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Exploring the energetic consequences and decision-making behaviours of polar bears (*Ursus maritimus*) foraging on common eider (*Somateria mollissima*) seaduck eggs on Mitivik Island, Nunavut

by

Patrick Mathiew Jagielski

A Thesis
Submitted to the Faculty of Graduate Studies
through the Great Lakes Institute for Environmental Research
in Partial Fulfillment of the Requirements for
the Degree of Master of Science
at the University of Windsor

Windsor, Ontario, Canada

2020

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Exploring the energetic consequences and decision-making behaviours of polar bears (*Ursus maritimus*) foraging on common eider (*Somateria mollissima*) seaduck eggs on Mitivik Island, Nunavut

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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is result of joint research, as follows: I am the sole author of Chapter 1 (General Introduction) and Chapter 4 (General Discussion), and am the primary author of Chapters 2 and 3. Chapter 2 and 3 are co-authored with Dr. Cody Dey, Dr. Grant Gilchrist, Dr. Evan Richardson, and Dr. Christina Semeniuk. In regards to both co-authored chapters, the key ideas, primary contributions, study designs, data analysis, interpretation, and writing were performed by the primary author, and the contribution of co-authors was primarily through securing funding, data collection, data analysis, interpretation, and editing versions of the manuscripts.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-author(s) to include the above material(s) in my thesis.

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ABSTRACT

Climate change is projected to further degrade sea-ice conditions in the Arctic, causing disruptions in the foraging ecology of animals. Polar bears (*Ursus maritimus*) will likely continue to suffer declines in fitness if they are unable to supplement lost on-ice hunting opportunities with terrestrial resources. My thesis aimed to investigate whether polar bears accrue a net energetic gain from foraging on common eider (*Somateria mollissima*) eggs and whether the decisions they make when foraging on eggs are consistent with optimal foraging theory. Using aerial footage of bears foraging on common eider eggs, I estimated the energetic consequences of foraging on eggs, and examined polar bears' foraging performance as the resource was depleted. My results indicate that polar bears consumed eggs at a decelerating rate. While the proportion of time spent searching in the colony increased as the season advanced, the energetic cost of searching remained constant throughout the season as a result of similar costs of expenditure across locomotion and feeding. Overall, while some bears gain an energetic surplus from egg foraging, the benefits decline with nest density, resulting in a net loss. Further, my results indicate that as the resource depleted, polar bears did not adjust all their foraging decisions to match resource density. Bears increased their visitation rates to nests that were 'empty', despite visiting fewer nests overall. Polar bears did not adjust their movement to nest density, but did become less selective in their choice of which clutches of eggs to consume. Lastly, bears that capitalized on the visual cue of a flushing eider hen to locate nests also significantly increased the number of clutches they consumed.

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CHAPTER ONE General Introduction

Background

Many scientists now believe we are in the Anthropocene (Steffen et al. 2007), an epoch characterized by human-induced rapid environmental change (HIREC) (Sih 2013). In specific, humans are believed to be the dominating force influencing the global climate (Hansen et al. 2006; Santer et al. 2018), largely through emitting large volumes of CO₂ into the atmosphere, causing surface-area temperatures to rise (IPCC 2018; Foster et al. 2017). While most species on earth have experienced climatic perturbations somewhere along their evolutionary lineage, the rate at which organisms are now subjected to global warming is unprecedented (Kannan and James 2009). Indeed, climate-mediated habitat loss is regarded as one of the greatest threats to global biodiversity loss in the 21st century (Mantyka-pringle et al. 2012; Travis 2003; Staudinger 2013). While generalist species are thought to be robust and have a high capacity to cope with change, habitat-specialist species' narrower ecological niche elicits concern in a changing world (Colles et al. 2009). With regards to foraging, habitat specialists who demonstrate a greater capacity (i.e., flexibility) to incorporate alternative food items (i.e., diet-switching) from different habitat types into their diet when their main resource is in low abundance or unavailable entirely may be better equipped to adapt to a changing world (Beever et al. 2017). However, these alternate food resources do not always guarantee population- or- species persistence because the energetic cost of attaining these resources might outweigh their nutritional and caloric benefits (Humphries et al. 2004). In addition, an animal's ability to make optimal foraging decisions (Pyke 1977; Stephens and Krebs 1986) may be compromised in an altered environment where uncommon diet items are being

increasingly relied upon (Griffin et al. 2017). Therefore, there is growing concern for habitat specialists that may be unable to adapt to this rapid climatic perturbation (Foden et al. 2009).

To mitigate the deleterious threats of HIREC, predator habitat specialists (who are also adapted to foraging on a particular resource) will have to continue to optimize their foraging behaviours. Optimal foraging theory states that animals should attempt to maximize their net energetic gain in relation to procurement cost (MacArthur and Pianka 1966; Pulliam 1974; Pyke 1977; 1984). Thus, animals should choose the highest-quality items at all times and ignore lower quality ones, irrespective of their abundance (Schluter 1981). However, when high quality food items diminish or become unavailable entirely (e.g., as a result of climate-mediated habitat loss), the foraging animal should incorporate lower-quality food items into its diet (Schluter 1981; Bergerud 1983; Steenhof and Kochert 1988; Kjellander and Nordström 2003). Quantifying the profitability of diet-switching (i.e., net energy gain) will require knowledge of the species' intake rate, energetic value of the item, and the energetic cost of searching for, handling, and consuming it (i.e., benefit-cost, Schoener 1971). The energy used to procure a resource (i.e., searching and foraging), and the subsequent net energetic gain (energy intake minus cost of procurement) can therefore be quantified with knowledge of the species' bioenergetics (i.e., energetic cost of physiological and behavioural activities performed throughout the day) (Hayssen and Lacy 1985; Nagy 1987). Given that energy is the 'currency of life' (Baldwin and Bywater 1984) and maximizing energetic gain facilitates fitness (i.e., survival and reproductive success) (Pyke 1977; Stephens and Krebs 1986), examining the energetic benefits and costs of diet-switching under HIREC is an ideal first

approach to understanding the potential contributions these diets may have on both individuals and populations as a whole (Humphries et al. 2004).

Underlying foraging behaviours are fine-scale decisions animals make in an attempt to improve their efficiency and hence maximize their net energetic returns. Indeed, animal decision-making involves more than simply finding the highest quality resource at the lowest cost as there exists uncertainty with regards to resource distribution and resource quality. Thus, animals must also decide: (1) among which patches of varying resource quality to exploit and for how long, (2) which searching patterns to adopt when moving within patches (and across landscapes) varying in resource distribution, (3) which items to consume versus ignore upon encounter, and (4) which information cues about resource quality and/or location to process and ignore upon encounter (Pyke 1977; Budaev et al. 2019). Natural selection has shaped organisms' decision-making heuristics to perform well (i.e., near optimally) the majority of the time across situations they are expected to encounter throughout their lifetime (Fawcett et al. 2013; 2014). However, if the environment under HIREC is sufficiently distinct from what the habitat-specialist is adapted to, these animals' decision-making heuristics may be compromised as a result of a mismatch in their cue-response systems (Sih 2013; Sih et al. 2019). For example, continuing to use previously-adaptive strategies to assess habitat and resource quality after the environment has changed may cause organisms to choose low-quality options that should be ignored, or avoid good-quality options that should be pursued (Schlaepfer et al. 2002; Robertson and Hutto 2006; Gilroy and Sutherland 2007). In some instances, the environment is so poor after HIREC that animals are ultimately constrained and unable to respond adaptively, regardless of the decisions they make (Sih

2013). Conversely, some animals are able to adjust and thrive in newly altered environments (e.g., urban pests and invasive species, Sih et al. 2010; Lowry et al. 2013). Given the outcome of a species' response to altered environmental conditions is difficult to predict (Wong and Candolin 2015), exploring their behavioural patterns when foraging (i.e., decisions) will aid in determining whether an organism maintains the capacity to maximize its efficiency when making foraging decisions in habitats to which they are not specifically adapted.

Studying the adaptive capacity of organisms to rapid environmental change is now at the forefront of ecological research (Bellard et al. 2012). Given that the incorporation of supplementary diet items does not guarantee an energetic surplus for an individual (Humphries et al. 2004), it is imperative to quantify both the energetic benefits and costs of diet-switching to informatively predict whether reliance on an alternative diet item will be able to mitigate lost foraging opportunities. Further, because foraging efficiency affects energy maximization, reproductive fitness, and survival (Pyke 1977; Stephens and Krebs 1986), and HIREC is expected to decouple species' adaptive decision-making capabilities (Griffin et al. 2017), it is becoming increasingly important to test whether individuals will behave as optimal foragers. If species are able to adjust their behaviours to optimize their energetic gain, this may eventually facilitate adaptation to these altered conditions over multiple generations (Sih 2013). In essence, studying the foraging of animals under HIREC requires examination of both broad- and- fine- scale behaviours related to net energetic gains.

Study System

The Arctic is changing faster than any other place on earth due to a phenomenon called polar (or Arctic) amplification, resulting from multiple synergistic interactions (e.g., albedo effect and cloud cover impacting radiation) causing surface temperatures to increase (Serreze and Barry 2011). Temperatures are rising at two to three times the global average rate and the spatiotemporal extent of sea-ice is declining faster than model projections had anticipated (Koenigk et al. 2013; Stroeve et al. 2007). New data predict the Arctic will be seasonally ice-free around mid-21st century (Thackeray and Hall 2019). The prevailing evidence suggests that most Arctic biota (across all trophic levels; e.g., phytoplankton to mammals) are experiencing shifts in abundance and distribution, and most marine mammals and birds are experiencing phenological shifts in their breeding and foraging ecologies (Descamps 2017; Frederiksen 2017).

Polar bears (*Ursus maritimus*) are apex marine predators that inhabit the circumpolar Arctic, and their reliance on the sea-ice for travelling, mating, and foraging (Thiemann et al. 2008) makes these habitat specialists particularly vulnerable to climate change. Polar bears use the sea-ice as a platform to hunt their primary prey, ringed (*Phoca hispida*) and bearded (*Erignathus barbatus*) seals (Stirling and Archibald 1977), but they are also known to opportunistically hunt walrus (*Odobenus rosmarus*, Calvert and Stirling 1990), beluga whales (*Delphinapterus leucas*, Lowry et al. 1987), and narwhals (*Monodon monoceros*, Smith and Sjare 1990) when locally available (see Galicia et al. 2015).

Every spring, polar bears have a critically short window of opportunity to put on the majority of their yearly fat reserves by intensively hunting the newly born cohort of

seal pups (Stirling and Øritsland 1995). Polar bears that inhabit seasonal-ice regions (i.e., areas of the Arctic that are ice-free during the summer months) migrate onto land when the sea-ice retreats in early summer. Polar bears must therefore accumulate enough fat reserves prior to sea-ice breakup to sustain themselves during the summer months when access to marine mammals is limited (Stirling and Derocher 1993; 2012). Arctic sea-ice is now melting earlier in the spring (and refreezing later in the fall) in many areas of the polar bears' range (e.g., southern Beaufort Sea, Atwood et al. 2016; Chukchi Sea, Rode et al. 2015a; Hudson Strait, Foxe Basin, and Hudson Bay, Sahanatien and Derocher 2012), consequently forcing bears onto nearshore terrestrial environments prematurely, causing them to spend considerably more time on land than they have in the past. This increased terrestrial occupancy is being increasingly studied by scientists as polar bears are unable to efficiently conserve energy while on land (Whiteman et al. 2015), and consequently lose approximately 1.0 kg of body mass per day⁻¹ when fasting (Pilfold et al. 2016). Data from some subpopulations suggest that bears are not accumulating enough fat reserves prior to sea-ice breakup (Stirling et al. 1999; Obbard et al. 2016), which has resulted in declining reproductive success (Laidre et al. 2020) and population declines (Stirling and Derocher 2012).

Polar bears are certainly known to eat while on land (e.g., Russell 1975; Derocher et al. 1993; Derocher 2012; Gormezano and Rockwell 2013ab; Gormezano et al. 2017), and some scientists hypothesize that polar bears will be able to adapt to longer terrestrial occupancy by incorporating terrestrial resources into their diet (e.g., Dyck and Kebreab 2009; Gormezano and Rockwell 2015). However, unless high-energy food resources are found (e.g., beached whale carcass), the notion of adapting to lengthier terrestrial

occupancy seems highly unlikely as terrestrial resources are spatially and temporally variable, and tend to be energetically inferior to seals (Rode et al. 2015b), but see (Pagano et al. 2019). Further, terrestrial resources will require different pursuit tactics (e.g., chasing, climbing and grazing; Smith et al. 2010; Gormezano et al. 2016; Stempniewicz 2017) than what bears typically employ on the sea-ice (i.e., sit-and-wait, Stirling 1974), so bears may not possess the capacity to make optimal foraging decisions for land-based diet items, although see (Gormezano et al. 2017).

