



Polar bear foraging on common eider eggs: estimating the energetic consequences of a climate-mediated behavioural shift

Patrick M. Jagielski^{a,*}, Cody J. Dey^a, H. Grant Gilchrist^b, Evan S. Richardson^c, Christina A. D. Semeniuk^a

^a Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada

^b Science and Technology Branch, Environment and Climate Change Canada, Ottawa, ON, Canada

^c Science and Technology Branch, Environment and Climate Change Canada, Winnipeg, MB, Canada

ARTICLE INFO

Article history:

Received 14 April 2020

Initial acceptance 8 June 2020

Final acceptance 28 September 2020

MS. number: A20-00257R

Keywords:

common eider

East Bay Migratory Bird Sanctuary

eggs

energetic benefit–cost

foraging

Mitivik Island

polar bear

Somateria mollissima

terrestrial resource

Ursus maritimus

Climate-mediated phenological shifts can cause species to lose access to their primary prey while increasing opportunities for alternative-prey encounters. Species that are able to capitalize on alternative resources could potentially profit from prey-switching should the benefits of procuring these alternative resources outweigh their acquisition costs. Polar bears, *Ursus maritimus*, use sea ice as a platform to hunt seals, and individuals inhabiting the southern-most extent of their range rely on accumulated fat reserves to sustain themselves during the increasingly lengthy ice-free season. In response to declining access to their primary prey through documented sea ice loss, some polar bears are foraging on the eggs of birds in lieu of hunting opportunities on ice, as their onshore arrival is increasingly overlapping with birds' breeding schedules. To gain a better understanding of the energetic consequences of this behaviour, we used aerial drones to record polar bears foraging on sea duck eggs (common eider, *Somateria mollissima*) on Mitivik Island, Nunavut, Canada. Using these data, we examined variation in individual polar bear foraging behaviours and estimated the energetic benefits and costs associated with foraging on common eider eggs. Because of low costs associated with nest searching and consumption, the energetic cost of foraging remained relatively constant throughout the 2-week observation period. However, we found that as the common eider breeding season progressed, polar bears consumed eggs at a lower rate as they depleted the nesting colony and spent proportionally more time searching for nests. Collectively, this foraging pattern led to an overall declining trend in the net energy gained from egg consumption. Foraging on common eider eggs during increasingly lengthy ice-free seasons is apparently beneficial for polar bears, but only during a limited window of opportunity. By coupling energetic estimates with detailed behavioural data collected through aerial videography, this study provides a quantification of both the benefits and costs of egg consumption for polar bears.

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Foraging decisions are often driven by an animal's physiological state and the environment in which it lives (Day, Kyriazakis, & Rogers, 1998). Optimal foraging theory (OFT) 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). Animals foraging on nonrenewable resources will deplete prey over time and should therefore adjust their searching behaviours in accordance to changes in resource density (Curio, 2012), by either abandoning the patch at some optimal threshold (Charnov, 1976), or switching to

alternative prey, else risk incurring a missed opportunity cost, expending unnecessary energy and potentially going into an energetic deficit. Climate change is expected to decouple traditional predator–prey relationships, while simultaneously introducing novel interspecific interactions (Bastille-Rousseau et al., 2018). 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 & Pianka, 1966). Variation in behavioural tactics may occur in response to sudden shifts in the timing and abundance, and therefore accessibility of food resources

* Correspondence: P. M. Jagielski, Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave, Windsor, ON, N9B 3P4, Canada.
E-mail address: PatrickMJagielski@gmail.com (P. M. Jagielski).

resulting from climatic changes (Wong & Candolin, 2015). Prey switching is often observed among generalists shifting their foraging from low to high resource availability (e.g. red foxes, *Vulpes vulpes*; Kjellander & Nordström, 2003), but is also exhibited by food 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, *Rangifer tarandus*, calves 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, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012).

The effects of climate change on ecological systems are projected to be most pronounced in the Arctic (Descamps et al., 2017; Post et al., 2013; Wassmann, Duarte, Agusti, & Sejr, 2011). 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 that is a key habitat for many species (Stern & 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, Derocher, & Stirling, 2008), which makes them particularly vulnerable to climate change. Polar bears are specialized predators that use the sea ice as a platform to hunt (almost exclusively) seals (Derocher, Lunn, & Stirling, 2004; Stirling & Archibald, 1977; Stirling & McEwan, 1975), and they rely on accumulating enough fat reserves prior to sea ice breakup to sustain themselves on land during the ice-free season (Stirling & Derocher, 1993, 2012; Stirling & Øritsland, 1995) when foraging opportunities are limited (Rode, Robbins, Nelson, & Amstrup, 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 & Gormezano, 2009; Sahanatien & Derocher, 2012; Smith, Elliott, Gaston, & Gilchrist, 2010). Consequently, displaced bears are coming ashore with reduced fat reserves (Obbard et al., 2016; Stirling, Lunn, & Iacozza, 1999) that have been linked to declines in reproductive output and population size (Atkinson & Ramsay, 1995; Stirling & Derocher, 2012).

