Research Paper

Heightened heart rate but similar flight responses to evolved versus recent predators in an Arctic seabird

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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 seabirds and their eggs by the polar bear (*Ursus maritimus*) is a consequence of bears shifting to terrestrial food resources through a shortened seal-hunting season. We examined antipredator responses in a colony of nesting Common Eiders (*Somateria mollissima*) on East Bay Island, Nunavut, Canada, which is exposed to established nest predators, such as arctic fox (*Vulpes lagopus*), but also to recent increases in polar bear nest predation due to the bears' lost on-ice hunting opportunities. Given eiders' limited eco-evolutionary experience with bears, we aimed to experimentally contrast eider responses to the recent predation pressure by polar bears to those induced by their more traditional mammalian predator, the arctic fox. Our goal was to characterize whether this population of eiders was vulnerable to a changing predator regime. Using simulated approaches of visual stimuli of both predator types, we measured eider heart rate and flight initiation distance as physiological and behavioral metrics, respectively, to characterize the perceived risk of and subsequent response to imminent threat posed by these two predators that differ in historical encounter rates. Eider heart rates were more responsive to impending visual cues of arctic foxes compared to polar bears, but birds responded behaviorally to all simulated threats with similar flight initiation distances. Results suggest eiders may not perceive the full risk that bears pose as egg and adult predators, and are therefore expected to suffer negative fitness consequences from this ongoing and increasing interaction. Eiders may therefore require conservation intervention to aid in their management.

Rythme cardiaque plus élevé mais réaction de vol similaire face aux prédateurs évolués par rapport aux prédateurs récents chez un oiseau marin de l'Arctique

RÉSUMÉ. Dans l'Arctique, la dynamique prédateur-proie change en raison des modifications qui adviennent dans la phénologie des glaces de mer. La fréquence accrue de la prédation par l'ours blanc (*Ursus maritimus*) d'oiseaux marins nichant en colonie et de leurs œufs découle du fait que les ours se tournent vers les ressources alimentaires terrestres en raison de la saison de chasse aux phoques plus courte. Nous avons examiné les réactions anti-prédation d'Eiders à duvet (*Somateria mollissima*) nichant en colonie sur l'île d'East Bay, au Nunavut, Canada, qui sont exposés à des prédateurs de nids établis, tels que le renard arctique (*Vulpes lagopus*), mais aussi à une hausse récente de la prédation de nids par l'ours blanc en raison de la perte d'occasions de chasse sur la glace pour l'ours. Compte tenu de l'expérience éco-évolutive limitée des eiders avec les ours, nous avons cherché à contraster de façon expérimentale les réactions des eiders à la pression de prédation récente par les ours blancs avec celle induite par leur prédateur mammifère plus traditionnel, le renard arctique. Notre objectif visait à déterminer si cette population d'eiders était vulnérable à un changement de régime de prédation. Au moyen d'approches simulées de stimuli visuels des deux types de prédateurs, nous avons mesuré le rythme cardiaque des eiders et la distance d'initiation de vol comme mesures physiologiques et comportementales, respectivement, pour caractériser le risque perçu et la réaction subséquente à la menace imminente posée par ces deux prédateurs, qui diffèrent dans leur taux de rencontres historique. Les fréquences cardiaques des eiders augmentaient davantage avec les signaux visuels imminents de renards qu'à ceux d'ours, mais les oiseaux réagissaient à toutes les menaces simulées avec des distances d'initiation de vol similaires. Nos résultats indiquent que les eiders ne perçoivent peut-être pas tout le risque que représentent les ours en tant que prédateurs d'œufs et d'adultes, et qu'ils devraient donc subir des conséquences négatives en termes de condition physique du fait de cette interaction continue et croissante. Une intervention visant la conservation des eiders pourrait donc être nécessaire.

Key Words: *antipredator behavior; arctic fox; arctic nesting seabird; Common Eider; heart rate response; polar bear; predation threat*

INTRODUCTION

Climate change is predicted to have a variety of biological and ecological consequences, from advancements in seasonal reproduction dates and migration (Thackeray et al. 2010) to distributional shifts toward more productive landscapes (e.g., Killengreen et al. 2007, Jepsen et al. 2008) and to altered species interactions (e.g., Gilg et al. 2009, Hamilton et al. 2017). As species respond to climate change by shifting the timing and degree of

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inter-specific spatial overlap, interactions may be altered between predators and prey (reviewed in Donnelly et al. 2011), such that rare interactions, relative to the prey's main predator(s), become more common. Because effective antipredator responses are dependent on the ability of prey to perceive predators as a threat, threat assessment of a predator can provide insight into a prey's ability to adapt to the increasing frequency of interactions (Ehlman et al. 2019). Prey have evolved various antipredator adaptations that lower their risk of predator confrontation and enhance their likelihood of escape if confronted (Lima and Dill 1990, Guiden et al. 2019). However, although some prey will have the necessary mechanisms to adaptively respond to unfamiliar or uncommon predators, others may exhibit maladaptive responses (Salo et al. 2007, Sih 2013, Sih et al. 2016, Ehlman et al. 2019). Prey's experience with a predator on both evolutionary (i.e., experience over multiple prey generations) and ecological timescales (i.e., recent experience over a prey's lifetime) influences their ability to detect and respond adaptively to the threat posed by increased encounters with a relatively rare predator (Carthey and Blumstein 2018). Moreover, prey are more likely to identify a predator as a threat and respond accordingly (i.e., adaptively) if the predator shares archetypal similarity to predators to which they have adapted in terms of sensory (e.g., visual, olfactory, acoustic), behavioral (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 recent threat (Ehlman et al. 2019). By contrast, if prey fail to adequately recognize a threat, naïve prey can either lack an antipredator response altogether or display an inappropriate one (Carthey and Blumstein 2018, Guiden et al. 2019). Consequently, increased interactions with relatively rare predators may have larger negative effects on prey populations than do traditional predators (Salo et al. 2007), placing already vulnerable prey populations at higher risk of decline.

Physiological metrics can indicate a prey's awareness of a predator, and vertebrates can display neurophysiological responses to stressors in the absence of or preceding any behavioral responses (reviewed in Ydenberg and Dill 1986, Weston et al. 2012). For example, an animal's cardiac stress response often occurs in less than one second of threat detection, where the sympathetic and parasympathetic nervous systems release circulating catecholamines (i.e., epinephrine and norepinephrine) and acetylcholine, which have a direct effect on heart rate (reviewed in Lang et al. 1997, Sapolsky et al. 2000, Carravieri et al. 2016). Monitoring the magnitude of heart rate changes during predator encounters can provide a reliable measure of a prey individual's assessment of a stimulus and perceived risk (Ydenberg and Dill 1986, Nephew et al. 2003, de Villiers et al. 2006, Viblanc et al. 2015, Wascher et al. 2022). Like changes in heart rate, stress-induced physiological mechanisms prepare the body for overt action, facilitating subsequent behavioral responses (e.g., predator avoidance), such as flight (escape) responses (e.g., Gabrielsen et al. 1977). Flight initiation distance (FID), the distance at which prey can be approached by a perceived threat prior to fleeing, is a commonly used metric to quantify the behavioral stress response to predation risk (e.g.,

Blumstein 2006, Tarlow and Blumstein 2007). Because of the energy costs associated with flight behavior as well as the concomitant downstream survival and reproductive fitness consequences, prey should modulate their flight response according to their perception of risk. Generally, prey tend to flee sooner (i.e., at greater distances) to higher perceived levels of predation risk (Ydenberg and Dill 1986, Cooper and Frederick 2007). The evaluation of physiological and behavioral responses, both independently (Nephew et al. 2003) and in concert, can 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). Consequently, this information will provide a better characterization of the vulnerability of prey to predation attempts that are increasing in frequency and intensity, thereby better informing predictions of higher-level population responses and subsequent conservation measures (see Bro-Jørgensen et al. 2019).

