Linda J. Gormezano



A collection of her published work

Linda J. Gormezano was a valued student in the Department of Ornithology at the American Museum of Natural History and member of the Hudson Bay Project . After completing her Ph.D., she remained an active researcher in the Department, publishing more of her papers before moving to Montana. Once she completed her degree, her affiliation with the Hudson Bay Project changed from a student to a Principal Investigator. Until her untimely death, she oversaw our polar bear research program. Her leadership on that front will be sorely missed.

Having Linda as a graduate student was every professor's dream. She was highly motivated, worked incredible hours, strove for perfection and was happy to debate everything I threw her way. She intended to work on coyotes in Westchester County but when I offered the opportunity to shift to polar bears in the Canadian Arctic she jumped on board and became fascinated with the project, the Arctic and especially the people. She spent many hours collecting Traditional Knowledge from members of both the Inuit Community and especially the Cree First Nation.

Linda was an excellent listener and her discussions with Cree Elders were part of what ultimately set her on a course of using non-invasive techniques to study polar bears. Other researchers' use of invasive techniques such as darting and tagging is anathema to the aboriginal world view. To meet this challenge, Linda acquired one of the loves of her life. Quinoa is a Dutch Shepherd that she trained from a 6-monthold pup to seek and find polar bear scat. Despite scientific "experts" who claimed she would find nothing (many of them still feel polar bears "fast"), she and Quinoa found more than 1200 piles of scat in 3 years. She brought the samples to the American Museum of Natural History and pains-takingly sorted each to identify and quantify the contents. Those data formed the core of her dissertation and allowed her to provide insights on several novel aspects of polar bear foraging and nutrition.

Publishing scientific work through the peer review system is always difficult but even more so when your findings are at odds with popularized views. There is an unfortunate overtone in the world of polar bears that is powered more by opinion than hard core science. Far too many that call themselves scientists and experts are actually advocates connected to not-for-profit organizations that fund themselves through public fears that iconic species such as the polar bear will soon go extinct. Linda's work focused on a simple theme – "What are the bears actually doing?" Tragically, her simple truth that the bears are "adapting" and trying to make the best of a changing situation struck a sour note with many of those who have influence over scientific journals.

Linda, being the exceptionally determined individual she was, never yielded but sought advice from our late colleague Robert L. Jefferies (Dr. Bob) who told her: "Stay your course. Good science, properly done, thoroughly documented and well written, will ultimately win the day". Fortunately for polar bears and the rest of us, Linda took his advice, stuck to it and her papers began to flow. It is rare indeed that a graduate student displays that level of perseverance (and grit) – but that was Linda.

It is rarer still that a graduate student and, later, a junior colleague can alter the trajectory of a long-term (38 year old) research program. When Linda first joined the Hudson Bay Project as a student she argued with Dr. Bob and me that we should expand our efforts from simply looking at the interplay of an herbivore (the snow goose) and its forage plants to a community level and incorporate research on polar bears that, because of climate change, were becoming an increasingly important player in the ecosystem. We listened, gave her a chance and the rest is history, well documented in this collection of her work.

Thanks to Linda's perseverance, the world view on the fate of polar bears is changing. Many scientists are duplicating her results and even more are challenging the fatalist attitude of the advocates of doom and gloom. Linda always ended her papers with admonitions that we do not know enough and that there is still more to learn. I and the Hudson Bay Project team, especially its new members from the University of North Dakota including Susan Felege, Brian Darby and their students, have agreed to take up her challenge and have committed ourselves to continuing and building on her work. We shall keep her vision and dream alive - I know of no more fitting and well-deserved tribute.

RF Rockwell



Field work was a key component of Linda's research - one that brought her endless joy.

Linda's peer-reviewed papers are reproduced from the journals in chronological order in the following pages. They are:

- Rockwell, RF, <u>LJ Gormezano</u> and D Hedmann. 2008. Grizzly Bears in Wapusk National Park, Northeastern Manitoba. Canadian Field-Naturalist 122(4) 323-326.
- Rockwell, RF and <u>LJ Gormezano</u>. 2009. The early bear gets the goose: climate change, polar bears and lesser snow geese in Western Hudson Bay. Polar Biology 32:539-547.
- Rockwell, RF, <u>LJ Gormezano</u> and DN Koons. 2011. Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay? Oikos 120: 696-709.
- Iles, DT, SL Peterson, <u>LJ Gormezano</u>, DN Koons and RF Rockwell. 2013. Terrestrial predation by polar bears: not just a wild goose chase. Polar Biology 36:1373-1379.
- <u>Gormezano, LJ</u> and RF Rockwell. 2013. What to eat now? Shifts in terrestrial diet in western Hudson Bay. Ecology and Evolution 3(10): 3509–3523.
- <u>Gormezano, LJ</u> and RF Rockwell. 2013. Dietary composition and spatial patterns of polar bear foraging on land in western Hudson Bay. BMC Ecology 13:51.
- <u>Gormezano, LJ</u> and RF Rockwell. 2015. The energetic value of land-based foods in Western Hudson Bay and their potential to alleviate energy deficits of starving adult male polar bears. PLOS ONE DOI:10.1371/journal.pone.0128520.

Linda had 3 additional papers on her polar bear work in various stages of revision. Her Hudson Bay Project colleagues and I will see to it they are published. In addition, she had 2 papers in revision with H. Brian Underwood who is seeing to their completion.

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A black and white version of this photo appears on the cover of Volume 122, Number 4 (Oct–Dec 2008) of the Journal and is referred to in the text of Rockwell, Gormezano and Hedman 122:323-326.

Grizzly Bears, Ursus arctos, in Wapusk National Park, Northeastern Manitoba

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Rockwell, Robert, Linda Gormezano, and Daryll Hedman. 2008. Grizzly Bears, Ursus arctos, in Wapusk National Park, northeastern Manitoba. Canadian Field-Naturalist 122(4): 323-326.

