Title: Predatory Cue Use in Flush Responses of a Colonial Nesting Seabird During Polar Bear Foraging

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Funding

This work was supported by Baffinland Iron Mines, Environment and Climate Change Canada, The Liber Ero Foundation (to CJD), Mitacs (Grant number IT04216), Natural Sciences and Engineering Council (Grant number 06768); and The University of Windsor.

Declaration of Interest: none

Acknowledgments

We thank the 2017 and 2019 East Bay Island field crew for their assistance with logistics and data collection. Specifically we thank Mike Janssen, Jake Russell-Mercier, and Bronwyn Harkness from Environment and Climate Change Canada; Josiah Nakoolak, Jupie Angootealuk, Clifford Natakok, and Bob Hansen for their expertise and assistance in the field. We are grateful for the opportunity to work in Qaqsauqtuuq (Inuit Nunangat) and the community of Coral Harbour. Drone use was authorized by Environment and Climate Change Canada Animal Care permits EC-PN-17-026 and EC-PN-19-026, and by Nunavut Wildlife Research permits WL-2017-030 and WL-2019-027. We thank Lincoln Savi for assistance with drone flight operations and planning during the 2019 field season. The creation of Figure 1 was done using the “Provinces and Territories of Canada” layer accessed via ESRI online. Writing of this manuscript was greatly facilitated by the soundtrack of The Witcher 3: Wild Hunt.

Highlights

- Polar bear predation of nesting seabirds has increased due to climate change, but bird behavioural responses to these predators has not been investigated
- We used drone videography to investigate polar bear foraging in a common eider colony, and recorded 200 flush events from 193 individual birds in 2017
- We demonstrate more direct angles of visual gaze and travel by bears result in more conspicuous nest flushes by eiders
- However eiders were more inconspicuous in their flushes when more gulls were present

Abstract

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 more direct angles of visual gaze and travel angle by polar bears resulted in conspicuous nest flushes by eiders (β = -0.236 ± 0.059), whereas the presence of herring gulls (*Larus argentatus*) resulted in more discrete flushes of hens walking from their nests (β = -0.181 ± 0.059). Shorter flush initiation distances between eiders and approaching bears resulted in greater nest predation by polar bears (β = -0.203 ± 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 make appropriate behavioural decisions to reduce 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.

Keywords: Common eider (*Somateria mollissima)*, Polar bear (*Ursus maritimus*), predator cues, Dynamic Risk Assessment, drones, path analysis

Introduction

Nest predation is a primary cause of reproductive failure in many species of birds (Côté and Sutherland 1997, Newton 1998, Smith et al. 2010b); thus predators apply strong selective pressure on avian nesting behaviour, especially risk-assessment behaviours during predator encounters at the nest (Ricklefs 1969, Montgomerie and Weatherhead 1988, Martin 1995, 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 and 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 (Curio 1975, Curio 1983, Rytkönen and Soppela 1995, Martin et al. 2000a, Tvardíková and Fuchs 2011, Congdon et al. 2020).

Risk assessments performed by incubating parents on predators are not static; rather, Dynamic Risk Assessment (DRA) 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 and 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 Jr and Frederick 2007). Some predator cues are well known to play a role in DRA and subsequent prey responses, including predator body size (Templeton et al. 2005), travel speed (Cooper Jr 2006), and direction of travel (Burger and 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 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 and Fleming 2011, Davidson and 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 and Klvaňa 2004). In combination, multiple sources of cues/information should be used by prey to better inform decision making (Sih 1992, Munoz and Blumstein 2012), 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 and Kamil 2000, Leavell and Bernal 2019). As such, investigating DRA 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' eco-evolutionary experience with a given predator, as prey are generally poorer at responding to unfamiliar/novel predators than those they have experience with (Saul and Jeschke 2015, Ehlman et al. 2019). In the context of climate-induced environmental change, exposure to unfamiliar/rare predators is an important and yet still largely under-studied aspect of predation risk assessments (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 birds species (e.g., Wiles et al. (2003), Blackburn et al. (2004), Wanless et al. (2007), 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 which risk adult/nest survival. Nonetheless, 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 then determining the consequences of those responses should be informative to predicting persistence of a prey species (Carthey and Banks 2014, Carthey and 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 (Iverson et al. 2014, Prop et al. 2015, Barnas et al. 2020b). 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.) (Laurila 1989, Bolduc and

Guillemette 2003a). 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 (Rockwell and Gormezano 2009, Smith et al. 2010a, Prop et al. 2015). Once onshore and within a colony, bears can destroy hundreds of eider nests in a relatively short period of time, leading to near complete colony failure in some years/sites (Rockwell and Gormezano 2009, Gormezano et al. 2017, Barnas et al. 2020b, Jagielski et al. 2021a, Jagielski et al. 2021b). Predictive modeling suggests that nesting eiders should disperse, and shift to 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 and Gochfeld 1981, Carter et al. 2008, Kyle and Freeberg 2016, Maziarz et al. 2018, Goumas et al. 2019), 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” (i.e., respond in a manner that would have led to predation by a real predator) to artificial predator cues 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 (Weissburg et al. 2014, Peers et al. 2018). 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 (Götmark and Åhlund 1984, Åhlund and Götmark 1989, Götmark 1992, Bêty and Gauthier 2001). 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 (Brisson-Curadeau et al. 2017, Mulero-Pázmány et al. 2017, Barnas et al. 2018). Fixed-wing drones in other systems have been shown to have little behavioural impact on nesting eiders (Ellis-Felege et al. 2021) and 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 measure two behavioural responses of eiders; 1) Flush Initiation Distance (hereafter FID: commonly used to describe "Flight Initiation Distance" (Cooper Jr and 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)), and 2) the behavioural style in which each bird flushed from her nest. Using predictions from DRA theory, we hypothesized that faster polar bear approaching travel speed, as well as more direct angles of approach and gaze should result in greater flush distances, indicating adult eiders prioritizing their own survival in the face of a threatening predator. Conversely, shorter flush distances would indicate eiders are investing more in protecting their current clutch of eggs. We also predict that eiders would flush inconspicuously with indirect angles of approach and gaze by bears and 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 (Figure 1). East Bay Island is a small (approximately 24 ha) island comprised 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 8m), 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 et al. (2021b).

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, Criscuolo et al. 2000, Bottitta et al. 2003, Fast et al. 2007). On East Bay Island, the primary nest predators of eiders are herring gulls (*Larus argentatus*, 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 et al. 2021b). Bears typically arrive ashore during eider egg-laying and early incubation stages of eiders (Jagielski et al. 2021b). 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 et al. 2021b).

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 multi-rotor drones from July 10th to 20th in 2017 (Jagielski et al. 2021b). Briefly, when bears 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 between approximately 30 to 55m Above Ground Level (AGL) 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), and only when environmental conditions permitted drone operation (e.g., clear weather, wind < 10km^{-hr}). 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 et al. 2020a), see Supplemental Materials #1.

We collected 995 minutes 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 30m AGL. This filtering step resulted in 166.3 mins of video to review, from 15 drone flights, across five days of bear foraging (July 11, 15, 16, 19, and 20), from 4 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 v10.7.1 (ESRI, Redlands, CA), and a georeferenced map of East Bay Island (see *Drone Video Review* below). For filtered videos, the estimated mean area ± SD was 1023 ± 195m^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 (Identity Concealed For Review) reviewed video of polar bear foraging for flushing eider hens using Windows Film & TV application v.10.200022.11011.0 (Microsoft Corporation, Washington, United States). 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, 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 datetime of drone flights and time of flush within each video to estimate the datetime 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 non-reproductive 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 is 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 and Jónsson 2015).

We used a georeferenced, true colour, 3cm Ground Sampling Distance (GSD) orthomosaic of East Bay Island produced from drone imagery acquired in June 2019 to estimate flush initiation distance of eiders to polar bears. For details on the image acquisition and creation of this orthomosaic, see Drone Reporting Protocol #2 in Supplemental Materials 2 (Barnas et al. 2020a). 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 datasets, 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 (Supplementary Materials #3, section 1.1). 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 in vacating her nest. We recorded three qualitative categories of flush style: walking = an eider who walked off her nest, jumping = an eider who more quickly ran or jumped off her nest and flying = an eider who 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 of time. Although polar bears are known to capture and kill nesting female eiders (Gormezano et al. 2017), we are primarily focused on the risk polar bears pose to eider eggs rather than the adult.

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 (Supplemental Materials #3, section 1.2). We estimated polar bear movement speed (m^{-s}) by estimating the location of the bear 10 seconds prior to an eider flush, calculating the distance traveled by the bear over those 10 seconds, and dividing distance by 10 to estimate movement in m^{-s} (Supplemental Materials #3, section 1.3). 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 number of gulls into three categories, Absent (0 gulls), Low (1-5 gulls), and High (> 5 gulls) (Supplemental Materials #3, section 1.4).