Polar bears are increasingly foraging on eggs in avian colonies as earlier sea-ice retreat is causing bears to overlap with breeding birds (e.g., Rockwell and Gormezano 2009; Smith et al. 2010; Prop 2015). In particular, polar bears inhabiting the west coast of Spitsbergen, east Greenland, and the Hudson Strait, Foxe Basin, and Hudson Bay regions (including Mitivik Island) are now inadvertently matching their arrival to the breeding schedule of colonial nesting common eider (*Somateria mollissima*) seabirds as declining sea-ice conditions are outpacing the birds' ability to adjust their laying phenology (Iverson et al. 2014; Prop et al. 2015; Dey et al. 2017). Given that common eiders are ground-nesting colonial species (over 1000 nests per hectare) (Schmutz et al. 1983; Chaulk et al. 2004), their nests are both easily accessible and densely populated making them potentially profitable to foraging bears. While an egg diet will likely not support entire polar bear subpopulations (Dey et al. 2017), it may provide energy to some individuals (Rockwell and Gormezano 2009). Determining the energetic contribution eggs make to bears during the ice-free season, and whether bears have the capacity to adjust their foraging decisions to a decline in resource abundance of alternative prey, will provide insight into whether bears can offset lost on-ice hunting opportunities, likely

through strategies such as diet mixing (Gormezano and Rockwell 2013a). Indeed, individuals within a population able to maximize foraging efficiency on alternative prey items may be able to facilitate adaptation to longer terrestrial residency times.

While scat analysis (which was the primary technique used for most polar bear terrestrial diet studies, Gormezano and Rockwell 2013ab; 2015) can inform what bears are eating and how much those items comprise the bears' overall diet, little is revealed about how those items were obtained by the bears (e.g., movement modes and time allocation) – which would ultimately affect the energetic return per unit of effort. For example, polar bears' energetic reward when hunting geese will vary greatly depending on how long they choose to chase the birds (Gormezano et al. 2016). Drones have recently emerged in ecological studies as powerful, cost effective, and minimal-impact tools to monitor animal behaviour (Christie et al. 2016). Drones have proven effective in monitoring otherwise difficult to observe megafauna, and have provided detailed and informative behavioural insight, all with minimum apparent behavioural disturbance to the focal species (Nieukirk et al. 2018), including Ursids (Ditmer et al. 2015; Barnas et al. 2018). Given that we know very little about *how* polar bears forage within an avian colony (specifically on eggs), drones are an ideal (i.e., non-invasive) approach to capture direct behaviour of foraging bears. Indeed, aerial footage allows the observer to track searching and foraging behaviours, which can then be assigned energetic values (i.e., estimation of benefits and costs). Further, it allows the observer to track foraging behaviours (that have arguably never been seen before) to determine whether bears' decision-making heuristics (which would affect the magnitude of their energetic return)

follow expectations of optimal foraging theory in this increasingly important terrestrial environment.

Thesis objectives

The overall objectives of my thesis are to determine whether foraging on common eider seaduck eggs provides an energetic benefit to polar bears and whether their decision-making heuristics are consistent with predictions of optimal foraging theory in this avian system.

My study took place on Mitivik Island in northern Hudson Bay, Nunavut (Fig. 1) in 2017. Mitivik Island is home to a long-term (est. 1996) research program where common eider population monitoring is carried out annually (Buttler et al. 2011; Henri et al. 2018). In recent years, polar bears have been arriving onto Mitivik Island progressively earlier, and overlapping with the eiders' breeding schedule, as the spatiotemporal extent of sea-ice in the Hudson Strait has been declining (Iverson et al. 2014). Mitivik Island is an excellent system to quantify the benefits and costs of bears foraging on sessile, depleting resources because it is an isolated ecosystem where bears are free to forage on a high density of eggs with very little disturbance and competition from other predators, such as arctic foxes (*Vulpes lagopus*). Polar bear foraging behaviour was recorded with drones (Fig.2) approximately midway through the eiders' breeding season.

In **Chapter 2, *Polar bear (Ursus maritimus) foraging on common eider (Somateria mollissima) eggs: Estimating the energetic consequences of a climate-mediated behavioural shift***: My objective was to quantify the energetic benefits and costs of polar bears foraging on eider eggs and how this benefit/cost relationship changes

across the eider breeding season. I hypothesized that as the study period progressed (and nests depleted) the profitability of foraging on seaduck eggs would diminish. I found that bears who arrive early to Mitivik Island are able to capitalize on the abundance of nests and gain an energetic surplus that can potentially mitigate lost seal-hunting opportunities. However, the energetic profitability declines as the colony depletes.

In **Chapter 3, *Examining polar bear (*Ursus maritimus*) decision-making as they forage in a large common eider (*Somateria mollissima*) seaduck colony:*** My objective was to determine whether polar bears forage on alternative prey in a manner consistent with optimal foraging theory. I hypothesized that, given the restricted window of opportunity, bears would adjust their behaviours in the context of a depleting resource so that their net energetic gains would be maximized. I found that as egg abundance declined, bears were unable to adjust their behaviours to match resource availability. I discuss how the energetic cost is likely negligible in this system, but posit that, should these behaviours continue post colony depletion or across the landscape in other bird colonies, they may begin to carry an energetic cost and impact polar bear body condition.

In **Chapter 4, *Conclusions:*** I briefly summarize and interpret my findings, then discuss their implications to the broader scope of polar bear terrestrial foraging ecology and resultant impacts on polar bear population persistence and predictive modelling. Lastly, I discuss my study's limitations and provide suggestions for future research.

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Figures

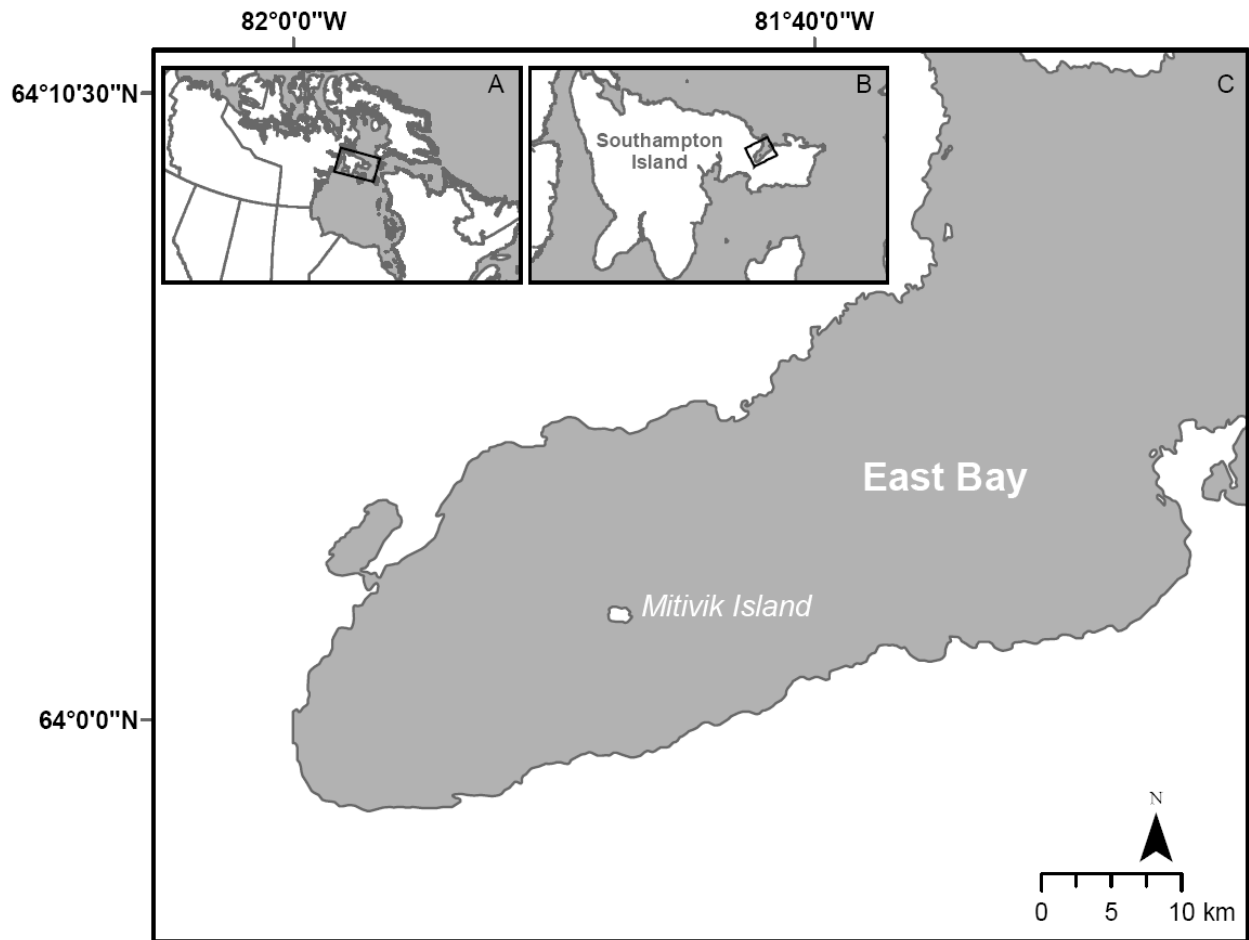


Figure 1. 1 Map of study area. Panel: a) General location (northern Hudson Bay), b) Regional location (Southampton Island), c) Study site (Mitivik Island)



Figure 1. 2 Drone hovering above and filming a polar bear foraging in the Mitivik Island eider colony on July, 2017

CHAPTER TWO Polar bear (*Ursus maritimus*) foraging on common eider (*Somateria mollissima*) eggs: Estimating the energetic consequences of a climate-mediated behavioural shift

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Introduction

Foraging decisions are often driven by an animal's physiological state and the environment in which it lives (Day et al. 1998). Optimal foraging theory states that animals should consume resources that maximize their net energetic gains and continue pursuing these resources until they become unavailable or unprofitable to pursue (Pyke 1984). If climate change alters a species' ability to access their primary food resource, their capacity to adapt will be influenced by whether they can incorporate alternative food items into their diet, and if these will be able to offset the potential risks of malnutrition, declining body condition and/or starvation. At a minimum, the energetic and nutrient benefits from consuming these alternative resources must outweigh their pursuit costs (MacArthur and Pianka 1966). Variation in behavioural tactics may occur in response to sudden shifts in the timing, abundance, and therefore accessibility of food resources resulting from climatic changes (Wong and Candolin 2015). Prey switching is often seen in generalists shifting their foraging from low to high resource availability (e.g., red foxes (*Vulpes vulpes*), Kjellander and Nordström 2003), but is also exhibited by specialists when their primary prey is no longer accessible or profitable to pursue. For example, lynx (*Lynx canadensis*) prey primarily on snowshoe hares (*Lepus americanus*) when their numbers are abundant, but will switch to hunting caribou calves (*Rangifer tarandus*) and other species of hare when snowshoe hare numbers crash (Bergerud 1983). Flexible foraging strategies such as prey switching may become increasingly important if

climatic changes cause temporal and spatial shifts in primary prey availability. Therefore, quantifying the energetic consequences of foraging on novel resources is becoming a major focus for ecologists studying the adaptive capacity of animals responding to human-induced, rapid ecological change (Bellard et al. 2012).

The effects of climate change on ecological systems are believed to be most prevalent in the Arctic (Wassmann et al. 2011; Descamps et al. 2017). Air temperatures in the Arctic are increasing at two to three times the global average rate (Koenigk et al. 2013), and there has been a rapid decline in the spatiotemporal extent of sea-ice which is a key habitat for many species (Stern and Laidre 2016). Polar bears (*Ursus maritimus*) inhabit the circumpolar arctic and their reliance on sea-ice for travelling, mating, and foraging is well known (Thiemann et al. 2008), which makes them particularly vulnerable to climate change. Polar bears are specialised predators that use the sea-ice as a platform to hunt (almost exclusively) seals (Stirling and McEwan 1975; Stirling and Archibald 1977; Derocher et al. 2004). In seasonal ice zones, polar bears rely on accumulating enough fat reserves prior to sea-ice breakup to sustain themselves on land during the ice-free season (Stirling and Derocher 1993; 2012; Stirling and Øritsland 1995) when foraging opportunities are limited (Rode et al. 2015). Across several polar bear subpopulations, changes in sea-ice phenology are driving bears onto nearshore terrestrial environments progressively earlier (e.g., Derocher et al. 2004; Rockwell and Gormezano 2009; Smith et al. 2010; Sahanatien and Derocher 2012). Consequently, displaced bears are coming ashore with reduced fat reserves (Stirling et al. 1999; Obbard et al. 2016) which have been linked to declines in reproductive output and population size (Atkinson and Ramsay 1995; Stirling and Derocher 2012).