Given the decline in seal-hunting opportunities, land-based food items will become more critical to polar bears as they begin occupying terrestrial environments for longer periods. While polar bears are known to opportunistically consume a wide variety of resources on land (Derocher, 2012; Derocher, Andriashek, & Stirling, 1993; Gormezano, Ellis-Felege, Iles, Barnas, & Rockwell, 2017; Gormezano & Rockwell, 2013b; Russell, 1975), 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 & Kebreab, 2009; Gormezano & Rockwell, 2015). This assertion warrants further research (Rode et al., 2010, 2015) given that the energetic costs of foraging were not considered in these studies (although see Gormezano, McWilliams, Iles, & Rockwell, 2016). While it is plausible that opportunistic foraging on the locally available resources can contribute to energetic gains for polar bears during the summer months (i.e. diet mixing, Gormezano & Rockwell, 2013a), it is important to determine whether the caloric benefits of these resources outweigh the energetic costs of attaining them. This trade-off consideration is

especially true for low-calorie items such as vegetation, berries and bird eggs, which potentially serve as a source for macronutrient intake (Gormezano & Rockwell, 2013a) but need to be consumed in high quantities to meet the high daily energetic requirements of polar bears (see Pagano, Durner, et al., 2018).

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, *Cephus grylle*: Divoky, 2011; lesser snow geese, *Anser caerulescens caerulescens*: Rockwell & Gormezano, 2009; Iles, Peterson, Gormezano, Koons, & Rockwell, 2013; barnacle geese, *Branta leucopsis*, glaucous gulls, *Larus hyperboreus*: Prop et al., 2015; and common eiders, *Somateria mollissima*: Dey et al., 2017; Iverson, Gilchrist, Smith, Gaston, & Forbes, 2014; Prop et al., 2015). One species that may be particularly vulnerable to nest predation by polar bears is the common eider duck (hereafter, 'eider'), a large sea duck that typically breeds on low-lying islands in colonies with densities reaching up to 1000 nests per hectare (Chaulk, Robertson, & Montevecchi, 2004; Schmutz, Robertson, & Cooke, 1983). As a result, eider eggs found in ground nests are easily accessed and could provide a potentially profitable target for foraging bears. For example, during a 96 h 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 & Gormezano, 2009). Indeed, such additional energetic gains may prove beneficial in prolonging polar bears' capacity to survive on land during the summer months when few resources are available (Pilfold et al., 2016).

To understand whether foraging on eider eggs generates a net energetic gain for polar bears, we investigated under an OFT framework 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 using aerial drones, and we 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.

METHODS

Study Site

This study took place in the East Bay Migratory Bird Sanctuary on Mitivik Island. This is a small (24 ha) island located near Southampton Island, Nunavut, in northern Hudson Bay (64°1'47.0"N, 81°47'16.7"W; Fig. 1). Mitivik Island is situated in Southampton Island's East Bay, a seasonally ice-free region that serves as an important summering ground for polar bears of the 'Foxe Basin subpopulation' (Sahanatien, Peacock, & Derocher, 2015; Stapleton, Peacock, & Garshelis, 2016). Mitivik Island is flat and characterized by low-lying (<8 m in elevation) tundra and granite



Figure 1. Map of study area: (a) general location (northern Hudson Bay); (b) regional location (Southampton Island); (c) study site (Mitivik Island). Our study site is home to a long-term (~1996) research programme where common eider population monitoring is carried out annually (Buttler, Gilchrist, Descamps, Forbes, & Soos, 2011; Henri, Jean-Gagnon, & Gilchrist, 2018).

rocks, interspersed with small ponds (Fig. 2a). It supports the largest known nesting colony of common eiders (*S. m. borealis*) in the Canadian Arctic (8000 pairs between 2002 and 2013: Jean-Gagnon et al., 2018; with more recent estimates of 1500–1700 breeding pairs in 2017). In recent years, earlier sea ice break ups in June have noticeably resulted in bears coming onshore during eider duck egg-laying and incubation periods (i.e. late June to early July; 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 10–20 July 2017, which is approximately midway through the eiders' incubation period (2017 mean arrival (Julian) date: 172.12 ± 0.22 days (21 June); median arrival date: 172.25 ± 0.31 days (21 June); mean lay date: 175.65 ± 0.60 days (25 June) median lay date: 175.71 ± 0.83 days (25 June); Love, Gilchrist, Descamps, Semeniuk, & Bêty, 2010). 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 m above the focal bear and videos were recorded at a resolution of 2700×1520 pixels, at 30 frames/s (Fig. 2b). Although bears were observed migrating towards Mitivik Island in late May (P. M. Jagielski, personal observation), their presence was discouraged by the eider research team (i.e. late-May to 10 July) for safety purposes during the daytime, although some egg predation likely occurred at night (a duration of 4–7 h). During this study's period (10–20 July), bears were allowed to forage freely (i.e. were not chased off the island). Bears were recorded between 0530 and 2030 hours whenever (1) they were present and active on Mitivik Island (we did not record bears that were sleeping

or resting for long periods) and (2) weather conditions were suitable for drone operation. Although 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. Dey & E. S. Richardson, personal observation). Filming started as soon as the researchers noticed a bear on the island and finished when the bear (1) went to sleep or (2) left the island. At times there were multiple bears on the island, so a focal bear was haphazardly chosen based on activity; filming then transitioned to other bears as soon as the focal bear fulfilled criterion (1) or (2) above. In cases when there was some recording overlap (i.e. more than one bear filmed at the same time), the video with the earliest time stamp was placed in first succession.

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 to be a different bear. Individuals were also considered to be different bears between days as we had no way of proving otherwise. Because of the overhead flight altitude used in this study, we were unable to accurately sex the bears, so our analysis does not consider between-sex differences in foraging energetics; however, there was little noticeable differentiation in bear size among our sample, but we nevertheless assigned two weight classes to each individual to represent an average female and male from the Foxe Basin sub-population (see below). In total, we differentiated 20 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. Dey, personal observation).



