Increasing nest predation will be insufficient to maintain polar bear body condition inthe face of sea-ice loss

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Running head: Polar bear predation of common eider nests

Climate change can influence interspecific interactions by differentially affecting species-specific phenology. In seasonal ice environments, there is evidence that polar bear predation of Arctic bird eggs is increasing because of earlier sea ice break-up, which forces polar bears into near-shore terrestrial environments where Arctic birds are nesting. Because polar bears can consume a large number of nests before becoming satiated, and because they can swim between island colonies, they could have dramatic influences on seabird and seaduck reproductive success. However, it is unclear whether nest foraging can provide an energetic benefit to polar bear populations, especially given the capacity of bird populations to redistribute in response to increasing predation pressure. In this study, we develop a spatially explicit agent-based model of the predator-prey relationship between polar bears and common eiders, a common and culturally important bird species for northern peoples. Our model is composed of two types of agents (polar bear agents, and common eider hen agents) whose movements and decision heuristics are based on species-specific bioenergetic and behavioral ecological principles, and are influenced by historical and extrapolated sea ice conditions. Our model reproduces empirical findings that polar bear predation of bird nests is increasing, and predicts an accelerating relationship between advancing ice break-up dates and the number of nests depredated. Despite increases in nest predation, our model predicts that polar bear body condition during the ice-free period will continue to decline. Finally, our model predicts that common eider nests will become more dispersed and will move closer to the mainland in response to increasing predation, possibly increasing their exposure to land-based predators, and influencing the livelihood of local people that collect eider eggs and down. These results show that predator-prey interactions can have non-linear responses to changes in climate, and provides important predictions of ecology change in Arctic ecosystems.

Introduction

Climate change can have a variety of impacts on animal populations (Walther *et al.*,

2002). Although direct climatic effects on animal physiology undoubtedly influence

species distributions (Pearson & Dawson, 2003), the most important impacts of climate

change are expected to be caused by changes in biotic interactions (Brooks & Hoberg, 2007; Milazzo *et al.*, 2013). Since species differ in their ability to disperse, climate change can lead to novel, or altered, interspecific interactions (e.g. predator-prey relationships, host-parasite interactions). These biotic changes can cause dramatic influences on ecological communities (Gilman *et al.*, 2010), and can lead to the loss of biodiversity via extirpation or extinction of species (Harley, 2011; Cahill *et al.*, 2012). Biotic changes involving top predators could be especially important, since predators can cause trophic cascades via influences on prey demography and behavior (Schmitz *et al.*, 1997; Fortin *et al.*, 2005). Therefore understanding the influence of climate change on predator-prey relationships should be a major goal of ecology.

The polar bear (*Ursus maritimus*) is an apex predator in circumpolar Arctic ecosystems. Northern polar regions have experienced greater climate warming than other areas of earth (Hansen *et al.*, 2006), including rapid changes in the spatial and temporal extent of sea ice (Stroeve *et al.*, 2014). Polar bears rely on sea ice as a platform to hunt seals and other marine mammals, and reductions in sea ice have been linked with decreasing body condition (Stirling *et al.*, 1999; Obbard *et al.*, 2016), lower reproductive success (Molnár *et al.*, 2011), and population decline (Regehr *et al.*, 2007; Bromaghin *et al.*, 2015; Lunn *et al.*, 2016) in some polar bear subpopulations. In seasonal ice environments (areas where sea ice is not present year-round), polar bears migrate from marine to near-shore terrestrial environments each summer as ice melts. Importantly, climatic warming has caused progressively earlier ice break-up, and progressively later freeze-up, in many areas of the Artic (Iverson *et al.*, 2014), and as a result, polar bears

are spending more time on land compared with historical periods (Derocher *et al.*, 2004; Rode *et al.*, 2015a). Since the loss of Arctic sea ice is expected to continue (Overland & Wang, 2007), the change in the distribution of polar bears has the potential to influence a variety of species in terrestrial and marine ecosystems, especially given that polar bears can become opportunistic omnivores when they don't have access to their primary prey (Gormezano and Rockwell 2013).

