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Changes in the distribution of nesting Arctic seaducks are not strongly related to variation in polar bear presence

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Abstract: Contemporary climate change is predicted to expose some species to altered predation regimes. Losses of Arctic sea ice are causing polar bears to increasingly forage on colonial seaduck eggs in lieu of ice-based hunting of marine mammals. Although polar bear predation of bird eggs has now been widely documented, it is unclear whether this change in predator behavior is having population-level consequences for Arctic breeding birds. In this study, we tested whether changes in the number of common eider nests on 76 islands in Hudson Strait, Canada, were related to variation in polar bear presence. We found that polar bear sign detected during eider breeding surveys was strongly correlated with spatial patterns of polar bears observed during aerial surveys. However, changes in eider nest count did not appear to be clearly related to polar bear sign at either the island scale or the island-cluster scale. This results of this study, therefore, suggest that the spatial overlap between eiders and polar bears varies across the landscape, but patterns of polar bear spatial variation do not seem to have driven large-scale redistribution of nesting common eiders.

Key words: Ursus, predator–prey, seabird, global warming, sea ice.

Résumé : Il est prévu que les changements climatiques contemporains exposeront certaines espèces à des régimes de prédation transformés. Les pertes de glace de mer arctique font en sorte que les ours polaires se nourrissent de plus en plus d'œufs de canards de mer coloniaux plutôt que de chasser sur la glace les mammifères marins. Alors que la prédation des œufs d'oiseaux par les ours polaires est maintenant bien documentée, on ignore si ce changement de comportement des prédateurs a des conséquences à l'échelle de la population pour les oiseaux nicheurs de l'Arctique. Dans cette étude, les auteurs ont vérifié si des changements dans le nombre de nids d'eiders communs sur 76 îles du détroit d'Hudson, Canada, étaient liés à la variation de la présence des ours polaires. Ils ont constaté que les signes de la présence d'ours polaires détectés lors des études de la reproduction des eiders étaient fortement corrélés avec les répartitions spatiales observées lors des relevés aériens. Toutefois, des changements dans le nombre de nids d'eiders ne semblaient pas être clairement reliés aux signes de la présence d'ours polaires tant à l'échelle de l'île qu'à celle d'un groupe d'îles. Les résultats de cette étude suggèrent donc que le chevauchement spatial entre les eiders et les ours polaires varie à travers le paysage, mais les patrons de variation spatiale des ours polaires ne semblent

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pas avoir entrainé une redistribution à large échelle des eiders communs nicheurs. [Traduit par la Rédaction]

Mots-clés : Ursus, prédateur–proie, oiseau de mer, réchauffement climatique, glace de mer.

Introduction

Nest site selection is an important determinant of fitness in birds. Because offspring survival varies among habitats (e.g., Clark and Shutler 1999), and offspring have limited mobility, there is strong selective pressure for parents to choose optimal nesting sites. In most species, nest site selection is thought to have evolved primarily in response to predation risk (Gotmark and Post 1996; Eggers et al. 2006) as predators are the primary cause of reproductive failure and may also consume care-providing parents (Lima 2009). Climate change can lead to shifts in predation regimes by impacting the distribution, population size, and composition of predator communities (Wilmers et al. 2007; Harley 2011). As a result, climate change may be altering patterns of nest site selection for many species.

In the Arctic, climate change is leading to increased polar bear (*Ursus maritimus* Phipps, 1774) predation of common eider (*Somateria mollissima* (Linnaeus, 1758); hereafter "eider") eggs (Smith et al. 2010; Iverson et al. 2014; Prop et al. 2015). Historically, consumption of bird eggs by polar bears was rare (Gormezano and Rockwell 2013) because polar bears focused on hunting marine mammals from the sea ice during the time that most birds were breeding. However, polar bears are now a major cause of reproductive failure for duck and goose populations in Hudson Bay (Rockwell and Gormezano 2009; Iles et al. 2013), Hudson Strait (Iverson et al. 2014), and in Greenland and Svalbard (Prop et al. 2015). In addition, recent models suggest that nest predation by polar bears will accelerate with advances in the date of ice break-up (Dey et al. 2017), and nest predation levels are expected to remain high even if polar bear populations show significant declines (Dey et al. 2018).

