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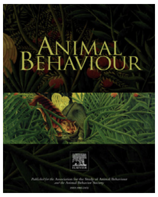

Predatory cue use in flush responses of a colonial nesting seabird during polar bear foraging

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Nest predation is a primary cause of reproductive failure in birds; thus, predators apply strong selective pressure on nesting behaviour, especially risk assessment behaviours during predator encounters at nests. Prey's risk assessments are not static; rather, dynamic risk assessment theory predicts that prey assess risk in real-time and update it according to changes in cues posed by the predator(s). We used drone videography to film nest-flushing behaviours of common eiders, *Somateria mollissima*, in response to foraging polar bears, *Ursus maritimus*, on East Bay Island (Nunavut, Canada). We assessed how cue use influenced flushing behaviour and nest fate in a path analysis using 200 observations of 193 eiders in 2017. Our most supported model found that more direct angles of visual gaze and travel angle by polar bears resulted in conspicuous nest flushes by eiders ($\beta = -0.236 \pm 0.059$), whereas the presence of herring gulls, *Larus argentatus*, resulted in more discrete flushes of hens walking from their nests ($\beta = -0.181 \pm 0.059$). Shorter flush initiation distances between eiders and approaching bears resulted in greater nest predation by polar bears ($\beta = -0.203 \pm 0.076$). We found no support that an eider's visibility from the nest influenced any component of flushing behaviour. We suggest that during encounters with bears, eiders are capable of assessing risk and making appropriate behavioural decisions to reduce the chances of nest loss. However, as the colony experienced heavy predation by bears in 2017, behavioural responses alone appear to be insufficient to mitigate polar bear predation at the population level.

Nest predation is a primary cause of reproductive failure in many species of birds (Côté & Sutherland, 1997; Newton, 1998; Smith, Pullin, et al., 2010); thus, predators apply strong selective pressure on avian nesting behaviour, especially risk assessment behaviours during predator encounters at the nest (Martin, 1995; Montgomerie & Weatherhead, 1988; Ricklefs, 1969; Schmidt, 1999). However, the responses of incubating birds can vary depending on the relative predation risk, as different predators pose different levels of risk to either the incubating parents or their clutch (Montgomerie & Weatherhead, 1988). Selection should therefore favour the ability of individuals to assess types and levels of risks posed by different predator archetypes and make appropriate behavioural decisions in a given environmental context (Congdon et al., 2020; Curio, 1975, 1983; Martin, Martin, et al., 2000; Rytkönen & Soppela, 1995; Tvardíková & Fuchs, 2011).

Risk assessments performed by incubating parents on predators are not static; rather, dynamic risk assessment theory predicts that prey should assess risk in real-time and update it according to any changes in cues posed by the predator(s) (Kleindorfer et al., 2005; Tvardíková & Fuchs, 2011). In doing so, prey can optimize time spent on profitable behaviours (e.g. remaining on nest to incubate eggs) and make the decision to flee (e.g. abandon the nest to prioritize adult survival) only when predation risk outweighs the benefits of remaining (Cooper & Frederick, 2007). Some predator cues are well known to play a role in dynamic risk assessment and subsequent prey responses, including predator body size (Templeton et al., 2005), travel speed (Cooper, 2006) and direction of travel (Burger & Gochfeld, 1981). A combination of these predator characteristics should be considered by prey during decision making. For example, a large-bodied predator that is quickly

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approaching a nest on a direct angle may be perceived as a greater risk than a slow-moving, small predator approaching more tangentially. However, there is increasing experimental evidence suggesting that prey can perceive even more subtle cues such as the orientation of the predator's head or eyes (Bateman & Fleming, 2011; Davidson & Clayton, 2016), presumably providing prey with finer-scale predation risk information to inform their behavioural responses (Sang-Im Lee et al., 2013). The perception of predator cues may additionally be influenced by characteristics of the prey's environment such as relative cover (Albrecht & Klvaňa, 2004). In combination, multiple sources of cues/information should be used by prey to better inform decision making (Munoz & Blumstein, 2012; Sih, 1992), but this may also incur a neurological cost associated with attentional constraints (i.e. paying attention to multiple cues at once may prove distracting from a single, more important cue) (Dukas & Kamil, 2000; Leavell & Bernal, 2019). As such, investigating dynamic risk assessment and cue use by prey should consider how individuals incorporate multiple cues simultaneously rather than each in isolation.

Cue use and reliable risk assessments are also modulated by a prey species' ecoevolutionary experience with a given predator, as prey are generally poorer at responding to unfamiliar/novel predators than those they have experience with (Ehlman et al., 2019; Saul & Jeschke, 2015). In the context of climate-induced environmental change, exposure to unfamiliar/rare predators is an important and yet still largely understudied aspect of predation risk assessment (Blumstein et al., 2019). For example, the introduction of novel nest predators has shown to increase nest failure rates and cause eventual population decline in a diversity of bird species (e.g. Blackburn et al., 2004; Wanless et al., 2007; Wiles et al., 2003; but see Didham et al., 2005; Palmas et al., 2020). It is thought that contributors to these declines may be due to the bird species' (1) inability to recognize novel predator cues and/or (2) inappropriate responses to predator cues that risk adult/nest survival. Nevertheless, naïve prey may still exhibit some degree of general antipredator behaviours even if a predator is unfamiliar (Carter et al., 2008). As such, quantifying behavioural responses to novel predators and determining the consequences of those responses should be informative to predicting persistence of a prey species (Carthey & Banks, 2014; Carthey & Blumstein, 2018).

An increasingly studied nest predator–prey dynamic that has arisen due to rapid changes in environmental conditions is the growing predation of common eider, *Somateria mollissima* (hereafter ‘eiders’), nests by polar bears, *Ursus maritimus*, in the Arctic (Barnas, Iles, et al., 2020; Iverson et al., 2014; Prop et al., 2015). Eiders that breed in the Arctic typically nest colonially on small islands offshore to reduce predation by terrestrial mammals (i.e. Arctic foxes, *Vulpes lagopus*) and exhibit extremely high nest attendance rates to reduce predation by avian predators (*Larus* sp.) (Bolduc & Guillemette, 2003a; Laurila, 1989). However, recent climate-induced reductions in spring sea ice have led polar bears in some populations to spend increasing time on land (Cherry et al., 2013), resulting in overlap with nesting birds (Prop et al., 2015; Rockwell & Gormezano, 2009; Smith, Elliott, et al., 2010). Once onshore and within an eider nesting colony, bears can destroy hundreds of eider nests in a relatively short period, leading to near complete colony failure in some years/sites (Barnas, Iles, et al., 2020; Gormezano et al., 2017; Jagielski, Dey, Gilchrist, Richardson, Love, et al., 2021; Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021; Rockwell & Gormezano, 2009). Predictive modelling suggests that nesting eiders should disperse and nest in lower-density colonies to reduce polar bear predation (Dey et al., 2017), although empirical data has not yet confirmed whether this is occurring at the population level (Dey et al., 2020). At the individual level, there may be nesting behaviours that reduce the likelihood of nest failure by polar bears, but these have not yet been examined. Investigating the predatory cues of polar bears on which eiders rely during flush responses and how those flush responses impact eider reproductive success will provide a better understanding of behavioural interactions between eiders and polar bears, thereby better informing predictions of higher-level population responses (see Bro-Jørgensen et al., 2019).

Here we use drone video of polar bears foraging within an eider colony to examine the relationships between several predator/environmental cues and the response of nesting eider hens using path analysis. Although several experimental studies have examined the effects of predator cues on prey behaviour often using human researchers or predator models as surrogates for predators (Burger & Gochfeld, 1981; Carter et al., 2008; Goumas et al., 2019; Kyle & Freeberg, 2016; Maziarz et al., 2018), we focused instead on a ‘remote’ drone approach for several reasons. First, experimental approaches using artificial predators (e.g. human researchers or predator models) may not realistically represent cues expressed by real predators. Individuals that respond ‘poorly’ to artificial predator cues (i.e. respond in a manner that would have led to predation by a real predator) remain in the study population, thereby skewing observed prey responses in a way that would not occur in natural settings and obfuscate any assumed fitness consequences (Peers et al., 2018; Weissburg et al., 2014). Second, field-based approaches to investigating prey responses to predators is often further complicated by the presence of researchers in the field, which is likely to impact the behaviours of both predators and prey (Bêty & Gauthier, 2001; Götmark, 1992; Götmark & Åhlund, 1984; Åhlund & Götmark, 1989). The advent of drone technology (Chapman, 2014) allows wildlife researchers the opportunity to observe predator–prey interactions (Fortune et al., 2017; Jagielski, 2020) while reducing researcher disturbance to wildlife (Barnas et al., 2018; Brisson-Curadeau et al., 2017; Mulero-Pázmány et al., 2017). Fixed-wing drones in other systems have been shown to have little behavioural impact on nesting eiders (Ellis-Felege et al., 2021) or polar bears (Barnas et al., 2018); thus, rotary-wing drones may reduce disturbance when investigating behavioural interactions between eiders and bears on East Bay Island (see below).

We estimated the effects of several polar bear cues (travel speed, direction of travel, direction of gaze) on eider flushing behaviours while simultaneously examining the numbers of native predators (herring gulls, *Larus argentatus*) in the area and an environmental variable accounting for visibility from nests. We measured two behavioural responses of eiders: (1) flush initiation distance (hereafter FID), commonly used to describe ‘flight initiation distance’ (Cooper & Frederick, 2007) as the distance between the bird and the predator when the bird decides to flee, but co-opted here to describe flushing by birds (Blumstein, 2010); (2) the behavioural style in which each bird flushed from her nest. Based on dynamic risk assessment theory, we predicted that faster approach speeds and more direct angles of approach and gaze by polar bears would result in greater flush distances, indicating that adult eiders prioritize their own survival in the face of a threatening predator. Conversely, shorter flush distances would indicate that eiders invest more in protecting their current clutch of eggs. We also predicted that eiders would flush inconspicuously in response to indirect angles of approach and gaze by bears and in response to higher number of gulls, so as to leave their nest undetected and avoid presenting visual cues to predators.

METHODS

Study Area and Species

This study was conducted at a long-term research station on East Bay (Mitivik) Island, within the East Bay (Qaqsauqtuuq) Bird Sanctuary of Southampton Island, Nunavut, Canada (Fig. 1). East Bay Island is a small (approximately 24 ha) island composed of low-lying vegetation (predominately graminoids, mosses and lichens), granite rock outcrops and snowmelt ponds. Topography of the island is flat (total elevation change, approximately 8 m), although larger rock outcrops can obscure fields of view for ground-nesting birds and predators. The study site supports the largest eider colony in the Canadian Arctic, hosting up to 8000 breeding pairs each year between 2002 and 2013 (Jean-Gagnon et al., 2018), although since that time the colony appears to have been declining (500–1700 pairs estimated in 2017; Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021).

Eiders on East Bay Island generally reuse historical ‘nest bowls’, which are circular depressions in the ground that have been used in previous years by nesting individuals. Nest bowls tend to be located in areas with higher deposits of organic materials (insulating mosses), often situated within and around rock outcroppings (Fast et al., 2010). Once incubation begins, eiders tend to remain on the nest and rarely take recess events to drink or feed (Bottitta, 1999; Bottitta et al., 2003; Criscuolo et al., 2000; Fast et al., 2007). On East Bay Island, the primary nest predators of eiders are herring gulls (hereafter ‘gulls’), although gulls are generally unable to access eider eggs while the attendant female remains on the nest. Polar bear foraging on eider nests on East Bay Island has been increasing in recent years (Iverson et al., 2014; Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021). Bears typically arrive ashore during eider egg laying and early incubation (Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021). Initially, rates of nest discovery by bears are high, but this declines as bears deplete the number of nests available. Eventually, most nests fail due to polar bears (Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021).