In particular, there is growing evidence that polar bear predation of bird nests is becoming more common as a result of climate change (e.g., Drent and Prop 2008; Smith et al. 2010; Iverson et al. 2014; Prop et al. 2015). Historically, polar bear predation of bird nests was rare (Gormezano & Rockwell, 2013; Iverson *et al.*, 2014; Prop *et al.*, 2015), and Arctic breeding birds would have had little selective pressure to evolve anti-predator strategies for polar bear predation. However, since polar bear onshore migration is tightly linked with sea-ice dynamics, this shore-directed movement is becoming progressively earlier as sea-ice break-up dates advance (Stirling *et al.*, 1999). While the migration and nesting phenology of Arctic breeding birds has also generally advanced (e.g., Dickey et al. 2008; Love et al. 2010), it has done so much more slowly than the advance in sea ice break-up (e.g. 0.16 days per year advance in *Anser caerulescens* nesting vs. 0.72 days per year advance in ice break-up; Rockwell and Gormezano 2009). As a result, polar bears and Arctic breeding birds are now present in near-shore environments with greater temporal overlap, and polar bears are increasingly preying on seabird eggs (Smith *et al.*, 2010; Prop *et al.*, 2013, 2015; Iverson *et al.*, 2014). Indeed, Iverson et al. (2014) demonstrated that polar bear

presence at large common eider (*Somateria mollissima*) and thick-billed murre (*Uria lomvia*) colonies has increased seven-fold between 1987 and 2012, and that interannual variation in polar bear presence was strongly predicted by the length of the ice-free period. Similarly, polar bears were almost never observed at five large mixed-species colonies in Spitsbergen and eastern Greenland from 1975-1995, but now there are an average of between 5 and 20 'bear days' per year (Prop *et al.*, 2015). Some authors have suggested that by foraging on bird nests, polar bears could mitigate predicted losses in condition (Dyck & Kebreab, 2009; Gormezano & Rockwell, 2015), but it is unclear whether this is realistic because the costs of searching for eggs is high relative to the energetic reward (Rode *et al.*, 2015b) .

In this study, we focus on the changing predator-prey relationship between polar bears and common eiders (*Somateria mollissima*). Common eiders are important species in many Arctic ecosystems because they are large-bodied and numerous. Since common eiders feed primarily on marine invertebrates (Waltho & Coulson, 2015), they are an important vector for energy flow from the relatively productive Arctic marine environment to the relatively unproductive Arctic terrestrial environment (Michelutti *et al.*, 2009; Mallory *et al.*, 2015). Common eider eggs and ducklings are an important prey source for predatory mammals (e.g. foxes) and birds (e.g. herring gulls) (Waltho & Coulson, 2015); and common eider feces are an important source of nutrients for terrestrial Arctic plant and insect communities (Nik Clyde, *unpublished data*). Additionally, in many areas, adult common eiders are hunted for meat, and their eggs and down are collected from nests by northern people. Common eiders typically nest in dense congregations on

near-shore islands, which is thought to be an adaptation to avoid predation by terrestrial mammals (Waltho & Coulson, 2015). However, since polar bears are capable of long distance swimming in cold water (Pilford *et al.*, 2016), and can consume a large number of eggs before becoming satiated (Best, 1977), they can cause intense local predation effects on island colonies. Indeed, in mixed-species colonies (including common eider) in Svalbard, polar bears have consumed > 90% of nests in some seasons (Prop *et al.*, 2015), and polar bears have caused near complete reproductive failure in several recent years at East Bay Island, the largest known common eider colony in the Canadian Arctic (Grant Gilchrist, *unpublished data*). Additionally, a landscape wide survey of eider colonies in Hudson strait from 2010-2012 estimated that polar bears had visited 34% of island colonies (Iverson *et al.*, 2014), which suggests that climate induced changes in polar bear behavior could have widespread impacts on common eider populations.