Figure 2. (a) Footage of a drone approaching a foraging polar bear, encapsulating physical characteristics of Mitivik Island. (b) Drone footage of a polar bear approaching a full common eider nest (circled in red) and encapsulating the approximate average view of bears foraging in this study.

A total of 995 min of polar bear foraging footage were recorded from 65 drone flights. 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 (~22 min/battery) for the drones used in our study. We considered it a new foraging bout for each individual bear (if it foraged more than once per day) during each day when there was a considerable time gap (mean = 167 min; median = 62 min; statistical range = 426 min) in filming a focal animal due to changes in activity (e.g. swimming or resting) before returning to forage and/or as a result of having to replace batteries. In total, we differentiated 31 distinct foraging bouts across the study that ranged from 2.85 to 134 min (mean = 32 min; median = 26 min). Importantly, ‘foraging bout’ was used as our unit of observation for our statistical analysis (see below).

Ethical Note

All precautions were taken to minimize any disturbance to polar bears during this study. Researchers were stationed behind an electrified bear fence and flew the drones at an altitude that elicited low behavioural responses in bears, likely due to (1) an appropriate flying altitude of 30–55 m, (2) the ambient noise of waterfowl and a herring gull, *Larus argentatus*, colony buffering the sound of the

drone and (3) bears being distracted by flying herring gulls. When bears did react to the drone (e.g. looked up), we positioned the drone higher in the air. We observed no eiders flushing from their nests due to the presence of the drone, although we acknowledge that without definitive evidence, bears (and potentially eiders) may have experienced a physiological response (Ditmer et al., 2015; Weimerskirch, Prudor, & Schull, 2018).

All flights in this study were considered ‘direct line-of-sight’. The research project held the operational permits required at the time (2017) including an Environment and Climate Change Canada Animal Care permit (No. EC-PN-17-026) and a Nunavut Wildlife Research Permit (No. WL 2017-030).

Please refer to the Drone Reporting Protocol (Barnas et al., 2020) in the Appendix for complete details of flight operations.

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 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'. 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 standing, sitting, lying down and walking while ingesting an egg (i.e. handling time/eating).

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 (1) estimates of the caloric content of eider eggs (1090 kJ/egg; Swennen & Meer, 1995), (2) the mean clutch size of 2.85 eggs for eiders at Mitivik Island (Love et al., 2010) and (3) 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 modest decline in caloric value of avian eggs across incubation (Romanoff & Romanoff, 1967), and therefore, our calculations may produce slight 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 energy used in time 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 rates per minute 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, Carnahan, et al. (2018):

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

where $\dot{V}O_2$ is in ml of O_2 per g per h and speed is in km/h, and following the energetic formula from Watts, Øritsland, and Hurst (1987), where 1 litre of O_2 consumed is equal to 19.66 kJ. We estimated polar bear movement at 3.4 km/h as they walked over the flat ground of the island, which was the average walking speed for bears in Pagano, Carnahan, et al. (2018). Together, these values produced an estimated energetic cost of movement of 16.67 kJ per kg per h. We estimated the energy use of bears when standing (i.e. during searching) and when ingesting eggs (when standing, sitting and lying down) using the same methods, but with a speed of 0 km/h. This produced an estimated energy use rate of 8.65 kJ per kg per h, which is 40% higher than estimates of resting metabolic rate for polar bears (e.g. combined from Pagano, Carnahan, et al., 2018, Pagano, Durner, et al., 2018). We produced estimates of energy use for polar bears weighing 255 kg and 580 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 580 kg).

Statistical Analyses

To estimate the benefits and costs of foraging on eider eggs, and how these benefits and costs change with resource density, we chose to explore four functional relationships with our data set a

priori, rather than use a best-fit statistical model with lesser biological relevance (in the optimal foraging field). 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 = 31), 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 variables, we considered the following foraging behaviours: (1) the rate of clutch consumption per min (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 and (4) the rate of net energetic gain per min.

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 dependent variables we fitted the following four models.

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

$$y = a \quad (2)$$

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

$$y = mx + b \quad (3)$$

(3) A power law model of resource density (Marquet et al., 2005), where the response variable (y) increases or decreases in nonlinear ways depending on nest density (foraging bout order) (x), where (β) is a normalization constant and (a) is the law's exponent. This model was selected as a candidate model due to the expected convex relationship between search time and resource density. OFT suggests animals should be able to retain low searching levels when resources are in high abundance and only accelerate search effort as resource density declines (Curio, 2012). Additionally, energy use rates should be tightly related to searching activity, which would also then produce a nonlinear fit to the data.

$$y = \beta x^a \quad (4)$$

(4) 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 maximum value for the dependent variable, and (b) is the x value at which the dependent variable achieves half its maximum value. This model was selected as a candidate model as it is similar in shape to the Holling type II functional response model (with adjusted parameterization; Bolker, 2008). Often observed in foraging ecology studies of prey consumption rates with no prey switching (as is the case here where we are exclusively focusing on one prey type) (Holling, 1959), this model is also applicable to net energy gain rate since it should be tightly associated with the number of clutches bears consume.