Eiders typically nest on small nearshore islands and can be found in densities of up to 1000 nests per hectare (Chaulk et al. 2004). Nest site selection and colonial nesting behaviour (i.e., nesting in high-density aggregations) are thought to have evolved primarily in response to the risk of predation by Arctic foxes (*Vulpes lagopus* (Linnaeus, 1758)) and large gulls (species of *Larus* Linnaeus, 1758) (Waltho and Coulson 2015). Unlike these traditional nest predators, polar bears can consume hundreds of eider eggs before being sated and can easily displace incubating hens from their nests. Additionally, polar bears are able to swim long distances to islands that would be unreachable by Arctic foxes (Pagano et al. 2012). As a result, the increasing importance of polar bears as a nest predator may be altering nest site selection for eiders, and may make previous nesting strategies (e.g., nesting in dense aggregations) maladaptive. If this is true, the breeding distribution of eiders should shift to reflect the change in the landscape of selection, either through direct dispersal of individual hens or through internal population processes (i.e., local changes in recruitment). However, no study to date has evaluated whether, or how, Arctic bird populations are altering their breeding distributions in response to increasing polar bear predation.

Here, we tested the hypothesis that spatial patterns of polar bear sign would be related to declines in the number of common eider nests in Hudson Strait, Canada. Such declines could occur either as a result of egg consumption by polar bears or as a result of non-consumptive predator effects (Peckarsky et al. 2008). We conducted our analysis at two scales. First, we tested whether observations of polar bear sign on islands were related to declines in the number of nests during the subsequent survey on each island. Second, we examined whether observations of polar bear sign across island clusters were related to

declines in nest numbers on islands in those clusters. We view these analyses as complementary, with island-level analyses exploring whether eider hens respond to a single polar bear intrusion, and cluster-level analyses exploring whether there has been a landscape-scale shift in nesting eiders in response to broad patterns of polar bear presence.

Materials and methods

Field methods

Our study was conducted in the Hudson Strait region of the Canadian Arctic (Fig. 1), which is one of the main breeding areas for northern common eiders, a subspecies of the common eider (*Somateria mollissima borealis* (C. L. Brehm, 1824)). In this region, sea ice break-up has advanced by about five weeks since the 1990s, and polar bear predation of eider nests is now very common at some sites (Iverson et al. 2014). Eiders typically nest on the many small (0.01–5 km^2), low-lying, nearshore islands, and researchers from Environment and Climate Change Canada have been monitoring eider nest numbers in Hudson Strait using boat-based surveys since the 1950s. Some of these data have been previously published (Falardeau et al. 2003; Gaston 2004; Iverson et al. 2014). In this study, we focus on data collected from 2010 to 2017, which used a standardized survey method and occurred during a period of increased polar bear predation of eider nests (Smith et al. 2010; Iverson et al. 2014).

The methods used for surveying islands were as follows: a group of 3–8 researchers walked in parallel transects separated by 10–15 m and counted the number of eider nests observed (both active and failed nests from the current year). Eider nests are easy to spot using this method because of limited vegetation and the presence of fresh down feathers in the nests (which provides insulation for the clutch). Typically, these transects were conducted until all nesting habitat was covered on each island. However, on some large islands a percentage of the nesting habitat was covered and the number of nests was estimated using linear extrapolations from the surveyed portion (79.8% of surveys covered all nesting habitat; mean percentage of nesting habitat surveyed across surveys = 94.9%). In addition, researchers recorded binary scores of whether polar bear sign was present on the island during the survey. Typical polar bear sign included footprints, fur, scat, crushed eider eggs in association with destroyed nests, and occasional direct observations of polar bears (see also Iverson et al. 2014). Survey locations were chosen based on a variety of factors, including varying study objectives over the study period, research priorities of local communities, and the logistical and safety issues associated with remote Arctic field work. As a result, survey frequency varied among sites (range of surveys per island = 2–5, range of intersurvey intervals = 1–7 years).