Drone Observations of Polar Bear–Eider Interactions

We collected aerial video of individual polar bears foraging on eider nests approximately midway through eider nest incubation using multirotor drones during 10–20 July 2017 (Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021). Briefly, when bears

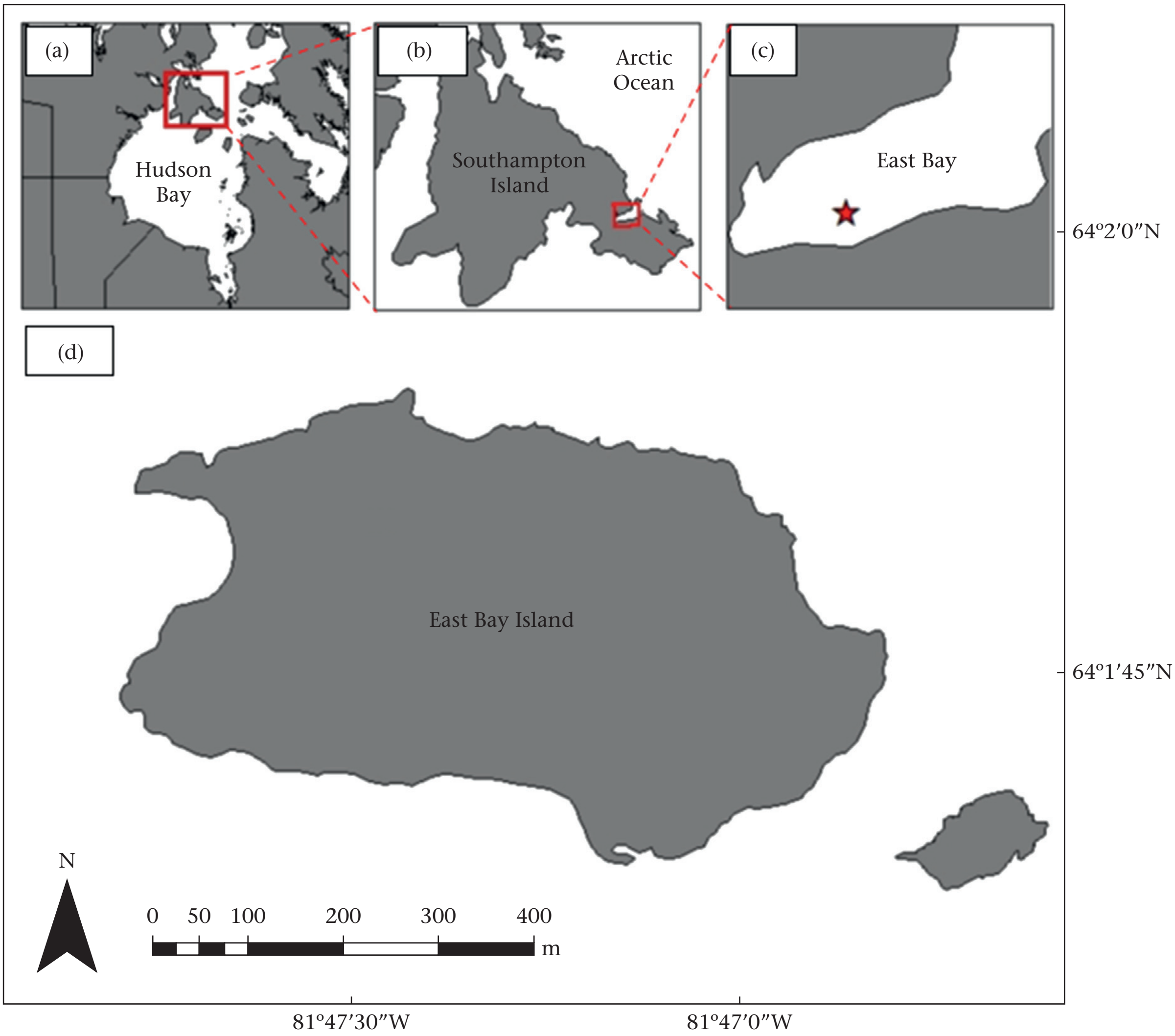

Figure 1. Map of the study location. (a) General study location in northern Hudson Bay. (b) Southampton Island, Nunavut, Canada. (c) East Bay of Southampton Island, location of study site indicated by red star. (d) East Bay Island, Nunavut, Canada. Inset map layers for Canadian Provinces and Territories provided by ESRI online (https://www.arcgis.com/home/item.html?id=d3fef65386df4e63b02d6e23bb98a1ee, accessed 1 September 2020).

were spotted by researchers on the island, a drone was deployed to perform a 'focal follow' of an individual bear. The drone hovered above the bear approximately 30–55 m above ground level and followed the bear during its foraging activity. We stopped filming during prolonged periods of bear inactivity. Bears were filmed during daylight hours (between 0530 and 2030 hours) and only when environmental conditions permitted drone operation (e.g. clear weather, wind <10 km/h). Since foraging activity of bears often took longer than the battery capabilities of the drone, filming of an individual bear's foraging bout often comprised multiple drone flights. The videos from these individual drone flights were subsequently stitched together for video review. For additional details and specifications of the collection of drone video for polar bear–eider interactions, we provide a Drone Reporting Protocol (as described by Barnas, Chabot, et al., 2020; see Supplementary material 1).

We collected 995 min of videography of polar bears foraging within the eider colony, representing 31 'foraging bouts' observed across 65 drone flights. Since recorded videos were variable with respect to altitude and viewing angle, to achieve an approximately constant-sized field of view, we only reviewed sections of video with an approximate straight down (nadir) view of polar bears and at the lowest flight altitude of approximately 30 m above ground level. This filtering step resulted in 166.3 min of video from 15 drone flights across 5 days (11, 15, 16, 19 and 20 July) on four individual polar bears. We estimated the field of view of these filtered drone videos by measuring the approximate length and width of the video frame for 10 random paused screenshots during eider flushes using the 'Measure' tool in ArcMap v.10.7.1 (ESRI, Redlands, CA, U.S.A.) and a georeferenced map of East Bay Island (see Drone Video Review below). For filtered videos, the estimated mean area ± SD was 1023 ± 195 m^2, indicating a reasonably consistent field of view. Hereafter, we only refer to these filtered sections of drone video featuring direct overhead views.

Drone Video Review

A single observer (A.F.B.) reviewed video of polar bear foraging for flushing eider hens using Windows Film & TV application v.10.200022.11011.0 (Microsoft Corp., Redmond, WA, U.S.A.). Video was reviewed on normal speed and paused at the moment an eider hen flushed from her nest to record variables of interest (see below). Due to the cryptic coloration of eiders, nests were often only located if the hen was observed flushing or had already flushed and left an open nest bowl with conspicuous eggs visible. If during review we identified a nest that was already vacated by the female, then we re-reviewed the footage to find the first observable flush, if possible. Review of eider flushes was also enhanced using video editing software (listed above) that kept track of individual nests by marking videos with nest indicators. If we could not observe the original flush for a nest in a drone video, we did not record a FID for that nest. We used the recorded start date/time of drone flights and time of flush within each video to estimate the date/time of each eider's flush (YYYY-MM-DD HH:MM:SS).

Since a flushing bird does not necessarily indicate the presence of a nest at that location (as it could represent a male or nonreproductive female), we only included flushes as being at nest locations if they met one of the following criteria: (1) visible eggs; (2) a visible nest bowl of down feathers/depression in the ground; (3) the bear stopped at the flush location and foraged (i.e. a prolonged period of the bear's nose down at that location); or (4) the flushing female returned back to the exact same location during the same video, indicating that she was attending to a clutch of eggs at that spot. We made the assumption that the observed flushing female was the attendant mother for that nest, although some female eiders have been known to briefly incubate nests of other females (Kristjansson & Jónsson, 2015).

To estimate FIDs of eiders to polar bears, we used a georeferenced, true colour (red, green, blue; RGB), 3 cm ground sampling distance orthomosaic of East Bay Island, produced from drone imagery acquired in June 2019. For details on the image acquisition and creation of this orthomosaic, see Drone Reporting Protocol 2 in Supplementary material 2 (Barnas, Chabot, et al., 2020). We were able to identify nest locations of flushing eiders and bears by matching patterns of rock outcrops and other landscape features (e.g. pond edges, mossy patches) between the 2017 video of flushing eiders and the 2019 island mosaic. The georeferencing of eiders and bears should not be impacted by the time gap between these two imagery data sets, as the physical landscape characteristics used for matching the 2017 video and 2019 imagery do not drastically change on an annual basis due to a lack of human activity and geophysical/erosion events on the island. Identifying locations of eider nests on the island mosaic was aided by the presence of historically used nest bowls, as these are distinct features present on the map that are often reused by eiders in following years (Fast et al., 2010). Nests were marked on the island mosaic within ArcMap and assigned a unique nest identification (nest ID), which allowed us to re-identify females that had repeat encounters with bears in subsequent videos (if that nest had not failed due to bear predation during the previous encounter).

We estimated bear location for each flush event as an approximate point at the base of the bear's neck in the middle of the shoulder girdle, similarly using landscape features in the video and mosaic to estimate positions (for more details, see Appendix, Georeferencing Eider Nests and Bear Locations to Measure Flush Initiation Distances). Using the location of the eider nest and the bear, we measured FID as the distance between these two points at the moment of eider flush using ArcMap's 'Measure' tool. For each eider flush, we recorded a flush style describing the type of behaviour the eider exhibited when vacating her nest. We recorded three qualitative categories of flush style: walking = the eider walked off her nest; jumping = the eider quickly ran or jumped off her nest; flying = the eider flew directly off her nest, clearly indicated by flapping wings. Although subjective, these responses represent increasingly visible and progressive flush responses; from walking to jumping to flying. Additionally, we recorded whether or not a nest was predated (Hanson, 2006) by polar bears (nest fate). This was indicated by observing a bear consuming eggs and/or lowering its head down in the eider nest for an extended period. Although polar bears are known to capture and kill nesting female eiders (Gormezano et al., 2017), we were primarily focused on the risk that polar bears pose to eider eggs rather than to the adults.

We recorded several measures of predator cues at the moment that eider hens flushed. For polar bears, we estimated whole circle bearings (directional values from 0 to 359, where north = 0, east = 90, south = 180, west = 270) for the bear's direction of travel and head orientation (hereafter 'gaze') using the 'Add Geometry' tool in ArcMap. Direction of travel was estimated as a straight line travelling from the posterior end of the bear's body through the shoulder girdle (i.e. the direction the bear was facing). Direction of gaze was estimated as a straight line travelling from the base of the neck at the shoulder girdle through the anterior portion of the bear's head (i.e. the direction the bear's head was pointing). We estimated the whole circle bearing of the bear's point location towards the focal nest at the moment of flush and used this to calculate the smallest angle between the bearing towards the nest and the bearing of travel/gaze, where smaller and larger angles represent more direct and indirect approaches/gazes, respectively (see Appendix, Estimating Polar Bear Travel and Gaze Angles). We estimated polar bear movement speed (m/s) by estimating the location of the bear 10 s prior to an eider flush, calculating the distance travelled by the bear over those 10 s, and dividing distance by 10 to estimate movement in m/s (Appendix, Estimating Polar Bear Movement Speed). Lastly, because eider behaviour may be influenced by the presence of other predators in addition to bear foraging, we recorded the number of herring gulls viewable in the video frame at the moment of flush. We binned the number of gulls into three categories: absent (0 gulls); low (1–5 gulls); high (>5 gulls) (Appendix, Estimating Number of Gulls).

Since prey behaviours are influenced by the amount of environmental information available to them (Schmidt et al., 2010), eiders with a greater field of view from their nest may make different behavioural decisions (i.e. FID, flush style) relative to those with less information available. For each eider nest location, we calculated the proportion of area in a 30 m radius (area ≈ 2827 m^2) that was visible to the nesting female using ArcMap's ‘Viewshed’ tool and a 3 cm digital surface model (Rogers et al., 2020) generated with structure-from-motion in Pix4Dmapper v.4.4.12 (Pix4D, Prilly, Switzerland) using the same RGB drone imagery collected in 2019. Briefly, within a 30 m radius for each eider nest location, the ‘Viewshed’ tool calculates whether other surface locations are visible to the nest location based on the elevation of surrounding points and potentially obstructing features (e.g. large boulders). We chose a 30 m radius based on the maximum observed FID of eiders (25.7 m; see Results). We included a vertical offset of 14 cm for eider nest locations to account for the approximate height of a female eider's eyeline while sitting on her nest (measured using a decoy male eider in an upright sitting position). We used the amount of visible area (m^2) in each eider's viewshed to calculate the proportion of the 30 m radius buffer visible (see Appendix, Estimating Eider Viewsheds). Although our calculated viewshed did not consider the height of polar bears (as taller bears may be more visible to nesting eiders), our metric should have provided an index of visibility from an eider's nest.