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 30m radius circle (area ≈ $2827m^2$) that was visible to the nesting female using ArcMap's *Viewshed* tool and a 3cm Digital Surface Model (Rogers et al. 2020) generated using Structure-from-Motion using the same RGB drone imagery collected in 2019. Briefly, within a 30m 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 30m radius based on the maximum observed FID of eiders (25.7m, see Results). We included a vertical offset of 14cm for eider nest locations to account for the approximate height of a female eider's eyeline while sitting on her nest (measured 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 30m radius buffer visible (Supplementary Materials #3, section 1.5). Although our calculated viewshed does not consider the height of polar bears (as taller bears may be more visible to nesting eiders), this metric should still provide 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, and 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 dataset. 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 (Figure 2). We also fit 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 re-coded them as dummy and ordinal variables where appropriate. Polar bear travel angle and gaze angle were positively correlated (Pearson correlation coefficient = 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 as Absent, Low, and High, and flush style as Walk, Jump, and Fly (where walking off nest is considered a “low” value, and increasing through jumping and flying as “high”). 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 8 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 through FID and flush style (Figure 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 AICc for small sample size, where models were considered competitive if they fell within Δ2 AICc (Burnham and Anderson 2002, Shipley 2013, Hennin et al. 2018). 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 v10.7.1 (ESRI, Redlands, CA). All other data manipulation and variable calculations were done in RStudio v3.6.2 (R Core Team 2017) using package *geosphere* for spatial data (Hijmans et al. 2017), *lubridate* for datetime data (Grolemund and 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 July 11 (n= 61), 15 (n=99), 16 (n=39), and 19 (n=1) in 2017; seven of these flushes were repeat observations by individuals on different days. No flushes were observed during foraging bouts on July 20, which may reflect the high level of bear predation that had occurred on previous days (i.e., relatively few eider nests were active by July 20). Of the 200 flush events used 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 ± 4.1m (range: 0.9-25.7m) from the bear and the number of flush styles observed was similar among types (Walk Off = 66, Jump Off = 66, and Fly Off = 68) (Figure 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 (Figure 5). Mean polar bear speed prior to flushes was 0.5 ± 0.3m^{-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 (Figure 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 fit of Model #6 and Model #7 was consistently "adequate" based on multiple measures (Model #6: CFI = 0.565, TLI = 0.348, RMSEA = 0.135, and SRMR = 0.112; Model #7: CFI = 0.593, TLI = 0.146, RMSEA = 0.154, and SRMR = 0.104), where "good" model fit is indicated by CFI > 0.9, TLI > 0.95, RMSE< 0.1, SRMR< 0.08. Interestingly, all models including a path from FID to flush style, received higher support than those models without that path (Table 1).

From our most competitive path model (Model #6), we found lower angle sums (i.e., more direct angles of travel and gaze) of polar bears resulted in more obvious flush response such as jumping or flying ($\beta = -0.236$, SE = 0.059, $P < 0.001$). We found that lower eider FIDs (i.e., closer bears) resulted both in more obvious flush responses s ($\beta = -0.437$, SE = 0.054, $P<0.001$) and subsequent nest loss by polar bears ($\beta = -0.203$, SE = 0.076, $P<0.05$), but the opposite relationship between gull presence and flush styles, as higher gull numbers evoked more inconspicuous "walk off" style flushes ($\beta = -0.181$, SE = 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 (Figure 5A). In Model #7 we found that eiders flushed at shorter distances when polar bears were moving faster ($\beta = -0.164$, SE = 0.068, $P<0.05$), but found no significant effects of angle sum, proportion viewshed visible, or number of gulls on FID (Figure 5B). Standardized estimates of path coefficients from all endogenous variables to flush style were similar in both Model #6 and #7 (Figure 5).

Discussion

Our findings reveal novel insights on the behavioural responses of eiders when leaving their nests, by demonstrating that individuals behave according to DRA 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 eider. Eiders have evolved a mass-loss incubation strategy which relies on females remaining concealed on their nest for as long as possible (Bolduc and 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 feel 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 anti-predator 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 refugia), 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 (Sih 1992, Munoz and Blumstein 2012), but due to costs associated with attentional constraints not all cues are considered equally during flush responses (Dukas and Kamil 2000, Leavell and 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 et al. 2021a). Our top model indicated flush styles are informed by FIDs, but that our measured cues were not greatly influential on 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 the next top supported model shows that slower moving polar bears result in greater FIDs, suggesting 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 and Guillemette 2003b), however as the majority of our observations came from July 11 – 15 (5 days), we did not explore ~~D~~date as a proxy for incubation date~~y~~ 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 and Coulson 2015).

Flight Initiation Distance Informs Flushing Style

Our observed mean FID (9.1m) falls within the reported FIDs of nesting eiders to researcher disturbance reported in the literature (4-8m: Kay and Gilchrist (1998); 16m Mallory (2016); 2.4-3.4m 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 “eye-line” of bears would have a higher chance of gaining attention. Distraction displays have previously been described in eiders (McNair 1981, Kay and Gilchrist 1998), 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 and 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 employed by relatively few individuals (perhaps learned through prior exposures to polar bears), 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. ~~and a~~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 et al. (2000a), but see Martin et al. (2000b)), 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 this 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 (Gaston and Elliott 2013, Iverson et al. 2014, Barnas et al. 2022). 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 anti-predator response that is effective on the scale of individual encounters with polar bears. In other words, eiders appear to be capable of performing DRA by sensing the predator- and environmental cues associated with a foraging polar bear, and differentially employ appropriate flushing behaviours to minimize 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, and it may be that the general confusion induced by multiple flushing eiders makes it difficult for bears to sometimes 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 is 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 et al. (2021b)), 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 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, Dey et al. 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 and 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 (Love et al. 2010, Chaulk and Mahoney 2012), 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.

Supplemental Materials

1) Drone Reporting Protocol for the drone video collection of polar bears foraging in a common eider colony in 2017
2) Drone Reporting Protocol for the drone imagery collection and production of the 2019 East Bay Island orthomosaic
3) Technical details and examples of georeferencing eider nests and polar bear characteristics

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Table 1 Model selection results for conceptual path diagrams relating exogenous predator and environmental variables to endogenous variables for common eider (*Somateria mollissima*) flushing behaviours and nest fate. Model ID indicates the candidate model structures detailed in Figure 2.

Model Rank	Model ID	K	Log Likelihood	AICc	∆AICc	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

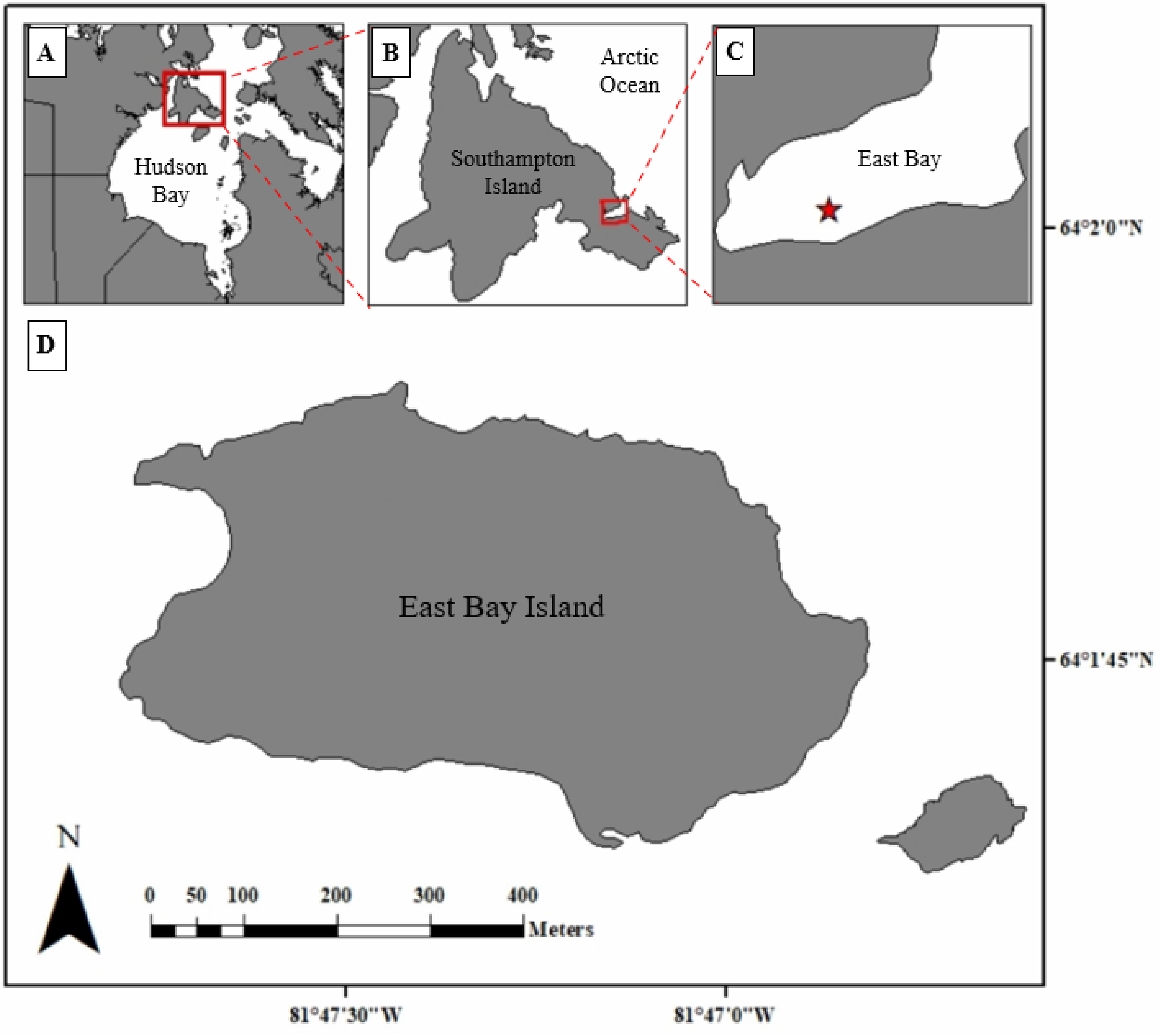

Figure 1. Map of the study location, A) General study location in northern Hudson Bay, B) Southampton Island, Nunavut, Canada, C) East Bay of Southampton Island, location of study site indicated by red star, D) East Bay Island, Nunavut, Canada. Canadian Provinces and Territories inset map layers provided by ESRI online, accessed September 1st, 2020.