Here, we model interactions between polar bears and common eiders using agent-based modelling, a technique that employs the creation of simulated 'agents' which behave according to specified behavioral rules (Wilensky & Rand, 2015). Agent-based models (ABMs) are becoming increasingly common in ecology and conservation biology (Grimm & Railsback, 2013) because of their ability to incorporate individual-level variation, account for complex interactions both among individuals, and between individuals and their environment, and to incorporate cross-discipline data and methods (McLane *et al.*, 2011). ABMs are a promising tool for understanding the influence of climate change on interspecific interactions because climate change can influence

individuals at a number of levels (e.g. by affecting physiology, behavior, growth, conspecific interactions, phenology, etc.), and this complexity can be naturally incorporated in ABMs. As a result, ABMs allow the prediction of the emergent effects (i.e. outcomes that are not simply additive results of underlying processes) of climate change, which generally make prediction challenging in ecological systems. We built the model using a combination of literature and field-derived data on polar bears and common eiders, and behavioral rules from general, and species-specific, foraging ecology, bioenergetics and behavioral ecology. Our model included both historical and predicted sea ice data, which allowed us to validate our model (Grimm *et al.*, 2005) using empirical patterns of polar bear behavior, and to make predictions about polar bear nest predation behavior in the future.

Materials and Methods

Model overview

We built an agent-based model to address three primary questions: 1) To what degree will common eider nest predation by polar bears change in response to climate change? 2) Will foraging on eider eggs mitigate observed and predicted declines in polar bear body condition?, and 3) How will changes in nest predation influence the distribution of common eider nests? We built this model in Netlogo (Wilensky, 1999)version 5.3 and have included the complete complete code in the Supplementary Information. A complete description of the model, including descriptions of all model processes (using the ODD protocol; Grimm et al. 2010), and the methods used to parameterize, calibrate, verify and validate the model, are included in the Supplementary TRACE (TRAnsparent

and Comprehensive model evaludation) document (Schmolke *et al.*, 2010; Augusiak *et al.*, 2014; Grimm *et al.*, 2014). Below, we briefly outline the major model components and their behavior, but readers interested in the details of these components should consult the TRACE document.

Model components and landscape

Our ABM included 2 types of digital agents representing polar bears and common eider nests/hens. They interacted on a simulated island archipelago landscape that is typical of common eider nesting habitat in Foxe Basin and Hudson Strait, Canada (and in many other areas of the circumpolar Arctic). The landscape was two-dimensional, and was composed of square cells each representing an area of 50 m by 50 m, with a total landscape area of 100 km by 17.5 km. The cells belonged to one of three types; mainland cells, island cells and water cells. Island cells varied in their habitat quality, which influenced the nesting success of local eider agents. For each model run we created a new random landscape that adhered to rules regarding the distribution and location of islands (see Figure S1 in TRACE). For further details consult Section 2.5 and 3.2 of the TRACE document.

The model proceeded in discrete time-steps representing 30 minutes (i.e. 48 steps per day). During each time-step, the polar bear agents acted, and then the eider nest agents acted, according to the general outline in Figure 1A. Each model run continued for 50 sequential eider breeding seasons (representing years 1990-2039). The model began each year on the date that the first eider nest was initiated, and ran until all eider

nesting had been completed for that year. Then, the model skipped forward to the start of the next breeding season. See Section 2.3 of TRACE for more details.

Eider nest agents

Eider nest agents were programmed to perform 3 main behaviors during each model year: they chose a nest site, they initiated nesting on a given date dependent on the annual climate (with earlier nesting in years with earlier ice break-up), and they incubated their nest. After choosing a nest site, the agents were immobile for the remainder of the model year. Their decision of where to nest was influenced by philopatric tendencies (Sonsthagen *et al.*, 2009; Öst *et al.*, 2011), as well as the outcome of their nest (success or failure) from the previous season. In order to avoid additional model complexity, the total population size of eider nest agents remained constant throughout the model run, although individual eider nest agents died and this mortality occurred between breeding seasons. See Section 2.7, 3.3 and 3.6 of TRACE for more details.