$$y = \frac{ax}{b + x} \quad (5)$$

For each behavioural attribute we fitted the four functional relationships described above and used Akaike's information criterion corrected for small sample sizes (AIC_c) (Symonds & 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 a likelihood ratio test, and its parsimony using evidence ratio tests (Wagenmakers & Farrell, 2004). All models were fitted with a Gaussian error distribution and identity link functions. Statistical analyses were performed in R v.3.4.4 (R Core Team, 2019) using 'tidyverse' (Wickham, 2017) and 'broom' (Robinson, 2014) packages for 'tidy' script, 'nlstools' (Baty et al., 2015) package for nonlinear modelling and 'MuMIn' package for multimodel selection (Allwood et al., 2005). Figures were created using the 'ggplot2' (Wickham, 2016), 'cowplot' (Wilke, 2016) and 'gridExtra' (Auguie, 2017) 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 (i.e. approximately 30% of clutches in 2017). As the season progressed, bears consumed clutches at a decelerating rate until the colony depleted to a point where locating nests proved challenging. Earlier in the season (10–17 July; foraging bouts 1–24), bears consumed >20 clutches during 10 of 24 foraging bouts and >10 clutches during 15 of 24 foraging bouts (statistical range = 66 clutches). In the last 3 days of filming (18–20 July; foraging bouts 25–31), all bears consumed fewer than eight clutches and three of those individuals (foraging bouts 28–31) consumed zero clutches. The relationship between the rate of clutch consumption and foraging bout order was best supported with the diminishing returns model (Table 1, Fig. 3a), which was significantly different when compared to the null model ($F_{30,29} = 13.89$, $P < 0.001$) and was highly likely to be the best model

fit from our set of candidate models (evidence ratio = 13). 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), which was significantly different when compared to the null model ($F_{30,29} = 4.47$, $P < 0.05$) and was twice as likely as the next most parsimonious model to be the best fit (evidence ratio = 2.3). While these results suggest the linear model was significantly different than the null and twice as likely to be the best fit against the null model, the null model was equally parsimonious when considering its delta AIC (i.e. $\Delta AIC_c < 2$) (Burnham & Anderson, 2002), and we therefore suggest caution when interpreting these results.

Energy use rates stayed relatively constant throughout the season and particularly within weight classes of bears that we considered (i.e. 255 kg and 580 kg). Although the relationships between energy use rates and foraging bout order were best supported with the diminishing returns model (Table 1, Fig. 3c), these were not significantly different when compared to the null model (255 and 580 kg: $F_{30,29} = 2.75$, $P = 0.1$) and were only slightly more parsimonious than the null model (evidence ratio = 1.6). However, despite this constant and low rate of energy expenditure as bears slowly travelled over the island in search of nests, 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 weight classes were significantly different when compared to the null model (255 kg: $F_{30,29} = 13.82$, $P < 0.001$; 580 kg: $F_{30,29} = 13.67$, $P < 0.001$) and were highly likely to be the best model fit from our set of candidate models (evidence ratio = 13).

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 sea duck colony when they may have been previously still hunting seals on the sea ice (Iverson et al., 2014). We present evidence that foraging on eider eggs provides an energetic benefit to those polar bears arriving on the island in late June and early July. By contrast, 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 11-day study period as bears depleted eggs in this large sea duck 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 (~1600 nesting pairs in 2017), we expect that 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/ha (Chaulk et al., 2004), and that lone bears have the capacity to consume hundreds of clutches in a short period (Gormezano et al., 2017; this study). However, this may not apply to very small colonies breeding on geographically large landmasses as locating nests at these sites would become difficult. Nevertheless, 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. Importantly, polar bears depleting the entirety of the colony of nests potentially suggests that they were unable to abandon the island at some optimal threshold (Charnov, 1976), although this assertion is beyond the scope of this

Table 1

Candidate models for the number of clutches eaten per min, the proportion of time spent searching, and energy use and net energy gain for bears in each weight class (255 kg and 580 kg)

Models	df	logLik	AIC _c	ΔAIC_c	w _i
<i>Number of clutches eaten/min</i>					
Intercept only	2	3258.70	-6512.97	5.22	0.07
Linear	3	3257.99	-6509.09	9.10	0.01
Power law	3	3258.08	-6509.27	8.92	0.01
Diminishing returns	3	3262.54	-6518.19	0.00	0.91
<i>Searching proportion</i>					
Intercept only	2	3258.19	-6511.95	1.74	0.22
Linear	3	3260.29	-6513.69	0.00	0.52
Power law	3	3258.27	-6509.65	4.04	0.07
Diminishing returns	3	3259.29	-6511.70	2.00	0.19
<i>Energy use rates (255 kg)</i>					
Intercept only	2	3141.28	-6278.12	0.97	0.28
Linear	3	3142.17	-6277.45	1.64	0.20
Power law	3	3141.01	-6275.14	3.95	0.06
Diminishing returns	3	3141.01	-6279.09	0.00	0.46
<i>Energy use rates (580 kg)</i>					
Intercept only	2	3115.86	-6227.28	0.97	0.28
Linear	3	3116.75	-6226.61	1.64	0.20
Power law	3	3115.59	-6224.29	3.95	0.06
Diminishing returns	3	3117.57	-6228.25	0.00	0.46
<i>Net energy gain rates (255 kg)</i>					
Intercept only	2	3012.51	-6020.59	5.25	0.07
Linear	3	3011.82	-6016.74	9.10	0.01
Power law	3	3011.89	-6016.90	8.95	0.01
Diminishing returns	3	3016.37	-6025.84	0.00	0.91
<i>Net energy gain rates (580 kg)</i>					
Intercept only	2	3012.38	-6020.32	5.27	0.07
Linear	3	3011.70	-6016.52	9.07	0.01
Power law	3	3011.76	-6016.63	8.95	0.01
Diminishing returns	3	3016.24	-6025.59	0.00	0.91

logLik = log likelihood; AIC_c = Akaike's information criterion corrected; ΔAIC_c = delta AIC; w_i = Akaike weights. Best candidate models are shown in bold.