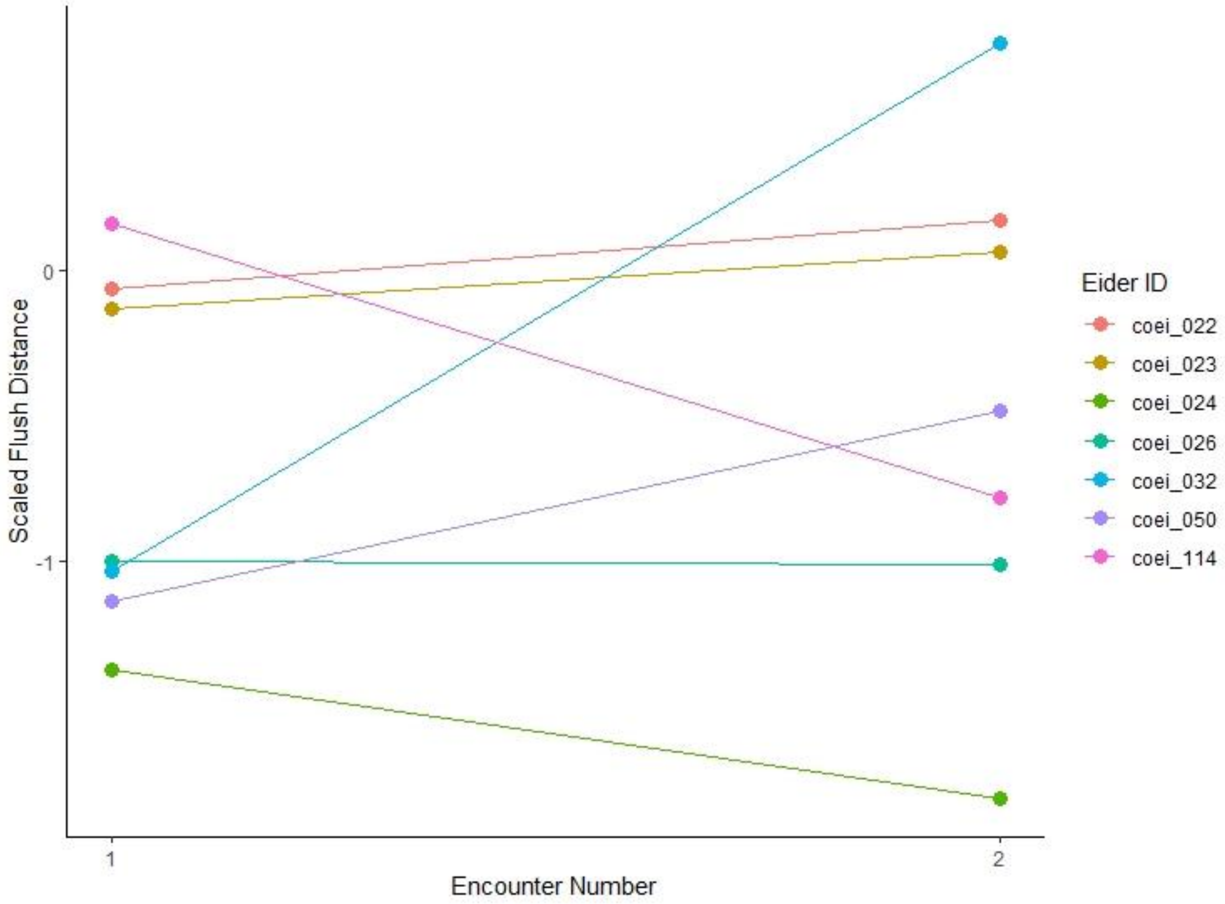

Figure 2 Scaled flush distance of individual common eiders (*Somateria mollissima*, n = 7) in response to first and second encounters with polar bears (*Ursus maritimus*).

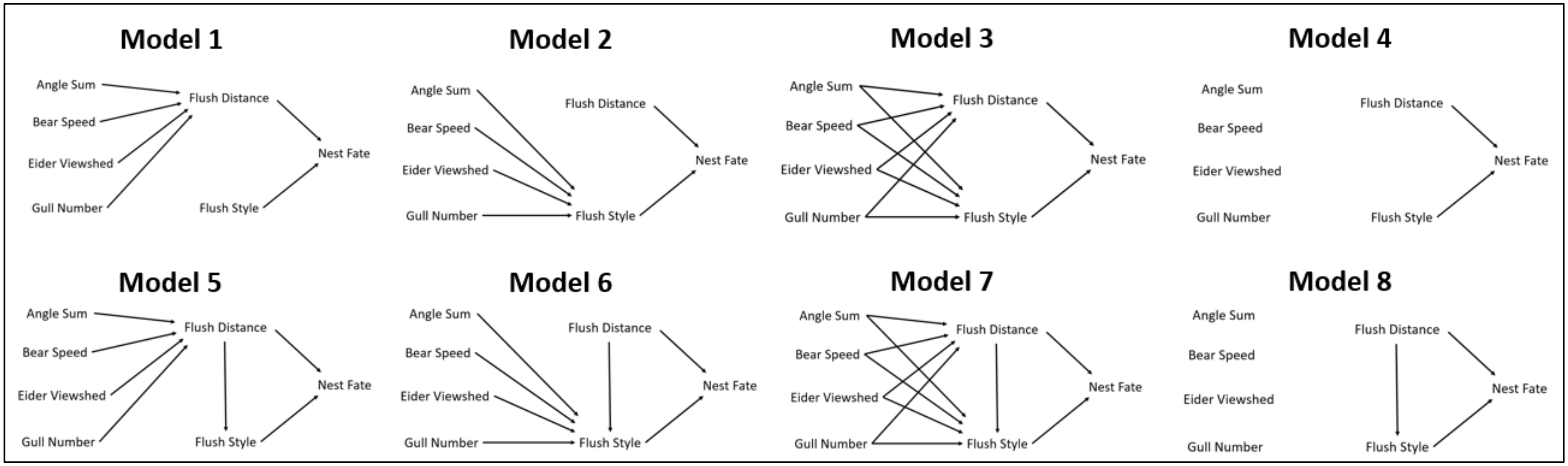

Figure 3. Candidate path diagrams relating predator and environmental cues to flushing behaviour and nest fate of common eiders (*Somateria mollissima*). Arrows represent conceptual unidirectional relationship between variables.

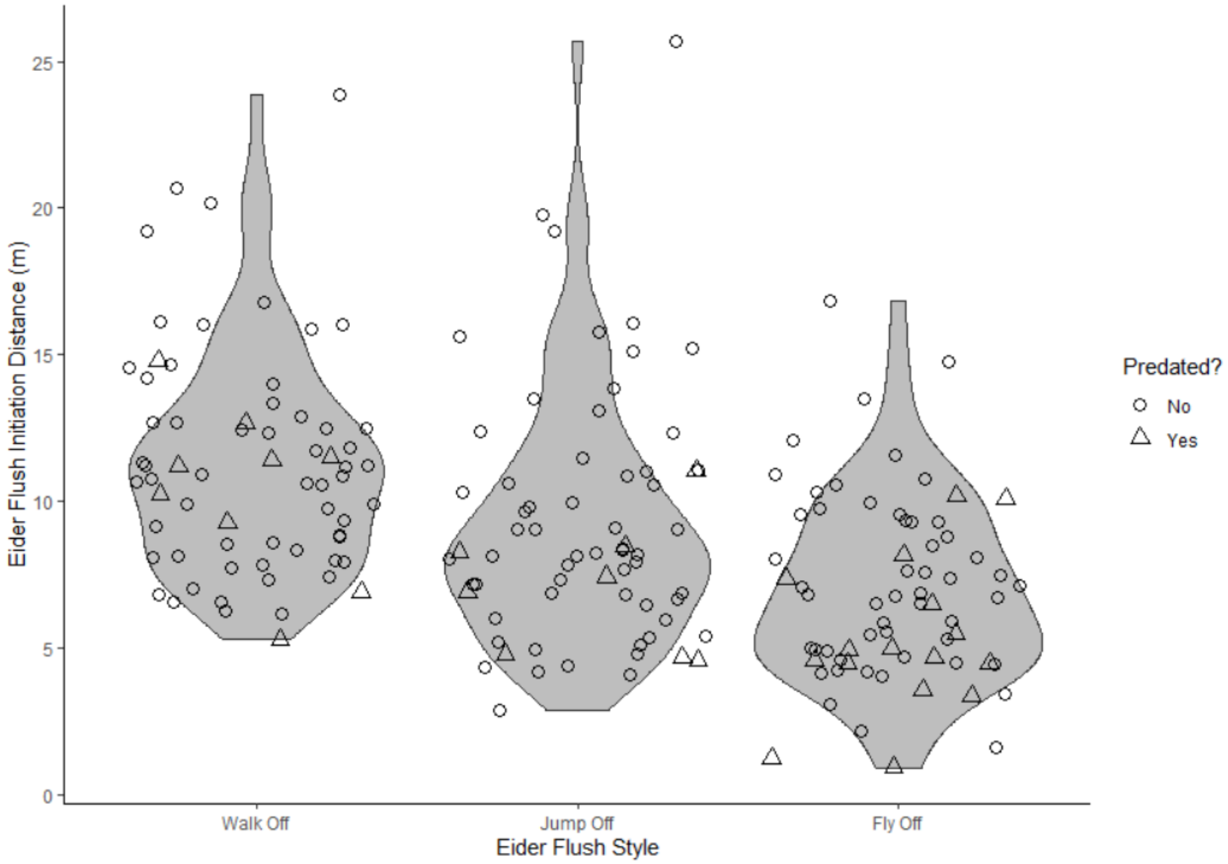

Figure 4. Raw data depicting relationship between flush style, flush initiation distance (m), and nest fate of common eiders (*Somateria mollissima*) in response to polar bears (*Ursus maritimus*). Measurements obtained from aerial drone video in July 2017 (n=200).

