Turner et al. 2006). For example, previously predator-naïve moose (*Alces alces*) whose calves had been killed by wolves made behavioural adjustments to reduce predation (i.e., increased vigilance and latency to resume feeding) within a single generation (Berger et al. 2001). Likewise, novel predation risk altered parental behaviour (i.e., increased nest attendance and reduced activity at nest) of New Zealand bellbirds (*Anthornis melanura*) (Massaro et al. 2008). Results from our work here suggest eider recognition templates to polar bears require further refinement and this can possibly be accomplished through learning. Female eiders have demonstrated the ability to learn in other contexts: for example, eiders implement the 'win-stay versus lose-switch' learning rule, in that they choose habitats that have yielded good reproductive success the previous summer (i.e., have high site fidelity), and avoid (i.e., by relocation) habitats that yielded poor reproductive success (Öst et al. 2011). Future work is required that compares perception of, and responses to polar bear predation risk between eider colonies with and without ontogenetic experience with bears to determine if eiders can learn over their lifetime and make breeding changes based on that learning (e.g., burrowing bettongs *Bettongia lesueur*, Steindler et al. 2020).

Another possible mechanism for rapid change is via phenotypic plasticity (i.e., the ability of a single genotype to produce more than one alternative phenotype in response to environmental variation) (e.g., Brookes and Rochette 2007). Indeed, species that show plasticity in antipredator responses might incur a selective advantage with climate-driven changes in predator-prey dynamics (Hendry et al. 2008, Ducatez et al. 2020). For example, orange-crowned warblers (*Vermivora celata*) exhibited adaptive phenotypic plasticity (i.e., shifts in nest site placement and adjustments to feeding rate) to reduce nest predation risk following experimental introduction of a novel avian nest predator (Peluc et al. 2008). Specifically examining consistency vs. plasticity of individual antipredator responses over time and across contexts provides insight into the stability vs. flexibility of traits, and their potential to evolve under natural selection (Dingemanse and Réale 2005, Sih et al. 2012, Sadoul et al. 2020). We detected a great degree of inter-eider variability in stress-induced flight initiation distance (FID) and heart rate responses (although repeated measures of these traits across time and situations could not be accomplished in this study). Eiders as a species exhibit flexibility in several life-history traits to variation in biotic and abiotic conditions, such as nesting phenology, egg/clutch size, and propensity to breed (Robertson 1995, Love et al. 2010, Chaulk and Mahoney 2012, Öst et al. 2018). However, FID to human approaches, a metric for boldness, showed high repeatability and has thus been deemed a valid personality trait in eiders (Seltmann et al. 2012). Furthermore, personality has been linked with physiological stress in this species (Seltmann et al. 2014) and was consistent with proactive and reactive stress coping styles (Koolhaas et al. 1999, Réale et al. 2010). For instance, reactive individuals are thought to be more sensitive to new information, store more information in long-term memory, and more readily modify their behaviours or defences when they do encounter a challenge (i.e., via plasticity), and thus are predicted to make faster progress in the face of change (Sih and Giudice 2012; e.g., zebrafish *Danio rerio*, Baker and Wong 2019; Sadoul et al. 2020). If variation in eider antipredator responses are indeed attributable to different coping styles (i.e., are a heritable trait), we might expect differential selection on individuals based on their differential capacity for learning and plasticity (Sih et al. 2012, Sadoul et al. 2020).