Here, we use an experimental approach to assess the perception and response of Arctic-nesting Common Eider ducks (*Somateria mollissima*, hereafter eider) to the predation risk posed by polar bears (*Ursus maritimus*) and arctic foxes (*Vulpes lagopus*). As an indirect effect of climate change, polar bears, a species traditionally dependent on ice as a platform to hunt marine mammals (Thiemann et al. 2008), are coming ashore earlier from a shortened seal-hunting season and are now temporally and spatially overlapping on land with colonial nesting eiders (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, Barnas et al. 2020, Jagielski et al. 2021a, Jagielski et al. 2021b). Polar bear presence in eider nesting colonies had been seldomly reported over the past century (e.g., Lønø 1970), but eider encounters with polar bears have steadily increased over the past few decades. These increased encounter rates are now associated with reduced nest success in some eider colonies, an impact far exceeding that caused by their traditional egg predators at some locations (Iverson et al. 2014, Prop et al. 2015).

Eider nesting strategies are suggestive of having evolved to predation from both avian (e.g., gulls, *Larus* spp.) and land-based mammalian egg predators (e.g., arctic fox; Larson 1960). Eiders nest primarily on small islands to avoid land-based mammalian predators (Larson 1960, Ahlén and Andersson 1970), and in many populations, hens form high-density nesting aggregations (Chaulk et al. 2007) for communal defense and predator warning (Schmutz et al. 1983, Mehlum 1991). Hens further 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). The main antipredator behavior toward polar bears during the eider breeding season is phenological avoidance. However, in Arctic-breeding populations, colonial nesting on islands may no longer ensure a reduction in nest predation by polar bears, because bears can swim to and from islands during the late-stage incubation and duckling-hatching period when ice begins to break up (Pagano et al. 2012). Further, recent documented bear presence in Arctic eider nesting colonies has been positively correlated with nest abundance (Iverson et al. 2014), suggesting that aspects of current eider breeding ecology are no longer effective for avoiding bears (Dey et al. 2017).

Given the rapidly changing predation pressure posed by polar bears, it is unknown whether eiders currently have the adaptive capacity to respond to this increasing threat. Polar bears differ from eiders' more traditional mammalian predator, the arctic fox, in several predatory cues, such as body size (with bears approximately 3.5 times longer and 5 times taller than foxes; http://www.worldwildlife.org/species/arctic-fox, http://www.worldwildlife.org/species/polar-bear; Atkinson et al. 1996, Amstrup 2003, Brudnicki et al. 2011), and egg foraging styles (e.g., slower approach speed by bears, bears lumbering toward a nest as opposed to sneaking like foxes, and full nest predation by bears as opposed to partial predation by foxes; Bahr 1989, Gormezano et al. 2017, Jagielski et al. 2021a). Despite their differences, both predators can easily displace incubating eiders from their nests to gain access to their eggs, and both can prey on hens if they fail to leave (Bahr 1989, Gormezano et al. 2017). Therefore, eiders must modulate their responses to both predators to optimize the trade-off between investing in current reproduction and future survival and reproductive success. Eiders that breed on near-shore islands are now at increasing risk of predation by both predators (Birkhead and Nettleship 1995, Iverson et al. 2014) across the entire breeding season. 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) and across different stages of their life cycle, such as during migration and overwintering (Cox and Lima 2006). However, it is still unknown how eiders perceive and respond, both physiologically and behaviorally, to the increasing risk posed by polar bears, and whether these responses differ in relation to arctic foxes. In our simulated predator approach, we quantified eider antipredator responses (both changes in heart rate and FIDs) to the threat of a simulated approaching predator. Specifically, we tested the hypothesis that, because of the difference in new and historical encounter rates of arctic foxes and polar bears by eiders, incubating eiders should be relatively naïve and therefore have a lower perception of risk to polar bears compared to arctic fox. As such, we predicted that female incubating eiders approached by a simulated polar bear would exhibit a lower heart rate response and concomitantly shorter FIDs when compared to an arctic fox.

METHODS

Study species and area
This study was conducted on free-living eiders nesting at East Bay Island, Nunavut, Canada (64°02' N, 81°47' W), located in Southampton Island's Qaqsauqtuuq (East Bay) Migratory Bird Sanctuary (Fig. 1). East Bay Island hosts the largest known eider breeding colony in the Canadian Arctic (Inuit Nunangat) and is the only known colony within a 100-km radius (Legagneux et al. 2016). Eiders on East Bay Island initiate laying in late June/early July (Jean-Gagnon et al. 2018), and undergo a subsequent 24-day fasting incubation period (Parker and Holm 1990, Bottitta et al. 2003). The East Bay eider colony has experienced many population setbacks during the past 25 years. During 1997 to 2005, numbers fell dramatically from being overharvested in their overwintering grounds in southwest Greenland (Buttler 2009). With strict harvest regulations in place, the population began to recover (Burnham et al. 2012), but between 2005 and 2007, eiders on the island then experienced an avian cholera outbreak that

killed over 3000 adult females (Mallory et al. 2009) and resulted in a 90% reduction in duckling survival (Descamps et al. 2011). Eiders are now experiencing a high (almost daily) encounter rate with bears on the island in early July (Smith et al. 2010, Iverson et al. 2014, Jagielski et al. 2021a), with duckling recruitment rates in more recent years being close to zero (Gilchrist and Love, *personal observations*). Because of increasing frequency of bear visits, field work outside the safety of the research compound is limited during this time, and we therefore timed our study for the end of June 2019, during the laying/early incubation period of eider ducks.