Statistical Analysis

We constructed unidirectional (acyclic) path models (structural equation models without latent variables) to examine relationships between our measured exogenous variables (gaze angle, travel angle, bear speed, gull number, eider viewshed) and endogenous variables (FID, flush style, nest fate). As we only recorded repeat flushes for 3.6% of the individual eiders (7 out of 193; see Results), we did not include eider ID as a hierarchical random effect, but we did keep these repeated observations in the data set. We justified this based on a visual examination of eider flush distances against polar bear encounter number, which did not reveal any clear changes in flush distances (Fig. 2). We also fitted a linear mixed effect model to examine scaled flush distance as a function of the fixed effect for encounter number and a random effect of eider ID. We found no significant effect of encounter number ($\beta \pm SE = 0.21 \pm 0.33$, $P = 0.65$), and a likelihood ratio test showed that including the random effect of eider ID in this model did not significantly improve model fit ($\chi^2 = 0.86$, $P = 0.35$).To facilitate the use of categorical exogenous and endogenous variables (gull number category, flush style, nest fate), we recoded them as dummy and ordinal variables where appropriate. Polar bear travel angle and gaze angle were positively correlated (Pearson correlation: $r_{198} = 0.67$, $P < 0.0001$), so we created a new variable termed ‘angle sum’ as the linear combination of travel angle and gaze angle (where low values indicate more direct angles of approach/gaze and the opposite for high values). We recorded ordinal variables for gull category (absent, low, high) and flush style (as increasingly visible and progressive responses: walking, jumping, flying). To account for larger variances associated with flush distance and angle sum (compared to other variables), we rescaled these variables to a mean of zero.

We constructed eight candidate path diagrams relating our measured predator/environmental cues to the flushing behaviour of eiders, as well as their indirect effects on nest fate as mediated

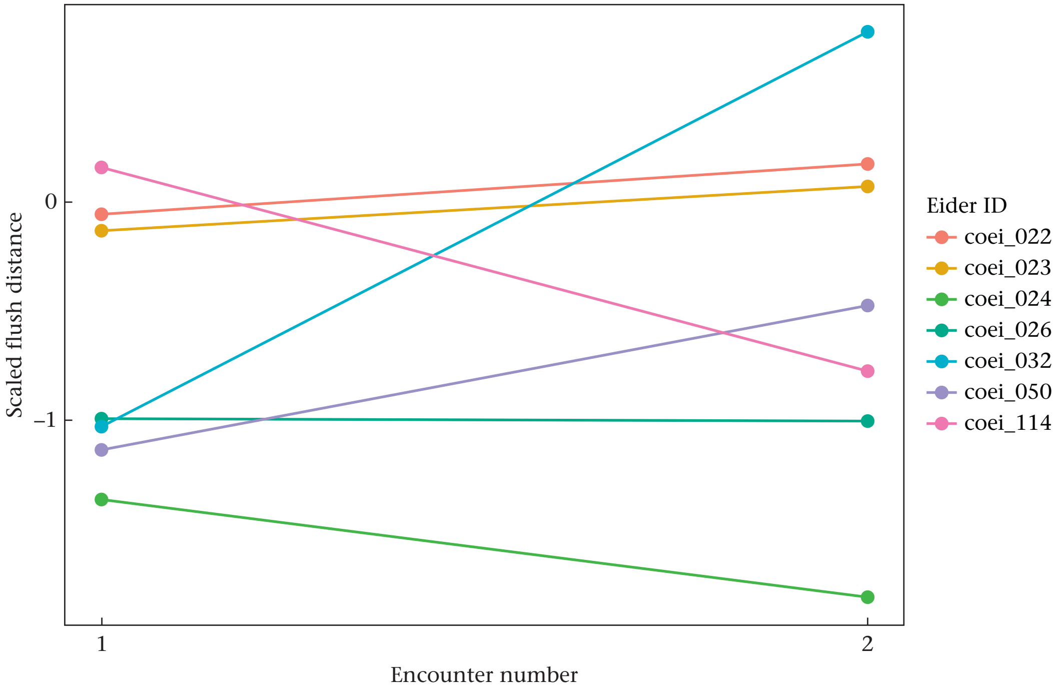

Figure 2. Scaled flush distances of individual common eiders ($N = 7$) in response to their first and second encounters with polar bears.

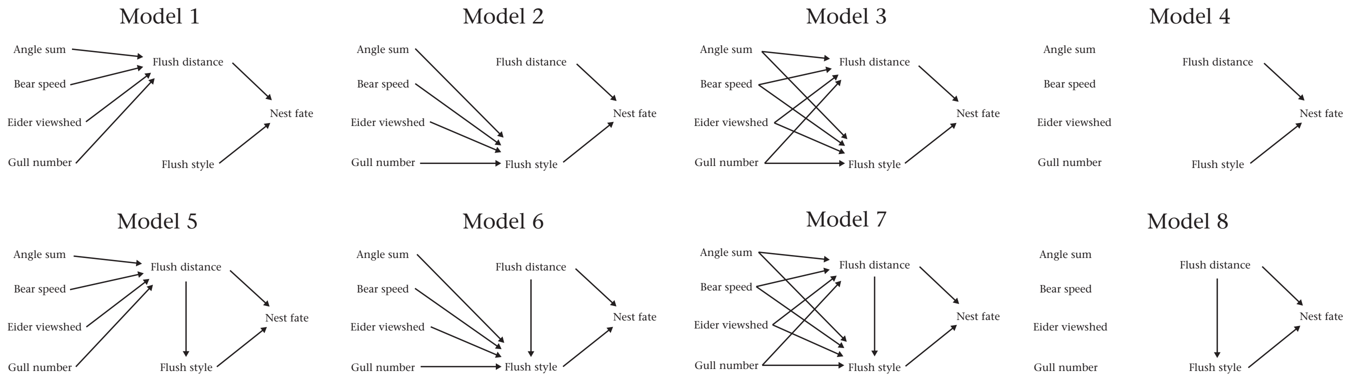

Figure 3. Candidate path diagrams relating predator and environmental cues to flushing behaviour and nest fate of common eiders. Arrows represent conceptual unidirectional relationships between variables.

through FID and flush style (Fig. 3). Briefly, we evaluated whether our exogenous variables were more influential on FID or flush style (or both), and whether flush style was also influenced by FID. We included a fully saturated 'global' model as well as a 'null' model where exogenous variables had no relationship to the mediating variables of FID and flush style. We explicitly kept the relationship between nest fate and FID/flush style constant in all models to estimate the effect of these variables on fate. Models were estimated with a maximum likelihood approach and evaluated based on Akaike's information criterion corrected for small sample size (AICc), where models were considered competitive if they fell within Δ2 AICc (Burnham & Anderson, 2002; Hennin et al., 2018; Shipley, 2013). For our most competitive path models, we estimated standardized partial path coefficients (with 95% CI) and commonly used fit indices for path models including comparative fit index (CFI), Tucker–Lewis index (TLI), root mean square error of approximation (RMSEA) and standardized root mean square residual (SRMSR).

All georeferencing and bearing calculations were done using ArcMap v.10.7.1. All other data manipulation and variable calculations were done in RStudio v.3.6.2 (R Core Team, 2017) using package 'geosphere' for spatial data (Hijmans et al., 2017), 'lubridate' for datetime data (Grolemund & Wickham, 2011), 'dplyr' for general data manipulation (Wickham et al., 2015), 'ggplot2' for data visualization (Wickham, 2016) and 'lavaan' for path analyses (Rosseel, 2012).

RESULTS

We observed 200 flush events from 193 individual eiders on 11 July ($N = 61$), 15 July ($N = 99$), 16 July ($N = 39$) and 19 July ($N = 1$) in 2017; seven of these flushes were repeat observations by individuals on different days. No flushes were observed during foraging bouts on 20 July, which may reflect the high level of bear predation that had occurred on previous days (i.e. relatively few eider nests were active by 20 July). Of the 200 flush events used

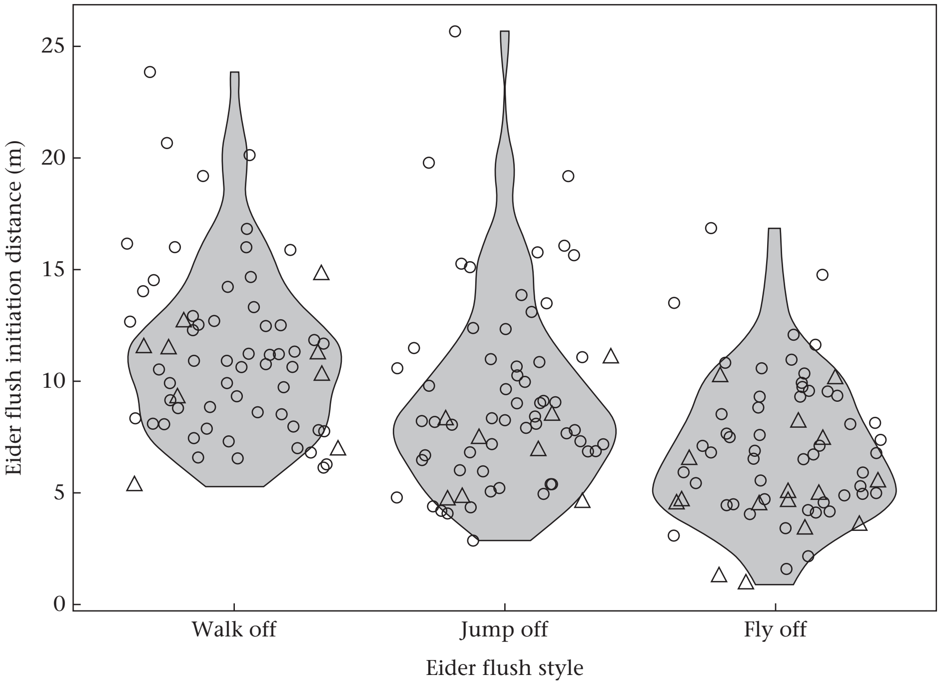

Figure 4. Raw data depicting the relationship between flush style, flush initiation distance (m) and nest fate (Δ = predated; ○ = not predated) of common eiders in response to polar bears. Measurements obtained from aerial drone video in July 2017 ($N = 200$).

for analysis, we observed 33 nests predated by polar bears. We did not observe any instances of adult eiders being captured and killed by polar bears. The overall mean FID of eiders was 9.1 ± 4.1 m (range 0.9–25.7 m) from the bear, with similar numbers of flush styles across events (walking = 66; jumping = 66; flying = 68; Fig. 4). Most observed flushes by eider hens were in response to bears moving and/or looking towards them, indicated by the combination of direct angles of polar bear travel and gaze direction at flush (Fig. 5). Mean polar bear speed prior to flushes was 0.5 ± 0.3 m/s (range 0–1.3 m/s), and mean proportion viewshed visible from eider nests was 0.22 ± 0.10 (range 0.07–0.59). We observed 49 eider flushes without gulls present, 80 with low numbers of gulls and 71 with high numbers of gulls (Fig. 5).

The path model with highest support was Model 6 ($K = 14$), which included direct paths from our exogenous variables to flush style only and a direct path from FID to flush style (Table 1). Notably, the next highest-ranked model was Model 7 (ΔAICc = 2.23, $K = 18$), which was the fully saturated model. For clarity we present parameter estimates from both models, as each had similar log likelihoods and Akaike weights (Model 6 LL = −936.2, $w = 0.752$; Model 7 LL = −932.6, $w = 0.246$) (see Arnold, 2010). Overall fits of Model 6 and Model 7 were consistently ‘adequate’ based on multiple measures (Model 6: CFI = 0.565, TLI = 0.348, RMSEA = 0.135, SRMR = 0.112; Model 7: CFI = 0.593, TLI = 0.146, RMSEA = 0.154, SRMR = 0.104), where a ‘good’ model fit is indicated by CFI > 0.9, TLI > 0.95, RMSE < 0.1 and SRMR < 0.08. Interestingly, all models including a path from FID to flush style received higher support than models without that path (Table 1).