Given the decrease in seal-hunting opportunities, land-based food items will become more critical to polar bears as they begin occupying terrestrial environments for longer periods of time. While polar bears are known to opportunistically consume a wide variety of resources on land (Russell 1975; Derocher et al. 1993; Derocher 2012; Gormezano and Rockwell 2013b; Gormezano et al. 2017), it is unclear whether the calories available from some of these resources outweigh their acquisition costs. Some authors have calculated the theoretical amount of calories from terrestrial food items available to bears during the ice-free season and have suggested that the available resources can help offset lost seal-hunting opportunities (e.g., Dyck and Kebreab 2009; Gormezano and Rockwell 2015). This assertion remains questionable (Rode et al. 2010; 2015) given that the energetic costs of foraging were not considered in these studies (although see Gormezano et al. 2016). While it is plausible that opportunistic foraging on the myriad of locally available resources (i.e., diet mixing, Gormezano and Rockwell 2013a) can contribute to energetic gains for polar bears during the summer months, it is critical to determine whether the caloric benefits of these resources outweigh the energetic costs of attaining them. This is especially true for low calorie (e.g., vegetation, berries, and bird eggs) resources as they would need to be consumed in high quantities to fulfill a polar bear's high daily energetic demand (see Pagano et al. 2018b).

There is growing evidence that polar bears are increasingly foraging on the eggs of cliff and ground nesting bird species at a variety of sites across the circumpolar Arctic (e.g., little auks (*Alle alle*), Stempniewicz 1993; thick-billed murres (*Uria lomvia*), Smith et al. 2010; black guillemots (*Cepphus grylle*), Divoky 2011; lesser snow geese (*Anser caerulescens caerulescens*), Rockwell and Gormezano 2009; Iles et al. 2013; barnacle

geese (*Branta leucopsis*), glaucous gulls (*Larus hyperboreus*), Prop et al. 2015; and common eiders (*Somateria mollissima*), Iverson et al. 2014; Prop et al. 2015; Dey et al. 2017). One species that may be particularly vulnerable to nest predation by polar bears is the common eider (hereafter, ‘eider’); a large seaduck that typically breeds on low-lying islands, and can form colonies with densities of over 1000 nests per hectare (Schmutz et al. 1983; Chaulk et al. 2004). As a result, eider eggs are an easily accessed and potentially profitable target for foraging bears. For example, during a 96-hour period on the La Pérouse Bay Research Station (near Churchill Manitoba, Canada), a lone bear devoured 206 nests in an eider colony and reportedly would have continued feeding had it not been chased away due to safety concerns (Gormezano et al. 2017). While predictive modelling work by Dey et al. (2017) suggests that foraging on eider eggs will be insufficient to maintain body condition in the face of projected sea-ice losses, it is plausible that bears who arrive early to breeding sites of colonial nesting species can accrue an energetic surplus within a given year (Rockwell and Gormezano 2009).

To understand if foraging on eider eggs generates a positive response to declining sea-ice conditions, we investigated the energetic benefits (i.e., the estimated caloric gain from egg consumption) and the energetic costs (i.e., costs associated with searching for and consuming eider eggs) of polar bears foraging on eggs in a large eider colony in northern Hudson Bay, Nunavut, Canada. To do so, we filmed polar bears foraging on eider eggs on Mitivik Island, and used these data, along with estimated energetic expenditures derived from existing literature studies on polar bear bioenergetics, to estimate the energetic benefits and costs of observed foraging behaviours. We predicted that when resources are in high abundance, bears would benefit energetically from

consuming eggs. However, bears arriving later to the eider colony would experience diminishing returns associated with resource depletion. As a result, we predicted that the profitability of foraging on eider eggs would decline over time. To our knowledge, this is the first study to provide an energetic quantification of polar bear foraging on eggs by examining direct behavioural data of bears foraging in the wild.

Materials and methods

Study site

This study took place on Mitivik Island, a small (24 hectare) island located near Southampton Island, Nunavut, in northern Hudson Bay (64° 01' 47.0" N, 81° 47' 16.7" W). Mitivik Island is situated in Southampton Island's East Bay, a seasonally ice-free region that serves as an important summering ground for many of the Foxe Basin subpopulation polar bears (Sahanatien et al. 2015; Stapleton et al. 2016). Mitivik Island is a relatively flat terrain characterized by low-lying (<8 m in elevation) tundra and granite rocks, interspersed with small ponds (Fig. 1), and supports the densest known nesting colony of common eiders (*S. m. borealis spp.*) in the Canadian Arctic (8000 pairs between 2002 and 2013 Jean-Gagnon et al. 2018, with recent estimates between 800-1200 breeding pairs). In recent years, changes in sea-ice phenology have aligned the onshore migration of polar bears onto Mitivik Island with the eiders' egg laying and incubation periods in late June to early July (Iverson et al. 2014). As a result, bears are arriving to the island when eiders are incubating and are foraging on eider eggs, presumably in an attempt to offset lost seal-hunting opportunities (Iverson et al. 2014).

Polar bear observations

We used DJI Phantom 3 Pro and 4 Pro drones (<https://www.dji.com/company>) to record polar bears foraging on eider eggs from July 10-20, 2017, which is approximately

midway through the eiders' incubation period (Love et al. 2010; Fig. 2). Although bears were migrating towards Mitivik Island in late May (P.M.J, pers. obs.), their presence was discouraged by the eider research team (i.e., late-May to July 10th) for safety purposes during the daytime (Fig. 2), although some egg predation likely occurred at night (between 4-7 hours). During this study's period (July 10-20), bears were allowed to forage freely (i.e., were not chased off the island). Bears were recorded between 0530 hrs and 2030 hrs (we did not film at night as the crew had to sleep) whenever they were present and active on Mitivik Island (i.e., we did not record bears that were sleeping or resting for long periods), and weather conditions were suitable for drone operation. Though predation events occurred at night during this time as well, we are confident that our study captured a large proportion of predation events, until bears ultimately depleted the entire colony (C.J.D and E.S.R, pers. obs. Fig. 2). Filming started as soon as the researchers noticed a bear on the island and finished when the bear: a) went to sleep or b) left the island. We note that at times there were multiple bears on the island and a focal bear was haphazardly chosen based on activity; filming then transitioned to other bears as soon as the focal bear fulfilled criteria a or b above.

The drone pilot and observer stood on the roof of a research cabin and launched/landed the drone within an electrified fence that surrounds the research station buildings. Drones were positioned between 30 and 55 meters above the focal bear and were recorded at a resolution of 2700 x 1520 pixels, at 30 frames per second. Importantly, the drones appeared to elicit minimal behavioural responses from the bears and we suspect that this was due (in combination) to: 1) an appropriate flying altitude, 2) the natural noise of a seaduck colony buffering the sound of the drone, and 3) bears being

attacked/annoyed and thus distracted by flying herring gulls (*Larus argentatus*)(C.J.D, pers. obs.); although we acknowledge that without definitive evidence, bears (and potentially eiders) may have experienced a physiological response (Ditmer et al. 2015; Weimerskirch et al. 2018).

We differentiated bears in order to track individuals' foraging behaviours (e.g., number of clutches eaten) throughout a 'foraging bout' – see description of foraging bout below. Bears were differentiated based on a combination of conspicuous markings, their size, our ability to keep track of the total number of bears observed per day, and time and date of video filming. If a bear was unrecognizable within the same day, it was considered a different bear. Individuals were also considered to be different bears between days as we had no way of proving otherwise. In total, we differentiated 19 individual bears, although we are aware that this estimate is likely high as some bears slept on pack ice and may have returned to forage the next day (C.J.D, pers. obs.).

A total of 1,028 minutes of polar bear foraging footage were recorded using the methods described above. These data were separated into distinct 'foraging bouts', which represented an observation of a single bear continuously foraging, but could be composed of one or more flights as a result of the flight time limitations (approx. 22 minutes per battery) for the drones used in our study. We considered it a new foraging bout when there was a significant time gap (> 20 minutes) in filming a focal animal as a result of having to replace batteries. In total, we differentiated 33 foraging bouts (some individuals foraged more than once in a day) that ranged from 5.7 to 134 minutes (mean = 34.5 minutes; median = 21.6 minutes). Importantly, 'foraging bout' was used as our unit of observation for our statistical analysis (see below).

Behavioural analysis

We used Solomon Coder version: beta 17.03.22 (<https://solomoncoder.com/>), a manual behavioural coding tool, to analyse polar bear foraging behaviour. Drone video footage was loaded into this interactive platform where we predefined behaviours of interest and then categorized bear behaviour during video playback. In reviewing each foraging bout, we recorded: 1) the number of clutches each polar bear consumed. A bear was only considered to have consumed a clutch when it was obvious that it had done so (i.e., its face was in a nest and the bear was seen chewing/licking; full clutch was clearly visible when approaching nest; and/or a hen was seen flushing from the nest before the bear approached). Any approaches to a nest not fulfilling the above criteria were considered an “empty-nest visit”. 2) The duration of time a bear spent walking and standing (i.e., searching), as well as the duration of time a bear spent standing, sitting, laying down, and walking while ingesting an egg (i.e., handling time/eating) were behaviours also included in the analyses.

Estimates of energetic gain and use

We estimated energetic gains for each foraging bout based on the number of clutches each polar bear consumed. The energetic value for each clutch was estimated based on: (i) estimates of the caloric content of eider eggs (1090 kJ per egg, Swennen and Meer 1995), (ii) the mean clutch size of 2.85 on Mitivik Island (Love et al. 2010), and (iii) a polar bear’s ability to digest protein and fat (83.7% and 97.3%, respectively, Best 1985), which are the primary components of an avian egg. These calculations resulted in an estimation that each clutch provides polar bears with 2803 kJ worth of energy (see supplementary material in Dey et al. 2017). We note however, that in our calculations we ignored the decline in caloric value of avian eggs across incubation (Romanoff 1967);

and therefore our calculations may produce modest overestimates as this study took place at approximately mid-breeding season (Love et al. 2010).

We estimated the energetic costs of foraging in an eider colony based on the amount of time polar bears spent searching for and handling eider eggs. Because videos in our study varied in length, we converted the unit of time for our analysis to per min^{-1} rates, and weighted the data to account for the contribution of longer-length videos. We used the formula describing the energetic cost of movement for polar bears (when searching and ingesting while walking) from Pagano et al. (2018a):

$$\dot{V}O_2 = 0.44 + 0.12 \times \text{speed}, \quad (\text{eq. 1})$$

where $\dot{V}O_2$ is in $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ and speed is in km h^{-1} , and the energetic formula from Watts et al. (1987) where 1 L O_2 consumed is equal to 19.66 kJ. We estimated polar bear movement at 3.4 km hr^{-1} as they walked over the flat ground of the island, which was the average walking speed for bears in Pagano et al. (2018a). Together, these values produced an estimated energetic cost of movement of $16.67 \text{ kJ kg}^{-1} \text{ hr}^{-1}$. We estimated the energy use of bears when standing (i.e., during searching), and when ingesting eggs (when standing, sitting, and laying down) using the same methods, but with a speed of 0 km/h. This produced an estimated energy-use rate of $8.65 \text{ kJ kg}^{-1} \text{ hr}^{-1}$, which is 40% higher than estimates of resting metabolic rate for polar bears (e.g., combined from Pagano et al. 2018ab) but were deemed appropriate given that bears standing at eider nests ingesting eggs were expending energy through jaw movement, postural costs and digestion. We produced estimates of energy use for polar bears weighing 255 kg and 579 kg, which represent the average masses for female and male polar bears from the Foxe

Basin subpopulation, respectively (Derocher 1991). Importantly, statistical analysis (see below) using a range of mass estimates produced qualitatively similar results; thus, in an effort to reduce unnecessary repeatability, we present just these two weight classes (255 kg and 579 kg) in this manuscript.

Statistical analyses

To estimate the benefits and costs of foraging on eider eggs, and how these benefits and costs change with resource density, we explored four functional relationships with our dataset. In each case, foraging bouts were considered as the unit of observation. We used foraging bout order as our independent variable (i.e., first recorded foraging bout = 1, last recorded foraging bout = 33) which captures not only time, but how resource density should decrease with time (since clutches are being consumed during each foraging bout). As our dependent variable we considered: 1) the rate of clutch consumption per min^{-1} (i.e., intake rate), 2) the proportion of time bears spent searching for nests (i.e., searching time divided by foraging time), 3) the rate of energy use per min^{-1} , and 4) the rate of net energetic gain per min^{-1} .