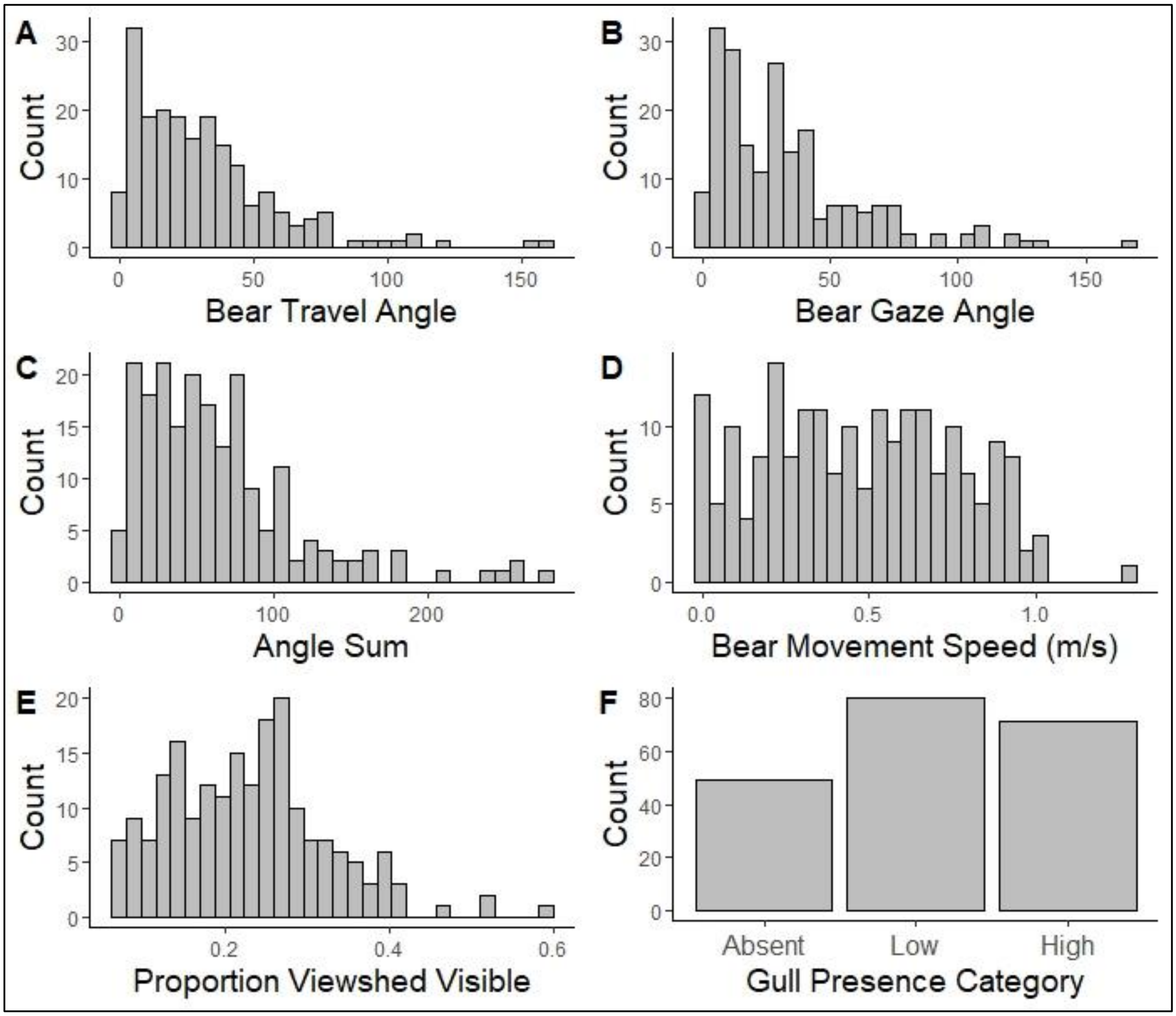

Figure 5. Raw data of predator and environmental cues collected during common eider (*Somateria mollissima*) flush events in response to polar bears (*Ursus maritimus*). A) Polar bear travel angle relative to eider nest location, B) polar bear gaze angle relative to eider nest location, C) Linear combination of a bear's travel and gaze angle, D) Polar bear travel speed (m/s) averaged over the 10 seconds prior to eider flush, E) proportion of an eider's viewshed that is visible from the nest location within a 30m radius, F) category of herring gull (Laru*s argentatus*) 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.

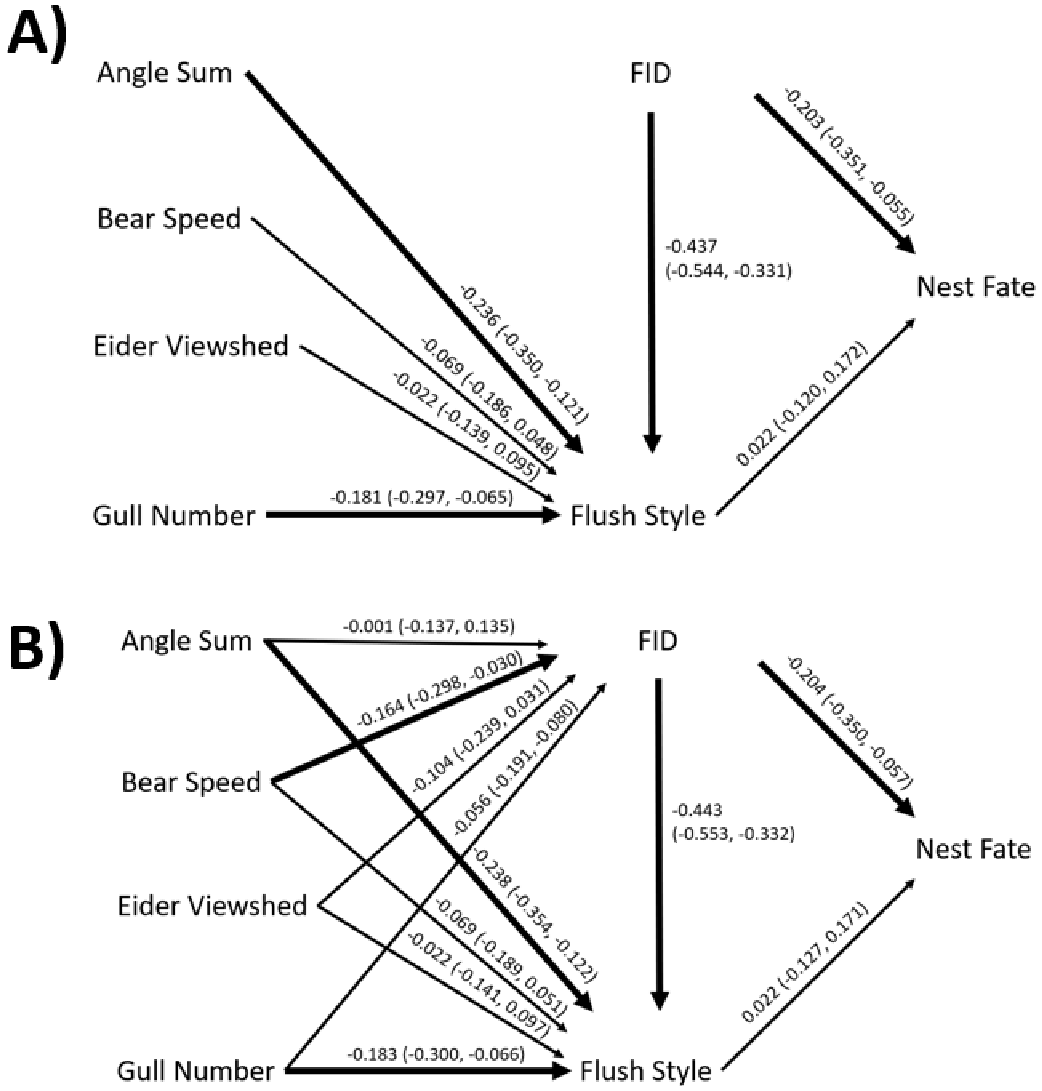

Figure 6. Standardized parameter estimates relating common eider (*Somateria mollissima*) flush style, flush initiation distance (FID)and nest fate to exogenous variables for the linear combination of polar bear (*Ursus maritimus*) travel and gaze angle, polar bear speed, proportion viewshed visible, and herring gull (*Larus argentatus*) 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).