From our most competitive path model (Model 6), we found that lower angle sums (i.e. more direct angles of travel and gaze) of polar bears resulted in more obvious flush responses such as jumping or flying ($\beta \pm SE = -0.236 \pm 0.059$, $P < 0.001$). Lower eider FIDs (i.e. closer bears) resulted both in more obvious flush responses ($\beta \pm SE = -0.437 \pm 0.054$, $P < 0.001$) and in more subsequent nest loss by polar bears ($\beta \pm SE = -0.203 \pm 0.076$, $P < 0.05$), but we found the opposite relationship between gull presence and flush styles, as higher gull numbers evoked more inconspicuous ‘walk off’ style flushes ($\beta \pm SE = -0.181 \pm 0.059$, $P < 0.005$). We did not find significant path coefficients for relationships between flush style and polar bear speed or proportion of viewshed visible, nor flush style and nest fate (Fig. 5a). In Model 7, we found that eiders flushed at shorter distances when polar bears were moving faster ($\beta \pm SE = -0.164 \pm 0.068$, $P < 0.05$), but we found no significant effects of angle sum, proportion viewshed visible or number of gulls on FID (Fig. 6b). Standardized estimates of path coefficients from all endogenous variables to flush style were similar in both Model 6 and Model 7 (Fig. 6).

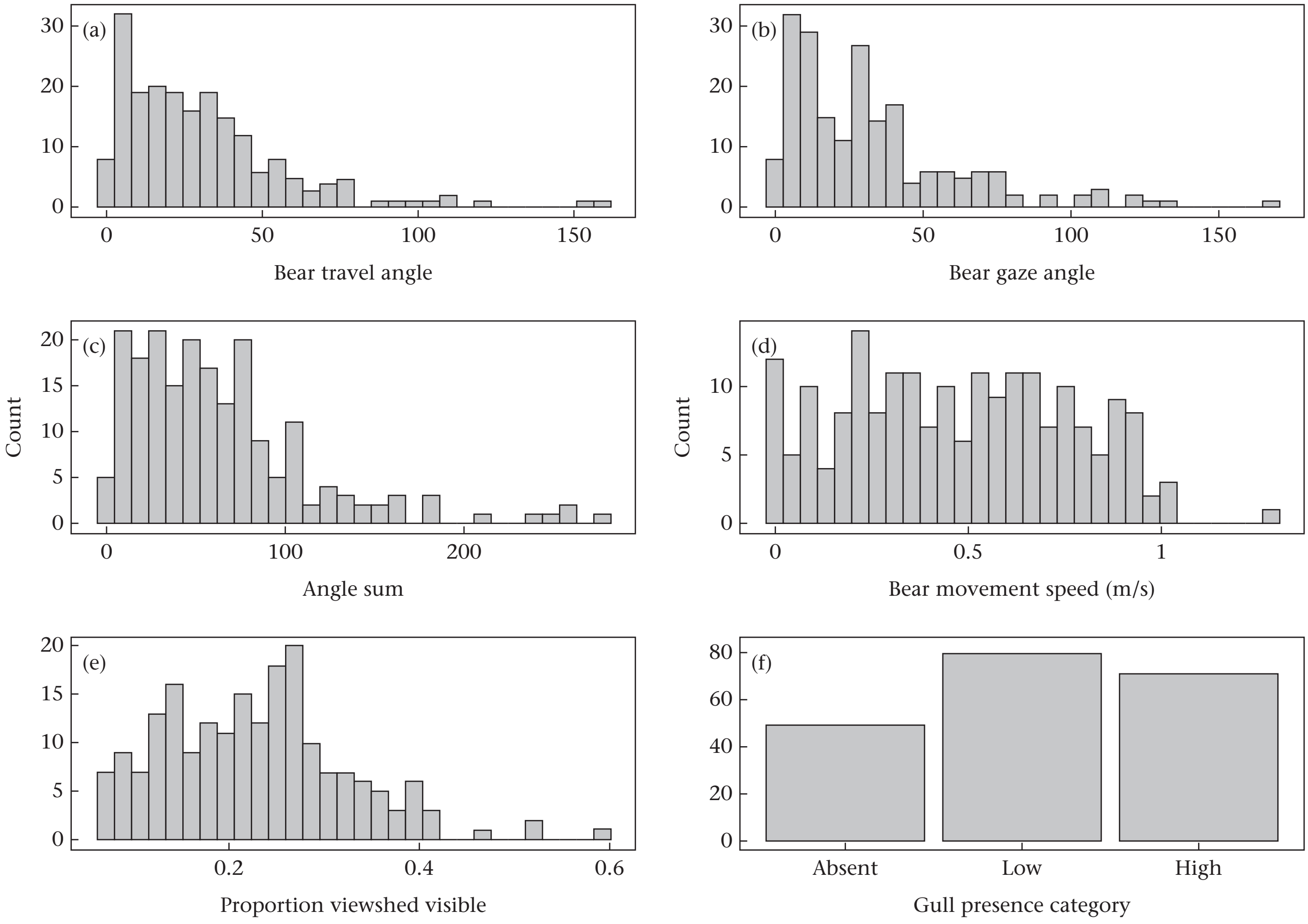

Figure 5. Raw data of predator and environmental cues collected during common eider flush events in response to polar bears. (a) Polar bear travel angle relative to eider nest location. (b) Polar bear gaze angle relative to eider nest location. (c) Linear combination of a bear's travel and gaze angle. (d) Polar bear travel speed (m/s) averaged over the 10 s prior to eider flush. (e) Proportion of an eider's viewshed that was visible from the nest location within a 30 m radius. (f) Category of herring gull abundance at the moment of eider flush (absent = 0 gulls; low = 1–5 gulls; high = >5 gulls). Data collected from 200 observations of eider flushes.

Table 1
Model selection results for conceptual path diagrams relating exogenous predator and environmental variables to endogenous variables for common eider flushing behaviours and nest fate

Model rank	Model ID	*K*	Log likelihood	AICc	ΔAICc	Akaike weight
1	6	14	-936.2143	1902.699	0	0.752
2	7	18	-932.5755	1904.93	2.231	0.246
3	8	10	-947.3683	1915.901	13.202	0.001
4	5	14	-943.7296	1917.729	15.03	0.000
5	2	13	-959.157	1946.271	43.572	0.000
6	3	17	-955.5182	1948.399	45.7	0.000
7	4	9	-968.0899	1955.127	52.428	0.000
8	1	13	-964.4511	1956.859	54.16	0.000

Model ID indicates the candidate model structures detailed in Fig. 3.

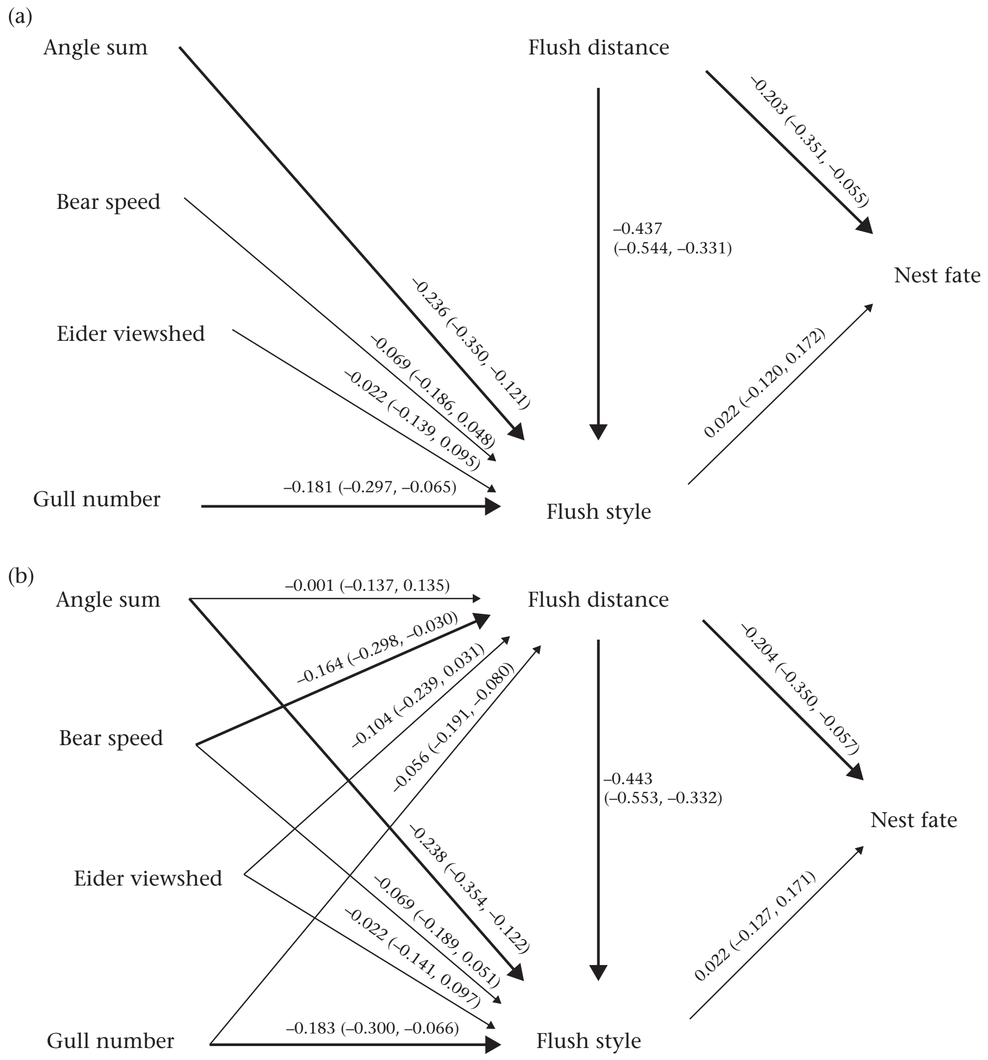

Figure 6. Standardized parameter estimates relating common eider flush style, flush distance and nest fate to exogenous variables for the linear combination of polar bear travel and gaze angle, polar bear speed, proportion of viewshed visible and herring gull number category. Estimates obtained from our most competitive path models based on AICc (a) Model 6 and (b) Model 7. Standardized estimated path coefficients for pathways displayed on arrows (95% CI in parentheses), bold lines represent statistically significant paths ($P < 0.05$).

DISCUSSION

Our findings reveal novel insights into the behavioural responses of eiders when leaving their nests, by demonstrating that individuals behave according to dynamic risk assessment theory by incorporating information on polar bear gaze and travel angle, as well as the number of herring gulls nearby. We demonstrate increased nest predation risk by polar bears for eiders that flush from their nests at shorter distances, but this risk is likely restricted to the immediate encounter between the bear and the eider. Eiders have evolved a mass loss incubation strategy that relies on females remaining concealed on their nest for as long as possible (Bolduc & Guillemette, 2003b; Garbus et al., 2018). This results in a behavioural trade-off between remaining on nest (reproductive investment) and flushing in response to a foraging bear (adult survival), although some aspects of flushing behaviour may act to increase nest survival (discussed below). Although the fit of our most competitive path models was not perfect, given the lack of investigation into nesting bird behavioural responses to foraging polar bears (but see Barnas et al., 2022), we believe that our analysis provides important preliminary investigations that can guide future studies.

Cue Use Impacts on Flushing Style and Flush Initiation Distance

We found no effect of an individual's view from their nest on flush responses, which is surprising given that nests with unobstructed views should provide more information when assessing predation risk and allow eiders to make the appropriate antipredator response (Fast et al., 2007). Since our viewshed metric did not account for polar bear height, it may be the case that most eiders had similar information on polar bear cues. A sampling bias may exist whereby nests with greatly decreased viewshed visibility (and thus increased shelter/cover) were observed less frequently from the drone in this study due to their concealment in the field and subsequently the collected video. It is more likely that viewshed is more informative for eiders initially selecting nest sites (e.g. thermal refuges), but flush responses are more informed by proximate stimuli such as predator presence. Multiple cue use in prey is well known to reduce ambiguity in predator risk assessments (Munoz & Blumstein, 2012; Sih, 1992), but due to costs associated with attentional constraints, not all cues are considered equally during flush responses (Dukas & Kamil, 2000; Leavell & Bernal, 2019).