We used a model selection framework to determine the shape that best fit the relationship between the dependent and independent variables. For each of the four relationships we fit:

1) An intercept-only (i.e., null) model, representative of no relationship between the variables (y) and (x), where (a) is the overall mean (or y-intercept).

$$y = a \quad (\text{eq. 2})$$

2) A linear model representative of a linear increase or decrease in the response variable (y), and nest density (foraging bout order) (x), where (m) and (b) are constants.

$$y = mx + b \quad (\text{eq. 3})$$

3) A diminishing returns model where the response variable (y) increases or decreases depending on nest density (foraging bout order) (x) and where (a) is equal to the rate needed for the response variable to reach its maximum value, and (b) is the constant required for the response variable to achieve half its maximum value. This model is similar in shape to the Holling type II functional response model (Holling 1959) often observed in foraging ecology studies.

$$y = \frac{ax}{b+x} \quad (\text{eq. 4})$$

4) A power law model (Marquete et al. 2005) where the response variable (y) increases or decreases in linear and non-linear ways depending on nest density (foraging bout order) (x), where (β) is a normalization constant and (α) is the law's exponent. This model is similar in shape to a generalized type III functional response model (Holling 1959) where rate is an accelerating function of resource density with saturation (Rosenbaum and Rall 2018).

$$y = \beta x^\alpha \quad (\text{eq. 5})$$

For each relationship we fit the four mechanistic models described above and used Akaike's information criterion corrected for small sample sizes (AIC_c) (Symonds and Moussalli 2011) to determine the best model fit from our model set. We tested

whether the best model had a significantly better fit than the null model (i.e., the intercept-only model) using an ANOVA. Further, we tested best models' goodness of fit through visual inspection and with a Shapiro-Wilks test (made available upon request). Statistical analyses were performed in R version 3.4.4 (R Core Team 2019) using the nlstools (Baty 2015), tidyverse (Wickham 2017), MuMIn (Allwood et al. 2005), and broom (Robinson 2014) packages. Figures were created using the ggplot2 (Wickham 2016), cowplot (Wilke 2016), and gridExtra (Auguie 2016) packages. Code will be made available upon request.

Results

Throughout the study period, we recorded polar bears consuming a total of 443 clutches in the eider duck colony on Mitivik Island, in East Bay. As the season progressed, bears consumed clutches at a decelerating rate until ultimately the colony depleted, resulting in three of four bears consuming no clutches in the last three days of the study period. The relationship between the rate of clutch consumption and foraging bout order was best supported with the diminishing returns model (Table 1., Fig. 3a) and was significantly different when compared to the null model ($F_{(32, 31)} = 15.028, p < 0.001$). As the season progressed, the time bears spent searching between nests increased. This relationship between proportion of time spent searching and foraging bout order was best supported with a linear model (Table 1., Fig. 3b) and was significantly different when compared to the null model ($F_{(32, 31)} = 4.4431, p < 0.05$).

Energy-use rates stayed relatively constant throughout the season and particularly within weight classes of bears that we considered (i.e., 255 kg and 579 kg). The relationships between energy-use rates and foraging bout order were best supported with

the diminishing returns model (Table 1., Fig. 3c) but were not significantly different when compared to the null model (255 and 579 kg: $F_{(32, 31)} = 2.92, p = 0.1$). However, despite this constant energy expenditure, net energy gain declined at an accelerating rate as the season progressed. The relationships between net energy gain rates and foraging bout order were best supported with the diminishing returns model (Table 1., Fig. 3d) and both were significantly different when compared to the null model (255 kg: $F_{(32, 31)} = 14.92, p < 0.001$; 579 kg: $F_{(32, 31)} = 14.72, p < 0.001$).

Discussion

Declines in the spatiotemporal extent of sea-ice have aligned the onshore arrival of polar bears onto Mitivik Island with the breeding schedule of eiders. Consequently, bears are foraging on eggs in this seaduck colony in lieu of missed seal-hunting opportunities (Iverson et al. 2014). We present evidence that foraging on eider eggs may have some energetic benefit to those polar bears arriving onto the island in early July while those polar bears arriving later experience diminishing returns due to resource depletion.

Our results indicate that clutch consumption rates declined (following a diminishing returns model) throughout the eleven-day study period as bears depleted eggs in this large seaduck colony. We suspect that the plateau pattern (early in the season) emerges as a result of bears being constrained by the amount of clutches they can physically ingest per unit time. Later in the season, clutch consumption rates decline nearly linearly as a result of decreasing encounter rates (Holling 1959). Because this colony is dense (Jean-Gagnon et al. 2018), we expect that the nests found at other sites would be depleted more quickly given that most eider ducks in polar environments typically nest in colonies of only 52.0 ± 141.9 nests per hectare (Chaulk et al. 2004), and

that lone bears have the capacity to consume hundreds of clutches in a short period of time (Gormezano et al. 2017). Therefore, while this terrestrial diet may benefit bears that arrive early to a colony, bears ultimately deplete the resource for themselves and for those individuals arriving later. Indeed, from July 10 to 16 (foraging bouts 1 through 20), bears consumed on average 17 clutches (48.5 eggs) per foraging bout (median = 14 clutches), while later in the season (July 17th to 20th; foraging bouts 21 through 33), bears consumed on average 9 clutches (25.5 eggs) per foraging bout (median = 5 clutches). In the last three days of filming (July 18 to 20; foraging bouts 27 through 33), all bears consumed fewer than 8 clutches and three of those individuals (foraging bouts 30 through 33) consumed 0 clutches.

For a resource to be energetically profitable, the energy gained must outweigh the pursuit cost (MacArthur and Pianka 1966). We found a positive linear relationship between the proportion of time bears spent searching for nests and the eider breeding season, suggesting that search time increases as a result of decreasing encounter rates. Despite this apparent increase in searching effort, the energetic cost of foraging on eggs remained relatively constant throughout the majority of the season within weight classes, since energy-use rates were balanced out by similarly negligible energetic costs associated with searching for and with eating eggs. That is, early in the season, bears are expending most energy through posturing, ingesting and digesting (relative to walking), while later in the season the source of energy expenditure was mainly through walking. Because polar bears possess efficient locomotion at routine walking speeds (i.e., preferred: $< 5.4 \text{ km h}^{-1}$; Pagano et al. 2018a), and egg foraging incurs very little energetic cost (even later in the season), on an individual level, eggs are probably one of the most

cost-effective resources for bears to pursue during the ice-free season (see Brook and Richardson 2002; Gormezano et al. 2016; but see Laidre et al. 2018). However, as we only quantified within-colony foraging behaviour, we caution that bears could incur additional energetic costs swimming between island bird colonies, thus necessitating studies at a larger geographic scale (Pagano et al. 2019). Moreover, because we stopped filming when the colony depleted, it is unknown whether more bears came onto the island (possibly driven by memory, curiosity, or residual scent of the colony) later in the season, a decision that would likely be costly.

During the summer months, hypophagic polar bears typically enter a slightly lower metabolic state as a means of conserving body condition (Robbins et al. 2012). However, because bears were actively foraging for eggs, we assumed a metabolic rate similar to bears foraging on the sea-ice. Therefore, polar bear field metabolic rates during the course of this study would have required them to consume on average approximately 52,000 kJ day⁻¹ (Pagano et al. 2018b). Given these energetic requirements, we can postulate that, on average, a polar bear would need to consume approximately 19 eider clutches (54 eggs) to satisfy its daily energetic demand. Our results show that, based on the average number of clutches consumed early in the season, bears can satisfy their daily energetic demand nearly twofold if they forage twice in one day, or for longer periods of time than we captured with the drones (e.g., during the night). Additionally, since we were unable to differentiate bears between days, it is plausible that some bears returned to forage over the course of several days, accruing even more calories than we were able to quantify. However, later arriving bears will experience diminishing energy returns associated with resource depletion. Moreover, the shape of the net energy gain model is

qualitatively similar to that of the clutches eaten model suggesting that the caloric value of eggs to polar bears is high relative to their acquisition cost. Nonetheless, the calories accrued via a seaduck-egg diet are minimal compared to what can be gained from an adult ringed seal (*Phoca hispida*, Stirling and McEwan 1975) and, in concordance with Dey et al. (2017), will most likely not be enough to maintain polar bear body condition during summer months in the face of increasing sea-ice loss, particularly when the eggs available to bears decline through depletion (as here) or following hatching.

As for any supplementary resource, to make a significant dietary contribution, the availability of eggs must be enough in terms of density, frequency, and accessibility to support polar bears at a population level (Rode 2015). To date, there has only been a handful of localized accounts of polar bears predating bird eggs (e.g., Stempniewicz 1993; Smith et al. 2010; Divoky 2011; Iles et al. 2013; Prop et al. 2015; specifically common eider: Noel et al. 2005; Iverson et al. 2014; Prop et al. 2015; Gormezano et al. 2017) suggesting that only a small number of bears are capitalizing on this resource. Indeed, although there are an estimated 305,400 breeding common eider females in northern Canada alone (Gilliland et al. 2009), eider population surveys conducted in the Hudson Strait (northern Hudson Bay) region showed that bear predation presence was only detected in 34% of surveyed islands, and was tightly linked to distance from the mainland (i.e., islands farther from the mainland experienced more polar bear predation, Iverson et al. 2014). Additionally, predictive modelling work by Dey et al. (2017) suggests that eiders may respond to increased predation pressure by dispersing closer to the mainland and nest in lower densities, making foraging on eider eggs less profitable for bears due to increased search costs (although this pattern has not yet been observed;

Dey et al. 2020). Despite there being an abundance of calories (theoretically) available to bears in the form of eider eggs, most colonies are not necessarily targeted (Iverson et al. 2014), and may become unavailable in the future should eiders shift their breeding locations (Dey et al. 2017). Therefore, only a small number of bears within a subpopulation would benefit energetically from egg foraging

Conclusion

Our results indicate that a small number of polar bears can potentially mitigate lost seal-hunting opportunities in July by foraging on eider eggs. Bears earlier to arrive on Mitivik Island had access to more nests and when combined with the low cost of foraging on eggs, translated to bears accruing net energetic gains. Within a relatively short time period, however (i.e., less than two weeks from filming), this foraging option was no longer profitable, suggesting a limited opportunity for a positive response to climate change. Our results provide the best available quantification of the energetic benefits and costs of egg foraging in polar bears (per unit time). Future work quantifying a bear's total behavioural budget while on Mitivik Island, and what effects, if any, air temperature has on polar bear hyperthermia (see Hurt et al. 1982) would contribute to further determining the benefits and costs of egg diets. In addition, examining the fine-scale decisions bears make when foraging in an eider colony would aid in determining if polar bears' decision-making heuristics remain optimal in this alternative environment. While our results show that some bears can profit energetically from foraging on eggs, the overall contribution eider eggs make to an entire population is probably small, reinforcing the importance of seal-hunting on ice to the overall persistence of polar bears.