Assuming rapid selection on personality and therefore the capacity to learn, how exactly could rapid learning that bears are a threat or adaptive plasticity help to mitigate the impacts of bear predation on eider nests? First, eiders that develop adaptive responses to polar bears by learning and/or plasticity may alter their nest defense behaviours (e.g., escape) to prevent bears from eating their nests in the short-term. In support of this outcome, recent work on Mitivik (East Bay) Island found polar bears ignore many nests in their immediate trajectory, but do use visual cues (i.e., flushing eider hens) to locate nests (Rockwell and Gormezano 2009, Jagielski et al. 2021a). Thus, a long-distance flush may be adaptive if the flushing hen is not seen by the polar bear, or if the bear is too far to locate exactly where the hen flushed (i.e., passive deceptive behaviour, Broom and Ruxton 2005, e.g., Charadriiformes sp., Smith and Edwards 2018) since an exposed nest does not guarantee predation by nearby bears. Additionally, an early escape may allow eiders time to cover their nests with insulating down before leaving the nest to protect their clutch from secondary predators and weather conditions (Mehlum 1991). Alternatively, it may also be adaptive for eiders to rely on crypsis and flush at a short distance only when they have been detected by bears if eider distraction displays are an effective strategy to draw bear's attention away from their nest (i.e., active deception, Kay and Gilchrist 1998). Although in recent years almost all nests on Mitivik Island have been consumed by the end of the breeding season (Jagielski et al. 2021b, pers. obs.), an earlier laying date paired with an appropriate antipredator behavioural response that extends the chance of nest predation could allow some females to successfully complete incubation and hatch ducklings. Alternatively, incubating eiders nesting in colonies facing bear predation that can perceive the risk bears pose to their eggs and themselves, and can therefore directly assess polar bear predation risk prior to the onset of breeding, may instead benefit from life history responses to bear predation risk by forgoing breeding altogether to avoid high survival costs of reproduction (reviewed in Lima 2009). Eider species are known to refrain from breeding in years and/or areas of high realized predation risk (e.g., steller's eider *Polystica stelleri*, Quakenbush et al. 2004; common eider, Öst et al. 2018). However, bears are predicted to increase nest predation as advances in ice breakup continue, and are known to return to eider colony locations year-after-year (Dey et al. 2017), thus, this strategy is likely not sustainable in these colonies. Finally, selection on personality and therefore the capacity to learn may allow females to avoid predation risk in the future if females also have the reproductive flexibility to shift from breeding in dense colonies to nesting alone or dispersed from other females. Indeed, since bear predation presence is density-dependent and linked to distance to the mainland (Iverson et al. 2014), bear foraging patterns are predicted to drive increased spacing of nests and large-scale relocation closer to the mainland to reduce egg predation by polar bears (Dey et al. 2017). Although this type of response has not been observed to date (Dey et al. 2020), with more experience and possible selection on personality some female eiders could learn to directly assess polar bear predation risk within their lifetimes and choose future nest sites that improve their long-term reproductive fitness.

Limitations and future directions

The current study sought to examine eider perception of risk to polar bears to predict fitness consequences resulting from this recent interaction. Naïve prey that cannot recognize a predator as dangerous and thus do not alter their response when confronted by that predator are expected to suffer fewer non-consumptive effects (e.g., changes in prey traits) from these predator encounters compared to encounters with their evolved predators for which they display risk-induced trait responses (Sih et al. 2009). However, non-consumptive effects of new/infrequent predators have been little studied (Anson et al. 2013). Persistent exposure to stressors can result in chronic elevation of glucocorticoid hormone levels which can have wide-ranging effects on bodily functions, from energy expenditure to immunosuppression to reproductive inhibition (Sapolsky et al. 2000, Criscuolo et al. 2005, Breuner 2011, Harms et al. 2015). Some consumptive effects of polar bear predation in eider colonies have been monitored (e.g., nest success, Iverson et al. 2014), but future work on eider responses to their recent predators could additionally quantify the non-consumptive effects by comparing physiological consequences (e.g., adrenocortical fear response) for eiders nesting in areas with and without bear suppression (e.g., using a landscape-scale manipulation of bear abundance, Anson et al. 2013, Hanssen et al. 2013). Such studies would also reveal whether there are synergistic impacts of polar bears on an eider hens' reproductive value in terms of direct clutch loss and female reproductive condition.

The lack of a discriminating FID response to a perceived threat may reflect eiders' reliance on crypsis as a defense during incubation, which may prevent the activation of the flight response (e.g., Seltmann et al. 2012) by increasing their tolerance to a detected predator (Ydenberg and Dill 1986, Fernández-Juricic et al. 2002), such as the arctic fox. However, other alternative measures of risk perception can be assessed in future studies. For instance, measures of tolerance can be incorporated into future studies by 1) linking physiology and behaviour to estimate the gap distance between when eiders become alert (e.g., change in heart rate from baseline, also known as alarm response;

Löw et al. 2008, and/or increased vigilance) to a predator and flush (Fernández-Juricic et al. 2002); or 2) quantifying the amount of time that the focal hen is exposed to the threat stimulus before she flushes (e.g., time from start distance to flush in an experimental predator approach study). Moreover, post-escape responses (i.e., when eiders are less reliant on crypsis) such as displacement distance of an eider from its nest or latency to return to nest and resume incubation following a disturbance can have significant energy costs (e.g., locomotion costs and cost of reheating eggs) or risks (e.g., eggs exposed to predators and inclement weather). Thus, these post-flush responses should also reflect an incubating bird's perception of risk (e.g., Fernández-Juricic et al. 2006, Felton et al. 2018, Dehnhard et al. 2020), and future research should therefore examine these responses in greater detail.