We report on nine sightings of Grizzly Bears (*Ursus arctos*) in northeastern Manitoba in what is now Wapusk National Park. Although biological research in the region has been conducted regularly since 1965, all sightings have been made since 1996. The Grizzly Bears were seen either along rivers known to harbor fish or in an area known for berries.

Key Words: Grizzly Bear, Ursus arctos, Wapusk National Park, Manitoba, Canada.

Grizzly Bears (Ursus arctos) are reported to have been absent from Manitoba historically at least through 1989 (Banfield 1959, 1974; Harington et al. 1962; Banci 1991, McLellan And Bianci 1999). Some recent accounts and range maps have included Manitoba in the Grizzly Bear's regular range (e.g., Schwartz et al. 2003), while others indicate that the regular range ends north of the Manitoba border but list rare, extra-limital observations for at least two sites along the Hudson Bay coast of Manitoba (e.g., Ross 2002*). Increased encounters with Grizzly Bears in northern Manitoba could be the result of increased observational effort or the expansion of the species' range. The latter could indicate a geographic shift related to habitat changes or food availability in the core areas and/or the newly occupied territory or to growth or other changes in the demographic structure of the core population followed by dispersal into unoccupied habitat.

In this paper, we extend the work of Clark (2000) and update confirmed observations of Grizzly Bears in the coastal sections of the Hudson Bay Lowlands east and south of Churchill, Manitoba (in what is now Wapusk National Park). We confine our primary efforts to this region since research there has been ongoing since 1965 and at a consistent level since 1993. As such, any recent increase in the frequency of Grizzly Bear encounters is more likely to be related to increased presence of the animals than increased efforts to find them. Because this new National Park is in the process of developing its status and mission plans, we also speculate on how regular occupation of the park by Grizzly Bears could influence some of the other species that have historically occupied the area.

While there have been occasional reports of Grizzly Bears or their sign since the onset of research in this area (e.g. Figure 1), we have limited the observations for this paper to confirmed sightings, as suggested by Clark (2000). Confirmed sightings require that either



FIGURE 1. Claw marks assumed to be made by a Grizzly Bear were observed in the tundra along the north coast of Wapusk National Park on 29 May 2006. The penknife is 12 cm.

the large hump of muscle over the scapulae or the concave face typical of Grizzly Bears be clearly seen by individuals familiar with the species. Nine encounters are summarized in Table 1 and to our knowledge they are the only confirmed sightings for this region since research began in 1965. Seven of the nine have been made since 2003 and the locations of all nine are depicted in Figure 2. The photograph of the most recent observation appears on the cover of this issue of *The Canadian Field-Naturalist* and the animal clearly shows the diagnostic scapular hump and concave face of a Grizzly Bear.

Comparisons of photographs from the three 2008 observations (Table 1) suggest that the animal seen near Rupert Creek may not have been the same animal as the ones seen near Thompson Point since it ap-

Encounter	Date	Location	Details	Authority ¹
1	15 June 1996	58.23333N 93.06667W; Approximately 7 km inland near Thompson Point	Seen from fixed-wing survey plane and photographs were taken. Hump and concave face were clearly seen and are obvious in photograph.	Dale Humburg ^a
2	5 June 1998	58.33333N 93.03333W; Coastal beach ridge near Thompson Point	Seen from helicopter. Hump and concave face were seen clearly.	Doug Clark ^b
3	Summer 2003	Near the coast at the Owl River	Seen from helicopter and photographs were taken. Hump and concave face clearly visible.	Robert Rockwell ^c
4	Summer 2004	Near the coast at the Broad River	Seen from helicopter and photographs were taken. Hump and concave face are clearly visible.	Bob Reside ^d
5	6 July 2004	58.13515N 92.86322; Broad River cabin	Seen 3 metres from cabin door.	Melissa Gibbons ^e
6	Summer 2005	Near the coast at Rupert Creek	Seen from helicopter. Hump and concave face were clearly seen.	Bob Reside ^d
7	22 July 2008	57.56758N 92.55860W; Near coast north of Rupert Creek	Seen from fixed-wing aircraft and photographs were taken. Hump and concave face were clearly seen.	Shaun Bobier ^f
8	1 August 2008	58.28953N 93.00608; Near coast south of Thompson Point.	Seen from helicopter and photographs were taken. Hump and concave face were clearly seen.	Daryll Hedman ^g
9	9 August 2008	58.36613N 93.08047W; 2 km inland and 9 km north- west of Thompson Point	Seen from helicopter and photographs were taken. Hump and concave face clearly seen.	Robert Rockwell ^c and Linda Gormezano ^c

TABLE 1. Confirmed sightings of Grizzly Bears in Wapusk National Park.

¹ Individuals who saw the animal or examined the pictures and confirmed it was a Grizzly Bear. ^aDucks Unlimited, Memphis, Tennesse; ^bUniversity of Alberta, Edmonton, Alberta; ^cAmerican Museum of Natural History, New York, New York; ^dRiding Mountain National Park, Wasagaming, Manitoba; ^eWapusk National Park, Churchill, Manitoba; ^fManitoba Conservation, Churchill, Manitoba; ^gManitoba Conservation, Thompson Manitoba

pears to be substantially larger. In contrast, the individuals in the latter two sightings (that were made less than a week and less than 10 km apart) could not be distinguished. We suggest at least two different Grizzly Bears may have been present in Wapusk National Park in 2008.