These methods were reviewed and approved by Environment and Climate Change Canada as per the Canadian Council on Animal Care, and by the Nunavut Research Institute.

Statistical analysis

The analysis described below was conducted in *R* (R Core Team 2015), and depended on the *tidyverse* suite of packages (Wickham 2017) for data tidying and manipulation. To construct the figures presented in this paper, we used *ggplot2* (Wickham 2009) and *mapdata* (Becker et al. 2018). For spatial analyses we used the *geosphere* (Hijmans 2017) and *fpc* (Hennig 2015) packages. For generalized linear mixed modelling we used *glmmTMB* (Brooks et al. 2017). We also used the *DHARMa* package (Hartig 2019) to inspect the models' residuals with respect to predicted values and to expected quantiles. Additionally, we plotted the model residuals in two-dimensional space (i.e., based on their latitude and longitude) to evaluate

Fig. 1. Map of the study area. Insets show the two main areas where islands were repeatedly surveyed between 2010 and 2017, which allowed us to conduct analyses of changes in eider nest counts. Each dot indicates a single island (*n* = 76), with different colors indicating spatial clusters of islands (see cluster-level analysis in the text). Map created using *ggplot2* (Wickham 2009) with basemap data from the *mapdata* package (Becker et al. 2018).
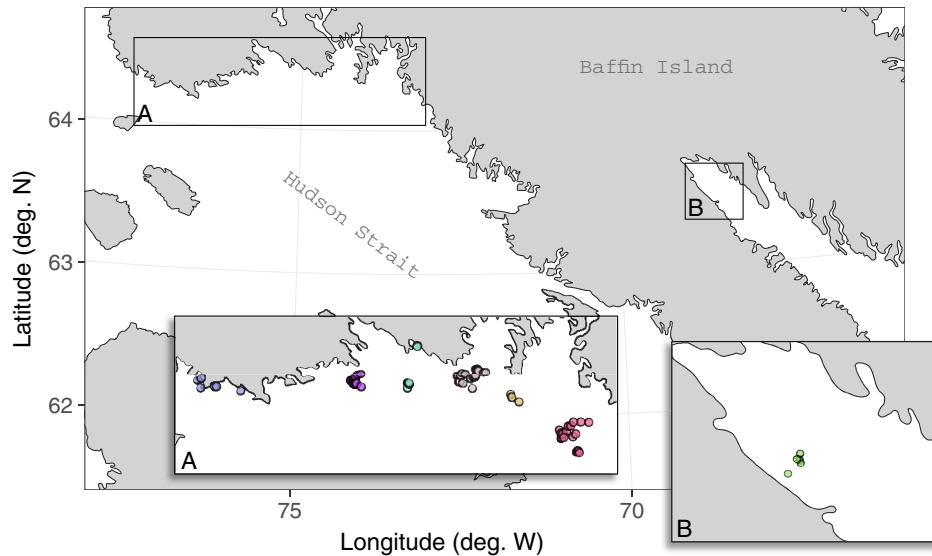
whether spatial autocorrelation was a concern, but found no evidence of spatial patterns in residual variance.

To help avoid misinterpretation of null hypothesis significance tests (NHSTs), we use the language of statistical "clarity" rather than statistical "significance" (as suggested by Dushoff et al. 2019). In this framework, NHSTs are reported with reference to whether they clearly show an effect in the positive or negative direction, which avoids obfuscation among the multiple meanings of the word "significant". However, we also emphasize effect sizes in our analysis by reporting and considering changes in odds or rate ratios (depending on the analysis), in adherence with the American Statistical Association's guidelines (Wasserstein and Lazar 2016). The code used for the analysis is available in the Supplementary Information (Files S1–S3)[1].

Validation of polar bear sign as a proxy for polar bear spatial distribution

To test if polar bear sign is a valid proxy for the spatial distribution of polar bears, we compared our observations of polar bear sign to polar bear location data gathered by Stapleton et al. (2016). These authors conducted aerial surveys of the Foxe Basin polar bear subpopulation during the ice-free season (August–October) in 2010. The areas surveyed by these authors included the Foxe Peninsula and northern Hudson Strait, which included the area around 91 islands we also surveyed in 2010. If our data on polar bear sign is indicative of the true variance in polar bear density, we would expect that more polar bears would have been sighted by Stapleton et al. (2016) near islands where polar bear sign was detected.