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Tables

Table 1 Candidate models for variables a-d, degrees of freedom (df), log-likelihood (logLik), Akaike's information criterion corrected (AIC_c), delta AIC (ΔAIC_c), Akaike weights (w_i). Best candidate models in bold

Models	df	logLik	AIC_c	ΔAIC_c	w_i
A clutch eaten rate					
Intercept	2	3687.91	-7371.413	8.12	0.017
Linear	3	3687.54	-7368.252	11.28	0.003
Powerlaw	3	3687.30	-7367.764	11.77	0.003
Diminishing returns	3	3693.18	-7379.530	0.00	0.977
b searching proportion					
Intercept	2	3689.31	-7374.223	0.64	0.289
Linear	3	3690.85	-7374.864	0.00	0.398
Powerlaw	3	3689.30	-7371.773	3.09	0.085
Diminishing returns	3	3690.29	-7373.754	1.11	0.228
c energy-use rates (255 kg)					
Intercept	2	3566.13	-7127.857	0.94	0.328
Linear	3	3565.95	-7125.067	3.73	0.081
Powerlaw	3	3565.71	-7124.599	4.20	0.064
Diminishing returns	3	3567.81	-7128.802	0.00	0.526
c energy-use rates (579 kg)					
Intercept	2	3566.13	-7073.735	0.94	0.328
Linear	3	3565.95	-7070.945	3.73	0.081
Powerlaw	3	3565.71	-7070.476	4.20	0.064
Diminishing returns	3	3567.81	-7074.679	0.00	0.526
d net-energy gain rates (255 kg)					
Intercept	2	3425.79	-6847.183	8.04	0.018
Linear	3	3425.42	-6844.013	11.21	0.004
Powerlaw	3	3425.18	-6843.532	11.69	0.003
Diminishing returns	3	3431.02	-6855.219	0.00	0.976
d net-energy gain rates (579 kg)					
Intercept	2	3425.79	-6846.795	8.04	0.019
Linear	3	3425.42	-6843.615	11.21	0.004
Powerlaw	3	3425.18	-6843.145	11.69	0.003
Diminishing returns	3	3431.02	-6854.694	0.00	0.974

Figures



Figure 2. 1 a) Footage of drone approaching a foraging polar bear and encapsulating Mitivik Island's physical characteristics, **b)** drone footage from above filming a polar bear approaching a full nest (circled in red) and encapsulating the approximate average view of bears foraging in this study

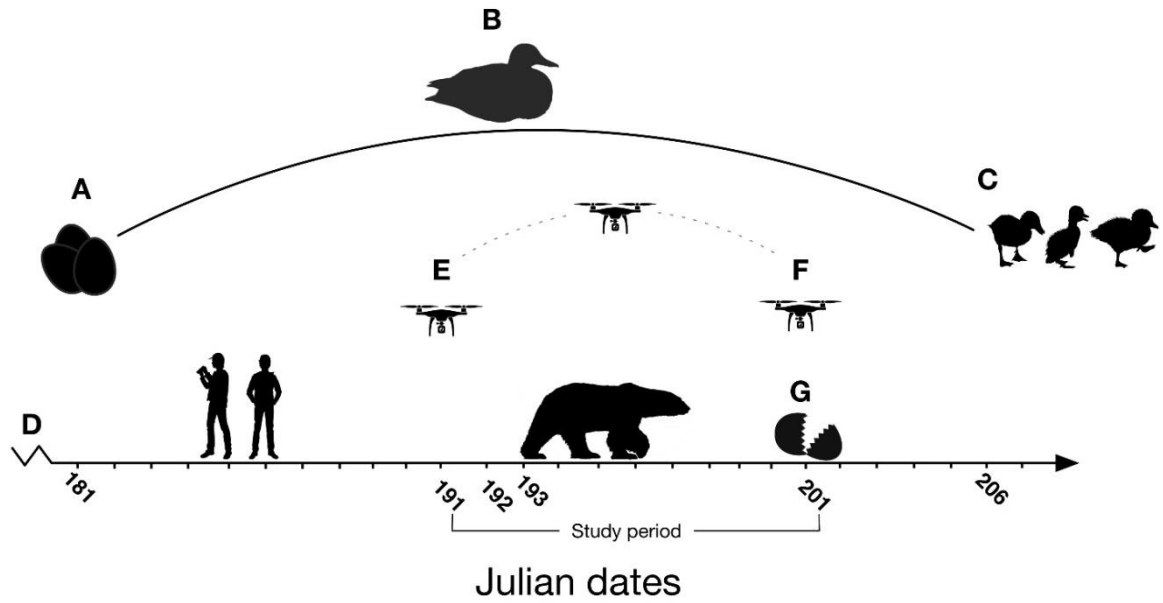


Figure 2. 2 Timeline schematic showing: a) eider mean laying date, b) mean mid-incubation date, c) mean hatch date, d) dates when eider researchers discouraged bears from coming onto the island (2017), e) to f) dates when bears were filmed (2017), g) date eider colony depleted (2017). Note: colony depletion occurred prior to mean hatch date. Data for a-c from Mitivik Island (2002-2008) (Love et al. 2010)

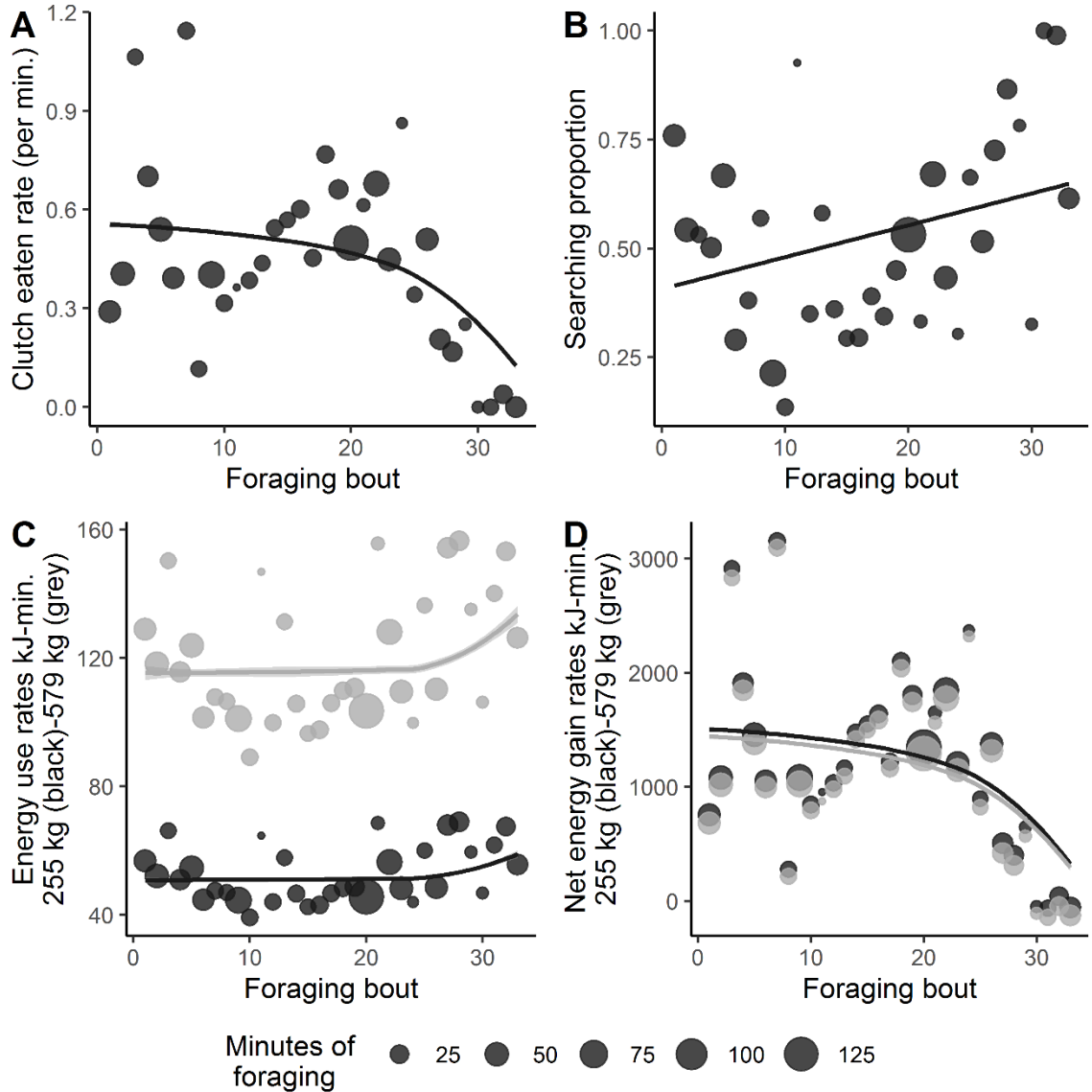


Figure 2. **a)** Clutch consumption rates (clutches per minute) during a foraging bout(s) decline following the diminishing returns model as the eider breeding season progresses. **b)** Proportion of time spent searching during a foraging bout(s) increases linearly as the eider breeding season progresses. **c)** Estimated rate of energy use (kJ per minute) increases following a diminishing returns model as the eider breeding season progresses for both polar bears estimated to weigh 255 kg and those estimated to weigh 579 kg. **d)** The rate of net energetic gain (kJ per minute) during a foraging bout(s) declined following a diminishing returns model as the eider breeding season progresses for both bears estimated to weigh 255 kg and 579 kg. Each data point represents a single foraging bout

CHAPTER THREE Examining polar bear (*Ursus maritimus*) decision-making as they forage in a large common eider (*Somateria mollissima*) seaduck colony

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Introduction

Understanding how animals make decisions is a fundamental goal in the field of ethology and behavioural ecology (Budaev et al. 2019; DeAngelis and Diaz 2019). An animal can be considered to have made a decision when it has gathered all possible information from the environment, evaluated its internal state, and weighed the trade-offs involved in pursuing the stimulus before choosing a behavioural outcome (Blumstein and Bouskila 1996; Mendelson et al. 2016). Foraging animals continually make decisions that affect their overall fitness (Dill 1987; Kohlmann and Risenhoover 1998; Stephens 2008), and it can be said they do so by following a set of rules to optimize their performance (Pyke et al. 1977; Stephens and Krebs 1986), enabling them to maximize their net-energetic return (MacArthur and Pianka 1966; Schoener 1971). Animals can at times deviate from expectations of optimality theory (i.e., perform sub-optimally), since ‘optimality’ can be constrained by various genetic, cognitive, physiological, and environmental mechanisms (DeWitt 1998; McNamara and Houston 2009; Giske et al. 2013; Fawcett et al. 2015; Marshall et al. 2015; Higginson et al. 2015; Vasconcelos et al. 2018). Nonetheless, natural selection has shaped these behaviours to overall be adaptive (i.e., no deleterious fitness consequence) within expected environmental contexts, with animals thus performing optimally on average (Houston 1987; Fawcett et al. 2013; 2014). However, under human-induced rapid environmental change (HIREC) (Sih 2013), animals such as predator generalists may need to increasingly incorporate non-preferred food items of low profitability into their diet when their main prey becomes unavailable. As a

consequence, this increasing reliance on the alternate diet may cause a mismatch in cue-response systems (i.e., previously adaptive behaviours may no longer be relevant in a functionally different environment), which can potentially cause animals to behave in a manner in which they are unable to maximize net benefits (Schlaepfer et al. 2002; Sih 2013; Sih et al. 2019). Whether these decisions pose any long-term negative consequences, or simply reflect a period of adjustment, first requires exploring whether foraging performance, and by extension, foraging decisions of animals follow predictions of optimal foraging theory.

When foraging within a patch, animals can limit energetic expenditure by tracking changes in resource abundance by using information gained from prey capture rates (Lima 1984; 1985; Shettleworth et al. 1988). This information allows individuals to determine an optimal time to abandon the patch (Charnov 1976; Green 1984) and move to another area, should profitable patches elsewhere exist within reachable distances. Animals can also modify their movement behaviours to match resource abundance by employing an extensive search mode, characterized by low sinuosity and fast locomotion when resources are in low abundance, and transition into an intensive search mode by slowing down movement and increasing sinuosity when a patch high in resources is encountered (i.e., area-restricted search (ARS), Curio 1976; Fryxell et al. 2008; Valeix et al. 2010). Animals are also capable of adjusting their selectivity (i.e., being ‘choosy’) against lower-quality items when resource abundance of their preferred diet item is greater (Emlen 1966; Gende et al. 2001), since the cost of consuming lower quality prey could be greater than ignoring the food item and searching for a higher quality one. Finally, animals that process (and use) environmental stimuli (hereafter ‘cues’) can

enhance their ability to locate diet items more quickly and efficiently than other foraging methods (i.e., random searching) (e.g., visual cues: Duncan and Jenkins 1998; Howery et al. 2000; Klinka et al. 2009).

Under anthropogenic rapid environmental change, however, these foraging decisions, intended to maximize efficiency, may no longer be optimal, or species may not be able to adjust their foraging behaviours accordingly. In the most extreme case, there may be no viable alternatives for animals, ultimately constraining them to their current situation (Sih 2013). Alternatively, behaviours may become optimal under HIREC when a new environment is sufficiently distinct to what the species is adapted to. For example, naïve individuals may spend time over-sampling their new environment to acquire valuable information aiding their ability to make more informed future decisions (Inglis et al. 2001; Greggor et al. 2019). More likely, foraging behaviours may be inefficient when foraging on less common diet items. For example, animals may continue to apply the same decision-making heuristics that were employed on their primary prey (shaped by past selection pressure), but prove costly in a new system (e.g., being selective, or ‘choosy’, in selecting habitats/resources when high quality ones no longer exist) (Crowley et al. 2019). Animals may also err by mis-assessing potentially valuable ‘unfamiliar-cues’, leading them to underutilize (or even ignore) the resource (Gilroy and Sutherland 2007). Because animals’ first response to HIREC is typically behavioural (Wong and Condolin 2015), the decisions they make (i.e., observable behavioural outcome) when foraging should play a key role when assessing their ability to cope with anthropogenic change (Sih et al. 2016; Buchholz et al. 2019). Given the premise that animals are expected to forage optimally (Pyke et al. 1977; Stephens and Krebs 1986),

examining the decision-making heuristics of animals increasingly relying on alternative resources will improve our understanding of the degree to which foraging performance in altered environments can be described by optimal foraging theory (Geary et al. 2020).