Given their enormous home ranges (11 400 km², Gau et al. 2004) and flexible habitat requirements (Schwartz et al. 2003), it is not surprising that Grizzly Bears have extended into areas such as Wapusk National Park that are only a few hundred kilometres south of their regular range. Three confirmed observations of Grizzly Bears since 1990 north of Churchill, Manitoba, further support that interpretation. The dates and locations of those encounters are: 27 July 1990 at 59.56667°N, 94.86667°W (in Clark 2000); 13 September 2005 at 59.89944°N, 97.03889°W and 28 June 2007 at 59.39383°N, 94.77224°W (both D. Hedman, unpublished data).

Wapusk National Park contains ample supplies of animal and plant resources known to be used by Grizzly Bears (Barry 1967; Gau et al. 2002; Ross 2002*; Schwartz et al. 2003). Of particular note are the more than 50 000 pairs of nesting Lesser Snow Geese (*Chen caerulescens caerulescens*), a potential food source already being exploited by Polar Bears (Rockwell and Gormezano 2009). Nesting Snow Geese are found within the Grizzly Bear's range in Nunavut but are absent between there and Wapusk National Park. The park also contains substantial populations of Canada Geese (Branta canadensis) and both Caribou (Rangifer tarandus) and Moose (Alces alces). The park is rich in various arctic berries, especially cloudberries (Rubus chamaemorus) and blueberries (Vaccinium uliginosum) (R. L. Jefferies, personal communication). The streams associated with five of the nine sightings (Figure 2) contain fish (R. F. Rockwell, unpublished data), and the Thompson Point area, where the other four sightings occurred, was traditionally used by local Cree First Nation communities for berry harvests (Flora Beardy, personal communication). The inland portions of the park include extensive peat plateaus and outcroppings used for winter denning by Polar Bears (Ursus maritimus) (e.g., Clark et al. 1997). These could certainly provide Grizzly Bears with winter haven.

The presence of Grizzly Bears raises interesting potential issues for other species in Wapusk National Park. Grizzly Bears are known to be exceptionally efficient predators of both Caribou and Moose (Ross 2002*) and would place new predation pressure on those species. Such predation would provide competition for both Wolves (*Canis lupus*) and Polar Bears,

although Grizzly Bears are known to provide scavenging opportunities for other such species (Ross 2002*). Female Polar Bears and their new cubs become active in the early spring in the interior portions of the parks and if Grizzly Bears were also to den there, encounters between the two species would be likely but the outcomes uncertain. There are reports and speculation that Grizzly Bears kill and consume female Polar Bears and their cubs but also that Polar Bears may prey on denning Grizzly Bears (Taylor 1995; Doupé et al. 2007). Although such events might be rare, informed management plans for interior portions of Wapusk National Park should consider them. Finally, there are several reports of natural hybridization between Grizzly and Polar bears, the most recent being the wellpublicized hybrid harvested in 2006 near Sachs Harbor on Banks Island (Taylor 1995; Schliebe et al. 2006). Such hybridization could potentially complicate issues related to genetic integrity and identification of the two species and their hybrids.

The observations presented here are consistent with the range map presented in Schwartz et al. (2003) that includes northeastern Manitoba in the range of Grizzly Bears. It is not yet clear whether the individuals encountered are transients, perhaps making use of higher levels of seasonally available food, or are more permanent residents. Continued and especially consistent monitoring will help resolve the Grizzly Bear's status and establish whether their abundance is increasing in northeastern Manitoba.

Acknowledgements

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FIGURE 2. Locations of the nine confirmed Grizzly Bear sightings in Wapusk National Park. See Table 1 for numbers.

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ORIGINAL PAPER

The early bear gets the goose: climate change, polar bears and lesser snow geese in western Hudson Bay

R. F. Rockwell · L. J. Gormezano

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Abstract As climate change advances the date of spring breakup in Hudson Bay, polar bears are coming ashore earlier. Since they would have lost some of their opportunities to hunt ringed seals from a sea ice platform, they may be deficient in energy. Subadult polar bears appear to come ashore before more mature individuals and the earliest subadults are beginning to overlap the nesting period of the large colony of snow geese also occupying the Cape Churchill Peninsula. The eggs these bears are known to eat could make up some of their energy shortfall. The earlier these eggs are consumed during the snow goose nesting period, the greater would be the energy that is available. Recent studies have shown that the annual survival rate for subadult bears declined in contrast to that of prime aged individuals. If this reduction in survival is related to an increasing energy deficit, as suggested by some, the consumption of goose eggs may reverse the trend and help stabilize the population, at least for some period of time. The total number of polar bears that could benefit from this resource will depend on the increasing temporal overlap with the nesting period and on the foraging behaviors of individuals eating the eggs. It is likely that other food sources will also have to play a role if the polar bears are to persist.

Keywords Chen caerulescens \cdot Climate change \cdot Eggs \cdot Energy compensation \cdot Foraging behavior \cdot Polar bear \cdot Snow goose \cdot Ursus maritimus

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Introduction

With the release of many popular articles on the potential effects of global climate change on its fate and its recent reclassification as a "threatened species," attention is again being focused on the plight of the arctic's most visible and charismatic predator, the polar bear (*Ursus maritimus* Phipps). There is little doubt that the global climate is changing and even less that these changes are negatively impacting polar regions (e.g., Randall et al. 2007; Stroeve et al. 2007). Since polar bears depend on sea ice for many aspects of their life history (e.g., Stirling and Derocher 1993), the continuing sea ice declines and temperature ameliorations predicted by climate change models are reasons for concern.

Ringed seals (Phoca hispida Schreber) are the primary prey of polar bears throughout most of their range and account for the major portion of the bears' annual energy budget (Stirling and Øritsland 1995). Much of the energy gained from consuming seals occurs after March each year and is coincident with the production and maturing of ringed seal pups (Stirling and McEwan 1975). Unfortunately, this is the period most likely to be impacted by climate change (e.g., Stirling and Derocher 1993; Stirling and Øritsland 1995; Rosing-Asvid 2006). Polar bears are quite efficient using the ice to hunt seals in their subnivean lairs and at breathing openings (Stirling 1974; Stirling and Latour 1978). However, as the sea ice breaks up, it is increasingly difficult for the bears to capture seals. If climate change advances the date of breakup, the problems for polar bears will be exacerbated.