Abstract

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 more direct angles of visual gaze and travel angle by polar bears resulted in conspicuous nest flushes by eiders (β = -0.236 ± 0.059), whereas the presence of herring gulls (*Larus argentatus*) resulted in more discrete flushes of hens walking from their nests (β = -0.181 ± 0.059). Shorter flush initiation distances between eiders and approaching bears resulted in greater nest predation by polar bears (β = -0.203 ± 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 make appropriate behavioural decisions to reduce 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.

Keywords: Common eider (*Somateria mollissima)*, Polar bear (*Ursus maritimus*), predator cues, Dynamic Risk Assessment, drones, path analysis

Introduction

Nest predation is a primary cause of reproductive failure in many species of birds (Côté and Sutherland 1997, Newton 1998, Smith et al. 2010b); thus predators apply strong selective pressure on avian nesting behaviour, especially risk-assessment behaviours during predator encounters at the nest (Ricklefs 1969, Montgomerie and Weatherhead 1988, Martin 1995, 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 and 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 (Curio 1975, Curio 1983, Rytkönen and Soppela 1995, Martin et al. 2000a, Tvardíková and Fuchs 2011, Congdon et al. 2020).

Risk assessments performed by incubating parents on predators are not static; rather, Dynamic Risk Assessment (DRA) 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 and 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 Jr and Frederick 2007). Some predator cues are well known to play a role in DRA and subsequent prey responses, including predator body size (Templeton et al. 2005), travel speed (Cooper Jr 2006), and direction of travel (Burger and 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 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 and Fleming 2011, Davidson and 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 and Klvaňa 2004). In combination, multiple sources of cues/information should be used by prey to better inform decision making (Sih 1992, Munoz and Blumstein 2012), 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 and Kamil 2000, Leavell and Bernal 2019). As such, investigating DRA 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' eco-evolutionary experience with a given predator, as prey are generally poorer at responding to unfamiliar/novel predators than those they have experience with (Saul and Jeschke 2015, Ehlman et al. 2019). In the context of climate-induced environmental change, exposure to unfamiliar/rare predators is an important and yet still largely under-studied aspect of predation risk assessments (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 birds species (e.g., Wiles et al. (2003), Blackburn et al. (2004), Wanless et al. (2007), 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 which risk adult/nest survival. Nonetheless, 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 then determining the consequences of those responses should be informative to predicting persistence of a prey species (Carthey and Banks 2014, Carthey and 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 (Iverson et al. 2014, Prop et al. 2015, Barnas et al. 2020b). 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.) (Laurila 1989, Bolduc and

Guillemette 2003a). 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 (Rockwell and Gormezano 2009, Smith et al. 2010a, Prop et al. 2015). Once onshore and within a colony, bears can destroy hundreds of eider nests in a relatively short period of time, leading to near complete colony failure in some years/sites (Rockwell and Gormezano 2009, Gormezano et al. 2017, Barnas et al. 2020b, Jagielski et al. 2021a, Jagielski et al. 2021b). Predictive modeling suggests that nesting eiders should disperse, and shift to 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 and Gochfeld 1981, Carter et al. 2008, Kyle and Freeberg 2016, Maziarz et al. 2018, Goumas et al. 2019), 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” (i.e., respond in a manner that would have led to predation by a real predator) to artificial predator cues 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 (Weissburg et al. 2014, Peers et al. 2018). 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 (Götmark and Åhlund 1984, Åhlund and Götmark 1989, Götmark 1992, Bêty and Gauthier 2001). 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 (Brisson-Curadeau et al. 2017, Mulero-Pázmány et al. 2017, Barnas et al. 2018). Fixed-wing drones in other systems have been shown to have little behavioural impact on nesting eiders (Ellis-Felege et al. 2021) and 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 measure two behavioural responses of eiders; 1) Flush Initiation Distance (hereafter FID: commonly used to describe "Flight Initiation Distance" (Cooper Jr and 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)), and 2) the behavioural style in which each bird flushed from her nest. Using predictions from DRA theory, we hypothesized that faster polar bear approaching travel speed, as well as more direct angles of approach and gaze should result in greater flush distances, indicating adult eiders prioritizing their own survival in the face of a threatening predator. Conversely, shorter flush distances would indicate eiders are investing more in protecting their current clutch of eggs. We also predict that eiders would flush inconspicuously with indirect angles of approach and gaze by bears and 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 (Figure 1). East Bay Island is a small (approximately 24 ha) island comprised 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 8m), 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 et al. (2021b).

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, Criscuolo et al. 2000, Bottitta et al. 2003, Fast et al. 2007). On East Bay Island, the primary nest predators of eiders are herring gulls (*Larus argentatus*, 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 et al. 2021b). Bears typically arrive ashore during eider egg-laying and early incubation stages of eiders (Jagielski et al. 2021b). 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 et al. 2021b).

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 multi-rotor drones from July 10th to 20th in 2017 (Jagielski et al. 2021b). Briefly, when bears 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 between approximately 30 to 55m Above Ground Level (AGL) 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), and only when environmental conditions permitted drone operation (e.g., clear weather, wind < 10km^{-hr}). 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 et al. 2020a), see Supplemental Materials #1.

We collected 995 minutes 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 30m AGL. This filtering step resulted in 166.3 mins of video to review, from 15 drone flights, across five days of bear foraging (July 11, 15, 16, 19, and 20), from 4 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 v10.7.1 (ESRI, Redlands, CA), and a georeferenced map of East Bay Island (see *Drone Video Review* below). For filtered videos, the estimated mean area ± SD was 1023 ± 195m^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 (Identity Concealed For Review) reviewed video of polar bear foraging for flushing eider hens using Windows Film & TV application v.10.200022.11011.0 (Microsoft Corporation, Washington, United States). 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, 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 datetime of drone flights and time of flush within each video to estimate the datetime 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 non-reproductive 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 is 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 and Jónsson 2015).

We used a georeferenced, true colour, 3cm Ground Sampling Distance (GSD) orthomosaic of East Bay Island produced from drone imagery acquired in June 2019 to estimate flush initiation distance of eiders to polar bears. For details on the image acquisition and creation of this orthomosaic, see Drone Reporting Protocol #2 in Supplemental Materials 2 (Barnas et al. 2020a). 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 datasets, 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 (Supplementary Materials #3, section 1.1). 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 in vacating her nest. We recorded three qualitative categories of flush style: walking = an eider who walked off her nest, jumping = an eider who more quickly ran or jumped off her nest and flying = an eider who 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 of time. Although polar bears are known to capture and kill nesting female eiders (Gormezano et al. 2017), we are primarily focused on the risk polar bears pose to eider eggs rather than the adult.

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 (Supplemental Materials #3, section 1.2). We estimated polar bear movement speed (m^{-s}) by estimating the location of the bear 10 seconds prior to an eider flush, calculating the distance traveled by the bear over those 10 seconds, and dividing distance by 10 to estimate movement in m^{-s} (Supplemental Materials #3, section 1.3). 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 number of gulls into three categories, Absent (0 gulls), Low (1-5 gulls), and High (> 5 gulls) (Supplemental Materials #3, section 1.4).

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 30m radius circle (area ≈ $2827m^2$) that was visible to the nesting female using ArcMap's *Viewshed* tool and a 3cm Digital Surface Model (Rogers et al. 2020) generated using Structure-from-Motion using the same RGB drone imagery collected in 2019. Briefly, within a 30m 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 30m radius based on the maximum observed FID of eiders (25.7m, see Results). We included a vertical offset of 14cm for eider nest locations to account for the approximate height of a female eider's eyeline while sitting on her nest (measured 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 30m radius buffer visible (Supplementary Materials #3, section 1.5). Although our calculated viewshed does not consider the height of polar bears (as taller bears may be more visible to nesting eiders), this metric should still provide 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, and 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 dataset. 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 (Figure 2). We also fit 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 ($\beta \pm \text{SE} = 0.21 \pm 0.33$, $P = 0.65$), 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 re-coded them as dummy and ordinal variables where appropriate. Polar bear travel angle and gaze angle were positively correlated (Pearson correlation coefficient = 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 as Absent, Low, and High, and flush style as Walk, Jump, and Fly (where walking off nest is considered a “low” value, and increasing through jumping and flying as “high”). 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 8 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 through FID and flush style (Figure 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 AICc for small sample size, where models were considered competitive if they fell within Δ2 AICc (Burnham and Anderson 2002, Shipley 2013, Hennin et al. 2018). 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 v10.7.1 (ESRI, Redlands, CA). All other data manipulation and variable calculations were done in RStudio v3.6.2 (R Core Team 2017) using package *geosphere* for spatial data (Hijmans et al. 2017), *lubridate* for datetime data (Grolemund and 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 July 11 (n= 61), 15 (n=99), 16 (n=39), and 19 (n=1) in 2017; seven of these flushes were repeat observations by individuals on different days. No flushes were observed during foraging bouts on July 20, which may reflect the high level of bear predation that had occurred on previous days (i.e., relatively few eider nests were active by July 20). Of the 200 flush events used 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 ± 4.1m (range: 0.9-25.7m) from the bear and the number of flush styles observed was similar among types (Walk Off = 66, Jump Off = 66, and Fly Off = 68) (Figure 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 (Figure 5). Mean polar bear speed prior to flushes was 0.5 ± 0.3m^{-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 (Figure 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 fit of Model #6 and Model #7 was consistently "adequate" based on multiple measures (Model #6: CFI = 0.565, TLI = 0.348, RMSEA = 0.135, and SRMR = 0.112; Model #7: CFI = 0.593, TLI = 0.146, RMSEA = 0.154, and SRMR = 0.104), where "good" model fit is indicated by CFI > 0.9, TLI > 0.95, RMSE< 0.1, SRMR< 0.08. Interestingly, all models including a path from FID to flush style, received higher support than those models without that path (Table 1).