Polar bear agents

Polar bear agents had more complex decision making heuristics and cognitive abilities than eider agents (Figure 1B), and were also able to move around the landscape. Their behavior was dependent on their energetic state (measured by Quetelet's body condition index), their ability to sense the environment, and also on their knowledge of the environment (i.e. memory) gained from past experiences. Polar bear agents that were in poor condition actively searched for eider nests, while those in good condition

only foraged on nests they encountered opportunistically, consistent with the expectations of risk-sensitive foraging theory (Caraco *et al.*, 1980; Bateson, 2002) and anecdotal evidence that young bears and females with cubs are more likely to forage on bird nests (e.g. Iles *et al.,* 2013). Polar bear agents could detect nearby eider nests through olfaction, and used visual cues to guide their movement (i.e. they would swim towards islands when searching for nests). Polar bear agents also remembered the location of eider colonies from previous years, and used this information to guide their searching behavior. The total population size of polar bear agents remained constant throughout the model run, however individual polar bear agents died from general sources of mortality between eider breeding seasons in order to maintain realistic age distributions and associated energetic variables. Additionally, some adult female polar bears had accompanying cubs or yearlings, which influenced their energetic demands and movement rates. See Section 2.4, 2.7, 3.1, 3.3 and 3.5 of TRACE for more details

Sea ice modelling

We included two ice metrics in our model: the date of ice break-up and the date of ice freeze-up. The ice break-up date determined the mean eider nest initiation date, as well as the mean date that polar bears appeared on the landscape (simulating their migration from offshore pack ice to near-shore environments). The ice freeze-up date determined the amount of time that polar bear agents could not access their primary prey (seals), and therefore influenced polar bear behavioral decision-making by influencing the amount of time they expected to fast (polar bear agents predicted how long they would need to fast based on the ice freeze-up date from the previous year).

For the first 25 years in each model run, we used historical data from satellite images of Foxe Basin (1990-2014) to determine the ice break-up and freeze-up dates. For the second 25 years of each model run, we extrapolated ice break-up dates for 2015-2039. See Section 2.7 and 3.4 of TRACE for more details.

Model parameterization and calibration

Our model was parameterized with data from previously published studies, from long-term datasets on polar bear and common eider ecology, and from recent field research. A list of model parameters is included in Table S1 and in Section 2 and Section 3 of the TRACE document. Additionally, two model parameters (the nest clumpiness coefficient, and the variation in nesting habitat) were calibrated through inverse determination, and are detailed in Section 6 of the TRACE document. Our model was designed to make general predictions about interactions between polar bears and common eiders. However we parameterized our model with sea-ice, landscape, and species-specific data from Foxe Basin and Hudson Strait whenever possible, as this is one of the main areas where there is data available about direct interactions between these species (e.g. Iverson et al. 2014), as well as good background data on polar bear and common eider biology. When data from Foxe Basin and Hudson Strait were not available, we prioritized data from adjacent areas (e.g. Hudson Bay, Ungava Bay, Baffin Bay), which are seasonal ice regions where common eiders and polar bears are also sympatric.

Model validation

We performed comprehensive testing to evaluate and validate our model, including using pattern oriented modelling techniques (Grimm *et al.*, 2005). When models reproduce patterns observed in real systems that were not included during model design, users can gain confidence that the model represents the essence of a system, and therefore is useful for predicting various outcomes (Grimm *et al.*, 2005; Grimm & Railsback, 2011). Even greater confidence in a model's utility can be gained when a model reproduces patterns of a real system at multiple levels (e.g. from individual agent 'physiology' up to system-level dynamics). Importantly, our model reproduced empirical results of polar bear bioenergetics, including a similar rate of daily mass loss, and changes in mass across years, observed in natural populations (Arnould & Ramsay, 1994; Derocher & Stirling, 1995; Atkinson *et al.*, 1996; Stirling *et al.*, 1999; Polischuk *et al.*, 2002; Obbard *et al.*, 2016). Similar to observations in Iverson *et al.*, 2014, polar bear agents in our model were more likely to visit eider colonies that had more nests, were on larger islands, and were further from the mainland. Finally, large eider colonies in our model were also stable over the 50-year modelling period, similar to observations that large eider colonies persist for long time periods (Sonsthagen *et al.*, 2009; Waltho & Coulson, 2015). Further details are available in Section 8 of the TRACE document.