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[1]Supplementary material is available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/as-2019-0017.

In their paper, Stapleton et al. (2016) show the locations of sighted polar bears on a map of the aerial survey area. We georeferenced their published map using *QGIS* (QGIS Development Team 2018) and extracted the latitude and longitude of all polar bear sightings for each of the two years. Then, for each of the 91 islands we surveyed in the region covered by Stapleton et al. (2016), we calculated the mean distance to the five closest polar bears sightings from Stapleton et al.'s (2016) aerial surveys. We used this value (mean distance to five closest bears) as the sole predictor variable in a binomial family generalized linear model. In this model, bear sign (yes/no) was included as the response variable.

Comparing changes in eider nest counts to island-scale bear sign

We tested whether the presence of polar bear sign was associated with changes in the number of eider nests. As polar bears typically arrive on eider breeding islands towards the end of the incubation period, the presence of polar bears should influence future nest counts on an island more than nest counts in the current year (as most breeding females will already have decided where to nest in the current year). Therefore, we tested whether changes in nest counts between subsequent surveys on an island were influenced by the presence or absence of polar bear sign during the initial survey at that island.

We constructed a linear mixed model with the change in nest counts between surveys as the response variable (i.e., $\log(\text{nest count}_{subsequent} + 1) - \log(\text{nest count}_{initial} + 1)$). Data for the change in nest count was available for 141 survey pairs conducted on 76 islands. For fixed effects we included bear sign at the initial survey (from each survey pair) and the number of years between surveys. We also included a random intercept for island ID to account for repeated measures on some islands.

Comparing changes in eider nest counts to cluster-scale bear sign

Our cluster-level analysis explored broader patterns in eider response and polar bear distribution by considering the frequency of polar bear sign within spatial clusters of islands, and also using a single measure of the change in nest count for each island (i.e., the change between the first and final survey at each site within the study period). The reasoning behind this analysis is that polar bears show high site fidelity during the ice-free season (Derocher and Stirling 1990; Stirling et al. 2004; Cherry et al. 2013; Sahanatien et al. 2015). As a result, some areas have consistently high bear density, whereas other areas have consistently low bear density, a pattern frequently reported by local guides during our field research. Cluster-scale measures of polar bear sign may, therefore, be good predictors of changes in nest counts on individual islands.

To cluster islands based on their geographical distribution, we first calculated a distance matrix (based on the geodesic distance between islands) for our set of 76 islands. Then, we performed partitioning around medoids clustering (Kassambara 2017), using the number of clusters that maximized average silhouette width (Rousseeuw 1987). This analysis grouped islands into seven geographic clusters that contained a range of 3–20 islands (Fig. 1). Next, we calculated the cluster-scale polar bear index based on the proportion of surveys conducted in that cluster that observed bear sign, which ranged from 0 (polar bear sign never detected in the cluster) to 0.39 (polar bear sign detected on 39% of surveys in the cluster).

To analyze if nesting eiders had shifted distribution in response to cluster-scale variation in polar bear presence, we used a linear mixed model with change in nest count over the study period as the response variable (i.e., $\log(\text{nest count}_{final} + 1) - \log(\text{nest count}_{initial} + 1)$). The cluster-scale polar bear index, and the number of years between the first and final survey at each island, were included as fixed effects. We also included a random intercept for each cluster to account for repeated sampling within clusters.