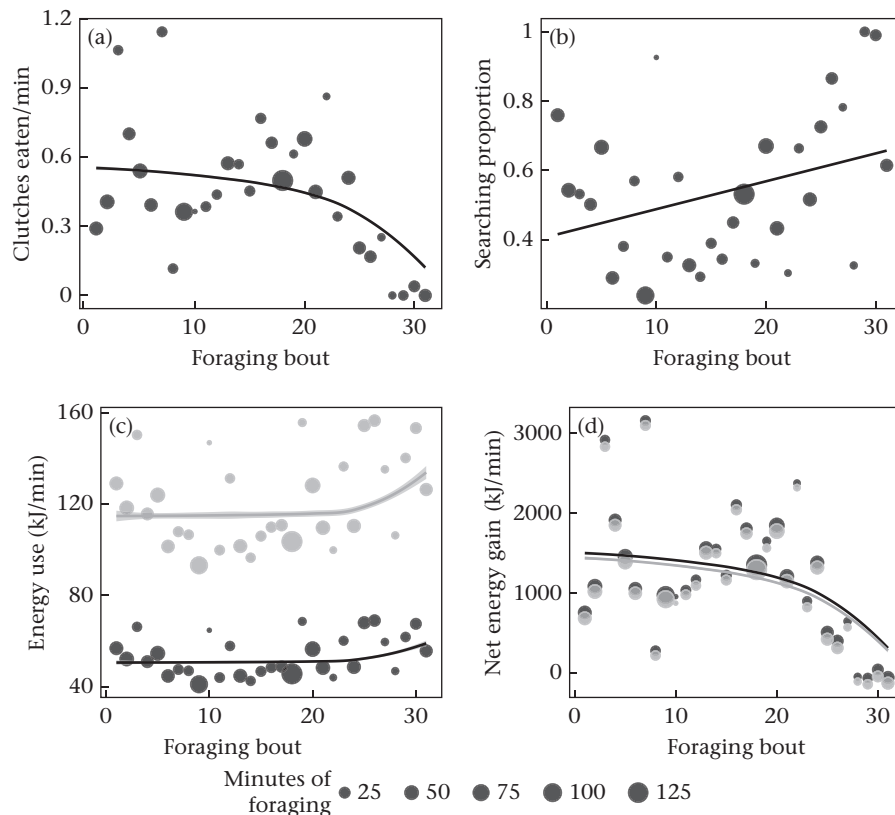


Figure 3. (a) Common eider clutches consumed/min by polar bears during foraging bouts as the eider breeding season progressed. (b) Proportion of time polar bears spent searching for nests during foraging bouts as the eider breeding season progressed. (c) Estimated rate of polar bears' energy use (kJ/min) during foraging bouts as the eider breeding season progressed for polar bears estimated to weigh 255 kg (grey circles and lines) and those estimated to weigh 580 kg (black circles and lines). (d) Estimated rate of polar bears' net energetic gain (kJ/min) during foraging bouts as the eider breeding season progressed for bears estimated to weigh 255 kg and 580 kg (symbol designations as in (c)). Each data point represents a single foraging bout.

present study as it would require knowledge of all the available seabird colonies and energetic calculations associated with travelling between them.

For a resource to be energetically profitable, the energy gained must outweigh the pursuit cost (MacArthur & Pianka, 1966). Given that the island is small and the colony is dense, we would expect that early in the season, when the colony was full of nests, time spent searching would remain relatively constant (while increasing later in the season as the colony is depleted) as bears should have adjusted their searching behaviour to limit movement and increase intake rates (Curio, 2012). However, we found a likely 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 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 attributed to walking. Because polar bears possess efficient locomotion at routine walking speeds (i.e. preferred: <5.4 km/h; Pagano, Carnahan, et al., 2018), and searching for eggs 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 & Richardson, 2002; Gormezano et al., 2016; but see Laidre, Stirling, Estes, Kochnev, & Roberts, 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 geographical scale (Pagano, Atwood, Durner, & Williams, 2020). 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, Lopez-Alfaro, Rode, Tøien, & Nelson, 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 (Pagano, Durner, et al., 2018). Given these energetic requirements, we can postulate that, on average, a polar bear would need to consume approximately 19 eider clutches to satisfy its daily energetic demand. Our results show that, based on the number of clutches consumed early in the season, some bears can satisfy their daily energetic demand within one foraging bout, and likely even gain an energetic surplus if they forage for longer periods than we captured with the drones (e.g. during the night). However, later-arriving bears will experience diminishing energy returns associated with resource depletion. While those individuals that forage on eggs early in the season can potentially accrue enough calories to extend the amount of time they can survive on land during the summer months (Pilfold et al., 2016), the calories accrued via a sea duck egg diet are minimal compared to what can

be gained from an adult ringed seal, *Pusa hispida* (Stirling & McEwan, 1975). Therefore, in concordance with Dey et al. (2017), eggs alone will most likely not be enough to maintain polar bear body condition (at least at a population level) 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. Moreover, the shape of the net energy gain model was 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. The similar relationships between 'clutches eaten rate' and 'net energy gain rate' with decreasing resources further supports our supposition that bears did not abandon the colony at some optimal threshold (Charnov, 1976) and warrants, then, future research into optimal give-up times for polar bears foraging in avian colonies.