The circumpolar Arctic is an ecosystem undergoing rapid environmental change (Koenigk et al. 2013; Stern and Laidre 2016) that is causing a behavioural shift in the region's top predator, the polar bear (*Ursus maritimus*). Polar bears primarily feed off the sea-ice platform on seals and other marine mammals (Stirling and Archibald 1977; Galicia et al. 2015). However, changes in sea-ice phenology, as a result of climate change, are increasing the bears' reliance on alternative resources as they are prematurely migrating onto nearshore terrestrial environments and foraging on various land-based resources (e.g., Derocher 2012; Gormezano and Rockwell 2013ab; Gormezano et al. 2017) in lieu of missed ice-based hunting opportunities. The extent to which polar bears are now relying on terrestrial diet items necessitates examining the specific decision-making heuristics polar bears use, since terrestrial resources can potentially require different foraging tactics (e.g., climbing cliffs, Smith et al. 2010; chasing prey, Gormezano et al. 2016; and grazing, Stempniewicz 2017), and a different suite of cues (e.g., avian anti-predator responses, this study) than what bears use to catch seals on the sea-ice (Stirling 1974), potentially affecting their ability to maximize energetic returns. Indeed, reports of polar bears foraging on waterfowl eggs (*Anatidae spp.*) have increased in recent years (e.g., Rockwell and Gormezano 2009; Smith et al. 2010; Iles et al. 2013; Iverson et al. 2014; Prop et al. 2015) as changes in sea-ice phenology have aligned the bears' onshore arrival with the birds' breeding schedules. While polar bear foraging on seaduck eggs has been reported in the past (Loughrey 1956; Harrington 1965; Lønø

1970), these have mainly been incidental occurrences; therefore polar bears may not exhibit the same degree of foraging efficiency specific to terrestrial predation given they are considered seal-specialists (Stirling and Archibald 1977).

In this study we examine polar bears' fine-scale decision-making behaviours while foraging in a large common eider (*Somateria mollissima*) breeding colony on Mitivik Island in northern Hudson Bay, Nunavut. We use direct behavioural observations of polar bears foraging on a depleting resource of seaduck eggs. We apply a descriptive approach guided by classical optimality theory and previous empirical research on foraging behaviour to explore decision-making strategies of polar bears foraging on common eider eggs. In this study we examine whether foraging bears: (1) are able to track changes in resource availability using information gained from visiting already-empty nests; (2) adjust their movement behaviours (tortuous vs. straight-line) in accordance to resource density, (3) modify their 'selectivity' in ingesting clutches of eggs in accordance to resource availability, and (4) use visual cues (i.e., flushing eider hens) to increase egg consumption rates. Given this temporally restricted foraging opportunity, we hypothesize that bears would adjust their foraging decisions that would be expected to maximize their net energetic gains according to optimality theory. As the season progressed and resources diminished, we therefore predicted bears to: visit empty nests at a decelerating rate, decrease their movement sinuosity as a proxy for reduced time spent searching, and decrease selectivity and ingest more clutches upon encounter. We also expected that using visual cues would increase the number of clutches consumed.

Materials and methods

Study site

We conducted our research on Mitivik Island, a 24 hectare island characterized by low-lying (<8m) tundra interspersed with granite rocks and ponds and situated within Southampton Island's East Bay, in northern Hudson Bay, Nunavut (64° 01' 47.0" N, 81° 47' 16.7" W). This region of the Arctic is seasonally ice-free so much of the Foxe Basin subpopulation of polar bears use Southampton Island as a summering ground while they wait for the sea-ice to reform in the fall (Sahanatien et al. 2015; Stapleton et al. 2016). During the summer months (i.e., June to August), thousands (up to 8000 pairs between 2002 and 2013 Jean-Gagnon et al. 2018) of common eiders (*S. m. borealis spp.*) migrating from the coasts of Greenland and Atlantic Canada (Buttler et al. 2011) converge onto Mitivik Island and form a dense breeding colony on the island. Every spring and early summer, polar bears migrate northward through Mitivik Island to reach frozen ice in the Foxe Basin before the sea-ice completely disappears (H.G.G. pers. obs.), but their earlier arrival is now overlapping with incubating eider hens, and bears are foraging on eggs as a supplementary resource, presumably in an attempt to top-up their energetic reserves (Iverson et al. 2014; Chapter 2).

Polar bear observations

We recorded foraging bears with DJI Phantom 3 Pro and 4 Pro drones (<https://www.dji.com/company>) from July 10-20, 2017 between 0530 hrs and 2030 hrs. We initiated filming when conditions were suitable for flying and when bears were active. Bears were filmed as soon as researchers noticed them on the island and were recorded until they either left the island or were resting for extended periods. The drone pilot and observer were stationed on the roof of the research cabin and launched/landed

the drone within the electrified fence surrounding the research station. Drones were flown above the focal bear at altitudes that elicited minimal apparent behavioural responses (see Chapter 2), although we cannot say for absolute certainty that bears and eiders were not affected physiologically (Ditmer et al. 2015; Weimerskirch et al. 2018). Videos were recorded at 30 frames per second at a resolution of 2700 x 1520 pixels. In total, we recorded 1,028 minutes of polar bear foraging footage. Video data were binned into distinct ‘event orders’ (i.e., foraging bouts), which represented a near continuous observation of a bear foraging. Whenever there was a significant time gap (> 20 minutes) in filming a focal animal (as a result of switching out the drone’s battery), we considered it a new event. Our dataset consists of a maximum of 19 individual bears with 33 distinct foraging events that range from 5.7 to 134 minutes (mean = 34.5 minutes; median= 21.6).

Behavioural analyses

We used Solomon Coder version: beta 17.03.22 (<https://solomoncoder.com/>), a manual behavioural coding tool, to analyse polar bear foraging behaviour. We loaded drone video data into this program and categorized bear behaviour (during video playback) based on predefined behaviours of interest. In reviewing each event, we recorded: 1) “***Total number of nests visited***”: sum of clutches eaten, empty nest visits, and nests ignored (see below for descriptions of behaviours). 2) “***Empty nests visited***”: number of empty nests a bear was considered to have visited when it was clearly evident there were no eggs in the nest cup (see ‘clutches eaten’ description). 3) “***Sinuosity***”: number of turns a bear made when searching for nests. We only considered it a turn when it was clearly visible that a bear abruptly (i.e., in 1-5 bear strides) veered a minimum of 45 degrees from its heading during locomotion or changed directions (i.e., turned left, right, or 180 degrees) after briefly stopping. We did not consider it a turn when a bear gradually (i.e., in > 5 strides)

veered into another direction. 4) “*Nests ignored*”: number of nests a bear was considered to have ignored when it walked up to a full clutch and did not consume the eggs (see ‘clutches eaten’ description). Because it was clearly evident when a bear inspected a nest and ignored it, we hypothesised that this was due to a polar choosing not to consume eggs (possibly due to bird feces on the eggs as a result of the eiders’ defence mechanism when flushed from their nest; McDougall Milne 1978). For the purposes of this study, we assumed nests were ‘ignored’ due to a bear’s reduced preference for soiled eggs. 5) “*Visual cues ignored and used*”: number of visual cues a bear *ignored* (i.e., eider hen(s) flushing from nest) when it was clear that the focal bear had observed at least one duck flush (i.e., head was facing in the same direction as flushing hen(s)), and did not approach the newly abandoned clutch. Conversely, a bear was considered to have *used* a visual cue when it was clearly evident that it had observed (i.e., head was facing in the same direction as flushing hen(s)) at least one duck flush, switched its current heading, and approached the newly abandoned clutch. 6) “*Clutches eaten*”: number of clutches a bear was considered to have eaten when it was clearly observable that it was chewing, licking, and/or yolk was dripping when its face was in the nest. In addition, to further confirm an eating event, a full clutch had to be clearly visible upon approach, and/or a hen was seen flushing from the nest when the bear approached. Any approach to a nest not fulfilling the above criteria was considered an ‘empty nest visit’. In addition to these foraging behaviours, we also recorded the duration of time a bear spent walking and standing (i.e., searching), as well as the duration of time a bear spent foraging: searching, and sitting, laying down, and walking while ingesting an egg/s.

Statistical analyses

For our response variables we analyzed: a) the total number of nests visited, b) the number of empty-nest visits, c) sinuosity, d) the number of nests ignored, and e) number of clutches eaten. For variables a-d, we used event order as our continuous independent variable (i.e., first recorded event = 1, last recorded event = 33) which serves as a proxy for resource density (since bears are continually consuming nests). For variable e, we used proportion of cues used (i.e., cues used divided by the sum of cues used and cues ignored) as our predictor variable, which encompasses the entire suite of events when a cue(s) was present and available for a bear to use, to test whether using visual cues enhances bears' ability to locate more nests. See Table 1 for model overviews. For all our models, we added search time (i.e., time spent walking and standing for each bear's foraging event) as a fixed effect to account for differences in filmed-video lengths. We tested our data with generalized linear models GLMs (Bolker et al. 2009) and accounted for overdispersion found in the data by using negative binomial distribution models.

All statistical analyses were performed in R version 3.4.4 (R Core Team 2019) using the *tidyverse* (Wickham 2017) and *glmmTMB* (Magnusson et al. 2017) packages. Figures were created using the *ggplot2* (Wickham 2016), *ggeffect* (Lüdecke 2018), *cowplot* (Wilke 2016), and *gridExtra* (Auguie 2016) packages.

Results

As the eiders' breeding season progressed, bears significantly decreased their total number of nest visits (Fig 1a); however, bears marginally increased their visits to empty nests during the same period (Fig 1b). There was no significant change in sinuosity with an increase in event order (Fig 2a). Bears significantly ignored fewer nests as event order

increased (Fig 2b); and the number of clutches bears consumed increased significantly when a greater proportion of visual cues were used (Fig 3; Table 2).

Discussion

Changing sea-ice conditions have created a phenological overlap between polar bears' onshore migration onto Mitivik Island and the common eiders' breeding schedule.

Consequently, bears are foraging on eggs in this large seaduck colony, presumably in an attempt to make up for lost on-ice seal-hunting opportunities (Iverson et al. 2014; Chapter 2). Our study is the first to use direct observations to examine polar bear decision-making heuristics when foraging on seaduck eggs. Based on these direct behavioural observations, our results indicate bears are not yet foraging in a manner consistent with optimal foraging theory, in that they do not appear to adjust all their behaviours in the context of a depleting resource. We discuss each foraging decision in terms of the contexts under which these behaviours could be considered suboptimal, costly, or pose no negligible costs.

As the eiders' breeding season advanced, polar bears' total visits to nests (i.e., clutches eaten, empty nests, and nests ignored) declined; however, simultaneously, bears increased their empty nest visits. This pattern reveals that the proportion of nests bears encounter at the end of the season are increasingly 'empty', and suggests bears were potentially unable to track the depleting colony efficiently (Lima 1984; 1985; Shettleworth et al. 1988). However, this behaviour may not be suboptimal (or without obvious fitness costs) in this particular system, at least until the colony is completely depleted. That is, given that Mitivik Island is small, the energetic cost of locomotion in this system is negligible (Chapter 2), and so inefficient tracking of resources may not be

particularly detrimental to bears here. In addition, because terrestrial foraging has only recently become an increasing occurrence for polar bears, naïve individuals may not have previous experience foraging in an avian colony, so they may be gathering information through sampling to help aid future foraging events in avian systems (Inglis et al. 2001; Greggor et al. 2019). However, we suspect that tracking efficiency may become an important consideration at a landscape scale in larger colonial-nesting avian systems where bears travel across many islands (e.g., Hudson Strait region, Iverson et al. 2014). Furthermore, this behaviour would become truly sub-optimal should bears remain on the island and continue their search long after colony depletion.