Sensitivity of model outputs to uncertainty in parameter values and model rules

We tested whether uncertainty in parameter values, as well as uncertainty in model rules influenced the outputs from our model in Section 7 of the TRACE document. To perform this analysis, we randomly varied 11 key parameters within intervals of

uncertainty, and tested how each parameter contributed to variance in model outputs. In brief, uncertainty in parameter values caused negligible changes in male polar bear body condition and nest distribution, and moderate changes in total nest depredation and female polar bear body condition. Uncertainty in most parameters explained less than 1% of the variation in model outcomes across model runs (Table S5). However, uncertainty in polar bear search efficiency (a'), how much eider agents adjust nesting phenology in response to climate (V), and the relationship between female polar bear body condition and behavior (Q_{crit-f}), each explained between 18.3 % and 22.5 % of the variation in nest predation (Table S5), and uncertainty in eider nesting phenology explained 14.5 % of the variation in the change in female polar bear body condition. As a result, these parameters should be the focus of future empirical research in this system in order to improve predictive capabilities.

Simulations and model analysis

Because our model contained stochastic (i.e. non-deterministic) processes, the results from individual model runs varied. To understand the general findings of our model and expected error around those predictions, we ran batches of model runs in BehaviorSpace (Wilensky & Shargel, 2002) and exported the results to R (R Core Team, 2015) for statistical analysis, using the *lme4, MuMIn and ggplot2* packages (Wickham, 2009; Bartoń, 2015; Bates *et al.*, 2015). To analyze the relationship between ice break-up date and nest depredation, we fit three mixed-effects models to the results from 100 model runs (Table 1). The statistical models considered were a linear, quadratic and exponential fit, and we compared the fit of these models with AIC (with

low AIC indicating better model fit; Akaike 1974). The response variables and fixed effects for each model are outlined in Table 1. To account for shared variance in observations from the same model run, we included model run as a random intercept in each model. To explore the model predictions for changes in polar bear body condition over time, we ran a linear mixed effects model (LMM) including one observation for each bear agent for each year, in each of 100 model runs. In this model, we used the Quetelet body condition of each polar bear agent (i.e. the body condition at the end of the model year) at the time of freeze-up as the response variable. The fixed effects included in this model were the model year, the sex of the polar bear agent, the ageclass of the polar bear agent (adult or subadult), as well as an interaction between sex and year (to test for differential responses between male and female polar bear agents), and the interaction between age class and year (to test for differential responses between adults and subadults). We included model run as a random intercept to account for shared variance among observations from the same model run. We centered the year variable in this model in order to improve the interpretation of main effects in the presence of interactions (Schielzeth, 2010). We used three variables to analyze changes in the distribution of eider nest agents: 1) the variance in number of nest agents across island cells, which is high when nests are highly clumped, 2) the mean distance from the mainland to each nest agent, and 3) the number of nest agents on the 10 islands that had the most eider nest agents at the start of a model run (i.e. in model year 1990). This latter variable was measured because many northern peoples collected eider down and eggs, and often visit the same colonies year after year because they represent a reliable resource. Therefore, changes in the number of nests

on large colonies can influence the livelihoods of northern peoples. Because these three variables were dependent on the model landscape and influenced by variability between model runs, we standardized each variable by considering the change in each variable across the model run (i.e. value at model year 2039 – value at model year 1990). Then, we compared the change in each variable in runs conducted with, and without, polar bear agents, using Welch's two-sample t-tests, in order to assess the influence of nest depredation on eider distribution.