This is particularly true for polar bears living in western Hudson Bay, near the southern limit of the species, where impacts of global change are expected to be felt sooner (e.g., Skinner et al. 1998; Derocher et al. 2004; Ferguson et al. 2005). Further, polar bears in this region normally

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shift to a terrestrial existence during a 4- to 5-month icefree period and are thought not to forage to any great extent, subsisting instead on stored fat reserves (e.g., Watts and Hansen 1987; Ramsay and Stirling 1988; Ramsay and Hobson 1991; Derocher et al. 1993, 2004; Stirling and Derocher 1993; Stirling et al. 1999; Stirling and Parkinson 2006). Since much of that fat is acquired during the period just prior to breakup (e.g., Stirling and Derocher 1993), any shortening of the spring hunting period could have profound effects. Recent analyses have shown declines in the body condition, reproductive success, survival and population size of polar bears in the western Hudson Bay population coinciding with an advance in spring sea ice breakup (e.g., Stirling et al. 1999; Regehr et al. 2007).

Although there have been some suggestions that increased terrestrial foraging during the ice-free period might provide some compensation for lost seal-hunting opportunities (Lunn and Stirling 1985; Derocher and Stirling 1990; Derocher et al. 1993, 2000; Dyck and Romberg 2007), there is a pervasive view that such foraging will not be adequate (e.g. Stirling and Derocher 2007). That view is driven in part by the metabolic expenses associated with terrestrial foraging. Lunn and Stirling (1985), for example, computed that the calories gained from consuming one of the many flightless (molting) geese in the Churchill (Manitoba) region would not likely compensate for the energetic cost of chasing it down.

Ironically, the advance in spring sea ice breakup that may be leading to the energy shortfall for polar bears may also provide some relief by making a more energy-efficient, terrestrial resource available. As the date of sea ice breakup advances, it is increasingly likely that some polar bears will arrive on shore when members of the large nesting colony of Lesser Snow Geese (Anser caerulescens caerulescens Linnaeus, henceforth snow geese) located on the Cape Churchill Peninsula are still incubating eggs. Polar bears are known to eat snow goose eggs (Abraham et al. 1977; Madsen et al. 1989; L. J. Gormezano, unpublished data) and since obtaining such a resource would not involve the high costs of a chase across the tundra, the eggs could compensate for some of the energy deficit associated with lost seal-hunting opportunities. The obvious questions are whether polar bears and nesting geese will increasingly overlap and how much energy is available for the bears.

In this article, we take advantage of well-studied populations of both species to examine the overlap of polar bears and nesting snow geese in their annual use of the terrestrial environment and to estimate the extent to which the bears will increasingly overlap the nesting period, assuming current climate trends continue. We also estimate the energy available to polar bears from snow goose eggs and examine both how this changes across the nesting period and how it could compensate for missed opportunities to eat seals when spring breakup occurs earlier. Finally, we consider the potential importance of this resource to polar bear persistence in light of what is known about the bears foraging on goose eggs.

Methods

Study site and spatial overlap of snow geese and polar bears

This study centers on polar bears and snow geese found in and around the northern coastal portion of Wapusk National Park, located approximately 30 km east of Churchill, Manitoba, Canada [see Rockwell et al. (2009) for details on the Park]. The polar bears are designated as part of the western Hudson Bay (WH) population (Aars et al. 2006) that occurs along the coast and adjacent inland habitat of Nunavut, Manitoba and Ontario during the ice-free season (typically from July to mid-November; Stirling et al. 2004). The snow geese are part of the Mid-Continent population (Abraham and Jefferies 1997). While the region's snow geese historically nested primarily near La Pérouse Bay, the colony has grown both numerically and geographically and now occupies a substantial portion of the Cape Churchill Peninsula, extending from La Pérouse Bay to the Broad River (Fig. 1). There are large concentrations where the density reaches 20 nests ha^{-1} . Most of the intervening habitat contains 1–5 nests ha⁻¹ with a few stretches (<5 km each), where density averages <1 nest ha⁻¹. The area depicted in Fig. 1 is also used during the spring, summer and early fall by many of the region's polar bears and forms the spatial basis for interaction between the two species.

Advances in the timing of snow goose nesting

Data on nesting phenology have been collected since 1968 as part of a larger, long-term study of snow geese, and methodological details are given in Cooke et al. (1995). While a portion of those data (1973–1993) were evaluated by Skinner et al. (1998), the entire data set (1968–2007) is used in our present analyses. We examined the data for any change in mean hatching date over 40 years with linear regression and estimated the rate of change and its confidence limits from that analysis. As part of our snow goose monitoring, sightings of polar bears within the nesting area have been recorded whenever possible and detailed records have been kept since 2000 when regular helicopter-based coastal snow goose surveys were begun.

Advances in the timing of sea ice breakup

Four studies have examined the advance of ice breakup in the portions of Hudson Bay that are relevant to the WH polar bear population (Stirling et al. 1999, 2004; Stirling and

Polar Biol (2009) 32:539–547

Fig. 1 Nesting Lesser Snow Geese are associated with over 100 km of coastline on the Cape Churchill Peninsula. South and southeast of the original La Pérouse Bay colony, they nest up to 15 km inland. Northwest of the Broad River, they nest up to 5 km inland. Many of the polar bears found in the Cape Churchill Peninsula use this section of coastline during spring, summer and fall

Parkinson 2006; Regehr et al. 2007). While all used similar approaches, the studies spanned different years and may have used slightly different criteria or procedures to define breakup dates. We assumed, however, that each study was internally consistent and as such would provide comparable estimates of the rate in advance of breakup. We extracted data from the graphs presented in each paper and estimated the rate of change in date of breakup over years using linear regression. We formed a weighted mean estimate across the four studies, using the inverse of the variances of estimates as weights to compensate for differences in parameter confidence. We compared the rates of change in hatching date and sea ice breakup following procedures outlined by Zar (1999).