As for any supplementary resource, to make a significant dietary contribution relative to bear conservation, the availability of eggs must be enough in terms of density, frequency and accessibility to support polar bears at a population level (Rode et al., 2015). To date, there has only been a handful of localized accounts of polar bears preying on bird eggs (e.g. Divoky, 2011; Iles et al., 2013; Prop et al., 2015; Smith et al., 2010; Stempniewicz, 1993; specifically common eider eggs: Gormezano et al., 2017; Iverson et al., 2014; Prop et al., 2015; Noel, Johnson, O'Doherty, & Butcher, 2005), 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, as polar bears actively forage on Mitivik Island, herring gulls have been observed capitalizing on exposed clutches (H. G. Gilchrist, personal observation), which likely serves to further reduce the availability of eggs as an alternative resource. Eiders themselves have evolved antipredation adaptations that may deter predators in the short term (Forbes, Clark, Weatherhead, & Armstrong, 1994; McDougall & Milne, 1978) but also influence the availability (and hence profitability) of this alternative resource. For instance, eiders may respond to predation pressure by skipping breeding the following year after an unsuccessful nesting attempt (Jean-Gagnon et al., 2018; Öst et al., 2018), or disperse from their nesting site following nest failure (Öst et al., 2011). Indeed, Kurvinen, Kilpi, Nordström, and Öst (2016) demonstrated that eiders have shifted their preferred breeding habitats inland to avoid increasing predation pressure on islands from white-tailed sea eagles, *Haliaeetus albicilla*. While it is still unknown whether such responses are occurring at the Mitivik Island colony, Inuit reports from the community of Coral Harbor suggest a neighbouring eider colony – closer to the mainland – is increasing in size (H. G. Gilchrist, personal communication). Intuitively, it seems that such perturbation by polar bears cannot persist indefinitely without eiders experiencing major population consequences (Hanssen & Erikstad, 2013; Hanssen, Moe, Bårdsen, Hanssen, & Gabrielsen, 2013). However, it has been suggested that eiders in the northern Hudson Strait may be able to offset polar bear predation pressure through climate-induced increased breeding propensity and, to a lesser extent, through an increase in clutch size at least in the next 25 years (Dey et al., 2018; but see Lehtikoinen, Kilpi, & Öst, 2006).

As evidenced here and in other systems (e.g. Abraham & Sydeman, 2006; Kowalczyk, Reina, Preston, & Chiaradia, 2015; Robinson, Thayer, Sydeman, & Weise, 2018; Víkingsson et al., 2014), when primary predator–prey relationships are decoupled due to

climate change, species that exhibit behavioural flexibility are able to opportunistically capitalize on alternative resources as would be expected from optimal foraging theory (Pyke, 1984). However, while such prey switching may be profitable in the short term, it cannot go unabated indefinitely as 'topological rewiring' is sure to occur (Bartley et al., 2019). For instance, prey switching by common murre, *Uria aalge*, due to variability in ocean conditions is endangering at-risk Chinook salmon, *Oncorhynchus tshawytscha*, along the west coast of the United States as they are incidentally consumed when co-occurring with murre's alternative prey (i.e. northern anchovies, *Engraulis mordax*; Wells et al., 2017). Due to the phenological overlap of red elderberry, *Sambucus racemosa*, blooms during the seasonal sockeye salmon, *Oncorhynchus nerka*, run caused by warmer spring temperatures, traditional ecological functions resulting from the dispersing of salmon carcasses by brown bears, *Ursus arctos*, will likely be altered as bears increasingly forage on berries (Deacy et al., 2017). Sea ice loss has already affected species' interactions and overall ecosystem dynamics across the circumpolar Arctic (Descamps et al., 2017; Post et al., 2013; Wassmann et al., 2011). The impacts of an apex predator increasingly switching its hunting of marine mammals from the sea ice to foraging on terrestrial prey such as on sea duck eggs will be complex (Juhász, Shipley, Gauthier, Berteaux, & Lecomte, 2020) and will likely have effects on several trophic levels in the Arctic, necessitating continual monitoring.

Conclusion

Our results indicate that a small number of polar bears can gain energy in late June and early July by foraging on common eider eggs when marine foraging opportunities are no longer available. While our results suggest that some bears can profit energetically from foraging on eggs, the overall contribution that eider eggs make to an entire population appears small, reinforcing the importance of seal hunting on ice to the overall persistence of polar bears. To fully understand the implications of our findings (beyond our study sample), we recommend long-term spatial and temporal studies to capture polar bear foraging behaviours across several colonies and seasons, as well as testing their foraging performance (i.e. efficiency) in the context of a depleting resource for a more comprehensive understanding of the benefits and costs of this climate-mediated behavioural shift.

Author Contributions

C.A.D.S., C.J.D., E.S.R. and H.G.G. conceived the study, C.J.D. and E.S.R. conducted the field work, P.M.J. analysed the data, C.J.D., P.M.J. and C.A.D.S. ran statistical analyses, P.M.J., C.J.D. and C.A.D.S. wrote the manuscript, E.S.R. and H.G.G. provided comments and suggestions to the manuscript and C.A.D.S., C.J.D., E.S.R. and H.G.G. obtained funding.