Polar bears did not adjust their movement to resource abundance as there was no significant relationship between sinuosity and event order. While it was not possible to accurately assess bear locomotion speed, our results are nonetheless inconsistent with what would be expected from foraging theory (i.e., area-restricted searching, Curio 1976), in which animals should adjust time spent searching based on resource quality and abundance. For example, elk (*Cervus elaphus*) displayed higher sinuosity when foraging in high-quality vegetation patches, and transitioned to more straight-line movements when foraging in lower-quality ones (Fryxell et al. 2008). Similarly, African lions (*Panthera leo*) employed an area-restricted search when hunting near watering holes (i.e., where prey congregate) and discontinued this behaviour when >2km away from prime hunting territory (Valeix et al. 2010). As polar bears forage in avian colonies, they appear to forego consuming many nests in their direct foraging path (Rockwell and Gormezano 2009; P.M.J, pers. obs.). Given that polar bears have a highly developed sense of smell capable of locating seals hiding in their subnivean lairs (Smith 1980) and eider hens are

flushing as bears walk through the colony (P.M.J pers. obs.), it appears inefficient for polar bears to not adjust their searching movement to nest density. Indeed, the underlying premise of optimal foraging theory is minimizing time and energy when acquiring resources, which is particularly relevant for eggs as higher quality diet items are unavailable on Mitivik Island (no filmed bears chased or predated upon adult eiders or other animals) (Pyke et al. 1977; Stephens and Krebs 1986). Therefore, because common eiders nest in a clumped distribution (Chaulk et al. 2004), early in the season when nests were in high abundance, bears should have concentrated their time in a restricted area after locating a nest to increase their search efficiency, and then transition to opportunistic feeding as nests depleted to optimize their time and energy cost (Curio 1976). We suspect that the bears' inability to adjust their movements to resource abundance may result from i) satiation (and therefore no need to employ a search mode) or ii) inexperience foraging in an avian colony. We posit, however, that polar bears can potentially learn to specialize on egg foraging (Araújo et al. 2011). For example, Gormezano et al. (2017) reported seeing a bear methodically going from nest to nest and then island to island, consuming 206 common eider nests in a 96-hour period at the La Pérouse Bay Research Station, near Churchill Manitoba, Canada. They also speculate that a female and her cub have foraged in that same colony for two consecutive years. Should bears continually be driven onto nearshore terrestrial environments and overlap with eider incubation they may become more specialized and therefore optimize their search efficiency as bears are capable of learning to use resources if they have proven to be profitable in the past (Lunn and Stirling 1985).

Early in the season, polar bears displayed a higher degree of selectivity in the eggs they consumed and then relaxed their selectivity as the colony depleted, as evidenced by the declining trend in the number of nests ignored. Such selective foraging seems common amongst Ursids as it has also been documented in both grizzly (*U. arctos*) and black (*U. americanus*) bears during the salmon (*Oncorhynchus spp.*) run. When salmon were in high abundance, both species displayed selectivity towards higher quality fish (i.e., those that had not yet spawned), but became less selective and transitioned to spawned fish as the availability of salmon declined (Gende et al. 2001). The observation that polar bears can be ‘choosy’ when the colony was full may suggest bears were not in any energetic deficits, perhaps as a result of satiation from foraging in the colony, or potentially from having recently come off the sea-ice after consuming a seal. While selectivity in prey quality is optimal under natural conditions (Emlen 1966), under HIREC, such selectivity may prove costly as preferred prey availability and profitability become uncertain and unpredictable (Crowley et al. 2019). The long-term consequence of polar bear selectivity requires further study and is outside the scope of this present one.

The use of visual cues of flushing hens significantly influenced the number of clutches bears located and consumed, suggesting there is a benefit to learning this strategy. Indeed, under experimental settings, both ground squirrels (*Spermophilus beldingi*) and domestic cattle (*Bovidae spp.*) significantly increased their probability of locating a food item when aided with ‘novel’ visual cues (i.e., ‘new plant’ and ‘traffic barricades and cones’, respectively) (Duncan and Jenkins 1998; Howery et al. 2000). Similarly, black bears foraging on salmon significantly increased their probability of

locating fish when they used visual cues (i.e., salmon carcass) during the daytime (Klinka et al. 2009). Thus, capitalizing on the use of flushing eider hens as cues should be a strategy adopted continually once learned. Further, given that we did not incorporate the number of nests ‘visited-but then-ignored’ after utilizing a cue in our model, as ignoring a nest would entail an additional choice between ‘consume’ or ‘ignore’ and our objective was to demonstrate the utility of cues for clutch consumption, we suspect that our analysis underrepresents the total number of nests ‘located’ when utilizing a cue.

Interestingly though, bears do not universally nor consistently use this strategy, and this underutilization is particularly inefficient when the colony is full, as bears would have been able to more easily locate nests. We postulate that such underutilization may emerge because: i) bears may not have had enough opportunities foraging in an avian colony to learn this strategy, ii) flushing eider hens do not resemble cues bears typically experience so they are not perceived as valuable (i.e., ‘undervalued resource’, Gilroy and Sutherland 2007), or iii) bears were satiated (or near satiated) with no need to actively seek out cued-nests.

Polar bears are specialized marine mammal predators (Stirling and Archibald 1977; Galicia et al. 2015) that are adapted to hunting efficiently from a sea-ice platform (Stirling 1974). However, their ability to incorporate terrestrial diet items suggests they are able to generalize their diet when resources are limited (e.g., Gormezano and Rockwell 2013ab) as would be expected from optimal foraging theory (Pyke et al. 1977; Stephens and Krebs 1986), and likely reflects phenotypic plasticity as a result of polar bears’ shared ancestry with the omnivorous grizzly bear (Gormezano et al. 2017). It has been suggested that polar bears foraging on land use similar strategies to on-ice foraging,

including when ‘scavenging’ for eggs, and bears may therefore be able to adapt to a lengthier terrestrial residency (Gormezano et al. 2017). Our findings here suggest that polar bears’ foraging performance in the context of adjusting behaviours to match resource availability of alternative prey may not be fully maximized in an avian colony. However, these observations may be the result of various non-mutually exclusive reasons that do not carry an instantaneous fitness cost to polar bears. Not all bears are expected to be experienced egg foragers, and have yet to learn how to specialize on this diet item, ultimately constraining their ability to make optimal foraging decisions. Further, some individuals visiting Mitivik Island may simply be satiated, and any seemingly ‘suboptimal’ behaviours will carry negligible costs. Should bears continue to expend energy searching for nests post colony depletion or in other systems (e.g., larger but less nest-density islands), coupled with projected continued climate change impacts, these behaviours may begin to become costly, and potentially affect polar bear body condition. Indeed, a modelling study by Dey and colleagues (2017) predicts eider duck eggs in Hudson Strait will be insufficient long-term to offset a predicted decline in polar bear body condition. Our results suggest if polar bears continue their inability to adjust their behaviours, body condition may decline at an even greater rate than previously predicted. We suggest a long-term spatial and temporal study to better understand not only the long-term fitness consequences of polar bear foraging performance, but given conditions of traditional prey availability will continue to decline, the ecological implications of this predator-prey interaction as well.

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Tables

Table 2. 1 Models a-e

Models	Model variables
a	Total nest visits ~ event order + search time
b	Empty nest visits ~ event order + search time
c	Sinuosity ~ event order + search time
d	Nests ignored ~ event order + search time
e	Clutches eaten ~ event order + search time + proportion of cues used

Note: Overdispersion parameters θ for models prior to negative binomial modelling were: **a**=3.8, **b** =2.31, **c** = 4.52, **d** = 1.65, **e** = 4.12

Table 2. 2 variables, parameter estimates, standard errors (SE), Z scores, and P values for model a-e

Models	Variables	Estimates	SE	Z	P
a (total nests visited)	Intercept	2.608	2.259	11.544	<0.001
	Event order	-2.409	1.069	-2.253	0.024
	Search time	7.012	9.936	7.057	<0.001
b (empty nests visited)	Intercept	0.356	0.323	1.102	0.27
	Event order	0.024	0.013	1.841	*0.06
	Search time	0.000	0.000	4.966	<0.001
c (sinuosity)	Intercept	2.458	2.051	11.985	< 0.001
	Event order	3.452	9.170	0.376	0.71
	Search time	8.098	9.905	8.176	<0.001
d (nests ignored)	Intercept	0.821	0.485	1.691	0.091
	Event order	-0.089	0.022	-4.004	<0.001
	Search time	0.000	0.000	2.885	<0.01
e (clutches eaten)	Intercept	1.917	0.330	5.803	<0.001
	Event order	-0.049	0.018	-2.739	0.006
	Search time	0.000	0.000	5.551	<0.001
	Proportion of cues used	1.194	0.586	2.035	0.041

Significant P values shown in bold, *significant at the 10% level

Figures

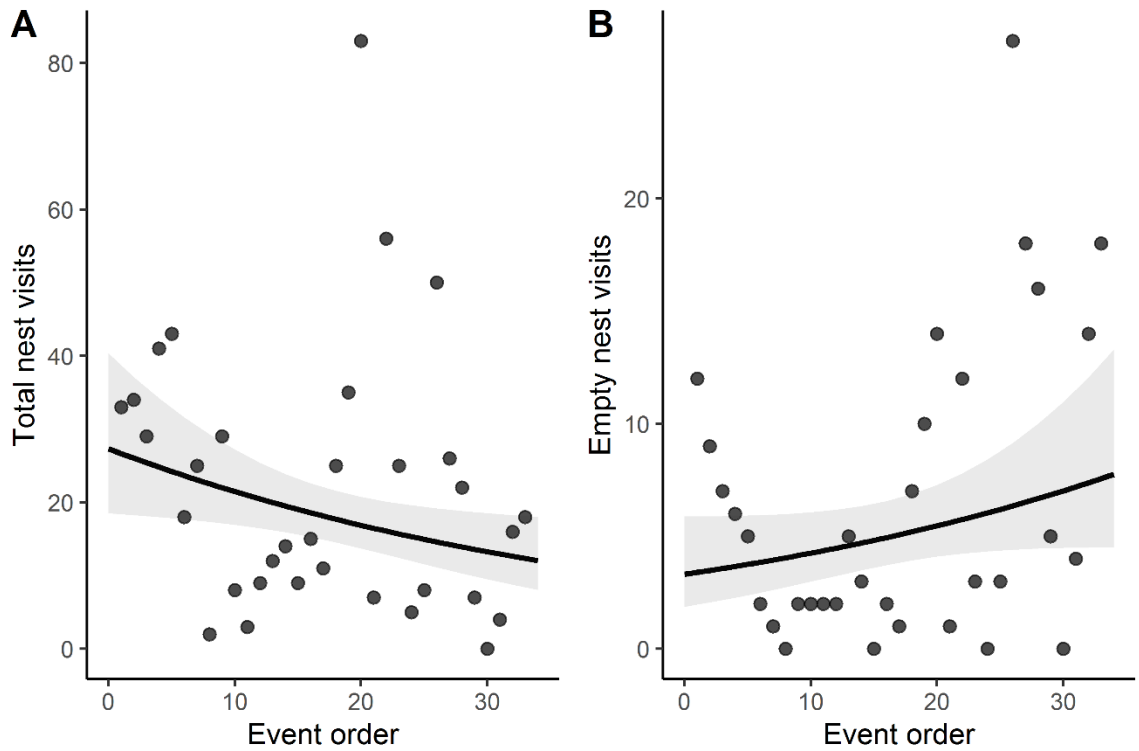


Figure 3.1 a) Total number of nests visited declined as the eider breeding season progressed. **b)** Empty nest visits increased as the eider breeding season progressed. Each data point represents a single event. Grey shading represents the confidence intervals around the predicted means

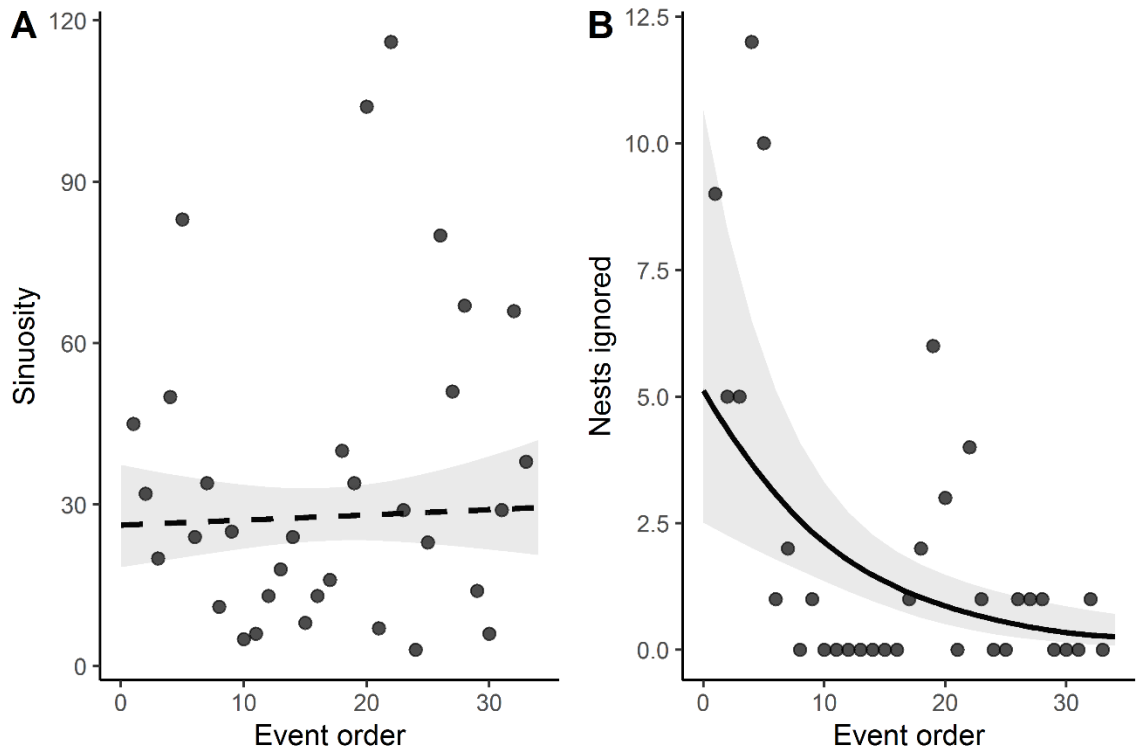


Figure 3. 2 a) Sinuosity stayed constant as the eider breeding season progressed. **b)** Nests ignored declined as the eider breeding season progressed. Each data point represents a single event. Grey shading represents the confidence intervals around the predicted means