From our most competitive path model (Model #6), we found lower angle sums (i.e., more direct angles of travel and gaze) of polar bears resulted in more obvious flush response such as jumping or flying ($\beta = -0.236$, SE = 0.059, $P < 0.001$). We found that lower eider FIDs (i.e., closer bears) resulted both in more obvious flush responses s ($\beta = -0.437$, SE = 0.054, $P<0.001$) and subsequent nest loss by polar bears ($\beta = -0.203$, SE = 0.076, $P<0.05$), but the opposite relationship between gull presence and flush styles, as higher gull numbers evoked more inconspicuous "walk off" style flushes ($\beta = -0.181$, SE = 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 (Figure 5A). In Model #7 we found that eiders flushed at shorter distances when polar bears were moving faster ($\beta = -0.164$, SE = 0.068, $P<0.05$), but found no significant effects of angle sum, proportion viewshed visible, or number of gulls on FID (Figure 5B). Standardized estimates of path coefficients from all endogenous variables to flush style were similar in both Model #6 and #7 (Figure 5).

Discussion

Our findings reveal novel insights on the behavioural responses of eiders when leaving their nests, by demonstrating that individuals behave according to DRA 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 eider. Eiders have evolved a mass-loss incubation strategy which relies on females remaining concealed on their nest for as long as possible (Bolduc and 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 feel 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 anti-predator 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 refugia), 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 (Sih 1992, Munoz and Blumstein 2012), but due to costs associated with attentional constraints not all cues are considered equally during flush responses (Dukas and Kamil 2000, Leavell and 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 et al. 2021a). Our top model indicated flush styles are informed by FIDs, but that our measured cues were not greatly influential on 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 the next top supported model shows that slower moving polar bears result in greater FIDs, suggesting 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 and Guillemette 2003b), however as the majority of our observations came from July 11 – 15 (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 and Coulson 2015).

Flight Initiation Distance Informs Flushing Style

Our observed mean FID (9.1m) falls within the reported FIDs of nesting eiders to researcher disturbance reported in the literature (4-8m: Kay and Gilchrist (1998); 16m Mallory (2016); 2.4-3.4m 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 “eye-line” of bears would have a higher chance of gaining attention. Distraction displays have previously been described in eiders (McNair 1981, Kay and Gilchrist 1998), 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 and 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 employed by relatively few individuals (perhaps learned through prior exposures to polar bears), 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 et al. (2000a), but see Martin et al. (2000b)), 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 this 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 (Gaston and Elliott 2013, Iverson et al. 2014, Barnas et al. 2022). 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 anti-predator response that is effective on the scale of individual encounters with polar bears. In other words, eiders appear to be capable of performing DRA by sensing the predator- and environmental cues associated with a foraging polar bear, and differentially employ appropriate flushing behaviours to minimize 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, and it may be that the general confusion induced by multiple flushing eiders makes it difficult for bears to sometimes 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 is 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 et al. (2021b)), 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 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, Dey et al. 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 and 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 (Love et al. 2010, Chaulk and Mahoney 2012), 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.

Supplemental Materials

1) Drone Reporting Protocol for the drone video collection of polar bears foraging in a common eider colony in 2017
2) Drone Reporting Protocol for the drone imagery collection and production of the 2019 East Bay Island orthomosaic
3) Technical details and examples of georeferencing eider nests and polar bear characteristics

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Table 1 Model selection results for conceptual path diagrams relating exogenous predator and environmental variables to endogenous variables for common eider (*Somateria mollissima*) flushing behaviours and nest fate. Model ID indicates the candidate model structures detailed in Figure 2.

Model Rank	Model ID	K	Log Likelihood	AICc	∆AICc	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

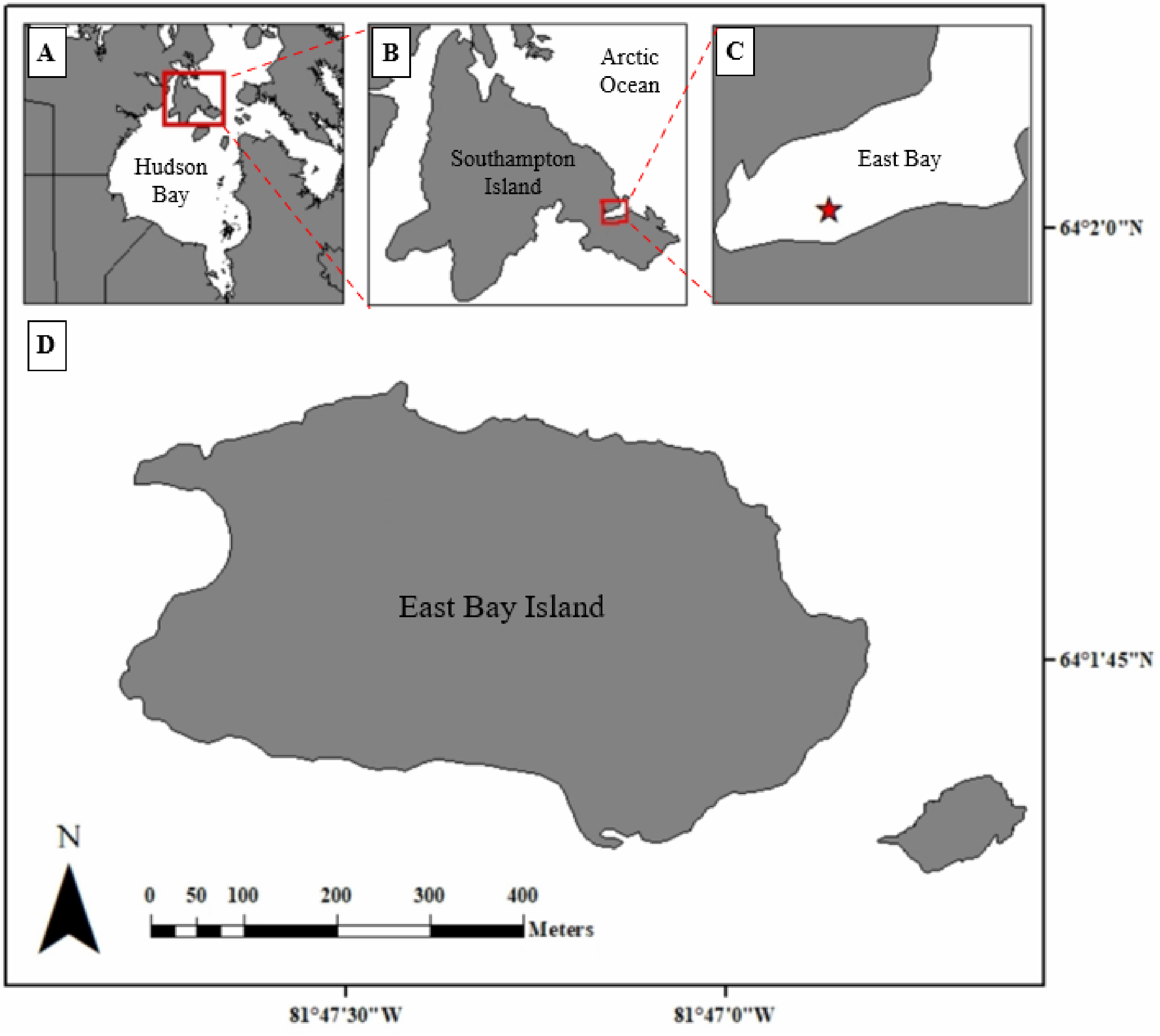

Figure 1. Map of the study location, A) General study location in northern Hudson Bay, B) Southampton Island, Nunavut, Canada, C) East Bay of Southampton Island, location of study site indicated by red star, D) East Bay Island, Nunavut, Canada. Canadian Provinces and Territories inset map layers provided by ESRI online, accessed September 1st, 2020.