Declaration of Interests

We declare that we have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Funding for this project was generously provided by Environment and Climate Change Canada, The University of Windsor, Mitacs, Baffinland Iron Mines, Natural Sciences and Engineering Council (NSERC) and The Liber Ero Foundation (C.J.D.). We thank Mike Janssen, Jake Russell-Mercier, Holly Hennin and Bronwyn

Harkness of Environment Canada for their logistical support. We especially thank Josiah Nakoolak, Jupie Angootealuk and Clifford Natakok for their years of expertise and support contributing to the research programme on Mitivik Island, East Bay. We also thank Bob Hansen for his assistance with field work. Finally, we thank Andrew Barnas for reviewing the manuscript and Drone Reporting Protocol and providing valuable feedback.

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Appendix

Drone Reporting Protocol

This protocol was written following [Barnas et al. \(2020\)](#) in order to provide more insight into techniques and specifications used in this study.

Project overview

Polar bear predation of common eider eggs is apparently increasing at some locations of the circumpolar Arctic ([Iverson et al., 2014](#); [Prop et al., 2015](#)). The aim of our research was to quantify the foraging energetics of polar bears while they depredated eggs from an eider colony in East Bay, Southampton Island, Nunavut, Canada. To do so, we used aerial drones to film polar bears from above as they foraged undisturbed in July 2017.

Drone systems and operation details

We flew DJI Phantom 3 Pro and 4 Pro rotary-wing (four propeller) drones (<https://www.dji.com/company>) (Fig. A1). While technically two distinct machines, we describe both models here in terms of the Phantom 4's specifications because of the similarities between the two models (for product details and to review the similarities (and differences) between the two models, see <https://www.dji.com/ca/phantom-4-pro?site=brandsite&from=nav>; <https://www.dji.com/ca/phantom-3-pro?from=buying-guides>). When entirely assembled with battery and propellers, these drones weigh 1388 g and are 350 mm in diagonal width (without propellers). Drones are powered by a single, removable LiPo 4S battery (15.2 V, 5870 mAh, 468 g), which has a maximum 30 min flight duration, but up to 10 min less when flying during our study (perhaps due to temperature). In polar regions, where temperatures are typically below 10 °C, even in summer months, as they were during this study, flight time limitations are often shorter. As per the operating instructions, it is not advised to fly these models in temperatures below 0 °C, during snow or rain events, or in wind conditions in excess of 10 m/s.

Field operations

This study took place during 10–20 July 2017, which coincided with the reproductive stage when eider ducks were incubating. Flights were not flown during inclement weather such as fog, rain or winds that exceeded 36 km/h.

Researchers operated the drones from behind an electrified fence, which safe-guarded them from polar bears. We also monitored the island for the arrival of bears from within wooden observation blinds. When a bear arrived on the island, the drone pilots were notified using hand-held radios and a flight was launched from within the fenced perimeter. Drones were launched as soon as a polar bear was observed arriving on the island and continued until the bear either went to sleep or left the island. When more than one bear was present, the researchers followed the bear that was actively foraging ('focal bear'). When a focal bear went to sleep or left the island, the team switched to filming other bears that were present. Most filming occurred during the most favourable light conditions between 0530 and 2030 hours. In total, we collected 185 raw video files with a total combined length of 1149 raw min from 65 drone flights.

Drone flights in this study were manually controlled by a single person using the Phantom 3/4 Pro remote controller (2.400–2.483 GHz), which is powered by a 6000 mAh LiPo 2S battery. We were operating in a remote, flat, treeless landscape with no obstructions or radio interference. Under these conditions, the Federal Communications Commission (FCC) maximum transmission distance is estimated to be 7 km.

Importantly, the pilot could view the live video feed from the camera of the drone itself using an iPad, which was mounted to the hand-held flight controller. On the iPad monitor, the pilot was also provided information on the drone's flight altitude, battery life and video settings.

During flights, drones were flown above and behind focal polar bears at roughly 30–55 m altitude. This altitude provided detailed video footage while ensuring that the bears were not disturbed. We intentionally flew the drone behind the polar bears and into the wind, which both stabilized the flights and lowered noise (Fig. A2).

The research team consisted of three people at any given time. Two people flew drones, while a third assisted with battery replacement. Two drones were used during a polar bear foraging bout to maintain as much continuous footage as possible. When a bear was located on the island from a distance, a single drone was launched to film the bear. After 20 min, the first drone was flown back to the camp to have its battery replaced, while a second was launched to ensure nearly continuous filming.

Payload, sensor and data collection

We collected high-resolution video footage using the Phantom 3 and 4 Pro drones flown at altitudes of 30–55 m above ground. Drones were equipped with a single 1-inch CMOS 20MP 4K video camera and a stabilizing gimbal with three axes (pitch, roll, yaw). Video was captured at 30 frames/s (2700 × 1520 pixels) using 'automatic ISO and focus' settings. (The technical specifications on the DJI Phantom 4 Pro camera system can be found at <https://www.dji.com/ca/phantom-4-pro>.) Pilots had a live view of the video footage, which was being simultaneously stored on a 32–128 gigabytes (GB) Secure Digital (SD) Card in Quick Time Movie (MOV). The video data were subsequently downloaded from these SD cards following flights.

Since flight altitudes and camera angles varied within and between flights, it was not possible to estimate the area captured by the video frame. However, we soon confirmed that this altitude and video resolution enabled us to clearly view polar bear foraging behaviour from above (e.g. whether or not they consumed an entire clutch of eider eggs from a nest).