The energy content of snow goose eggs

The protein and fat content of fresh and newly hatching (pipping) eggs of snow geese were estimated by Badzinski et al. (2001), and provide the basis for computing the energy that could be obtained by polar bears from eggs across the 24-day incubation period. We scaled their gram estimates of protein and fat to energy using the standard coefficients of 4.30 and 9.39 kcal g⁻¹, respectively (Robbins 1993; Schmidt-Nielsen 1997). We further scaled these by the digestibilities of protein and fat for polar bears (0.84 and 0.97, respectively) provided by Best (1985). This allowed us to estimate that a fresh egg would provide a polar bear with approximately 210 kcal and a nearly hatched neonate (at the end of the nesting period) would provide approximately 124 kcal. The energy content of an egg does not decline linearly during incubation, especially for the yolk for which more than 80% of the lipid consumption occurs during the final third of the incubation period (e.g., O'Connor 1984). Romanoff (1967) provided a daily accounting of the decline in the yolk content of the chicken egg and we modeled the decay in available energy of snow goose eggs (Y) across the incubation period (X) based



Cape Churchill

La Pérouse Bay

on those data $(Y = -0.01X^3 + 0.19X^2 - 1.03X + 210.87; R^2 = 0.99).$

We used this model to compute a profile of energy potentially available to polar bears over the nesting period (egg laying and incubation) of snow geese on the Cape Churchill Peninsula. In doing that, however, we had to account for the fact that while each goose has an incubation period of approximately 24 days, the entire colony is not synchronous (Cooke et al. 1995). In average years, nest initiation spans a 7-day period with a near symmetrical distribution of daily initiation peaking on day 4 (Cooke et al. 1995). Using our current colony size estimate of 48,855 pairs of snow geese (Ross et al. 2004; R. F. Rockwell, unpublished data), our detailed data on nesting phenology and assuming a modal clutch size of four, we calculated the number of nests that initiated on each of the 7 days and computed the energy they would provide during the 4-day egg-laying period and across the 24-day incubation period. We summed the daily contributions of these staggered initiation nests to generate an energy profile for the overall 33-day nesting period of the colony. The profile spans the period from initiation of the earliest nests through hatching of the latest ones.

In years of late melting snow, overall nest initiation is delayed, and the pattern and relative distribution of nest initiation is narrower and negatively skewed, while in early melt years, there is an advance of overall nest initiation and a positive skew to the distribution (Cooke et al. 1995; R. F. Rockwell, unpublished data). Energy profiles for such years were adjusted accordingly and compared to each other and a profile for an average year. It is important to note that we have not detected any spatial variation in initiation or hatch dates across the nesting area depicted in Fig. 1 (R. F. Rockwell, unpublished data).

The energy content of seals

There are limited data on the depredation of ringed seals by polar bears. The bulk of it is based on observations made during the 1970s at Radstock Bay on Devon Island in the central Canadian High Arctic by Stirling and his colleagues (Stirling 1974; Stirling and Archibald 1977; Stirling and Latour 1978). Those data and other unpublished observations are summarized by Stirling and Øritsland (1995). Estimates of the energy content of ringed seals of various age classes collected in Amundsen Gulf are summarized by Stirling and McEwan (1975). We used those data to estimate the average amount of energy polar bears obtain each day from seals in spring prior to break up. We focus on this metric since climate change is expected to "cost" polar bears days of spring seal-hunting opportunities.

Seal pups grow rapidly and increase in energy content through the spring and early summer (Stirling and McEwan 1975). Our daily energy intake computation accounted for both age structure and age-specific energy content of seals consumed by polar bears (Stirling and Øritsland 1995). We assumed that the energy came solely from the consumption of seal fat (Stirling and McEwan 1975) and that this would provide 9.39 kcal g^{-1} of gross energy (Robbins 1993; Schmidt-Nielsen 1997). We used the fat digestibility rate of 0.97 (Best 1977) to convert this to the energy available to polar bears. On average, a polar bear obtains approximately 22,432 kcal of energy per day from the consumption of seals.

For simplicity, we refer to this energy gain as a "seal day," denoting that it is the average energy a polar bear obtains per day consuming seals on the ice during the spring and early summer. Equivalently, it is the average daily energy lost when that hunting is prevented by reductions in the ice platform associated with climate change. While these estimates are based on seal depredation from further north and more than 3 decades ago, they were used by Stirling and Øritsland (1995) to develop a depredation and energy-based model that related polar bear and ringed seal abundances. They successfully applied this model across a wide geographic range of the Canadian High Arctic, and more recently Lunn et al. (1997) found that its predictions were applicable in western Hudson Bay. As such, the seal day estimate of 22,432 kcal is a reasonable approximation for our purposes.

Since it was not our intent to provide a full evaluation of daily and seasonal energy budgets for polar bears living on either geese or seals, we did not consider energy costs of searching, catching, consuming or digesting prey. Rather, we assumed that the overall field metabolic rate associated with walking through the nesting colony and eating eggs (density is 5–20 nests ha⁻¹ on much of the colony) would not be dissimilar from the rate assumed by Stirling and Øritsland (1995) for seal consumption based primarily on still hunts (77%) mixed with some stalking and chasing (Stirling 1974; see also Best 1985).