We demonstrate that eider flushing responses are contingent on perceived predator cues, which has implications for how polar bears may locate eider nests (Jagielski, Dey, Gilchrist, Richardson, Love, et al., 2021). Our top model indicated that flush styles are informed by FIDs, but our measured cues did not greatly influence FID itself. Previous work has found that eider FIDs are influenced by several environmental factors, including colony location, habitat characteristics, gull presence and degree of disturbance (Laurila, 1989). However, our next top-supported model showed that slower moving polar bears resulted in greater FIDs, suggesting that eiders assess slower-moving (potentially searching) predators as a greater risk. Eiders are known to increase incubation constancy as incubation date increases (Criscuolo et al., 2002; but see Bolduc & Guillemette, 2003b); however, as the majority of our observations came during 11–15 July (5 days), we did not explore date as a proxy for incubation date in our models. Similarly, incorporating information on eider age in future analyses (which we were unable to do here) would be informative, as eiders are a relatively long-lived species that may prioritize adult survival over reproduction (Waltho & Coulson, 2015).

Flight Initiation Distance Informs Flushing Style

Our observed mean FID (9.1 m) falls within the reported FIDs of nesting eiders to researcher disturbance reported in the literature (4–8 m: Kay & Gilchrist, 1998; 16 m: Mallory, 2016; 2.4–3.4 m: Seltmann et al., 2012). To the best of our knowledge there have been no rigorous examinations of eider FIDs in response to mammalian predators such as Arctic foxes or polar bears in the literature. As expected, shorter FIDs resulted in increasingly conspicuous flush responses in eiders, such as flying directly from the nest, and there are multiple potential interpretations of this finding. Polar bears that are closer to an individual's nest are likely perceived as riskier to both the adult bird and the nest contents, and these easily visible flush responses are simply escape behaviours intended to increase distance between the adult eider and the bear (i.e. prioritizing adult survival and abandoning the nest). Alternatively, the rapid movement of wings during/following flush may be interpreted as distraction displays, whereby eiders feign injury to lure the attention of predators away from the nest (i.e. risking adult survival and prioritizing nest survival). Further support for this interpretation stems from the finding that more direct angles of travel and gaze resulted in more conspicuous flush responses, as eiders in the immediate ‘eyeline’ of bears would have a higher chance of gaining attention. Distraction displays have previously been described in eiders (Kay & Gilchrist, 1998; Mcnair, 1981), but we did not find a significant effect of flush style (interpreted here as distraction behaviours) on nest fate. Distraction displays are common in cryptic-nesting birds but are less likely to evolve in colonial nesting species (Humphreys & Ruxton, 2020). In eider colonies, the distraction of a predator away from one nest may inadvertently direct the predator towards a nearby neighbouring nest that may be genetically related (Gochfeld, 1984; McKinnon et al., 2006). However, if this strategy is used by relatively few individuals (perhaps learned through prior exposures to polar bears), then these behaviours may benefit a small proportion of individual birds, given that the majority of other birds do not perform distraction displays. Feigning injury rather than escaping entirely inherently increases risk to the adult eider performing these behaviours, which would be indicative of eiders risking adult survival in favour of nest success. Although we did not observe any female eiders killed by polar bears during flushes, bears are capable of catching and killing adult eiders (Gormezano et al., 2017). Detailed observations of eider behaviour following flushes will provide greater insights to potential of eiders to distract and reduce nest predation, but this is beyond the scope of the current study.

Impact of Gull Presence on Flush Style

While direct angles of bear gaze and shorter FIDs led to visually obvious flush responses, increasing gull presence had a negative effect on flush style, resulting in more discrete flushes by eiders. Increasing activity at the nest may draw the attention of predators (Martin, Martin, et al., 2000; but see Martin, Scott, et al., 2000), and conspicuous flushes in the presence of visually acute avian predators are likely to increase risk to the exposed nest. We only examined eider behaviours in response to the number of gulls present at the moment of eider flush, as examining the interaction between eiders and gulls following flush was beyond the scope of the current study. Avian predators are thought to closely associate with polar bears foraging on colonial nesting birds and may capitalize on unattended eggs left by the incubating parent birds (Barnas et al., 2022; Gaston & Elliott, 2013; Iverson et al., 2014). Eiders may therefore be attempting to reduce gull predation in the presence of polar bears by leaving the nest without notice. It is also thought that eiders may reduce avian predator predation by covering eggs with insulating down feathers upon leaving (Opermanis, 2004).

Overall Impact of Eider Flush Responses on Nest Fate

We found that relatively few eider nests were predated by polar bears, given that 83.5% (167/200) of eider flush events observed in this study resulted in no egg loss to bears. However, to be clear, most of these nests eventually failed in the 2017 season due to bears (outside of our drone video samples). We tentatively suggest that eiders retain a general antipredator response that is effective on the scale of individual encounters with polar bears. In other words, eiders appear to be capable of performing dynamic risk assessment, by sensing the predator and the environmental cues associated with a foraging polar bear and differentially using appropriate flushing behaviours to minimize the probability of being killed, while simultaneously reducing the chances of nest predation by bears. Our finding of relatively few predation events of eider nests by polar bears is surprising. It may be that the general confusion induced by multiple flushing eiders sometimes makes it more difficult for bears to locate individual nests. However, a small chance of nest failure due to polar bear predation with each individual encounter is amplified due to repeat encounters throughout the nesting season. Our assessment of nest fate was restricted to the immediate encounter between the eider and bear, but the effect of bear encounters on eider nest fate for the remainder of their incubation is unclear. However, if polar bears are able to thoroughly search the entire nesting area, the majority of nests are likely to be discovered and consumed over time due to repeat encounters (as was the case in 2017; see Jagielski, Dey, Gilchrist, Richardson, & Semeniuk, 2021), suggesting that behavioural responses alone are insufficient to reduce nest failure.

Conclusions and Future Research Directions

Behavioural responses at the scale of individual encounters with polar bears may be more effective when coupled with additional changes in nesting strategies in response to increased bear predation. Eiders may engage in ‘predator swamping’ by nesting in dense colonies (Wilson et al., 2012), but this appears be ineffective against polar bears due to their ability to quickly consume hundreds of nests compared to the traditional predators of eiders (Gormezano et al., 2017). Simulation-based approaches predict that eiders should adjust nesting strategies to favour smaller, more isolated colonies (as opposed to larger high-density aggregations) in response to polar bear predation (Dey et al., 2017, 2018), but recent work in Canada's Hudson Strait did not find evidence of large-scale nest redistribution (Dey et al., 2020). This is surprising given an apparent lack of nest site fidelity observed in some eider populations following a year of unsuccessful nest attempts (Bustnes & Erikstad, 1993; Hervey et al., 2019). Future work should prioritize monitoring the nesting locations of females known to have experienced nest failure due to polar bears, which will help identify factors associated with nest redistribution in response to bears if they occur. Notably, our observations were only possible through using the emerging technology for drones, which may play a role in future studies of polar bear foraging behaviour in bird colonies (Jagielski et al., 2022).

Warming Arctic temperatures may inadvertently benefit eiders by allowing them to initiate egg laying and incubation earlier, resulting in early hatching (Chaulk & Mahoney, 2012; Love et al., 2010), which would normally occur far in advance of when bears would historically come on land. However, within increasing temperatures, polar bears are now arriving on land earlier, which is apparently generating a greater temporal overlap with eider incubation periods. Whether a mismatch between eider incubation and polar bear arrival on land can be re-established depends on the plasticity of eiders in responses to warming temperatures (e.g. can eiders advance laying dates faster than the advancement of polar bear arrival on land?). Other alterations to nesting strategies may involve increased rates of nest parasitism, whereby eiders lay eggs in nests of other females in the hopes of at least one nest being successful (Hervey et al., 2019). Regardless, predicting population responses of eiders to increasing rates of polar bear predation is likely to benefit from approaches that incorporate both individual-based behavioural responses (i.e. flushing behaviours) and colony level changes in nesting strategies (i.e. nesting locations, nest densities). As eiders play an important role in ecosystems as transporters of marine nutrients into terrestrial systems (Clyde et al., 2021) and serve as a source of sustenance and materials for northern communities (Henri et al., 2018), future investigations of eider responses to polar bears are warranted.

Author Contributions

Conceptualization: A.F.B., E.A.G., O.P.L., H.G.G., E.S.R., C.A.D.S.; Data curation: A.F.B., E.A.G., O.P.L., P.M.J., E.S.R., C.A.D.S.; Formal analysis: A.F.B., O.P.L., H.L.H., C.A.D.S.; Funding acquisition: O.P.L., H.G.G., E.S.R., C.A.D.S.; Investigation: A.F.B., E.A.G., O.P.L., P.M.J., C.M.H., H.G.G., H.L.H., E.S.R., C.J.D., C.A.D.S.; Methodology: A.F.B., E.A.G., O.P.L., P.M.J., C.M.H., H.G.G., H.L.H., E.S.R., C.J.D., C.A.D.S.; Project administration: O.P.L., C.M.H., H.G.G., H.L.H., E.S.R., C.J.D., C.A.D.S.; Resources: O.P.L., C.M.H., H.G.G., H.L.H., E.S.R., C.J.D., C.A.D.S.; Writing – original draft: A.F.B., E.A.G., O.P.L., H.G.G., C.A.D.S.; Writing – review & editing: A.F.B., E.A.G., O.P.L., P.M.J., C.M.H., H.G.G., H.L.H., E.S.R., C.J.D., C.A.D.S.

Data Availability

Data will be made available on request.

Declaration of competing interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2022.08.009.

References

Åhlund, M., & Götmark, F. (1989). Gull predation on eider ducklings *Somateria mollissima*: Effects of human disturbance. *Biological Conservation, 48*, 115–127.

Albrecht, T., & Klvaňa, P. (2004). Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology, 110*, 603–613.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. *Journal of Wildlife Management, 74*, 1175–1178.

Barnas, A. F., Chabot, D., Hodgson, A. J., Johnston, D. W., Bird, D. M., & Ellis-Felege, S. N. (2020). A standardized protocol for reporting methods when using drones for wildlife research. *Journal of Unmanned Vehicle Systems, 8*, 89–98.

Barnas, A. F., Darby, B. J., Iles, D. T., Koons, D. N., Rockwell, R. F., Semeniuk, C. A., & Ellis-Felege, S. N. (2022). Bear presence attracts avian predators but does not impact lesser snow goose daily nest attendance. *Journal of Avian Biology, 3*, Article e02840.

Barnas, A. F., Felege, C. J., Rockwell, R. F., & Ellis-Felege, S. N. (2018). A pilot(less) study on the use of an unmanned aircraft system for studying polar bears (*Ursus maritimus*). *Polar Biology, 41*, 1055–1062.

Barnas, A. F., Iles, D. T., Stechmann, T. J., Wampole, E. M., Koons, D. N., Rockwell, R. F., & Ellis-Felege, S. N. (2020). A phenological comparison of grizzly (*Ursus arctos*) and polar bears (*Ursus maritimus*) as waterfowl nest predators in Wapusk National Park. *Polar Biology, 43*, 457–465.

Bateman, P., & Fleming, P. (2011). Who are you looking at? Hadeda ibises use direction of gaze, head orientation and approach speed in their risk assessment of a potential predator. *Journal of Zoology, 285*, 316–323.

Bêty, J., & Gauthier, G. (2001). Effects of nest visits on predator activity and predation rate in a greater snow goose colony. *Journal of Field Ornithology, 72*, 573–586.

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science, 305*, 1955–1958.

Blumstein, D. T. (2010). Flush early and avoid the rush: A general rule of antipredator behavior? *Behavioral Ecology, 21*, 440–442.