Results

Nest predation

Our model qualitatively reproduced the observed increase in polar bear presence at large common eider colonies (Iverson *et al.*, 2014; see also Section 8.4 in the TRACE document), and predicts increases in nest predation as advances in ice-breakup continue (Figure 2). On average, our model predicts that 20.6 % (95% CI = [18.8, 22.3]) of common eider nests will be depredated by polar bears each year by 2039, with some model runs exceeding 40% nest depredation in certain years (Figure 2). We found that the number of nests depredated was strongly linked with the date of ice break-up, with earlier ice break-up leading to more depredation (Figure 2). This relationship was non-linear, and accelerating as ice break-up advanced, and was best fit by an exponential model (Table 1). This exponential model explained 75.5 % of the variance in nest predation (marginal R^2; Nakagawa and Schielzeth 2013).

Change in body condition

Despite increasing nest predation across years in our model (Figure 2A, polar bear agent body condition declined as model year increased (LMM: effect of year = -0.19, 95% CI = [-0.20, -0.18], p < 0.001; Figure 3). As expected, male polar bear agents had higher body condition scores than female polar bear agents (effect of sex = 20.7, 95% CI = [20.5, 20.8], p < 0.001; Figure 3), and subadults had lower body condition scores that adults (effect of age class = -3.98, 95% CI = [-4.13, -3.83], p < 0.001; Figure 3). There were also statistically significant interaction effects, such that female polar bear agents had a more dramatic decrease in body condition with year than did male polar bear agents (sex * year interaction = 0.04, 95% CI = [0.03, 0.05], p < 0.001; Figure 3), and subadults had a less dramatic decrease in body condition with year than adults (sex * age class interaction = 0.06, 95% CI = [0.05, 0.07], p < 0.001; Figure 3).

Change in eider nest agent distribution

Polar bear behavior caused eider nest agents to be significantly more dispersed in the landscape (mean change in variation with polar bear agents = -6.9, and without polar bear agents = 1.1, t-test, t = -11.8, df = 30.3, p < 0.001, Figure 4, Figure S5). Additionally, polar bear behavior caused significant decreases in the number of nests in large colonies (mean change in variation for runs with polar bear agents = -579.8, and without polar bear agents = -8.7, t = -7.5 df = 97.9, p < 0.001, Figure 4). Indeed, the 10 largest colonies decreased in size by an average of 19.6% over the 50-year modelling period. Additionally, polar bear predation caused eider nest agents to move significantly

closer to the mainland (mean change in runs with polar bear agents = -0.7 km, and without polar bear agents = 0.1 km, t = -9.1, df = 84.8, p < 0.001).

Discussion

Our model predicts that predation of common eider nests by polar bears will continue to increase over the next 25 years. Importantly, our model demonstrates that there is an accelerating relationship between the amount of nest predation and the advance in ice break-up. This emergent pattern is due to interactions among a number of climate-driven model processes: (1) earlier ice break-up leads to more available nests (fewer have completed incubation) that contain more energy (i.e. less energy has been lost during chick development), (2) longer ice-free periods lead to more polar bears being energetically stressed and encouraged to forage on nests, and (3) polar bear agents are better able to sample their environment and learn where eider nests are most concentrated when ice break-up is early. Prediction of this accelerating relationship would be challenging without techniques such as agent-based modelling, which can incorporate complex ecological interactions and account for variation in behavior among individuals. We believe that our predictions of increases in nest predation are likely conservative for several reasons: first, we assumed that polar bear body condition at ice break-up was not influenced by the date of ice break-up. However, the period before ice break-up is an important hunting period for polar bears as this is when seals reproduce (Stirling & Archibald, 1977). Since advances in ice break-up will shorten the amount of time polar bears can hunt for young seals, it is likely that polar bears will be in poorer condition at the start of the ice-free period as ice break-up dates advance, and polar

bears may increasingly rely on ancillary prey to maintain adequate condition. Second, our model does not account for carry-over effects in polar bear body condition between years. It is unclear whether there is a correlation between polar bear body condition in the fall and in the subsequent spring, but if such a carry-over effect does exist then increases in the date of ice freeze-up will also lead to decreases in polar bear body condition during subsequent ice free seasons. Finally, our model includes linear extrapolations of sea ice break-up and freeze-up dates for model years 2015-2039. However, there is some evidence that the decline in sea ice is accelerating (Stroeve *et al.*, 2007; Velicogna *et al.*, 2014), which could increase nest depredation by leading to even greater temporal overlap between bears and seabirds, and increased energetic stress in polar bears (e.g. see also, Towns *et al.*, 2009).