Fig. 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 (East Bay Island) within East Bay, Nunavut, Canada. Canadian Provinces and Territories map layers provided by ESRI online, accessed 30 May 2018.
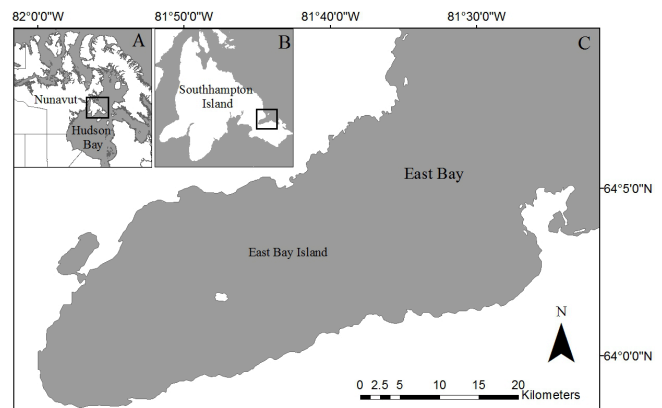
The predator system
Polar bears have been documented visiting our field site by local Inuit from the nearby community of Salliq (Coral Harbour), Nunavut, for decades and since researchers began to study the colony in 1997. However, the East Bay Island eider colony experienced a sevenfold increase in polar bear nest predation between the 1997–2001 and 2008–2012 study periods (Smith et al. 2010, Iverson et al. 2014). From 2005 to 2018, researchers have reported instances of arctic fox and polar bear presence on the island during the eiders' breeding season. Using these data, we calculated the range and mean number of days each species was sighted on the island. For safety purposes and to maintain the integrity of the colony for use in research, the presence of both polar bears and arctic foxes on the island was discouraged during the field season (late May to 29 June). Bears and foxes were therefore unable to forage freely prior to experimentation, and this was evident across 84 trail cameras deployed on the island for another project (Geldart et al., *unpublished manuscript*). Thus, we do not expect results to be influenced by within-season experience with predators.

Heart-rate monitoring
We deployed heart-rate monitoring equipment on active eider nests (n = 11) on 24 and 25 June 2019. Each nest was equipped

with an artificial egg heart-rate monitor (outlined in Geldart et al. 2022). Heart-rate monitors consisted of a 3D-printed plastic eider egg (sub-elliptical, 7.4 cm long x 4.8 cm 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 (approximately 183 cm long, 3.5 mm stereo plug; Fig. 2). The primary microphone was situated at the end of a 3D-printed plastic funnel for amplified sound, whereas the secondary microphone was placed within a hole and flush with the surface of the egg, to be used as a backup in case the eider shifted positions on the egg (i.e., off the primary microphone). Weight was caulked to the inside of the bottom half of the egg to help ensure the egg maintained the appropriate 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., approximately 11 to 12 days of continuous recording), the recorder was attached to an external assembled battery pack (with 24 AA lithium-ion batteries). See Table A1.1 in Appendix 1 for all recorder settings used. The recorder and battery pack were situated within a weatherproof, camouflaged storage box (29.0 cm long, 13.7 cm wide, 18.0 cm high).

We chose to deploy heart-rate monitoring equipment on nests located on the periphery of the island to limit disturbance from our experimental approaches in dense portions of the colony and to reduce variability in nest density and predator warning coming from nearby nests. However, nests selected for the current study did not differ from a group of additional nests monitored across the island (n = 38) in terms of lay date (i.e., range: 9 to 24 June and 10 to 24 June, respectively) and incubation stage (i.e., mean age of first laid egg on 25 June: average (± SD) of 4 ± 4 days and 4 ± 3 days, respectively).

We placed artificial eggs in nests containing 1 to 5 eggs at the time of equipment deployment. During deployment, the location of each study nest was marked by GPS for ease of relocation prior to experimental approaches. Study nests were each located an average (± SD) of 288 ± 151 m (range: 37–554 m) apart from each other (Fig. 3). The first-laid egg from each study nest was collected for another project (e.g., Smith et al. 2021) and was also immediately candled to estimate incubation stage (i.e., the number of days since an eider laid their first-laid egg on the day of heart-rate monitoring equipment deployment, allowing us to calculate incubation stage for the days of simulated-predator approaches; Weller 1956). 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 1 m from the nest, and the box and cable were secured and concealed under rocks from 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 h (range: 0.001–6.61 h), as measured by sounds on the heart-rate recordings of the experimenter vacating the area and the resumption of eider heart sounds. Experiments began approximately 14 h after the final heart-rate monitor had been deployed.

Fig. 2. Experimental heart rate recorders, with photographs of (A) separate halves of 3D-printed Common Eider (*Somateria mollissima*) egg (a), microphones (b), and funnel (c), two halves of plastic 3D-printed egg assembled (d), artificial eider egg covered with a balloon membrane (e); (B) digital audio recorder (Tascam DR-05X) (f) and external battery pack (g); and (C) storage box (h) and artificial-egg (i), ready for deployment. Ruler in image (A) and (C) is 150mm long for scale.
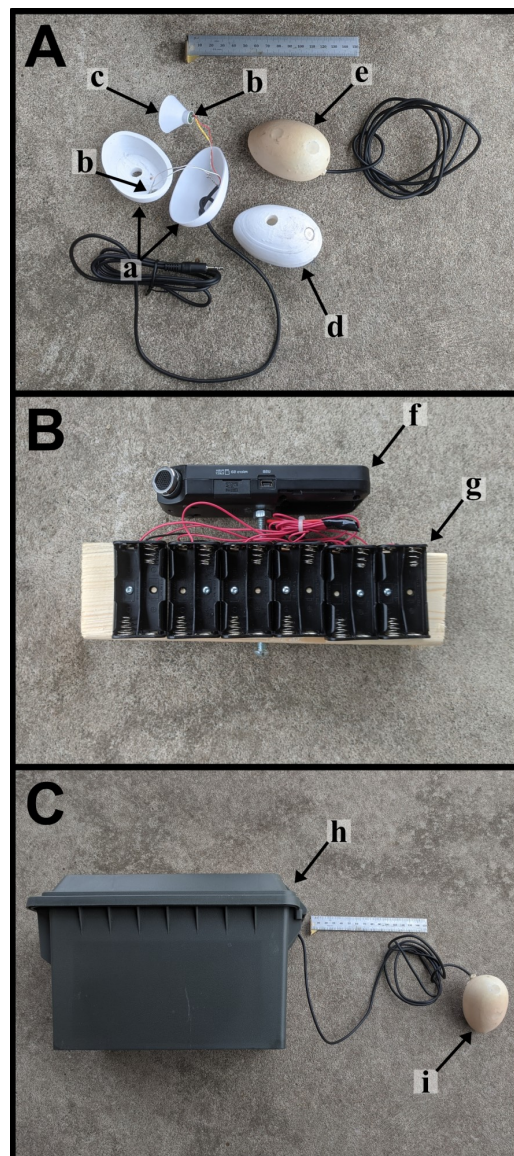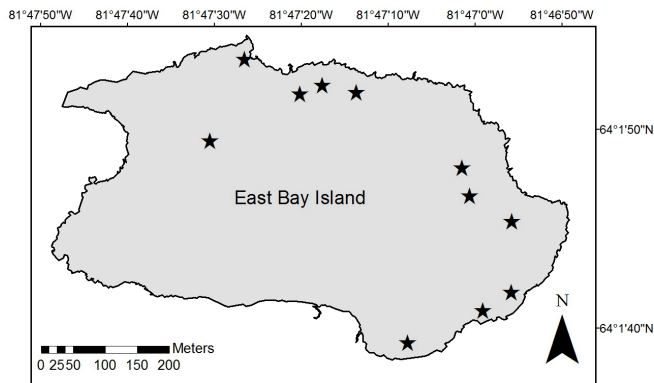
Fig. 3. Distribution of focal Common Eider (*Somateria mollissima*) nests (black stars) across East Bay Island, Nunavut, Canada. Map layer created using ArcMap v10.6.1 (Esri, Redlands, California, USA).