Measures of heart rate used in the current study (i.e., absolute heart rate and magnitude of heart rate change) allowed us to assess relative perceived risk across different visual predator stimuli and variation in realized polar bear predation risk. Across both our studies, we observed that eiders respond with both slight tachycardia and bradycardia when bears were present on Mitivik Island at various distances from eiders (*Chapter 3*) and when bears (and simulated predation threats) posed an imminent risk (i.e., directly targeted their nest, *Chapter 2*), respectively. To our knowledge, such a response pattern in heart rate is the first recorded in a free-living animal and therefore warrants further investigation with increased events ending in actual nest predation to quantify eiders' pattern of response to different stages of threat by polar bears. We assumed that modulation of heart rate has a fitness-driven role since stress-induced increases in heart rate responses can be energetically costly (e.g., European starlings

Sturnus vulgaris, Cyr et al. 2008). Hawkins et al. (2000) investigated the relationship between non-incubating eider resting heart rate and energy expenditure, but further work that simultaneously monitors heart rate and energy expenditure of incubating hens in the field is needed to determine if slight changes in heart rate in response to the threat of polar bear predation observed in the current study significantly alter metabolic energy use. Moreover, some heart rate responses (i.e., tachycardia) may not be long enough to expend significant amounts of energy (e.g., Cyr et al. 2008). Thus, further investigation of heart rate recovery time is needed to estimate the relative energetic costs of eliciting a mild heart rate response (e.g., Ellenberg et al. 2013), and obtain further understanding of perceived risk to threat (e.g., Viblanc et al. 2012).

Lastly, little is known on eiders' capacity to respond physiologically to predation stressors. To the best of our knowledge, only one study has quantified eider heart rate to threat (i.e., human handling) and used a small sample size (n=3) of non-incubating captive birds (Cabanac and Guillemette 2001); thus, their responses may not reflect responses by free-living nesting eiders. Future work that quantifies eider heart rate to simulated capture as a metric for eider maximum cardiovascular stress response is needed to be able to relate eiders' level of perceived risk to their maximum capacity to respond to risk in order to gain a better understanding of the biological significance of cardiac responses to polar bears.

Conclusion

Northern Inuit communities rely on eiders for sustenance such as meat, eggs, and down (reviewed in Waltho and Coulson 2015), therefore, any impacts to the eider population will not only cause ecological effects, but will also impact Northern communities socially. In addition, humans and bears are now in direct conflict for access to resources such as eider eggs, and the presence of polar bears while Inuit are interacting with eiders (i.e., down collecting, egg-picking) further places humans in direct predation risk (H.G.G. pers. comm.). As such, eider-polar bear interactions therefore have wide-ranging consequences. Local population decline in breeding eiders can occur as a result of egg consumption by polar bears or polar bear-induced eider dispersal or aggregation behaviour (i.e., non-consumptive effects). Collectively, results from my studies suggest that consumptive effects of polar bear predation are relatively more important to eider population dynamics, since eiders did not show optimal responses to polar bears. Future studies should link eider antipredator responses to polar bears and their associated consumptive (i.e., adult survival and recruitment) and potential non-consumptive consequences to determine the downstream population effects eiders are expected to endure as an indirect consequence of anthropogenic climate change. This knowledge can be used to refine the Nunavut and Canadian government management plans for the Mitivik Island eider population. For example, predator control (e.g., chasing polar bears as done in Hanssen et al. 2013; or use of nest exclosures such as electric fences, Lokemoen et al. 1982, Isaksson et al. 2007, Davies and Rockwell 2016, Storer et al. 2017) could mitigate the negative consequences (e.g., on recruitment) and conserve important eider populations. Moreover, as government and local communities plan to establish a Marine Protected Area in Northern Hudson Bay, increased population survey efforts in combination with knowledge from Northern communities could help identify potential nesting habitat that may be suitable for eiders to avoid overlap with their recent egg predator. Greater protection to Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary and other critical foraging and nesting habitat is needed to lessen the impact of human rapid environmental change in populations that endure high reproductive fitness consequences as a result of increased predation risk by polar bears.

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APPENDICES

Appendix A Heart rate recorder settings

Table A1. Tascam DR-05X recorder settings selected to record common eider (*Somateria mollissima*) heart rate

Settings	Selected Setting
File Format (FORMAT)	MP3 320kbps
Sampling Frequency (SAMPLE)	48k
Sampling Type (TYPE)	Stereo
Maximum File Size (SIZE)	2GB
Microphone Power (MIC POWER)	ON
Low Cut Filter Status (LOW CUT)	OFF
Prerecording (PRE REC)	OFF
AUTO TONE function (AUTO TONE)	OFF
AUTO TONE Length (TONE SECS)	1sec
AUTO TONE Volume (TONE VOL)	-12dB
Recording Automatically (AUTO REC)	OFF
Input Signal Level (LEVEL)	-6dB
Input Level	60

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