Results and discussion

Advances in the timing of snow goose nesting

The mean hatching dates of snow geese nesting on the Cape Churchill Peninsula from 1968 to 2007 are depicted in Fig. 2. There is a small but statistically significant advance in the mean date of hatching (and thus the nesting period) of snow geese over the 40 years of this study $[0.16 (\pm 0.07) \text{ days year}^{-1}; F_{1,37} = 4.18, P = 0.048]$. The rate of advance in hatching is consistent with the advance in the arrival date of snow geese at Delta Marsh, Manitoba, a known staging area for snow geese (Murphy-Klassen et al.



Fig. 2 The mean hatching date of Lesser Snow Geese nesting on the Cape Churchill Peninsula has advanced by $0.16 (\pm 0.07)$ days/year over the 40 years of the study

2005). It is important to note that the advance in mean date occurs in the face of a substantial amount of annual variation.

Advances in the timing of sea ice breakup and the onshore arrival of polar bears

The estimated mean rate of advance in sea ice breakup is $0.72 (\pm 0.23)$ days year⁻¹, which is substantially (and significantly, P < 0.02) higher than the advance in hatching date of the snow geese. Physical processes such as the "sea ice-albedo climate feedback mechanism" (Cury and Schramm 1995; Overpeck et al. 1997) suggest that sea ice breakup may proceed more rapidly both within and between years than land-based processes; so, this difference is not unexpected. The correlations between annual breakup estimates in the four studies and annual hatching date estimates are not especially high (r = 0.16 - 0.41), suggesting that goose nesting likely responds to additional variables that do not appear to be changing at the same overall rate as those affecting sea ice breakup (cf. Skinner et al. 1998). One implication is that there will be periodic annual mismatches when, for example, an early sea ice breakup may occur during the same spring as a late nesting period.

The date of sea ice breakup is a reasonable predictor of the onshore movement of polar bears (e.g., Stirling et al. 1999; Stirling and Parkinson 2006). However, the move is not immediate and does not initially involve all the polar bears, since the transition from initial sea ice breakup to an ice-free Hudson Bay can extend over several weeks (Gagnon and Gough 2005). Further, the order of onshore arrival is not random on the Cape Churchill Peninsula. During our spring and early summer coastal surveys, we generally observe subadult bears arriving ashore first, before any family groups or lone adults are seen (R. F. Rockwell, unpublished observations). This nonrandom pattern is perhaps not surprising, since the spring loss of sea ice-based platforms could increase competition for seal hunting and subadults would not fare well against prime-aged and larger adult males (M. A. Ramsay, personal communication).

Subadult bears are also the only ones that have thus far been observed during the nesting period on the Cape Churchill Peninsula. The mean arrival date of the first bear seen in the nesting area during 2000–2007 (for which we have consistent helicopter surveys across the entire area) is 23rd of June (\pm 3 days), and this overlaps the average nesting period for 2000–2007 by 2 days (see below). Given that the relative rate of advance in sea ice breakup is 4.5 times the advance in hatching date, we expect to see increasing numbers of polar bears earlier in the nesting period of the snow geese on the Cape Churchill Peninsula.

The energy available to polar bears from snow goose eggs

The amount of energy available to polar bears using the eggs of nesting snow geese changes over the nesting period. This is depicted in Fig. 3 for three chronological scenarios, an early year, an average year and a late year. As explained before, the relative pattern and distribution of nest initiation by the geese differ among these scenarios. As is clear in Fig. 3, however, these differences only lead to small and subtle changes in the shapes of the three energy profiles (e.g., the late year has a faster initial rise and terminates sooner). The primary difference among the profiles is their absolute position along the annual time axis. Together, the early and late examples depict the maximum range observed for the Cape Churchill Peninsula colony of snow geese.

In all three cases, the available energy increases as additional pairs begin laying and as they add eggs to their nests. The available energy declines slowly at first and then more rapidly as development progresses into its last 10 days and



Fig. 3 The energy available to polar bears from the eggs of nesting Lesser Snow Geese changes over the nesting period—rising during nest initiation, falling over the 24 days of incubation and reaching 0 when the goslings hatch and leave the nesting habitat. The relative position of the energy profile, as well as minor aspects of its shape, varies as a function of the date of nest initiation. See text for more detail

as increasing numbers of pairs take their hatching goslings out of the nesting area and onto brood-rearing habitat. The potential value of snow goose eggs would be substantially higher in years when sea ice breakup brought polar bears ashore during the first 14–16 days of the nesting period. Such a trend is anticipated under current climate change models and is expected periodically owing to annual mismatches between the timing of the nesting period and the timing of breakup.

Overlap of the snow goose nesting period by polar bears

The current situation for the Cape Churchill Peninsula is depicted in Fig. 4, where the mean date the first polar bear was seen on the nesting colony from 2000 to 2007 is indicated on the average energy profile computed for the same years. These years include an equal number of earlier and later nest initiation years (Fig. 2); so, while the absolute time scale is an "average", it is representative of this more recent period. On average, the earliest bear overlaps the last few days of the mean hatching period. The rates of advance of both the nesting period and polar bear arrival (as predicted by advance of sea ice breakup) are also indicated. If these trends both hold, polar bear arrival will overlap the mean of the hatching period in 3.6 years and the energy available then will represent an increase of more than 300% (from 4.24×10^6 to 17.02×10^6 kcal). If the trends hold for a decade, the overlap would have advanced by approximately 5.6 days and the energy available will have risen by more than 660% to 32.25×10^6 kcal.