Data processing

Raw videos files (185) were sorted using flight time logs and were subsequently 'stitched' together using video editing software (iskysoft <https://www.iskysoft.com/>), which generated continuous video files of focal bears as they foraged in the wild. Video footage collected while the drone commuted to and from its launch point (i.e. 'empty footage') was not included in our analysis. We also excluded video footage collected when (1) a bear was adjacent to the fenced perimeter and acting inquisitively towards us, (2) a bear was interacting with the wooden observation blinds (e.g. playing with the strings) and (3) a bear was lying down for extended periods (as we considered this nonforaging behaviour). After complete processing, we collected 995 min of video footage of bears foraging within the eider duck colony (mean bout length = 32 min; median bout length = 26 min; statistical range = 131 min; see [Table A1](#)).

It was often possible to distinguish individual bears by (1) the date and time of video filming, (2) field logs containing information such as number of bears on the island on a particular day and time and/or (3) individuals' characteristics (stains on fur, scars), or when females were accompanied by a cub. However, when a bear could not be distinguished from individuals observed during the same or previous day, it was considered to be a new individual. In total, we differentiated 20 individual bears and categorized them into 31 distinct foraging bouts.

Training

Pilots assembled and operated the drones for several weeks prior to travelling north, to practice flying and familiarizing themselves with software and battery characteristics.

Table A1

Summary of polar bear foraging bouts (bout number, date and bear identity) and video lengths of each foraging bout before and after processing (i.e. excludes 'interacting with blinds and people' and 'resting while lying down')

Polar bear foraging bout	Date	Bear ID	Video length (min) excluding 'empty' footage	Video length (min) after complete processing
1	10 July 2017	1	53.19	44.02
2	11 July 2017	2	70.98	51.75
3	11 July 2017	2	21.47	15.97
4	11 July 2017	2	32.82	32.82
5	15 July 2017	3	56.68	52.54
6	15 July 2017	4	38.60	38.60
7	15 July 2017	4	19.24	19.24
8	15 July 2017	5	17.17	17.17
9	15 July 2017	3	90.8	83.82
10	15 July 2017	3	17.02	2.85
11	16 July 2017	6	19.37	18.17
12	16 July 2017	7	17.35	16.29
13	16 July 2017	6	41.86	41.86
14	16 July 2017	8	19.86	17.67
15	16 July 2017	8	19.87	19.87
16	16 July 2017	9	20.84	20.84
17	16 July 2017	7	28.7	28.7
18	16 July 2017	6	136.08	134.21
19	17 July 2017	10	13.57	9.78
20	17 July 2017	11	58.92	58.92
21	17 July 2017	11	46.75	46.75
22	17 July 2017	12	5.79	5.79
23	17 July 2017	11	16.33	14.83
24	17 July 2017	13	52.88	43.68
25	18 July 2017	14	40.55	33.96
26	18 July 2017	15	34.97	29.76
27	18 July 2017	16	11.2	11.2
28	18 July 2017	17	7.20	7.20
29	18 July 2017	18	16.87	16.87
30	19 July 2017	19	26.29	25.44
31	20 July 2017	20	36.89	34.73
Total:		20	1090	995

Foraging bouts are listed in increasing order with respect to time and date (i.e. chronological order) to account for decreasing prey availability with time.



Figure A1. (a) Phantom 4 Pro hovering. (b) Phantom 3 Pro hovering. Photo credit: Evan Richardson.

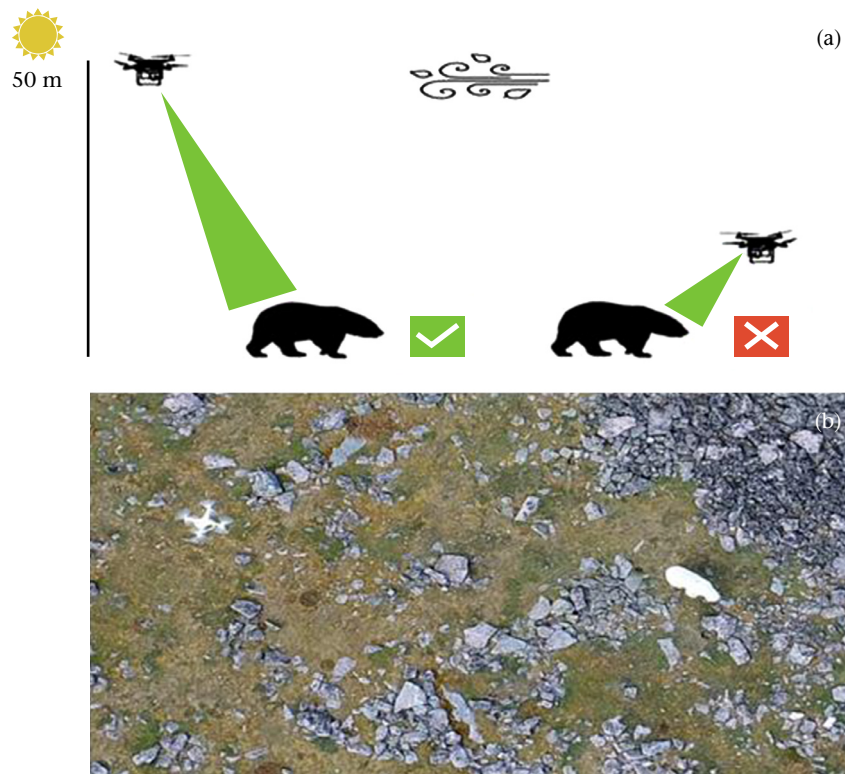


Figure A2. (a) Diagram representing the approach angle (i.e. from the rear of the bear) and flight altitude used in this study. (b) Picture of a drone filming a polar bear consuming a common eider clutch and an approximate representation of the researchers' field of view when analysing the data.