Fig. 4. Images of our experimental predator stimuli: 1.37 m diameter grey umbrellas with to-scale images of (A) polar bear (*Ursus maritimus*), (B) arctic fox (*Vulpes lagopus*), and (C) plain for control. Images include approximate measurements (cm, width and length) of the animal's head. Images sourced on the internet from Creative Common websites.


Predator-simulated experimental protocol

We used a randomized experimental predator-model approach to test the relative responses of birds to a visual representation of a bear and a fox, and a control. Predator models were adapted from Jones et al. (2016a). Visual predator stimuli consisted of to-scale images of the different predator types (i.e., polar bear and arctic fox) attached to 137 cm diameter grey umbrellas, with an additional plain, grey umbrella to serve as the control (Fig. 4). Images of a polar bear (approximately 41 cm long and 46 cm wide head, body sizes proportional to head; Fig. 4a) and arctic fox (approximately 15 cm long and 13 cm wide head, body sizes proportional to head; Fig. 4b) were sourced on the internet from Creative Common websites. The visual images represent realistic features that evoke strongest responses in prey: relative body-size differences (Stankowich and Blumstein 2005) and forward-facing head and eye gaze orientation (Carter et al. 2008, Bateman and Fleming 2011, Davidson and Clayton 2016). A previous study in our system also revealed higher responsiveness in eider flushing (i.e., jumping off nest, flying away) to more direct angles of travel and gaze of polar bears (Barnas et al. 2022). Each umbrella had a round slit covered with dark-colored mesh so that the experimenter could locate the study hen and monitor their behavior during an approach without eiders being able to see the experimenter. Our use of umbrellas to display visual predator cues therefore allowed us to remain concealed when taking necessary measurements during the approach, control the direction and pace of the predator stimuli, and offer a suitable control treatment (i.e., blank umbrella).

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 Microsoft Excel to control for possible habituation or sensitization. Each study eider was approached three times (i.e., once by each predator treatment) at 24-h intervals from 26 to 28 June 2019 to avoid any diel variation in antipredator responses (Ferguson et al. 2019). In preparation for each experimental approach, a single experimenter (E.A.G.),
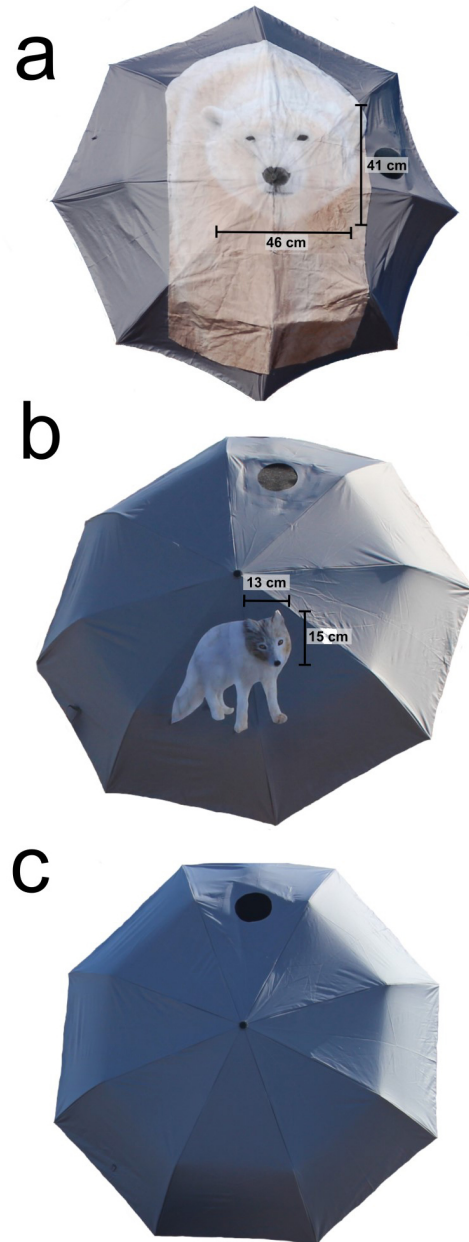
wearing camouflaged and nonreflective gear, crawled into the colony until they reached the location at which they planned to start the approach. Approaches began on average ± SD 22.3 ± 5.26 m (range: 15–33 m) from the study nests (i.e., distances at which the experimenter could spot the nest without disturbing the bird). If focal eiders were absent from their nest prior to an approach,

Fig. 5. Waveforms from heart sounds produced by an incubating focal Common Eider (*Somateria mollissima*) in Audacity v2.3.2 (Audacity Team 2019). At the end, the hen flushes, and heart beats were counted for three 10 s intervals before the hen flushed to a simulated predator approach.
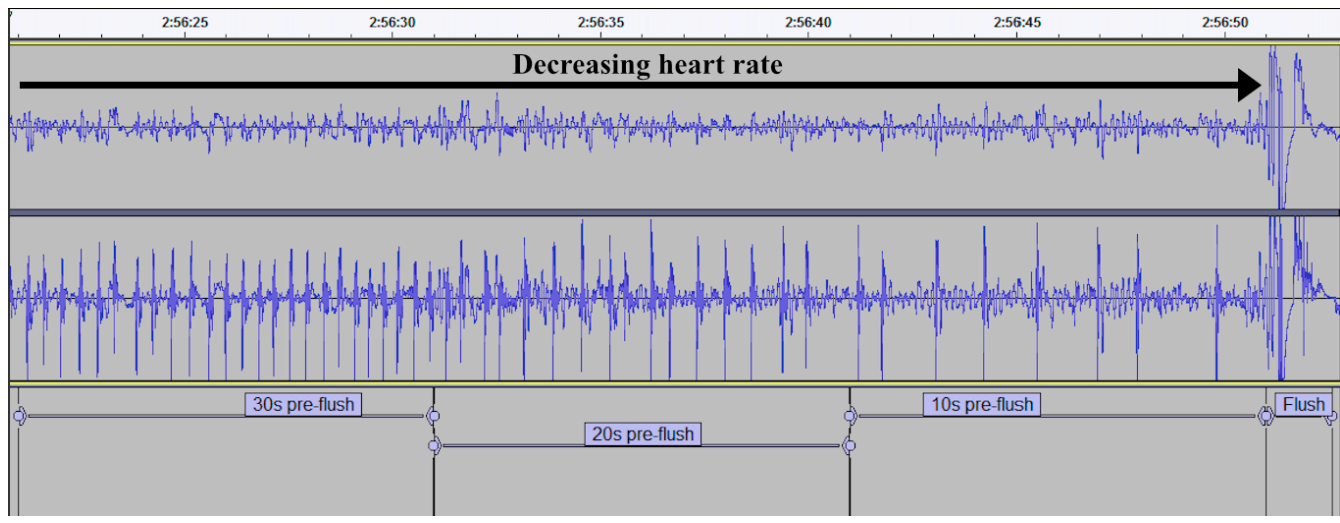
treatments for these individuals were excluded from the experiment (see Results). During each approach, a hand-held recording device was used by the experimenter to dictate all necessary data. To start the approach, the experimenter dictated the start time and slowly opened the umbrella, stood up, and began walking toward the study nest concealed behind the umbrella at a consistent pace of approximately 0.5 meters per second, making sure to keep the predator stimuli upward 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 subsequently measure the distance between the experimenter and the nest as soon as the hen vacated in response to the threat stimuli (i.e., FID) and recorded clutch size (number of eggs, including the artificial egg). Incubation stage during approaches ranged from 2 to 16 days (mean ± standard error [SE]: 6 ± 1 day) and clutch size ranged from 3 to 5 eggs (mean ± SE: 4 ± 0 eggs). When all necessary data were recorded, the experimenter covered the eggs with feather nest down before departing the area to protect the nest from predation by avian predators and extreme temperature. Neighboring focal nests were tested sequentially with a minimum of 11 minutes (mean ± standard deviation [SD]: 22 ± 16 minutes) between approach starting times. Cabanac and Guillemette (2001) found that elevated eider heart rates subsided after only two to three minutes following an acute stress; thus, given both the temporal and spatial distances between nests, we do not believe nearby approaches at one nest influenced responses of subsequent focal birds. Experiments were conducted in low wind, to minimize any disturbance caused by umbrella flutters.