Fig. 2. Validation of the use of bear sign observations taken during common eider breeding surveys as a proxy for polar bear presence on islands in Hudson Strait, Canada. Here we show the distance from each island to the five closest bears sighted during aerial surveys as a function of whether bear sign was sighted on the island (black = yes, grey = no). The top panel shows the distribution of mean distances to the five closest bears. The bottom panel shows the mean distances (black and grey dots) for each island separately, with horizontal bars indicating the range between the closest bear sighting (left-most extent of the bar) and the fifth closely bear sighting (right-most extent of the bar).
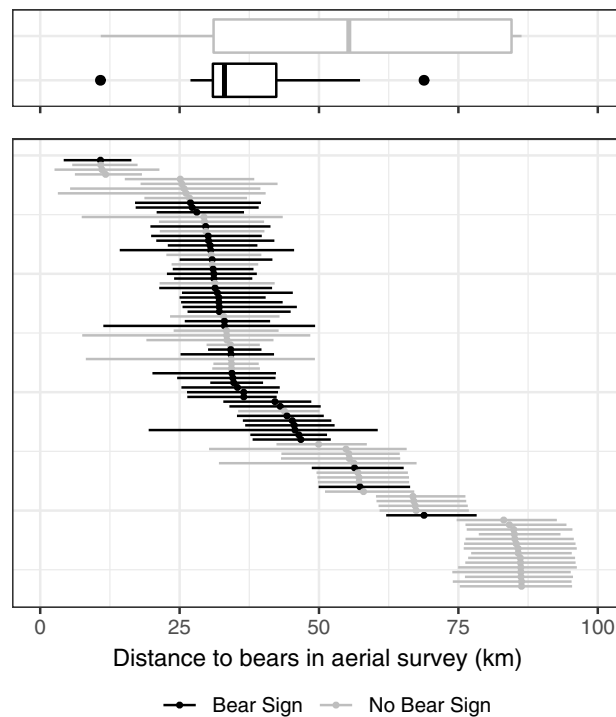
Results

Validation of polar bear sign as a proxy for polar bear spatial distribution

Polar bear sign was clearly more likely to be detected on islands that were closer to polar bears sighted during aerial surveys (Fig. 2). The odds of detecting polar bear sign increased by 4.4% (95% confidence interval = (1.9%, 6.8%), $P = 0.0007$) for every kilometer decrease in the mean distance to the five nearest bears sighted during the aerial surveys.

Comparing changes in eider nest counts to island-scale bear sign

Island-scale observations of polar bear sign did not clearly relate to changes in the number of nests on islands (Fig. 3A). The statistical model suggested that islands on which we observed polar bear sign had 18% fewer nests at the subsequent survey; however, there was considerable uncertainty in that estimate, with confidence intervals (95% CI) ranging from a 51% decline in nests to a 35% increase in nests ($P = 0.43$). The time between surveys was clearly related to change in nest count, with nest numbers increasing 15% per year between surveys (95% CI = (+2%, +31%), $P = 0.02$).

Comparing changes in eider nest counts to cluster-scale bear sign

Observations of polar bear sign at the scale of island clusters were also not clearly related to changes in eider nest counts (Fig. 3B). Model estimates suggested that increasing the

Fig. 3. Changes in nest count (A) between subsequent surveys and (B) over the survey period, for 76 islands in Hudson Strait, Canada. (A) Shows the relative change in nest count between surveys as a function of whether polar bear sign was observed during the previous survey on the focal island. (B) Shows the change in nest count relative to the cluster-scale polar bear index (i.e., the proportion of surveys conducted in that island-cluster that observed polar bear sign).

cluster-scale polar bear index from 0 to 0.39 (the maximum observed value) would result in a 31% decrease in nest count. However, the 95% confidence intervals for this estimate ranged from -39% to $+242\%$ ($P = 0.39$). There was also no clear effect of time on the number of nests in this model, with an estimated increase in nest count of 2.7% per year (95% CI $= (-9\%, +16\%)$, $P = 0.67$).

Discussion

Our study explored spatial patterns of polar bear presence on islands in Hudson Strait, and related these patterns to changes in the number of common eider nests. We demonstrated that polar bear sign is correlated with the spatial distribution of polar bears observed in aerial surveys (Fig. 1). However, we did not find a clear signal of changes in nest count relative to patterns of polar bear presence. Despite widespread evidence that polar bear predation of bird eggs is increasing (Smith et al. 2010; Gormezano and Rockwell 2013; Iverson et al. 2014; Prop et al. 2015), this study is the first, to our knowledge, to investigate the spatial patterns of polar bear presence in bird colonies and the response of Arctic bird populations to polar bears.