Blumstein, D. T., Letnic, M., & Moseby, K. E. (2019). In situ predator conditioning of naive prey prior to reintroduction. *Philosophical Transactions of the Royal Society B: Biological Sciences, 374*, Article 20180058.

Bolduc, F., & Guillemette, M. (2003a). Human disturbance and nesting success of common eiders: Interaction between visitors and gulls. *Biological Conservation, 110*, 77–83.

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

Bottitta, G. E. (1999). Energy constraints on incubating common eiders in the Canadian Arctic (East Bay, Southampton Island, Nunavut). *Arctic, 52*, 425–429.

Bottitta, G. E., Nol, E., & Gilchrist, H. G. (2003). Effects of experimental manipulation of incubation length on behavior and body mass of common eiders in the Canadian Arctic. *Waterbirds, 26*, 100–107.

Brisson-Curadeau, É., Bird, D., Burke, C., Fifield, D. A., Pace, P., Sherley, R. B., & Elliott, K. H. (2017). Seabird species vary in behavioural response to drone census. *Scientific Reports, 7*, Article 17884.

Bro-Jørgensen, J., Franks, D. W., & Meise, K. (2019). Linking behaviour to dynamics of populations and communities: Application of novel approaches in behavioural ecology to conservation. *Philosophical Transactions of the Royal Society B: Biological Sciences, 374*(1781), Article 20190008.

Burger, J., & Gochfeld, M. (1981). Discrimination of the threat of direct versus tangential approach to the nest by incubating herring and great black-backed gulls. *Journal of Comparative & Physiological Psychology, 95*, 676.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York. Springer.

Bustnes, J. O., & Erikstad, K. E. (1993). Site fidelity in breeding common eider *Somateria mollissima* females. *Ornis Fennica, 70*, 11–16.

Carter, J., Lyons, N. J., Cole, H. L., & Goldsmith, A. R. (2008). Subtle cues of predation risk: Starlings respond to a predator's direction of eye-gaze. *Proceedings of the Royal Society B: Biological Sciences, 275*, 1709–1715.

Carthey, A. J., & Banks, P. B. (2014). Naïveté in novel ecological interactions: Lessons from theory and experimental evidence. *Biological Reviews, 89*, 932–949.

Carthey, A. J., & Blumstein, D. T. (2018). Predicting predator recognition in a changing world. *Trends in Ecology & Evolution, 33*, 106–115.

Chapman, A. (2014). It's okay to call them drones. *Journal of Unmanned Vehicle Systems, 2*(2) (iii–v).

Chaulk, K. G., & Mahoney, M. L. (2012). Does spring ice cover influence nest initiation date and clutch size in common eiders? *Polar Biology, 35*, 645–653.

Cherry, S. G., Derocher, A. E., Thiemann, G. W., & Lunn, N. J. (2013). Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *Journal of Animal Ecology, 82*, 912–921.

Clyde, N., Hargan, K., Forbes, M., Iverson, S., Blais, J., Smol, J., Bump, J., & Gilchrist, H. (2021). Seaduck engineers in the Arctic Archipelago: Nesting eiders deliver marine nutrients and transform the chemistry of island soils, plants, and ponds. *Oecologia, 195*, 1041–1052.

Congdon, J. V., Hahn, A. H., Campbell, K. A., Scully, E. N., Yip, D. A., Bayne, E. M., & Sturdy, C. B. (2020). Acoustic discrimination of predators by black-capped chickadees (*Poecile atricapillus*). *Animal Cognition, 23*, 595–611.

Cooper, W. E., Jr. (2006). Dynamic risk assessment: Prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology, 112*, 858–864.

Cooper, W. E., Jr., & Frederick, W. G. (2007). Optimal flight initiation distance. *Journal of Theoretical Biology, 244*, 59–67.

Côté, I. M., & Sutherland, W. J. (1997). The effectiveness of removing predators to protect bird populations. *Conservation Biology, 11*, 395–405.

Criscuolo, F., Gabrielsen, G. W., Gendner, J. P., & Le Maho, Y. (2002). Body mass regulation during incubation in female common eiders *Somateria mollissima*. *Journal of Avian Biology, 33*, 83–88.

Criscuolo, F., Gauthier-Clerc, M., Gabrielsen, G. W., & Le Maho, Y. (2000). Recess behaviour of the incubating common eider *Somateria mollissima*. *Polar Biology, 23*, 571–574.

Curio, E. (1975). The functional organization of anti-predator behaviour in the pied flycatcher: A study of avian visual perception. *Animal Behaviour, 23*(1), 1–115.

Curio, E. (1983). Why do young birds reproduce less well? *Ibis, 125*, 400–404.

Davidson, G. L., & Clayton, N. S. (2016). New perspectives in gaze sensitivity research. *Learning & Behavior, 44*, 9–17.

Dey, C. J., Richardson, E., Mcgeachy, D., Iverson, S. A., Gilchrist, H. G., & Semeniuk, C. A. (2017). Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. *Global Change Biology, 23*, 1821–1831.

Dey, C. J., Semeniuk, C. A., Iverson, S. A., & Gilchrist, H. G. (2020). Changes in the distribution of nesting Arctic seaducks are not strongly related to variation in polar bear presence. *Arctic Science, 6*, 114–123.

Dey, C. J., Semeniuk, C. A., Iverson, S. A., Richardson, E., Mcgeachy, D., & Gilchrist, H. G. (2018). Forecasting the outcome of multiple effects of climate change on northern common eiders. *Biological Conservation, 220*, 94–103.

Didham, R. K., Ewers, R. M., & Gemmell, N. J. (2005). Comment on avian extinction and mammalian introductions on oceanic islands. *Science, 307*(5714), 1412.

Dukas, R., & Kamil, A. C. (2000). The cost of limited attention in blue jays. *Behavioral Ecology, 11*, 502–506.

Ehlman, S. M., Trimmer, P. C., & Sih, A. (2019). Prey responses to exotic predators: Effects of old risks and new cues. *American Naturalist, 193*, 575–587.

Ellis-Felege, S. N., Stechmann, T. J., Hervey, S. D., Felege, C. J., Rockwell, R. F., & Barnas, A. F. (2021). Nesting common eiders (*Somateria mollissima*) show little behavioral response to fixed-wing drone surveys. *Journal of Unmanned Vehicle Systems, 10*(1), 1–14.

Fast, P. L., Gilchrist, H. G., & Clark, R. G. (2007). Experimental evaluation of nest shelter effects on weight loss in incubating common eiders *Somateria mollissima*. *Journal of Avian Biology, 38*, 205–213.

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

Fortune, S. M., Koski, W. R., Higdon, J. W., Trites, A. W., Baumgartner, M. F., & Ferguson, S. H. (2017). Evidence of molting and the function of 'rock-nosing' behavior in bowhead whales in the eastern Canadian Arctic. *PLoS One, 12*, Article e0186156.

Garbus, S.-E., Lyngs, P., Garbus, M., Garbus, P., Eulaers, I., Mosbech, A., Dietz, R., Gilchrist, H. G., Huusmann, R., & Christensen, J. P. (2018). Incubation behaviour of common eiders *Somateria mollissima* in the central Baltic: Nest attendance and loss in body mass. *Acrocephalus, 39*, 91–100.

Gaston, A. J., & Elliott, K. H. (2013). Effects of climate-induced changes in parasitism, predation and predator–predator interactions on reproduction and survival of an Arctic marine bird. *Arctic, 66*(1), 43–51.

Gochfeld, M. (1984). Antipredator behavior: Aggressive and distraction displays of shorebirds. In J. Burger, & B. L. Olla (Eds.), *Shorebirds* (pp. 289–377). Boston: Springer.

Gormezano, L. J., Ellis-Felege, S. N., Iles, D. T., Barnas, A., & Rockwell, R. F. (2017). Polar bear foraging behavior during the ice-free period in western Hudson Bay: Observations, origins, and potential significance. *American Museum Novitates, 2017*(3885), 1–28.

Götmark, F. (1992). The effects of investigator disturbance on nesting birds. In D. M. Power (Ed.), *Current ornithology* (Vol. 9, pp. 63–104). Boston: Springer.

Götmark, F., & Åhlund, M. (1984). Do field observers attract nest predators and influence nesting success of common eiders? *Journal of Wildlife Management, 48*(2), 381–387.

Goumas, M., Burns, I., Kelley, L. A., & Boogert, N. J. (2019). Herring gulls respond to human gaze direction. *Biology Letters, 15*, Article 20190405.

Grolemund, G., & Wickham, H. (2011). Dates and times made easy with lubridate. *Journal of Statistical Software, 40*, 1–25.

Hanson, T. (2006). To predate or depredate: What's the word? *Bulletin of the Ecological Society of America, 87*(2), 128–131.

Hennin, H. L., Dey, C. J., Bêty, J., Gilchrist, H. G., Legagneux, P., Williams, T. D., & Love, O. P. (2018). Higher rates of prebreeding condition gain positively impacts clutch size: A mechanistic test of the condition-dependent individual optimization model. *Functional Ecology, 32*, 2019–2028.

Henri, D. A., Jean-Gagnon, F., & Gilchrist, H. G. (2018). Using Inuit traditional ecological knowledge for detecting and monitoring avian cholera among common eiders in the eastern Canadian Arctic. *Ecology and Society, 23*(1), 22.

Hervey, S. D., Barnas, A. F., Stechmann, T. J., Rockwell, R. F., Ellis-Felege, S. N., & Darby, B. J. (2019). Kin grouping is insufficient to explain the inclusive fitness gains of conspecific brood parasitism in the common eider. *Molecular Ecology, 28*, 4825–4838.