Heart-rate quantification

All nest monitoring equipment was retrieved on 19 July 2019. 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 (E.A.G.) 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., Fig. 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 the heart rate varied as the predator stimuli approached the incubating eider and the eider got closer to flushing (i.e., time until flush). We extracted all samples as .wav files and heartbeat sounds were counted aurally at least twice, and averaged to avoid measurement error and therefore increase accuracy of the counts.

We also opportunistically estimated focal eider heart rate to actual approaching polar bears on East Bay Island, where possible, to confirm responses to our simulated predator were similar to those to actual predators (see Appendix 2). Briefly, our heart-rate recordings of actual polar bear approaches were found to match response patterns to our simulated predator models, indicative of a naturally induced response.

The increasing rate of polar bear nest predation (Iverson et al. 2014, Dey et al. 2017) has made field work at this site increasingly dangerous during the eider reproduction period. Furthermore, with the cancellation of our Arctic field program for seasons 2020 and 2021 because of the Covid-19 pandemic (a communal decision by Inuit community members and our research team), we were further constrained in our sampling efforts. Nevertheless, by focusing our efforts on performing repeated measures on a small sample, we were able to test our treatments while balancing researcher and community safety and health, time limitations, and also limiting disturbance by researchers in an ecologically and culturally important population of birds.

Statistical analyses

Nine of our 11 study eiders produced usable heart rate and FID data, resulting in n = 21 clean heart-rate samples for the "polar bear" approach, n = 24 for control, and n = 27 for the "arctic fox." This resulted in n = 7 usable approaches using the "polar bear" stimulus, n = 8 for the control, and n = 9 for the "arctic fox" stimulus.

We analyzed both eider heart rate (beats/10 s) and 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 (nominal categorical with three levels: polar bear, arctic fox, control), time until flush (ordinal categorical: 10 s, 20 s, and 30 s before flush), and start distance (m; continuous) and their two-way interactions: predator treatment × time until flush interaction, predator treatment × start distance interaction, and time until flush × start distance interaction. We modelled eider FID as a function of predator treatment (categorical with three levels: polar bear, arctic fox, control), heart rate (beats/10 s; continuous) at the 30 s interval before flush, start distance (m; continuous), incubation stage (days; continuous), clutch size (continuous), and the interaction between predator treatment and heart rate. For the FID model, we chose heart rate at the 30 s interval before flush because it had the most complete dataset. We included incubation stage and clutch size in the model because Forbes et al. (1994) discovered an effect of parental investment on nesting female duck FID. Start distance was included in both heart rate and FID models since results from Blumstein's (2003) study suggest that animals respond sooner to a threat as starting distance increases. For both analyses, we included trial day (categorical with three levels: 26, 27, and 28 June) and eider ID (categorical: nine 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 using a Gaussian family and an identity link function 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) by using the backward elimination procedure, leaving in the final model only the fixed effects associated with the outcome, considering a 10% level of significance, a standard retention criterion for backward elimination (Bursac et al. 2008). The final model with retained fixed effects was refitted by using restricted maximum likelihood (REML) estimation. 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 report confidence intervals for all fixed effects (Nakagawa and Cuthill 2007, Fidler et al. 2018, Dushoff et al. 2019), and the contributed variance of random factors in our final models. Using the package *MuMIn* (Bartoń 2019), we additionally 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*.

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), and used α = 0.1 for all statistical significance tests to minimize type II errors (Baker and Mudge 2012, Mudge et al. 2012, Schumm et al. 2013). Model predictions and visualizations were done by using packages *ggeffects* (Lüdecke 2018) and *ggplot2* (Wickham 2016).

RESULTS

The predator system

From 2005 to 2018, observation log books by researchers revealed the number of days that arctic foxes were sighted on the island to range from 3 to 19 days (mean 9 days) throughout the eiders' prospecting, laying, and incubation stages. Thus, encounter rates with foxes on the island have occurred almost annually but for short durations, whereas since 2016, eiders have experienced continuous, daily co-occurrence with polar bears on the island (range: 5–31 days; mean: 17 days), often with more than one bear in attendance at a time.

Heart rate

Heart rate ranged from 3 to 39 beats/10 s (mean ± SE: 18 ± 3 beats/10 s) in response to the control, 6 to 49 beats/10 s (mean ± SE: 23 ± 3 beats/10 s) to arctic fox, and 2 to 26 beats/10 s (mean ± SE: 13 ± 2 beats/10 s) to polar bear. Our model with heart rate as a function of predator treatment and time until flush (marginal R^2 = 0.063, conditional R^2 = 0.899; Table 1) best explained our data according to our backward elimination approach, and it had the best model fit according to AICc (Table 2). In this model, we detected a statistically significant difference in eider heart rate in response to the predator treatment ($F_{2,49.40}$ = 14.91, P < 0.00001; Fig. 6a, Table 1), with eiders displaying a significantly higher heart rate in response to the arctic fox model than to both the control (Tukey's HSD: P = 0.001, estimate ± SE = -4.91 ± 1.41) and polar bear models (Tukey's HSD: P < 0.0001, estimate ± SE = -7.67 ± 1.42; least square [LS] means ± SE heartbeats: control 16.3 ± 4.40; arctic fox 21.2 ± 4.36; polar bear 13.5 ± 4.40). Heart rate in response to the polar bear stimulus was marginally lower than the control (Tukey's HSD: P = 0.055, estimate ± SE = 2.75 ± 1.40). Additionally, we detected a statistically significant change in heart rate with time until flush ($F_{2,48.90}$ = 2.47, P < 0.1): regardless of predator type, eider heart rate decreased the closer to flush (significant difference between 10 s and 30 s: Tukey's HSD: P < 0.05, estimate ± SE = -2.96 ± 1.36; Figure 6a; Table 1). Within our random effects structure, we detected the most variance for eider ID (Table 3), suggesting a large degree of inter-individual variation in heart rate. This was further supported by our large conditional R^2.