It is surprising that we found no clear evidence of a shift in eider breeding distribution away from areas with high polar bear presence. If polar bear presence is a good proxy for patterns of nest depredation, and if polar bear nest predation is additive to other sources of reproductive failure, then eiders should show a shift away from areas of high polar bear presence. However, these assumptions may not hold; although Iverson et al. (2014) found that eider nest success was clearly lower on islands with polar bear sign (22% of nests survived to the date of survey vs. 66% on islands without polar bear sign), the presence of polar bear sign does not imply that nest predation by polar bears occurred. It may be that the relationship between the intensity of nest predation and the presence polar bears co-varies with spatial features. For example, polar bear sign may be present on offshore islands that

polar bears use as rest sites while hunting marine mammals, and therefore declines in nest numbers would not necessarily be expected if high rates of predation on eider eggs are not also occurring at these sites. Unfortunately, it is not typically feasible to determine if individual eider nests have been subject to polar bear predation, and, therefore, we could not estimate polar bear predation rates in the current study. However, even in the absence of high rates of nest predation, eider hens could still relocate away from areas of high polar bear density if they perceive polar bears as predators. Such non-consumptive predator effects (e.g., the landscape of fear; Peers et al. 2018) are frequently observed in natural populations, and in some cases are known to have stronger effects on prey populations than consumptive predator effects (Peckarsky et al. 2008). Nesting eiders could also be compensated for high levels of polar bear nest predation in areas with high polar bear presence if there are other changes in environmental variables related to reproduction. Polar bear sign is more likely to be found on islands in areas with low local concentrations of sea ice (Iverson et al. 2014), however sea-ice decline and warmer temperatures have also been associated with increased eider breeding propensity and clutch size (Mendenhall and Milne 1985; Swennen 1991; Lehikoinen et al. 2006; D'Alba et al. 2010). As a result, areas with high polar bear presence may also be areas with high eider reproductive success (for those individuals that can avoid nest predation).

Although the current study suggests that nesting common eiders have shown a limited response to polar bears in Hudson Strait, changes in predation pressure (from other species) have led to changes in eider nest count in other studies (e.g., Sonsthagen et al. 2009; Hanssen et al. 2013; Waltho and Coulson 2015). However, it is currently unclear whether predators primarily cause local declines in breeding eiders through decreases in reproductive success (i.e., direct mortality on eggs) or by causing female eiders to disperse away from islands (i.e., non-consumptive effects). Predator establishment and (or) control have been linked with short-term changes in eider nest counts in Svalbard (Hanssen et al. 2013) and Alaska (Petersen et al. 2015), suggesting that non-consumptive predator effects (Peckarsky et al. 2008; Peers et al. 2018) may be involved. However, for novel or invasive predators it seems likely that consumptive effects would also be important, as prey should be naïve to this source of risk and may not show appropriate behavioural responses (Salo et al. 2007). Further studies examining the relative importance of consumptive and non-consumptive effects of novel predation regimes will be important in understanding the mechanisms through which climate change influences prey species such as eiders.

Some aspects of Arctic ecosystems are undergoing dramatic change in response to climate change (Wassmann et al. 2011; Fossheim et al. 2015). Here, we show that polar bear sign, which we frequently detected during breeding surveys for common eider seaducks, strongly relates to spatial patterns of polar bear distribution in aerial surveys. Nonetheless, we did not observe a strong shift in eider breeding distribution consistent with a response to polar bear predation. It may be that patterns of polar bear presence are not strongly related to patterns of nest predation, or breeding eiders may be somehow compensated for increased egg mortality in areas with high polar bear presence. Understanding the complexity associated with climate-mediated changes in predator behaviour will be challenging, but is crucial to building climate resilience for human and wildlife populations across the globe.

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Author contributions

Designed the study: HGG, SAI, and CADS. Collected the data: HGG, and SAI, with help from CJD. Analyzed the data: CJD. Wrote the paper: CJD, with input from CADS, HGG, and SAI.

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