Hijmans, R. J., Williams, E., Vennes, C., & Hijmans, M. R. J. (2017). *Geosphere: Spherical trigonometry (R package Version 1.5-14).* https://cran.r-project.org/web/packages/geosphere/index.html.
Humphreys, R. K., & Ruxton, G. D. (2020). Avian distraction displays: A review. *Ibis, 162*, 1125–1145.
Iverson, S. A., Gilchrist, H. G., Smith, P. A., Gaston, A. J., & Forbes, M. R. (2014). Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. *Proceedings of the Royal Society B: Biological Sciences, 281*, Article 20133128.
Jagielski, P. M. (2020). *Exploring the energetic consequences and decision-making behaviours of polar bears (*Ursus maritimus*) foraging on common eider (*Somateria mollissima*) seaduck eggs on Mitivik Island, Nunavut* (M.Sc. thesis). Windsor, ON, Canada: University of Windsor.
Jagielski, P. M., Barnas, A. F., Gilchrist, H. G., Richardson, E., Love, O., & Semeniuk, C. A. (2022). The utility of drones for studying polar bear behaviour in the Canadian Arctic: Opportunities and recommendations. *Drone Systems and Applications, 10*(1), 97–110.
Jagielski, P. M., Dey, C. J., Gilchrist, H. G., Richardson, E. S., Love, O. P., & Semeniuk, C. A. (2021a). Polar bears are inefficient predators of seabird eggs. *Royal Society Open Science, 8*, Article 210391.
Jagielski, P. M., Dey, C. J., Gilchrist, H. G., Richardson, E. S., & Semeniuk, C. A. (2021b). Polar bear foraging on common eider eggs: Estimating the energetic consequences of a climate-mediated behavioural shift. *Animal Behaviour, 171*, 63–75.
Jean-Gagnon, F., Legagneux, P., Gilchrist, G., Bélanger, S., Love, O. P., & Bêty, J. (2018). The impact of sea ice conditions on breeding decisions is modulated by body condition in an Arctic partial capital breeder. *Oecologia, 186*, 1–10.
Kay, M. F., & Gilchrist, H. G. (1998). Distraction displays made by female common eiders, *Somateria mollissima borealis*, in response to human disturbance. *Canadian Field-Naturalist, 112*, 529–531.
Kleindorfer, S., Fessl, B., & Hoi, H. (2005). Avian nest defence behaviour: Assessment in relation to predator distance and type, and nest height. *Animal Behaviour, 69*, 307–313.
Kristjansson, T. O., & Jónsson, J. E. (2015). Cooperative incubation behaviour in a super dense common eider *Somateria mollissima* colony. *Bird Study, 62*, 146–149.
Kyle, S. C., & Freeberg, T. M. (2016). Do Carolina chickadees (*Poecile carolinensis*) and tufted titmice (*Baeolophus bicolor*) attend to the head or body orientation of a perched avian predator? *Journal of Comparative Psychology, 130*, 145.
Laurila, T. (1989). Nest site selection in the common eider *Somateria mollissima*: Differences between the archipelago zones. *Ornis Fennica, 66*, 100–111.
Leavell, B. C., & Bernal, X. E. (2019). The cognitive ecology of stimulus ambiguity: A predator–prey perspective. *Trends in Ecology & Evolution, 34*(11), 1048–1060.
Love, O. P., Gilchrist, H. G., Descamps, S., Semeniuk, C. A., & Bêty, J. (2010). Pre-laying climatic cues can time reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Oecologia, 164*, 277–286.
Mallory, M. L. (2016). Reactions of ground-nesting marine birds to human disturbance in the Canadian Arctic. *Arctic Science, 2*, 67–77.
Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs, 65*, 101–127.
Martin, T. E., Martin, P., Olson, C., Heidinger, B., & Fontaine, J. (2000a). Parental care and clutch sizes in North and South American birds. *Science, 287*, 1482–1485.
Martin, T. E., Scott, J., & Menge, C. (2000b). Nest predation increases with parental activity: Separating nest site and parental activity effects. *Proceedings of the Royal Society B: Biological Sciences, 267*, 2287–2293.
Maziarz, M., Piggott, C., & Burgess, M. (2018). Predator recognition and differential behavioural responses of adult wood warblers *Phylloscopus sibilatrix*. *Acta Ethologica, 21*, 13–20.
Mckinnon, L., Gilchrist, H. G., & Scribner, K. T. (2006). Genetic evidence for kin-based female social structure in common eiders (*Somateria mollissima*). *Behavioral Ecology, 17*, 614–621.
Mcnair, D. B. (1981). Common eider plays ‘possum’. *Wilson Bulletin, 93*, 559–560.
Montgomerie, R. D., & Weatherhead, P. J. (1988). Risks and rewards of nest defence by parent birds. *Quarterly Review of Biology, 63*, 167–187.
Mulero-Pázmány, M., Jenni-Eiermann, S., Strebel, N., Sattler, T., Negro, J. J., & Tablado, Z. (2017). Unmanned aircraft systems as a new source of disturbance for wildlife: A systematic review. *PLoS One, 12*, Article e0178448.
Munoz, N. E., & Blumstein, D. T. (2012). Multisensory perception in uncertain environments. *Behavioral Ecology, 23*, 457–462.
Newton, I. (1998). *Population limitation in birds*. Academic Press.
Opermanis, O. (2004). Appearance and vulnerability of artificial duck nests to avian predators. *Journal of Avian Biology, 35*, 410–415.
Palmas, P., Jourdan, H., Debar, L., Bourguet, E., Rigault, F., Bonnaud, E., & Vidal, E. (2020). A conservation paradox: Endangered and iconic flightless kagu (*Rhynochetos jubatus*) apparently escape feral cat predation. *New Zealand Journal of Ecology, 44*, 1–8.
Peers, M. J., Majchrzak, Y. N., Neilson, E., Lamb, C. T., Hämäläinen, A., Haines, J. A., Garland, L., Doran-Myers, D., Broadley, K., & Boonstra, R. (2018). Quantifying fear effects on prey demography in nature. *Ecology, 99*, 1716–1723.
Prop, J., Aars, J., Bårdsen, B.-J., Hanssen, S. A., Bech, C., Bourgeon, S., De Fouw, J., Gabrielsen, G. W., Lang, J., & Noreen, E. (2015). Climate change and the increasing impact of polar bears on bird populations. *Frontiers in Ecology and Evolution, 3*, 33.
R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.r-project.org/.
Ricklefs, R. E. (1969). An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology, 9*. iv–48.
Rockwell, R., & Gormezano, L. (2009). The early bear gets the goose: Climate change, polar bears and lesser snow geese in western Hudson Bay. *Polar Biology, 32*, 539–547.
Rogers, S. R., Manning, I., & Livingstone, W. (2020). Comparing the spatial accuracy of digital surface models from four unoccupied aerial systems: Photogrammetry versus LiDAR. *Remote Sensing, 12*, 2806.
Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling and more (Version 0.5–12) (BETA). *Journal of Statistical Software, 48*, 1–36.
Rytkönen, S., & Soppela, M. (1995). Vicinity of sparrowhawk nest affects willow tit nest defense. *Condor: Ornithological Applications, 97*, 1074–1078.
Sang-Im Lee, S. H., Joe, Y.-E., Cha, H.-K., Joo, G.-H., Lee, H.-J., Kim, J.-W., & Jablonski, P. G. (2013). Direct look from a predator shortens the risk-assessment time by prey. *PLoS One, 8*(6), Article e64977.
Saul, W. C., & Jeschke, J. M. (2015). Eco-evolutionary experience in novel species interactions. *Ecology Letters, 18*, 236–245.
Schmidt, K. A. (1999). Foraging theory as a conceptual framework for studying nest predation. *Oikos, 85*(1), 151–160.
Schmidt, K. A., Dall, S. R., & Van Gils, J. A. (2010). The ecology of information: An overview on the ecological significance of making informed decisions. *Oikos, 119*, 304–316.
Seltmann, M. W., Öst, M., Jaatinen, K., Atkinson, S., Mashburn, K., & Hollmén, T. (2012). Stress responsiveness, age and body condition interactively affect flight initiation distance in breeding female eiders. *Animal Behaviour, 84*, 889–896.
Shipley, B. (2013). The AIC model selection method applied to path analytic models compared using ad-separation test. *Ecology, 94*, 560–564.
Sih, A. (1992). Prey uncertainty and the balancing of antipredator and feeding needs. *American Naturalist, 139*, 1052–1069.
Smith, P. A., Elliott, K. H., Gaston, A. J., & Gilchrist, H. G. (2010a). Has early ice clearance increased predation on breeding birds by polar bears? *Polar Biology, 33*, 1149–1153.
Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2010b). Effectiveness of predator removal for enhancing bird populations. *Conservation Biology, 24*, 820–829.
Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science, 308*, 1934–1937.
Tvardíková, K., & Fuchs, R. (2011). Do birds behave according to dynamic risk assessment theory? A feeder experiment. *Behavioral Ecology and Sociobiology, 65*, 727–733.
Waltho, C., & Coulson, J. (2015). *The common eider*. Bloomsbury.
Wanless, R. M., Angel, A., Cuthbert, R. J., Hilton, G. M., & Ryan, P. G. (2007). Can predation by invasive mice drive seabird extinctions? *Biology Letters, 3*, 241–244.
Weissburg, M., Smee, D. L., & Ferner, M. C. (2014). The sensory ecology of nonconsumptive predator effects. *American Naturalist, 184*, 141–157.
Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer.
Wickham, H., Francois, R., Henry, L., & Müller, K. (2015). *dplyr: A grammar of data manipulation (R package Version 1.0.9)*.
Wiles, G. J., Bart, J., Beck, R. E., Jr., & Aguon, C. F. (2003). Impacts of the brown tree snake: Patterns of decline and species persistence in Guam's avifauna. *Conservation Biology, 17*, 1350–1360.
Wilson, H. M., Flint, P. L., Powell, A. N., Grand, J. B., & Moran, C. L. (2012). Population ecology of breeding Pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. *Wildlife Monographs, 182*, 1–28.

Appendix

Georeferencing Eider Nests and Bear Locations to Measure Flush Initiation Distances

Georeferencing of common eider nests and polar bear locations was done using a 3 cm ground sampling distance orthomosaic of East Bay Island. This mosaic was produced using drone imagery collected in June 2019 with a DJI Phantom 4 Pro. For additional details on drone imagery collection and mosaic production, see Supplementary material 2. Estimating locations of eider nests and the bear at the moment of flush was done in ArcMap v.10.7.1 by identifying sets of unique landscape features in the 2017 video and finding those same features in the 2019 mosaic (see Fig. A1). We primarily used uniquely shaped rocks since these were not likely to change between 2017 and 2019. To facilitate more precise estimates of location, we often used multiple features to assist in the 'triangulation' of locations. We measured flush initiation distance as the distance between the eider nest and the bear location at the moment of flush using the 'Measure' tool.

Estimating Polar Bear Travel and Gaze Angles

We estimated whole circle bearings (WCBs) for the direction of the bear's travel, the direction of the bear's gaze and the direction from the bear's location to the focal eider nest. For clarification, WCBs are directional bearings from 0 to 359, where north = 0, east = 90, south = 180 and west = 270. Line segments for each of the three measurements were drawn in ArcMap, and then given WCBs to the nearest whole number using the 'Add Geometry' tool. From these bearings, we estimated the smallest angle between the bear's travel bearing and the bearing towards the nest (angle of approach), as well as the smallest angle between the bear's gaze bearing and the bearing towards the nest (angle of gaze) (see Fig. A2).

Estimating Polar Bear Movement Speed

To estimate polar bear movement speed prior to eider flush, we estimated the location of the bear at the moment of flush and 10 s prior to flush. We estimated the distance between the two locations using package 'geosphere' in R (Hijmans et al., 2017; R Core Team, 2017), rounded to the nearest 10 cm (see Fig. A3). We divided distances by 10 to obtain estimates of movement speed in m/s.

Estimating Number of Gulls

We estimated the number of gulls present at the moment eiders flushed by visually inspecting screenshots from the drone video. A single observer inspected images and counted the number of gulls present. While gulls were relatively easy to identify from the images, in the case of ambiguous identifications, we returned to the video to see if potential gulls moved at all during bear foraging when in view (see Fig. A4). If we were not able to positively identify a gull in an image beyond a reasonable doubt, we did not include it in the final total.

Estimating Eider Viewsheds

To estimate the proportion of area visible within a 30 m radius of each nest, we calculated viewsheds in ArcMap using the 'Viewshed' tool. Geoprocessing was done using ArcMap's 'ModelBuilder' to iteratively execute tools and procedures for each of the 193 unique eider nest locations. For each eider, we generated a 30 m polygon buffer and produced a raster clip from a 3 cm ground sampling distance digital surface model of East Bay Island generated from drone imagery acquired in June 2019. This was done to increase computational efficiency in estimating viewsheds only for the 30 m buffer area rather than a viewshed for the entire island for each eider nest location. We then estimated viewsheds for each eider's clipped digital surface model, including a 14 cm vertical offset to account for the approximate eye level of a nesting eider (as measured using a male sitting eider decoy, see Fig. A5). We then converted viewshed rasters to polygon layers and extracted the proportion of area occupied by visible cells within each layer. Summary statistics for each viewshed were exported to Microsoft Excel files. See Fig. A6 for a summary of the geoprocessing workflow described above.