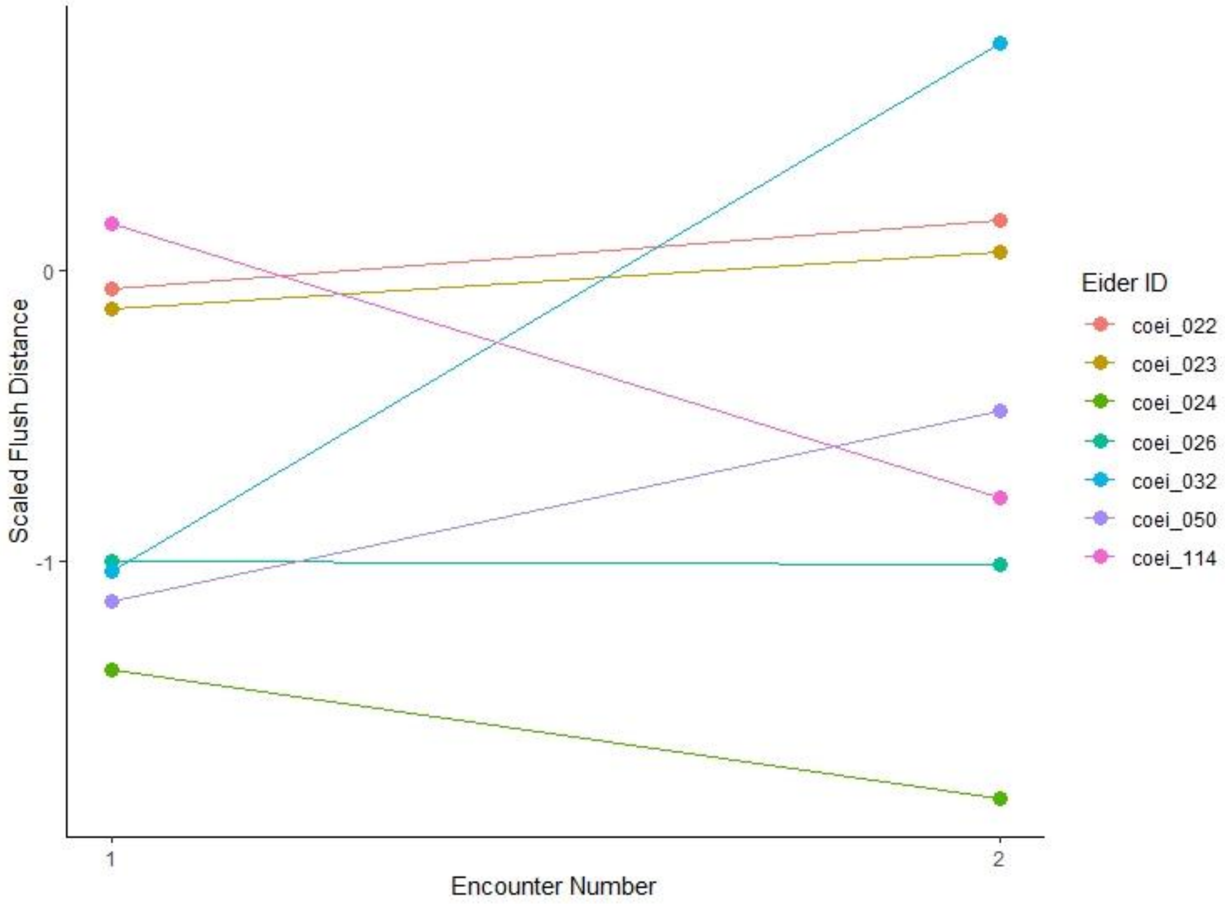

Figure 2 Scaled flush distance of individual common eiders (*Somateria mollissima*, n = 7) in response to first and second encounters with polar bears (*Ursus maritimus*).

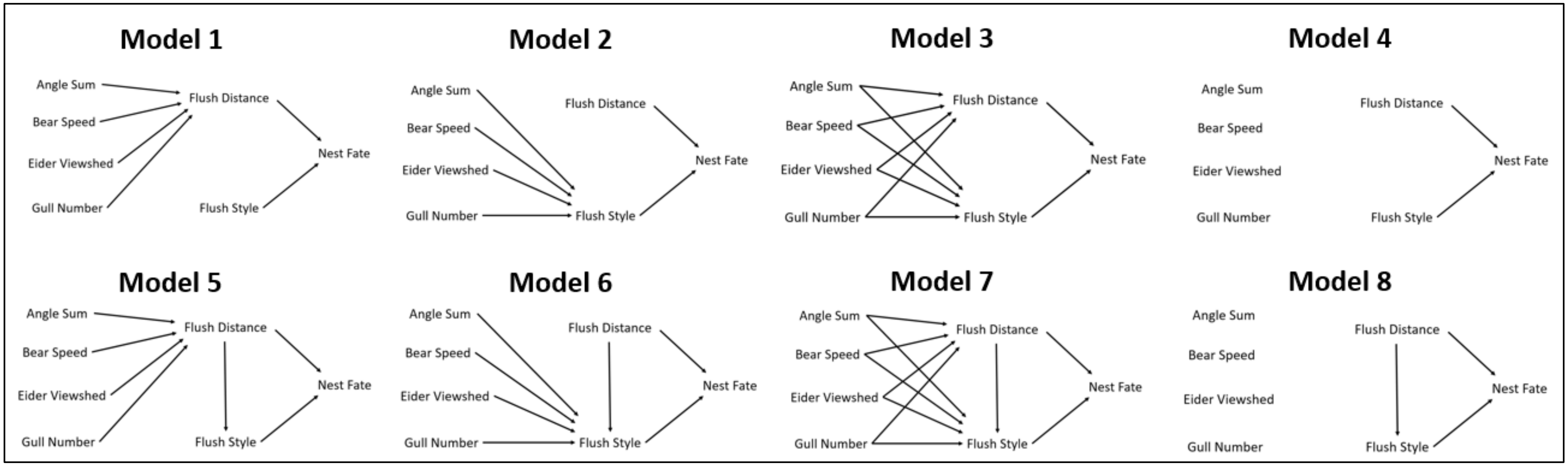

Figure 3. Candidate path diagrams relating predator and environmental cues to flushing behaviour and nest fate of common eiders (*Somateria mollissima*). Arrows represent conceptual unidirectional relationship between variables.

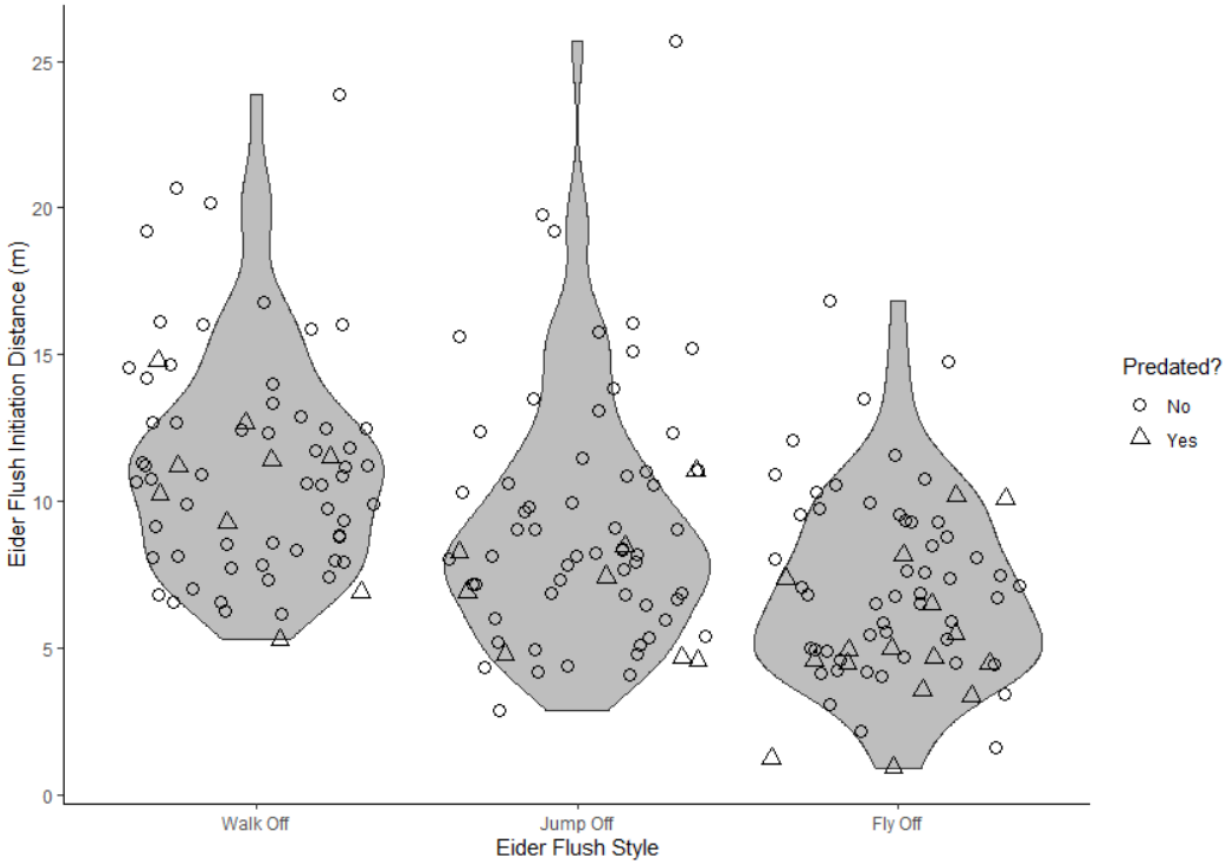

Figure 4. Raw data depicting relationship between flush style, flush initiation distance (m), and nest fate of common eiders (*Somateria mollissima*) in response to polar bears (*Ursus maritimus*). Measurements obtained from aerial drone video in July 2017 (n=200).