Flight initiation distance

Flight initiation distance ranged from 2.95 to 17.7 m (mean ± SE: 9.0 ± 2.1 m) in response to control, 3.2 to 15.1 m (mean ± SE: 7.9

Table 1. Mixed effect model results for fixed effects used to explain variation in heart rate among nesting Common Eiders (*Somateria mollissima*) on East Bay Island in the most competitive model according to backward stepwise regression and Akaike Information Criterion (AICc) model selection. CI, confidence interval.

Model parameter	Estimate ± SE	95% CI
Intercept	16.268 ± 4.39	7.23 to 25.21
Polar bear[†]	-2.755 ± 1.40	-5.45 to -0.07
Arctic fox[†]	4.911 ± 1.41	2.20 to 7.60
10 s until flush[‡]	2.092 ± 0.96	0.24 to 3.93
20 s until flush[‡]	0.351 ± 0.94	-1.45 to 2.16

[†]Reference category = control treatment.
[‡]Reference category = 30 s until flush.

Fig. 6. Incubating female Common Eider (*Somateria mollissima*): (a) heart rate (beats/10 s) depending on time until flush (s), and (b) flight initiation distance (m) in response to experimental approaches by simulated predators. Red points and vertical lines are based on model predicted values ± 95% confidence intervals, respectively.

Fig. 7. Incubating female Common Eider (*Somateria mollissima*) flight initiation distance (m) in response to eider heart rate (beats/10 s) at the 30 s interval before flush during experimental approaches by simulated predator. Solid and dashed lines are based on model predicted values ± 95% confidence intervals, respectively.
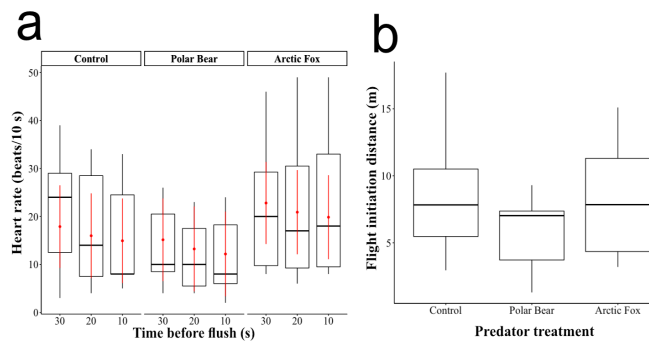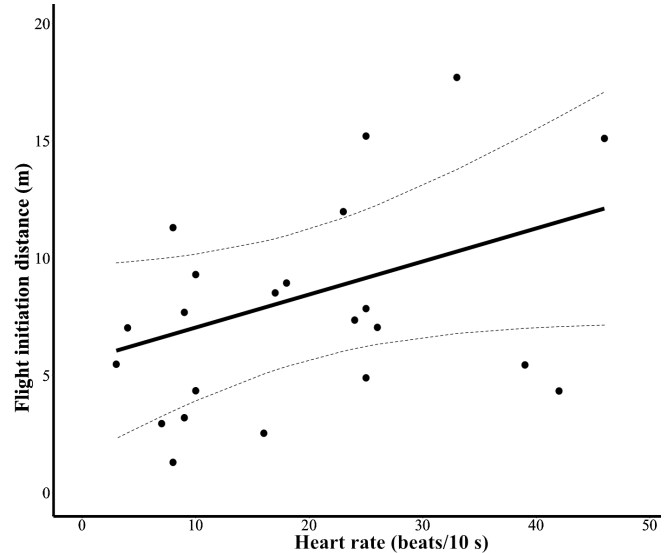

± 1.7 m) to arctic fox, and 1.3 to 9.3 m (mean ± SE: 6.2 ± 1.1 m) to polar bear (Fig. 6b). Heart rate at the 30 s interval before flush ranged from 3 to 46 beats/10 s (mean ± SE: 20 ± 3 beats/10 s). Our model with FID was best explained as a function of the single fixed effect of heart rate (marginal R^2 = 0.139, conditional R^2 = 0.764; Table 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 (Fig. 7). According to AICc, the final model received equal support to the intercept-only model (Table 5), in that variation in FID can also be explained by our random effect structure (conditional R^2 = 0.883, Table 4); namely, eider ID (Table 6), again suggestive of a large degree of inter-individual variation in behavior.

DISCUSSION

We experimentally demonstrated that incubating female eiders showed differential stress-induced heart rate responses to predator imagery, with eiders displaying a significantly higher heart rate in response to the arctic fox model than to both the control and polar-bear models, as well as a higher magnitude of response to the fox than bear when compared to the control.

However, birds did not show differential FIDs in response to the three predator stimuli. Although we acknowledge that our sample size is small in this present study (i.e., based on one year of experimentation), our results suggest that female eiders may not perceive the full risk posed by polar bears in comparison to arctic foxes, particularly given the recent documented increase in rates of polar bear encounter rates on colonies (Smith et al. 2010, Iverson et al. 2014, Prop et al. 2015, Dey et al. 2017, Jagielski et al. 2021a). Importantly, we also found a large degree of inter-eider variation in heart rate and especially FID responses, which we believe warrants further research to relate these responses to different coping styles. Here we discuss what our findings might suggest for the capacity of eider ducks to respond to their more recent primary egg predator, the polar bear, and detail possible fitness costs and downstream population effects from this climate-induced increase in nest predation by polar bears.

Differential heart rate responses to evolved predators

Given eiders' only recent increasing encounters with polar bears, and bears' archetypal differences with eiders' traditional mammalian egg predators, we hypothesized that eiders would be less responsive to approaching bears relative to arctic foxes. We found partial support for this prediction for eider heart rate only, in 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, and marginally lower heart rates when approached by a polar bear stimulus compared to a control stimulus. Eiders could have reacted to the experimental predation threats in two opposing ways: (1) by using an active

Table 2. Predicting Common Eider (*Somateria mollissima*) heart rate (beats/10 s) on the basis of 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. The null model is represented by "heart rate ~ 1."