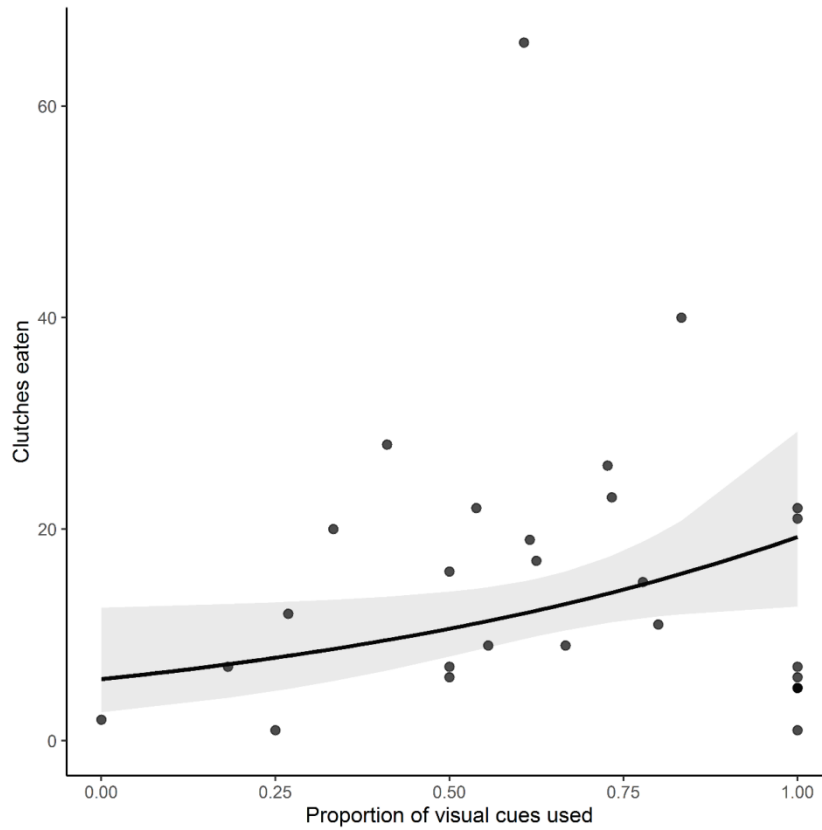


Figure 3. 3 Clutches eaten increased with an increase in the proportion of visual cues used (i.e., total cues detected and used to locate nests). Each data point represents a single event. Grey shading represents the confidence intervals around the predicted means

CHAPTER FOUR General Discussion

The spatiotemporal extent of sea-ice is rapidly declining in the circumpolar Arctic, resulting in reduced on-ice hunting opportunities for polar bears (Stern and Laidre 2016). Previous work suggests that polar bears are able to utilize terrestrial diet items to offset lost on-ice hunting opportunities (Gormezano and Rockwell 2015). However, because polar bears require a high-calorie diet (composed mainly of fatty-rich marine mammals) (Galicia 2015; Pagano et al. 2018), and terrestrial resources tend to be energetically inferior to marine prey, as well as spatially and temporally unreliable, some scientists believe that supplementary use of terrestrial diet items will be insufficient to support polar bears as they adjust to a rapidly transitioning Arctic ecosystem (Stirling and Derocher 2012; Rode et al. 2015). In this thesis I examined the energetic benefits and costs, as well as decision-making heuristics, of polar bear foraging on common eider eggs (on Mitivik Island, Nunavut), an increasingly relied-upon resource (Iverson et al. 2014). The objectives were to determine: (1) if bears gain an energetic surplus from foraging on eggs, and (2) if their foraging decisions were consistent with optimal foraging theory. To my knowledge, this study is the first to quantify the energetic benefits and costs and to examine the decision-making heuristics of polar bears feeding on eggs using direct behavioural observations from an unobstructed aerial vantage point (i.e., filmed with drones), which allows for practically non-invasive observations of animal behaviours that have likely never been witnessed before (Nieukirk et al. 2018).

The results of my work indicate a subset of polar bears that feed on common eider eggs, particularly those individuals who arrive early to the colony during the eider breeding season, can gain an energetic surplus from egg foraging as bears only need to

consume 19 clutches to achieve their daily energetic demand (Chapter 2). Therefore, since bears are capable of consuming hundreds of clutches in a short period of time (Gormezano et al. 2017), some individuals can offset several days of lost on-ice hunting opportunities. Indeed, while polar bears have access to a myriad of resources during the summer months (e.g., grasses, Stempniewicz 2017; caribou (*Rangifer tarandus*), Brook and Richardson 2002; fishes, Dyck and Romberg 2007; whale carcasses, Laidre et al. 2018; cliff-nesting birds, Smith et al. 2010; and running/flying waterfowl, Rockwell and Gormezano 2009), in terms of overall availability and relative ease of foraging per unit time given their nesting strategy, eider eggs may be the most profitable supplementary resource for polar bears since breeding common eider hens in the Canadian Arctic number at approximately 300,000 (Gilliland et al. 2009), and nest on low-lying islands with up to 1000 nests per hectare (Schmutz et al. 1983; Chaulk et al. 2004). Interestingly, though, scat analysis shows that avian eggs (including common eider) do not make up a substantial proportion of polar bears' overall summer diet (Gormezano and Rockwell 2013ab). Similarly, landscape surveys show that polar bears are only foraging in a small proportion (i.e., 34%) of available colonies (Iverson et al. 2014). Collectively, these observations, along with my results, suggest that in the short-term, eggs are a valuable, but underutilized resource. This observed underutilization may result from bears' natural tendency to follow remaining sea-ice rather than travel towards nearshore terrestrial environments to search for resources, a strategy which now has been suggested could be an ecological trap (Pagano et al. 2019).

Despite the contribution value of seaduck eggs, predictive modelling work suggests that a supplemental eider egg diet will not be enough to mitigate declining polar

bear body conditions as sea-ice extent continues to decline in the Eastern Canadian Arctic (Dey et al. 2017), despite eider populations remaining stable in the face of polar bear predation pressure (Dey et al. 2018). This contradictory pattern likely stems from the fact that sea-ice melt is predicted to advance earlier in the spring (Thackeray and Hall 2019), so polar bears will increasingly arrive onshore with larger energetic deficits that cannot be mitigated with eggs alone. Given the suspected importance of eider eggs to the contribution of polar bears' daily energetic requirements (based on my results), bears that forage in such a way that maximizes their energetic return should perform best under climate change. My results from Chapter 3 indicate, however, that polar bears do not adjust their behaviours to match resource availability according to the predictions of optimal foraging theory, which can potentially influence (i.e., increase) the rate at which polar bear body conditions are expected to decline (Dey et al. 2017). However, whether these behaviours carry a fitness cost is unknown without future field and modelling studies. Indeed, other factors not quantified in my thesis can influence the contribution and payoff of eggs to the polar bears' overall terrestrial diet (e.g., bear demography, availability of alternative food resources, and landscape-level distribution of resources). This study was limited both by a one-year sample size and our ability to track individual polar bears throughout and across days. Future studies that track polar bear behaviour on a 24-hour time scale (e.g., camera collars, Bowersock et al. 2015), including after they abandon the colony, would greatly improve our knowledge of how many clutches bears consume and how much net energy they gain throughout an entire 24-hour period. Following bears for extended periods will reveal if they are diet mixing or exclusively seeking out avian colonies, and would allow for a more realistic bioenergetic assessment

of the total contribution eggs make to bears' diet over the summer months. In addition, future studies should also examine individual bears' foraging behaviours between sexes and age classes (naïve sub-adults versus seasoned adults) as those variables will likely influence foraging efficiency (Sih et al. 2019).

In addition to field studies, the findings of my thesis can also be used to parameterize predictive 'agent-based' simulation models (Wilensky and Rand 2015) to improve existing estimates of polar bear egg foraging energetics (i.e., Dey et al. 2017). Agent-based models are a computer-simulation tool that uses real-world data to parametrize both a digital 'environment' and discrete digital 'agents' who inhabit this environment and make decisions based on programmed rules (Wilensky and Rand 2015). Agents can forage, grow, interact, reproduce, adapt and die (Railsback and Grimm 2011). In essence, agent-based models allow the operator to program complicated foraging decision-rules specific to individuals within a population, where population-level patterns then emerge from individual variation (DeAngelis and Diaz 2019), providing a more realistic, and therefore reliable, insight about the phenomenon being studied (i.e., compared to deterministic modelling) (McLane et al. 2011). This type of modelling approach can be especially relevant in systems where animal tracking is logistically challenging. Indeed, polar bear agents can be programmed, using evolutionary and ecological rules, to walk across a simulated landscape composed of multiple islands with nesting eider agents of varying densities, and make foraging decisions based on my findings; for example, not adjusting movement patterns in relation to resource abundance, or continue to search for nests long after the eider breeding season. Moreover, individual agents within a population can have differing past experiences and current states which

ultimately affect their decision-making and performance on a given task (Sih et al. 2019). Anecdotal evidence (this thesis) suggests that some individuals are able to forage more efficiently than others (e.g., consume large amounts of eggs, Chapter 2; and learn to capitalize on visual cues, Chapter 3) which would no doubt influence net energetic return. Incorporating such individual-level variation into simulation modelling to test whether those individuals who learn to optimize their foraging efficiency (e.g., agents who capitalize on all visual cues to locate nests) gain substantially more calories than my results were able to show, and how intraspecific conflicts affect foraging efficiency (e.g., vigilance, Brown 1999) would be of great importance to strengthen future modelling efforts. Ultimately, agent-based simulation approaches can estimate whether polar bear decision-making heuristics carry any long-term bioenergetic fitness costs impacting body condition, reproduction, and survival, which would more accurately predict the population-level consequences of foraging on eider eggs.

The Canadian Arctic is home to approximately two-thirds of the world's 20,000 to 25,000 polar bears (Vongraven and Peacock 2011), with 2,585 of those bears residing in the Foxe Basin (i.e., my study's subpopulation) (Stapleton et al. 2016). Polar bears are currently listed as species of 'special concern' based on the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2008), and, based on the best available evidence, their persistence into the near future is projected to remain under threat (Stirling and Derocher 2012; Laidre et al. 2020). With the circumpolar Arctic projected to keep warming into the foreseeable future (Thackeray and Hall 2019), polar bears inhabiting seasonal-ice regions will likely become increasingly more reliant on terrestrial food resources. For bears to be able to successfully transition onto land for lengthier

periods of time, the available resources must be able to mitigate any lost on-ice hunting opportunities (Rode et al. 2015). Finally, future research should monitor eider populations to determine if they will disperse and relocate to other breeding colonies (see Dey et al. 2017 and 2020), and therefore become less available (Dey et al. 2017), as it would have a further impact on the bears' overall energetic profitability. While eiders are projected to balance out this increased perturbation pressure by increasing their recruitment and clutch size (Dey et al. 2018), it should be of interest to conservation biologists to monitor eider populations if this perturbation continues. Further, given the potential for eider eggs to mitigate some lost hunting opportunities, the sustainability (and viability) of this predator-prey relationship should be continually monitored, as well. Nonetheless, my study provides the best available estimate of the energetic consequences of egg foraging within a single patch (i.e., Mitivik Island); and the egg-related decision-making heuristics explored here suggest bears can improve their foraging performance.

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