Accelerating nest predation cannot continue indefinitely in the absence of large increases in common eider populations, and such increases seem unlikely given the dramatic increase in nest predation documented in our model, and in empirical studies of common eiders (Iverson *et al.*, 2014; Prop *et al.*, 2015). Although our model does not account for demographic changes in eider populations due to polar bear predation, increasing predation could ultimately drive declines in common eider population size through decreased reproductive success and/or large-scale (i.e. between landscapes) relocation of nesting eiders. If local eider populations become sufficiently small and dispersed, polar bears might stop searching for common eider nests because the energetic cost of foraging would exceed the potential benefits. Such a response in common eider populations would likely occur slowly because eiders are long-lived and

highly philopatric (Öst *et al.*, 2011; Waltho & Coulson, 2015), however further modelling that includes demographic responses in both common eiders and polar bears will be essential to make long-term (i.e. more than 25 years in the future) forecasts of the impact of climate change on Arctic ecosystems.

Our model suggests that increases in common eider nest predation will be insufficient to prevent predicted declines in polar bear body condition in response to lengthening ice-free periods. This finding was consistent, even when key parameter values, and model rules, were varied (TRACE Section 7). Some studies have suggested that increased consumption of terrestrial resources could offset losses in ice-based hunting opportunities in western Hudson Bay (Dyck & Kebreab, 2009; Rockwell & Gormezano, 2009), although these studies have been criticized because polar bear body condition and survival has declined even as terrestrial resource use has increased (Rode *et al.*, 2010, 2015b). Realized changes in polar bear body condition will be dependent on the availability and usage of all terrestrial foods, and since our study only considers eider nests it is possible that increased use of other terrestrial food (e.g. caribou, vegetation, snow goose nests, marine mammal carcasses) could mitigate declines in polar bear body condition. We believe this is unlikely because most other terrestrial resources are challenging for polar bears to access. For example, caribou (*Rangifer tarandus*) are difficult for polar bears to catch (Brook & Richardson, 2002) and populations are declining across much of their range (Vors & Boyce, 2009), Arctic char (*Salvelinus alpinus*) are only available during anadromous migrations and in rivers that are shallow enough to facilitate capture, and most other bird species nest in lower density (e.g.

snow geese, *Chen caerulescens*) or in areas that are more challenging to access (e.g.

cliff nesting thick-billed murres), than eider nests. Additionally, it is important to point out

that varying the number of eider nests in our model up to 10000 eider nest agents

caused negligible changes in polar bear agent body condition compared with the base

model (Table S5), and therefore our model predicts body condition declines even when

nests are highly available. Nonetheless, changes in polar bear body condition will be

dependent on local ecology, and could differ from the results presented here

Interestingly, adult female polar bear agents showed the largest decline in condition in

our study (Figure 3). This could be due to the presence of dependent cubs, which

increase the energetic costs of nursing females and decrease their rate of movement

(see TRACE Section 2.7). Regardless of the mechanism, this finding is of particular

concern given that females must undergo prolonged periods of fasting in order to

reproduce, and female condition in the fall (when pregnant females enter maternity

dens) is an important predictor of reproductive success (Atkinson & Ramsay, 1995).

Indeed, energy budget models suggest that climate warming will lead to both increased

reproductive failure, and decreased mean litter size, in polar bears (Molnár *et al.*, 2011),

which could drive changes in polar bear demography and population size (Regehr *et al.*,

2007; Hunter *et al.*, 2010).