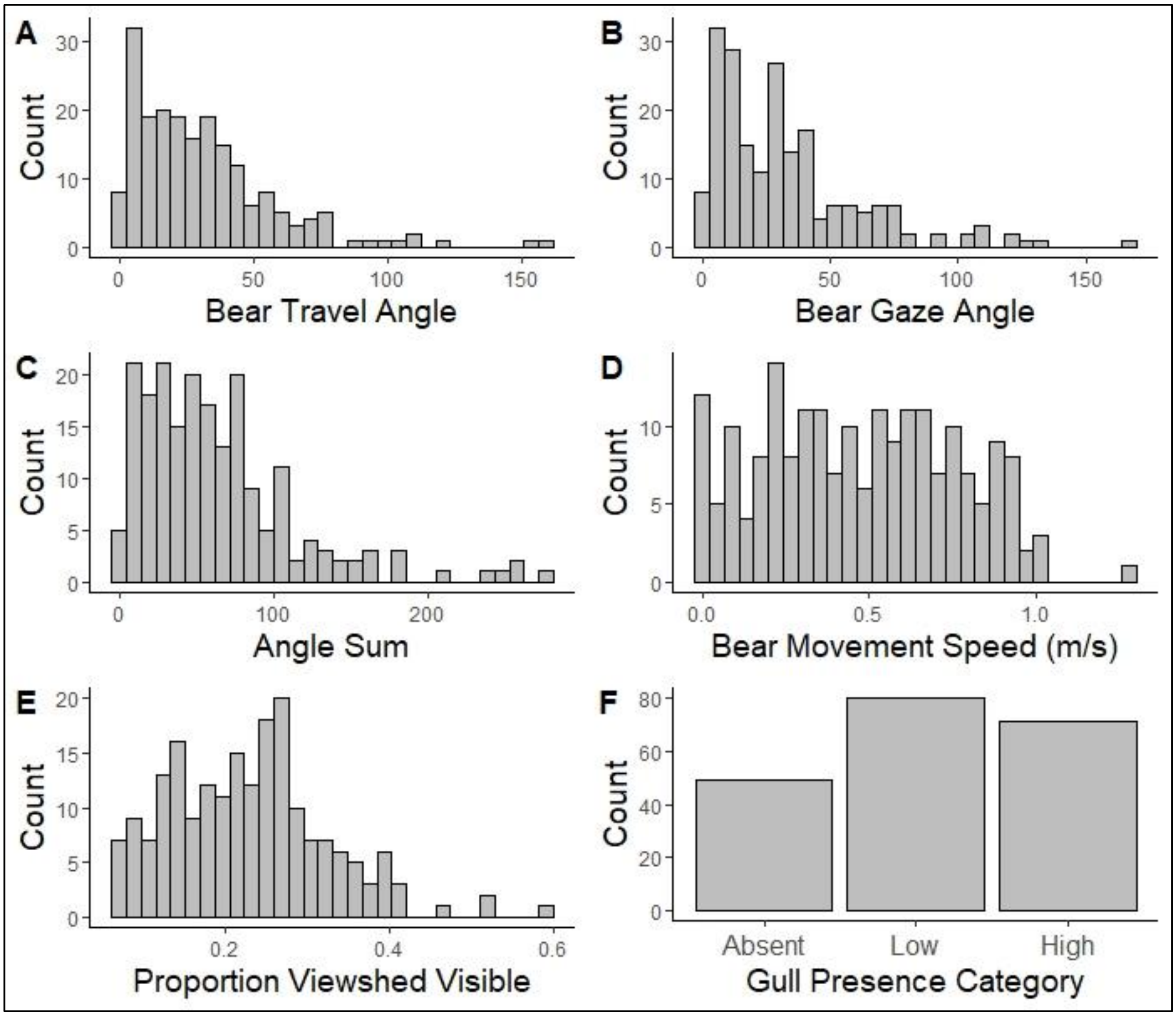

Figure 5. Raw data of predator and environmental cues collected during common eider (*Somateria mollissima*) flush events in response to polar bears (*Ursus maritimus*). A) Polar bear travel angle relative to eider nest location, B) polar bear gaze angle relative to eider nest location, C) Linear combination of a bear's travel and gaze angle, D) Polar bear travel speed (m/s) averaged over the 10 seconds prior to eider flush, E) proportion of an eider's viewshed that is visible from the nest location within a 30m radius, F) category of herring gull (Laru*s argentatus*) 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.

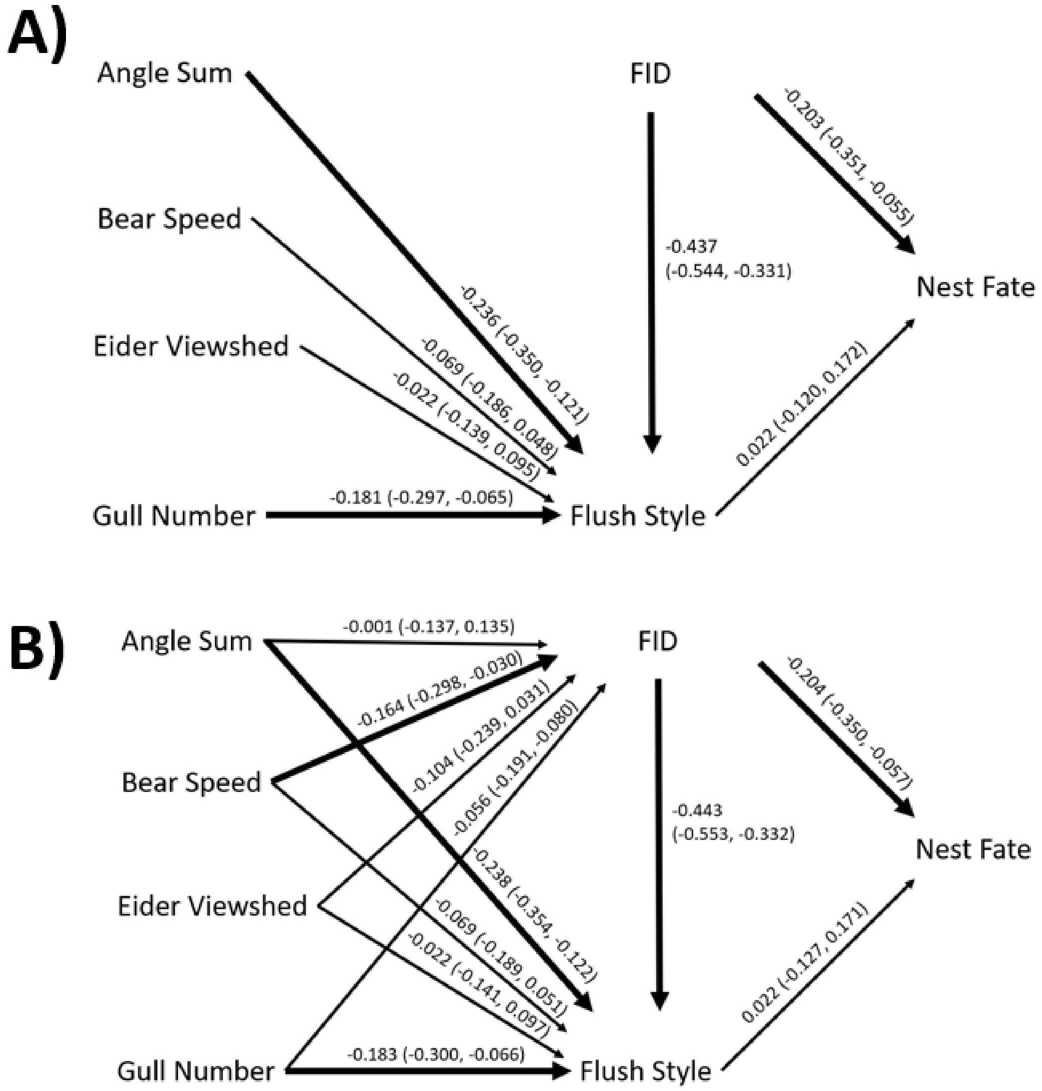

Figure 6. Standardized parameter estimates relating common eider (*Somateria mollissima*) flush style, flush initiation distance (FID)and nest fate to exogenous variables for the linear combination of polar bear (*Ursus maritimus*) travel and gaze angle, polar bear speed, proportion viewshed visible, and herring gull (*Larus argentatus*) 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).

Acknowledgments

We thank the 2017 and 2019 East Bay Island field crew for their assistance with logistics and data collection. Specifically we thank Mike Janssen, Jake Russell-Mercier, and Bronwyn Harkness from Environment and Climate Change Canada; Josiah Nakoolak, Jupie Angootealuk, Clifford Natakok, and Bob Hansen for their expertise and assistance in the field. This manuscript was greatly improved by the editor Dr. Andy Horn, as well as two anonymous reviewers. We are grateful for the opportunity to work in Qaqsauqtuuq (Inuit Nunangat) and the community of Coral Harbour. Drone use was authorized by Environment and Climate Change Canada Animal Care permits EC-PN-17-026 and EC-PN-19-026, and by Nunavut Wildlife Research permits WL-2017-030 and WL-2019-027. We thank Lincoln Savi for assistance with drone flight operations and planning during the 2019 field season. The creation of Figure 1 was done using the "Provinces and Territories of Canada" layer accessed via ESRI online. Writing of this manuscript was greatly facilitated by the soundtrack of The Witcher 3: Wild Hunt.

Animal Welfare Note

Details on ethical drone use in this study are detailed in the methods section of the main manuscript, as well as the detailed Drone Reporting Protocols in supplemental materials 1 and 2. Permits for animal study and drone use on East Bay Island are provided in the Acknowledgment section of the title page.

Author Contributions Statement

CRediT Statement

Conceptualization: AB, EG, OL, GG, ER, ES CS; Data curation: AB, EG, OL, PM, ER, ES, CS; Formal analysis: AB, OL, HH, CS; Funding acquisition: OL, GG, ER, ES, CS; Investigation: AB EG OL PM CH GG HH ER CD CS; Methodology: AB EG OL PM CH GG HH ER CD CS; Project administration: OL, CH, GG, HH, ER, CD, CS; Resources: OL, CH, GG, HH, ER, CD, CS; Writing – original draft: AB, EG, OL, GG, CS; Writing – review &editing: AB EG OL PM CH GG HH ER CD CS