Model	Model rank	K	AIC$_c$	ΔAIC$_c$	w_i
Heart rate ~ predator treatment + time until flush	1	8	422.2	0.00	0.726
Heart rate ~ predator treatment + time until flush + start distance	2	9	424.9	2.69	0.189
Heart rate ~ predator treatment + time until flush + start distance + predator treatment*start distance	3	11	426.8	4.59	0.073
Heart rate ~ predator treatment + time until flush + start distance + predator treatment*start distance + time until flush*start distance	4	13	430.4	8.18	0.012
Heart rate ~ 1	5	4	440.1	17.87	0.000
Heart rate ~ predator treatment + time until flush + start distance + predator treatment*start distance + time until flush*start distance + predator*time until flush	6	17	441.8	19.56	0.000

Table 3. Model parameter variance and standard deviation for random effects used to explain variation in heart rate among nesting Common Eiders (*Somateria mollissima*) on East Bay Island in the most competitive model according to backward stepwise regression and AICc model selection.

Model parameter	Variance ± SD
Eider ID	154.879 ± 12.45
Trial day	2.845 ± 1.69
Residual	19.011 ± 4.36

Table 4. Mixed effect model results for fixed effects used to explain variation in flight initiation distance (FID) among nesting Common Eiders (*Somateria mollissima*) on East Bay Island in the most competitive models according to backward stepwise regression and Akaike Information Criterion (AICc) model selection. CI, confidence interval.

Model parameter	Estimate ± SE		95% CI	
	FID ~ heart rate	FID ~ 1	FID ~ heart rate	FID ~ 1
Intercept	5.635 ± 2.07	8.553 ± 1.70	1.60 to 9.72	5.06 to 12.09
Heart rate	0.141 ± 0.08	NA	-0.01 to 0.30	NA

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. This latter response 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 1995, Alboni et al. 2008, Löw et al. 2008). We observed that eider heart rates generally decreased immediately prior to flushing regardless of predator 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 to all three experimental threat stimuli given the cryptic camouflage and nesting strategies of female eiders. Whereas 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 (i.e., bradycardia preceded by acceleration of heart rate; e.g., red deer *Cervus elaphus* calves, 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 maintained bradycardia right up until the point of flushing from their nests, suggesting that both tachy- and bradycardia are mechanisms for quick flight. Notably, despite our limited sample size, our mean heart rate values were largely within the ranges previously reported for eider diving bradycardia (mean 93–310 beats/min; Hawkins et al. 2000) and handling-induced stress studies (approximate mean 150–220 beats/min, Cabanac and Guillemette 2001). Altogether, our results indicate that eiders recognize both predator stimuli as a threat. Nonetheless, even as eiders went into bradycardia, they still exhibited a comparatively larger heart rate response to arctic foxes, suggesting a stronger recognition and response to these mammalian predators.

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 their more limited eco-evolutionary experience with polar bears compared to fox. We found that although eiders may differentially recognize an arctic fox and polar bear as a threat physiologically, contrary to our predictions, eiders did not display a difference in FID between the two predator stimuli, with eider ducks found to leave their nest within 1.3 to 17.7 m of an approaching threat stimuli (see Results). 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). However, 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

Table 5. Predicting Common Eider (*Somateria mollissima*) flight initiation distance (FID; m) on the basis of Akaike Information Criterion (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. The null model is represented by "FID ~ 1."

Model	Model rank	K	AIC_c	ΔAIC_c	w_i
FID ~ 1	1	4	129.4	0.00	0.437
FID ~ heart rate	2	5	129.5	0.11	0.414
FID ~ heart rate + clutch size	3	6	131.9	2.43	0.130
FID ~ heart rate + incubation stage + clutch size	4	7	135.7	6.27	0.019
FID ~ predator treatment + heart rate + incubation stage + clutch size	5	9	144.3	14.84	0.000
FID ~ predator treatment + heart rate + start distance + incubation stage + clutch size	6	10	151.3	21.83	0.000
FID ~ predator treatment + heart rate + start distance + incubation stage + clutch size + predator treatment*heart rate	7	12	168.5	39.08	0.000

Table 6. Model parameter variance and standard deviation for random effects used to explain variation in flight initiation distance (FID) among nesting Common Eiders (*Somateria mollissima*) on East Bay Island in the most competitive models according to backward stepwise regression and Akaike Information Criterion (AICc) model selection.

Model parameter	Variance ± SD	
	FID ~ heart rate	FID ~ 1
Eider ID	13.239 ± 3.64	19.521 ± 4.42
Trial day	0.800 ± 0.89	0.872 ± 0.93
Residual	5.289 ± 2.30	2.705 ± 1.64

by Guiden et al. 2019). Nevertheless, in a study of eider FID to actual polar bears and opportunistic egg-predator Herring Gulls, Barnas and colleagues (2022) similarly found FID to be insensitive to predator type; instead, predators differentially influenced flush style (e.g., walk, jump, or fly off nest).

We did, however, detect a weak link between stress-induced physiology and behavior in response to threat stimuli; birds in our study that responded with a higher heart rate to approaching predators were more likely to have longer FIDs. This is consistent with the two response strategies that animals employ when reacting to challenges (i.e., active versus passive defense strategies). For instance, eiders that had higher heart rates at 30 s 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 and Temple 1995, Alboni et al. 2008). Based on this, we would expect eiders to have the longest FID to foxes, for which they displayed the highest heart rate, and shortest to bears, for which they had the lowest heart rate. However, we failed to detect such a direct behavioral response in the current study. 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. Or, as mentioned above, eiders may employ different "flight-initiation" behaviors in terms of how they flush from the nest in response to differences in perceived threat (Barnas et al. 2022). Finally, our measured FID values were within the range previously reported in an eider human-approach study (approximate means 0–20 m, Seltmann et al. 2014), and actual polar bear study (9.1 ± 4.1 m, range: 0.9–25.7 m; Barnas et al. 2022).

Future directions in studies of seabird responses to predation risk

Although we experimentally tested sensitivity of eiders to visual cues of predators that historically differed in frequency, prey use multiple cues to assess threats and other tactics to respond to threats (Fernández-Juricic et al. 2002, Felton et al. 2018, Peers et al. 2018, Dehnhard et al. 2020; Barnas et al. 2022). For instance, the gap distance between when eiders become alert to a predator (e.g., change in heart rate from baseline and/or increased vigilance) and flush can be used to estimate threat tolerance (Fernández-Juricic et al. 2002, Löw et al. 2008). Threat tolerance, as well as post-escape responses, such as displacement distance of an eider from its nest or latency to return to nest and resume incubation following a disturbance, could reflect an incubating bird's perception of risk when they no longer rely on crypsis (e.g., Felton et al. 2018, Peers et al. 2018, Dehnhard et al. 2020). Future research should therefore examine these responses in greater detail. Moreover, our study should be complemented by a correlative study on eider responses to real predators and matched to nest fate, and to do so would increase the overall characterization of individual antipredator responses in natural conditions and ensuing consequences on population persistence.