Our model predicts increasing nest predation by polar bears despite the ability for eiders

to disperse within the landscape in response to increased predation. Common eiders

are thought to nest on islands primarily to avoid predation by terrestrial predators such

as foxes (Waltho and Coulson 2015). Even in island colonies, fox predation can still occur since foxes can reach some islands by crossing sea ice, and fox presence is more common on islands that are closer to the mainland (Iverson et al. 2014). Conversely, polar bear presence is more common on islands that are further from the mainland (Iverson et al. 2014; this study Figure S4), and eider nest agents in the current model shifted their distribution closer to the mainland in response to increased polar bear predation on off-shore islands. In our model, eider agents had no ability to assess polar bear predation risk. Instead, shore-ward movement of nests was simply due to increasing nest failure (and resulting nest dispersal) for eider agents nesting far from the mainland. If common eiders can directly assess polar bear predation risk and use this information when choosing a nest site, then shore-ward movement of nests may be even faster than predicted in the current model. Regardless of the mechanism, such a shoreward shift in distribution could increase the susceptibility of common eiders to predation by terrestrial predators, and further models that investigate eider reproductive success in multi-predator environments will be useful to understand both the direct and indirect effects of polar bear predation on common eiders. In our model, polar bear predation also caused eider nest agents to become more evenly dispersed in the landscape. Such an effect could have consequences for northern people who collect eider eggs and down, and hunt adult eiders for meat, since traditional hunting and gathering sites (i.e. large colonies that are stable for long time periods) will contain fewer nests (Figure 4).

Climate change is predicted to have profound effects on Arctic ecosystems through changes in biotic interactions (Brooks & Hoberg, 2007; Milazzo *et al.*, 2013). Here, we show that earlier ice-melt and resultant changes in species-specific phenology can have strong effects on predator-prey interactions. Our model reproduces observed increases in nest predation in Canada, Greenland and Svalbard, and predicts accelerating nest predation as climate warming continues even though common eiders disperse to avoid overlap with migrating polar bears. Furthermore, we show that increasing nest predation will not mitigate predicted declines in polar bear body condition caused by increases in the length of the ice-free period. As a result, the model presented in this paper should be a useful tool for predicting changes in Arctic ecosystems in response to climate change, and other anthropogenic activities. Additionally, our model identifies research gaps in our understanding of bear – eider interactions, and suggests that future studies on common eider nesting phenology, and polar bear foraging behavior, will improve the predictive capabilities of future modelling efforts.

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Table 1. Summary of model fits for the relationship between ice break-up date and the number of nests depredated. All statistical models were fit by the lmer function in *lme4* (Bates *et al.*, 2015) and included model run as a random intercept. Each model run contained 5000 nest agents and the statistical models consider the results from 100 model runs.

Model	Response variable	Fixed effects	AIC
linear	nests depredated	ice break-up date	68783
quadratic	nests depredated	ice break-up date + ice break-up date^2	68069
exponential	log (nests depredated)	ice break-up date	10632

Captions

Figure 1. A simplified flowchart of model processes. Panel A shows the order of actions taken by polar bear and eider nest agents during typical time steps, while panel B shows the decision tree for polar bear agent behavior (B). Further details of model processes are available in the supplemental TRACE document.

Figure 2. Patterns of nest predation in relation to model year (top) and ice break-up date (bottom). In the top panel, each grey lines indicates a single model run whereas the black line represents the average across all 100 model runs ($\pm$ 95% CI). In the bottom panel, grey points represent values from each model run (50 points per run) while black lines represent fitted values from an exponential mixed-effects model. Each model run was conducted with 5000 nest agents.

Figure 3. Body condition of polar bear agents at freeze-up across model years. Data shown are mean ($\pm$ 95% CI) values for adults (i.e. $\geq$ 5 years old: top) and subadults (3-4 years old: bottom) averaged across 100 runs.

Figure 4. Changes in eider nest agent distribution. On average, eider nest agents showed decreasing variance in nests per cell (i.e. more equal distribution; top) and the number of nests in the 10 largest colonies decreased (bottom) as model runs progressed. In each figure, grey lines are the results from a single model run, and the black line is the mean across all 100 model runs ($\pm$ 95% CI).