Fig. 4 Polar bears are beginning to overlap the nesting period of Lesser Snow Geese on the Cape Churchill Peninsula. Since the advance of onshore arrival of polar bears is estimated to be 4.5 times faster than the advance in the nesting period of the geese, the amount of energy available to the bears will increase as the overlap with the nesting period becomes earlier. The energy profile and the date on which the first polar bear was seen in the nesting area are averages for the period 2000–2007. The mean hatching date is 21st of June and mean date for the first bear's arrival is 23rd of June

Polar bear arrival and foraging on snow goose eggs

Given the current overlap of nesting period and polar bear arrival, the early bear needs to consume the eggs from approximately 43 nests to compensate for a one seal-day energy loss. There would be over 8,305 such nests still available, even at this late stage of the nesting period, and those nests represent a reservoir of compensation energy equivalent to more than 190 seal days. If the bear overlapped the nesting period 5.6 days earlier, it would only need to consume the eggs from 34 nests to compensate for a one seal-day loss. In that situation, the bear could forage from among 48,855 nests, a total reservoir of approximately 1,438 seal days that could be used by one or more polar bears. Although the nests are distributed across the entire nesting area depicted in Fig. 1, there are no sections where high concentrations of nests are more than 5 km apart, and while some nests are up to 15 km inland, most are within 5 km of the coast. Since there are numerous examples of individual polar bears traveling overland more than 50 km in a single day (D. Hedman, personal communication), the resource is readily available. The earlier bear, whether its overlap with a higher energy section of the nesting period results from a decade's advance due to climate change or to a seasonal mismatch between sea ice breakup and nesting period, would certainly get the better deal.

Consistent with the advance in sea-ice breakup, four of the six bears we observed during the nesting period over our 40-year study were seen since 2000. In all six cases, the bears were observed within the nesting area and their size and lack of facial scars were most consistent with them being subadults. In four cases, we were able to follow a portion of the individual's trail through the nesting colony. For one, there was no evidence of egg depredation despite the fact that tracks went right past several nests. In the other three cases, we located 5, 11 and 16 depredated nests along the portion of the trail we followed. These numbers are likely underestimates, since the exact trail was difficult to follow in some of the more vegetated and rocky sections of the nesting colony. Curiously, depredation was not continuous along the bears' trails, as depredated nests were found interspersed with intact nests.

In similar fashion, Smith and Hill (1996) reported that a lone polar bear consumed the clutches of eggs at only four of 36 Canada Goose (*Branta canadensis* Linnaeus) nests on Akimiski Island in southern James Bay on a single foray during the nesting period. Madsen et al. (1998) reported that polar bears depredated 135 eggs from 43 of 85 nests of Light-bellied Brent Geese (*Branta bernicla hrota* Linnaeus) on Svalbard in 1987 and 1991. Finally, Drent and Prop (2008) report that a single female polar bear and her cub consumed the eggs from 108 Barnacle Goose (*Branta leucopsis* Linnaeus) nests in a single day in 2004 on Svalbard. In describing that depredation, Drent and Prop (2008) note that the female and cub broke many of the eggs by pressing with their noses and then licking up the contents, consuming both partially developed goslings and egg residue. At one point, the bears left the goose colony, drank from a freshwater pond and then returned and continued eating eggs. Clearly, when opportunity arises, polar bears consume large numbers of goose eggs.

Taken together, these observations raise the question of whether a polar bear arriving ashore with a specific accrued energy deficit, for example four seal days, would forage only until that deficit was replaced or would the bear continue foraging until it ran out of nests, became satiated or, perhaps, gained too much weight to forage further (M. Ramsay, unpublished data). To our knowledge, there is little information available on this point, especially as it pertains to the consumption of migratory waterfowl eggs by polar bears. Reviewer 2 (personal communication) noted that one polar bear foraging on waterfowl eggs appeared to consume the contents of about 10 nests and then rest for up to an hour before resuming foraging. This may indicate at least a pattern of temporary satiation.

Our relevant observation on this point is of a subadult male that came ashore after the snow geese had hatched but while common eiders were still nesting in a dense colony at La Pérouse Bay. We observed the polar bear walk from island to island and consume all the eggs from 206 of the approximately 325 active common eider nests during an approximately 96-h period (P. Z. Matulonis, unpublished data). Unfortunately, the bear had to be chased from the area for safety reasons and we were unable to see if it would have consumed more clutches or had become satiated. Assuming the energy available to polar bears from eider eggs scales to the eggs' size relative to that of a snow goose egg, the bear's foraging yielded more than 170,000 kcal or approximately 7.5 seal-day equivalents in just 96 h.

These observations do not fully resolve whether arriving polar bears would simply satisfy any accrued energy deficit or gorge on an ephemeral resource. Polar bears are certainly known to gorge when otherwise scarce food is available (Amstrup 1986; Amstrup and Nielsen 1989). They can consume up to 10% of their body mass in 30 min and their stomachs can hold up to 20% of the their body mass (Best 1977). The literature on foraging in other bear species indicates that satiation likely does occur. Beckmann and Berger (2003), for example, showed that black bears (Ursus americanus Pallas) displayed satiation rather than gorging indefinitely on unlimited supplies of urban garbage. Similarly, studies of grizzly bears (Ursus arctos Linnaeus) indicate that they will consume large quantities of abundant salmon (exceeding 20% of their body mass), but will eventually stop and switch to berries and other vegetation even though salmon are still available (e.g., Hilderbrand et al. 1999).

Grizzly bears also exhibit highly selective foraging, only consuming certain parts of the salmon under some conditions, perhaps indicating that factors other than simple energy maximization may drive their foraging behavior (Gende et al. 2001). This was further explored by Robbins et al. (2007), who showed that captive grizzly bears, given access to abundant salmon and fruit, preferred a mixed diet rather than gorging indefinitely on salmon, again in contrast to simple energy maximization models. They showed further that the mixed diet actually increased rates of growth and mass accumulation. Whether polar bears, which have been shown to consume a variety of fruits and other vegetation (e.g., Derocher et al. 1993), would display a mixed foraging strategy, reducing consumption of snow goose eggs, and whether it would benefit them in a fashion similar to that shown for grizzly bears, is not currently known but certainly important.