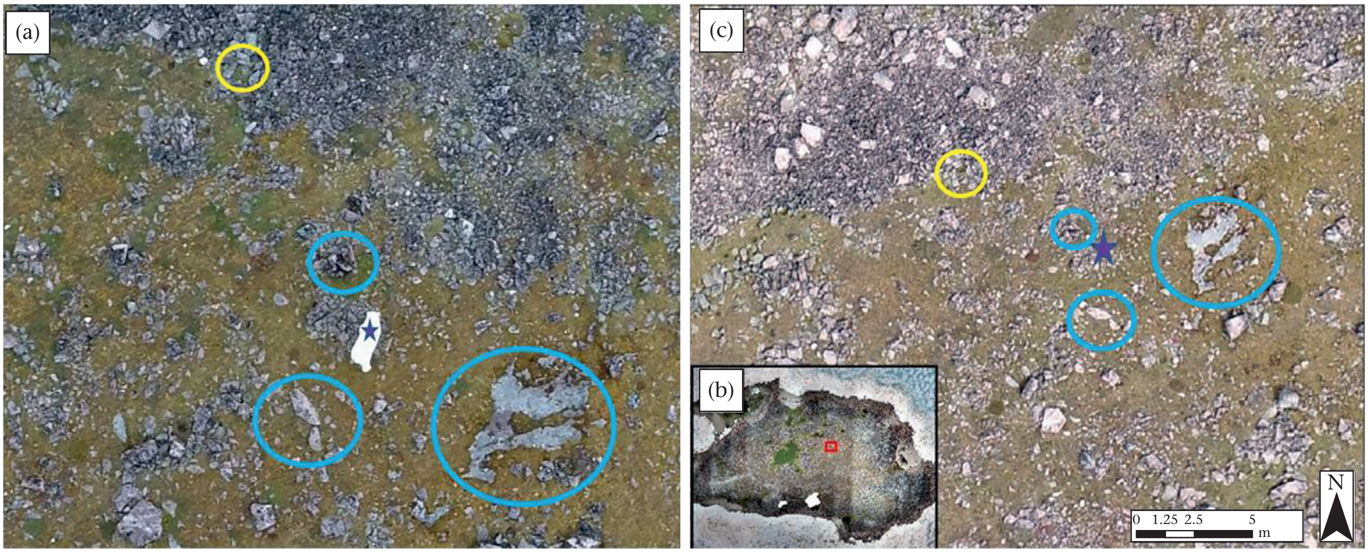

Figure A1. An example of georeferencing a common eider nest and a polar bear location at the moment of eider flush. (a) Original drone video paused at the moment of eider flush (cropped). Eider nest indicated by a yellow circle; polar bear indicated by a purple star. Blue circles indicate unique landscape features used to assist the observer in 'triangulating' the bear's location. Note the same process was used to locate eider nests, but for clarity, we have not included them in this figure. (b) Extent indicator for the general location of the flush event on East Bay Island. (c) The location of the eider nest and the polar bear on the georeferenced drone imagery mosaic of East Bay Island. Note the same landscape features (blue circles) on the mosaic used to estimate the polar bear location.

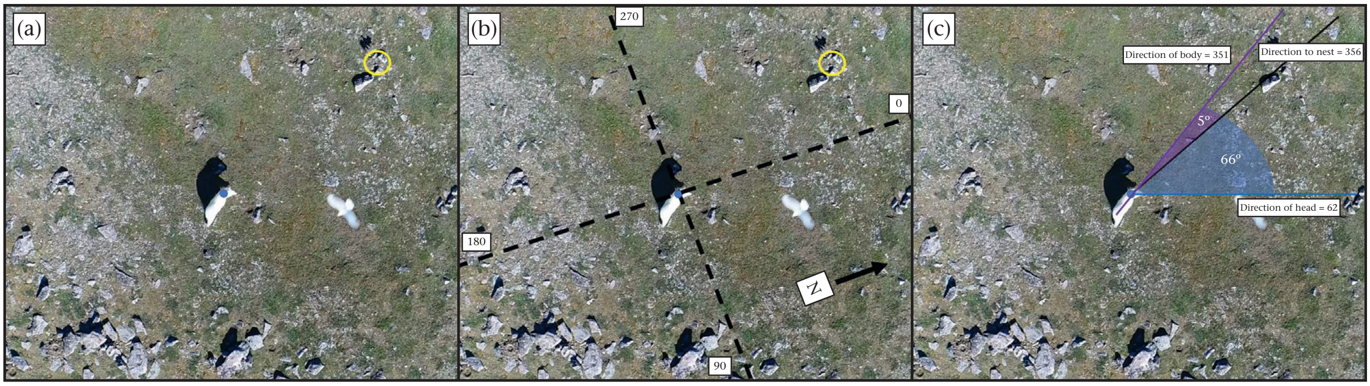

Figure A2. Estimating angles of approach and gaze between polar bears and common eider nests. (a) A cropped screen shot of drone video of a polar bear (blue dot) at the moment a female eider flushes from her nest (yellow circle). (b) An overlay of the cardinal directions for the view of this flush event and the respective whole circle bearings (WCBs). (c) Estimated WCBs denoting the bear's direction of travel (purple line), the direction of the bear's head (blue line) and the direction to the eider nest from the bear's location (black line). Estimates for smallest approach and gaze angles to the nest in this example are 5° and 66°, respectively.

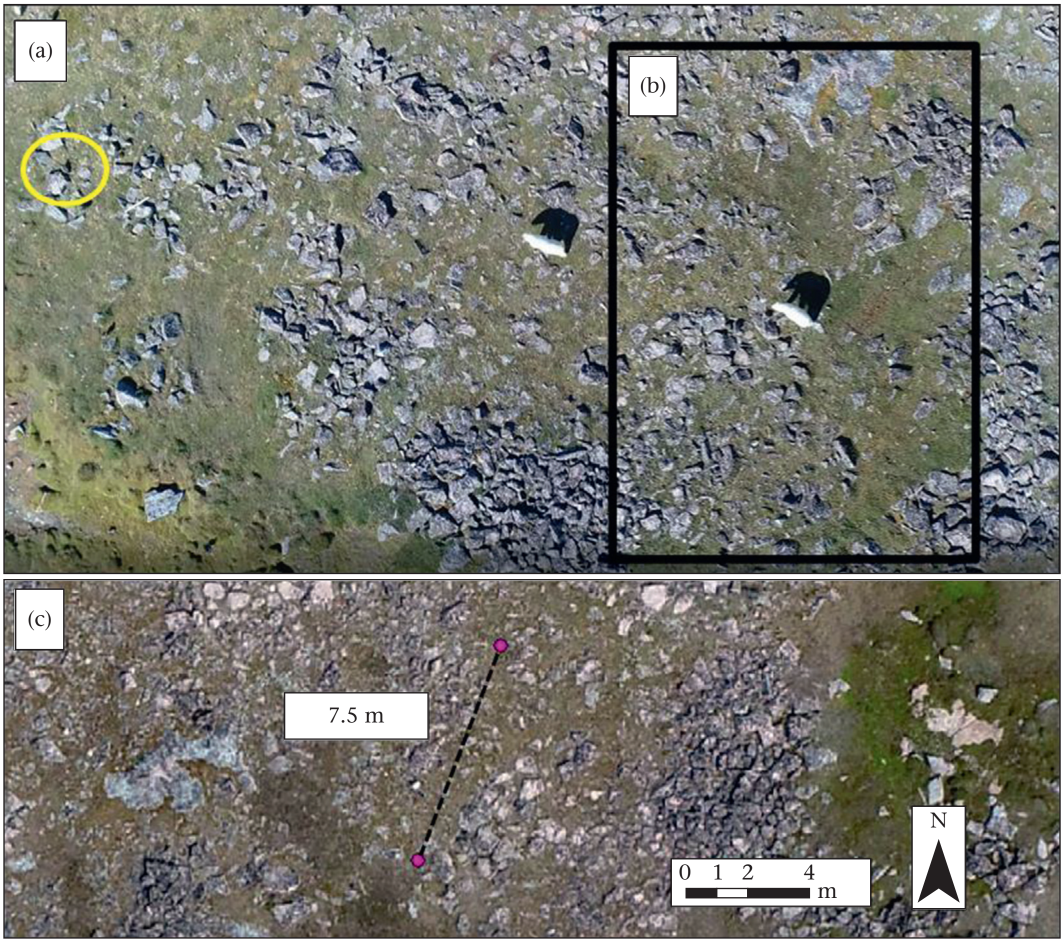

Figure A3. Estimating movement speed of polar bears prior to common eider flush. (a) Location of bear at the moment of eider flush. Nest indicated by yellow circle. (b) Location of the same bear, 10 s before flush, superimposed and aligned with the original image for clarity. (c) Georeferenced drone imagery used to estimate both locations and calculate the distance travelled over the 10 s prior to flush.

Figure A4. Estimating the number of gulls present at the moment of common eider flush from a screenshot of drone video. Eider nest indicated by blue circle, gulls indicated by purple circle, and an example of a potentially ambiguous white rock, which was excluded as being a gull (red circle).

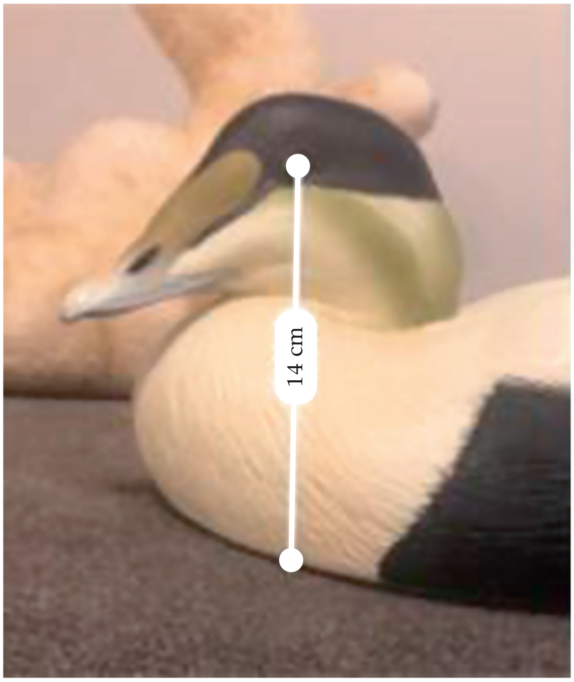

Figure A5. Estimated vertical offset for a common eider's eye level above ground using a sitting male eider decoy. Photo credit: Erica Geldart.

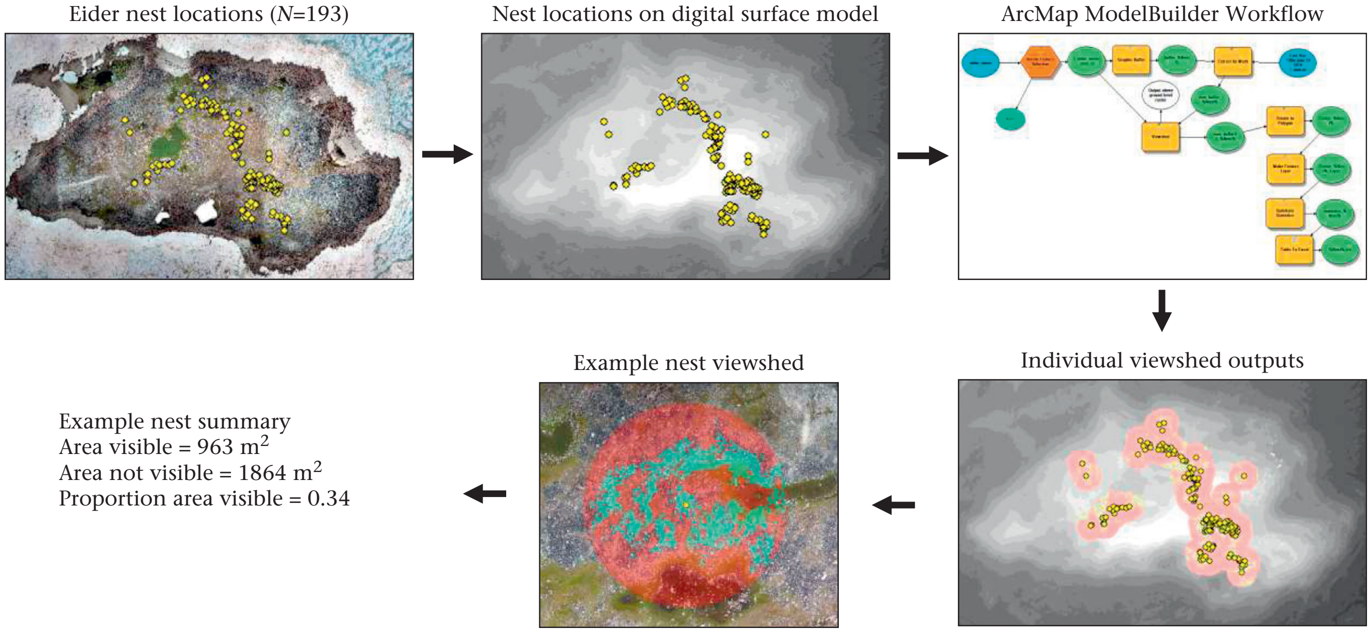

Figure A6. Geoprocessing workflow for calculating viewsheds for each common eider nest in ArcMap. Note the example nest viewshed has been overlaid on the original RGB mosaic at 70% transparency for comparison.