In the current study, eiders showed inter-individual variation in heart rate and FID responses to simulated predator approaches. This variation may be driven by experience with predators (potentially related to age). For example, incubating 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). Moreover, Jones et al. (2016b) showed that birds that witnessed an attack on a conspecific triggered a stress response, and such responses may enhance memory of the predator type and allow an individual to employ more appropriate antipredator behaviors in future encounters.

Although it was not logistically possible to determine eider hen age, it may credibly contribute to the variation seen between individuals in our system. In future work of this type, a larger sample size would allow for repeated predator approaches on each individual using the same predator models to examine repeatability of 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). In line with this, several studies have related individual variation in circulating corticosterone (CORT) to antipredator responses in waterfowl, and determined that CORT may differentially mediate physiological and behavioral responses to threats, and may therefore create inter-individual variation in sensitivity to threats (Kralj-Fišer et al. 2010, Seltmann et al. 2012). 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; B. Sadoul et al., *unpublished manuscript*). Thus, by characterizing the extent to which inter-individual responses are consistent across time and situations, and how these responses relate to individual coping style, one can anticipate differential selection on individuals based on their differential capacity for learning and plasticity (Sih et al. 2012), and make predictions on the adaptive capacity of different groups of individual eiders to respond to changes in predator regimes.

Eiders that develop adaptive responses to polar bears by learning and/or undergoing selection for individuals that display plasticity may alter their nest defense behaviors to prevent bears from eating their nests in the short term. In support of this outcome, recent work found polar bears ignore many nests in their immediate trajectory, but do use visual cues (i.e., flushing eider hens) to locate nests (Gormezano et al. 2017, Jagielski et al. 2021a). Thus, a long-distance or inconspicuous flush (i.e., walking as opposed to flying off nest) 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 behavior, Broom and Ruxton 2005; Barnas et al. 2022), because 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 adverse 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 bears' attention away from their nest (i.e., active deception, Kay and Gilchrist 1998; Barnas et al. 2022; Simone et al. 2022).

Upon successive failed reproductive attempts, eiders have been reported to start a replacement clutch at a new nest site within the colony following nest predation (Hanssen and Erikstad 2013), indicative that eiders can adjust their reproductive behaviors on the basis of past experience. Future work that is able to repeat our experiment on hens over multiple nesting attempts, or following confirmed nest predation by polar bears or arctic foxes, could uncover whether eiders show within-season learning of predation risk. This spatial shift in breeding distribution may not

be entirely adaptive; polar bear foraging is prey density–dependent and linked to greater distance to the mainland (Iverson et al. 2014). Consequently, this foraging pattern is predicted to drive increased spacing of eider nests and large-scale relocation closer to the mainland to reduce egg predation by polar bears (Dey et al. 2017), inadvertently increasing arctic fox predation instead. Although this type of response has not been observed to date (Dey et al. 2020), with more experience and possible selection for reproductive flexibility, some female eiders may nevertheless learn to directly assess polar bear predation risk within their lifetimes and choose future nest sites that improve their long-term reproductive fitness.

CONCLUSION

Predation pressure has been steadily increasing for Arctic and northern wildlife (Kubelka et al. 2021), and the consequences of a changing predation landscape on prey fitness are challenging to predict (Guiden et al. 2019). The lesser heart rate response of eiders to polar bear than to arctic fox suggests that eiders may not recognize polar bears as great a risk as arctic foxes (but still a risk, nonetheless). Given the unprecedentedly poor reproductive success (in terms of duckling recruitment) of eiders in recent years due to polar bear egg predation (Iverson et al. 2014), the East Bay Island eider population appears to be at risk of serious decline and therefore needs long-term monitoring. A more mechanistic understanding of predator-prey interactions, such as the study of heart rate and behavioral responses to predators, can improve the targeting and effectiveness of conservation measures (Suraci et al. 2022), by helping us identify which species/populations are most vulnerable to changing predator regimes and are in need of conservation efforts, for example. Whether eider responses to polar bears are learned or influenced by individual coping styles is an important avenue of study to predict selection for adaptive responses. Data from the current study can therefore be used as a first step in examining whether eiders are expected to have the capacity to evolve adaptive responses to increasing polar bear predation. By collecting experimental data on how animals behave in response to the uncertainty posed by recent predation by historically rare predators, future research can then 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).

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Appendix 1

1   Selected Tascam DR-05X recorder settings for "Heightened heart rate but similar flight
2   responses to evolved versus recent predators in an Arctic seabird"
3
4   Table A1.1 Tascam DR-05X recorder settings selected to record Common eider
5   (*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

6

Appendix 2

1   Eider responses to natural polar bear predation for "Heightened heart rate but similar
2   flight responses to evolved versus recent predators in an Arctic seabird"
3
4   We opportunistically estimated focal eider heart rate to actual approaching polar bears on
5   East Bay Island where possible to confirm responses to our simulated predator were
6   similar to those to actual predators. To find instances where eiders flushed in response to
7   polar bears, we reviewed a combination of the following synchronized remote-
8   monitoring equipment used for another set of projects: 1) footage from Browning trail
9   cameras (model: BTC-5HDPX) dispersed across the island to identify periods when
10   polar bears were present on East Bay Island (Geldart et al. In Review); 2) temperature
11   probe data (Tinytag® Plus 2, Smith et al. in prep) to determine instances when an eider
12   was off her nest; and 3) heart-rate recordings during these times to identify acoustic signs
13   that an eider had indeed vacated their nest (e.g., halt in the sound of incubating eider
14   heartbeats) and a polar bear visited their nest (e.g., sounds of bear eating eggs from focal
15   nest or breathing nearby). We confirmed three instances where focally-recorded eiders
16   flushed in response to a polar bear and had sufficient audio quality to count heartbeats
17   before flush. Two of these hens had bears predate their nests soon after she flushed and
18   we can confirm that bears were within spatial viewing distance to two eiders when they
19   flushed (i.e., were within her estimated viewshed; Geldart et al. In Review). Additionally,
20   bears arrived at the nest quickly after eiders flushed in all three instances (average ± SD:
21   9.33 ± 3.25 sec), suggesting eiders flushed in response to bears. We estimated heart rate
22   30-s, 20-s, and 10-s to flush consistent with the sampling of heart rate to simulated-
23   predator approaches (see **Heart-rate quantification** section).
24
25   Eider heart rate in response to actual polar bears on East Bay Island (n=3) averaged 12
26   beats/10s and generally decreased as eiders got closer to flushing: two eiders' heart rate
27   became continuously slower with reduced time until flush (i.e., across 30-10s sample
28   intervals: 12 to 10 to 8 and 11 to 9 to 5 beats/10s), whereas one initially increased their
29   heart rate followed by a decrease right before flush (i.e., 9 to 28 to 12 beats/10s). These
30   heart-rate results help to confirm that eider responses to a simulated polar-bear approach
31   is indicative of a natural response as eiders exhibited a similar pattern of decrease in
32   heart rate and the same magnitude of response.