The consumption of snow goose eggs by early arriving subadult polar bears raises two interesting behavioral issues. First, if subadults come ashore earlier than more mature members of the population, owing, perhaps, to competitive displacement, what will happen as they mature? Will they remain on the sea ice longer once they achieve a more competitive size or will they take advantage of experience and knowledge of resources and leave early to consume snow goose eggs in subsequent years? Results presented by Madsen et al. (1998) and Drent and Prop (2008) indicate that some individuals leave the sea ice regularly to eat goose eggs suggesting that the behavior becomes habitual at least for some polar bears.

Second, since eggs consumed earlier in the nesting period provide more energy, might individual polar bears be able to sense this and progressively come ashore earlier to exploit an even more valuable resource? Or is the consumption of goose eggs a simple opportunistic reaction to sea ice breakup that forces polar bears ashore? Observations that both immature and adult polar bears on Svalbard leave solid pack ice and consume eggs of light-bellied brent and barnacle geese early during their nesting period despite the availability of seals (Madsen et al. 1998; Carlens et al. 2006; Drent and Prop 2008) suggest that the use of goose eggs may not be exclusively driven by broken sea ice and the attendant difficulties of hunting seals. The observations with respect to both issues may be another example of the behavioral flexibility and adaptability of polar bears (e.g., Derocher et al. 2000).

Unlike prime-aged adults, the subadult age class of the WH population appears to have suffered a 2-5% decrease in annual survival for each week of advance in breakup (Regehr et al. 2007). If this is due to an accrued energy deficit, as they suggest, then the consumption of snow

goose eggs could improve bears' condition and stabilize or reverse the survival decline of this age class. Assuming that the age structure given by Stirling and Øritsland (1995) is generally applicable, this age class represents approximately 25% of the region's population. Given the high relative importance of survival to population growth, such a reversal could at least temporarily increase the near-term growth rate of the WH polar bear population (cf. Heppell et al. 2000; Koons et al. 2006).

General considerations

If climate change continues at its current or even an accelerated pace, polar bears will increasingly overlap the nesting period of snow geese on the Cape Churchill Peninsula. Energy available in the goose eggs could be used to offset some of the accrued deficits from lost seal-hunting opportunities with earlier portions of the nesting period providing the greatest energy. The earliest arriving polar bears will likely be members of the subadult age class, and they would be the first to benefit although the total number gaining from this resource will depend on individual foraging strategies. Competition could lead to a "tragedy of the commons" situation (Rankin et al. 2007), where individual self-interests degrade a resource the whole group could use. Preliminary simulations indicate that if more than 36% of the nests are depredated the snow goose colony would decline. Both Madsen et al. (1998) and Drent and Prop (2008) indicate that polar bear depredation on Svalbard is sufficient that it is impacting the resident goose populations.

While the energy from snow goose eggs may reduce or delay the immediate impact of climate change on the polar bears of this region, simple extrapolation of the available egg energy values indicate that other food sources will have to play a role if the polar bears are to persist in the long term. Polar bears display a high level of behavioral plasticity, capturing and consuming other prey while on land (e.g., Russell 1975; Derocher et al. 2000; Dyck and Romberg 2007; L. J. Gormezano, unpublished data). Such foraging, especially if it increases in frequency, could further mitigate losses of sea ice-based seal hunting. It is also possible that polar bears may increase their daily rate of seal capture prior to or during breakup, thus reducing their accrued energy deficit when arriving onshore. It is our view that in monitoring the health of this species, we should pay particular attention to the polar bears' diverse foraging abilities and their attempts to cope with environmental changes. We feel this is a better approach than making predictions based only on their historic behaviors in habitats that are themselves now changing.

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Trophic matches and mismatches: can polar bears reduce the abundance of nesting snow geese in western Hudson Bay?

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Climate change driven advances in the date of sea ice breakup will increasingly lead to a loss of spring polar bear foraging opportunities on ringed seal pups creating a phenological trophic 'mismatch'. However, the same shift will lead to a new 'match' between polar bears and ground nesting birds. This new match will be especially prevalent along the Cape Churchill Peninsula of western Hudson Bay where both polar bears and nesting snow geese are abundant. Easily foraged goose eggs will provide at least some of the earlier arriving polar bears with compensation for the energy deficit accrued through lost seal hunting opportunities. We examine the potential impact of changes in the extent and pattern of polar bear egg predation on snow goose abundance using projection models that account not only for increases in the temporal overlap of the two species but also for autocorrelation and stochasticity in the processes underlying polar bear onshore arrival and snow goose incubation. Egg predation will reduce reproductive output of the nesting lesser snow geese and, under all but trivial rates, will lead to a reduction in the size of their nesting population on the Cape Churchill Peninsula. Stochasticity associated with the asymmetrical advances in polar bear onshore arrival and the snow goose incubation period will lead to periodic mismatches in their overlap. These, in turn, will allow snow goose abundance to increase periodically. Climate driven changes in trophic matches and mismatches may reduce snow goose numbers but will not eliminate this over-abundant species that poses a threat to Arctic landscapes.

Global climate change has led to shifts in the phenology of numerous species of plants and animals (Parmesan and Yohe 2003). Owing to inherent differences among species in their physiological tolerances, reaction norms and life histories, it is not surprising that their responses to even similar trends in climate change are not the same (Both et al. 2009). When the species affected are also ones that occur at different trophic levels in the same or linked ecosystems, mismatches in their normal trophic interactions may develop (Both et al. 2009). As many of those trophic interactions involve the transfer of nutrients and/or energy, these mismatches can reduce the success of one or more of the interacting species, reduce biodiversity and destabilize ecosystems (Visser and Both 2005).

One interesting climate related mismatch that spans trophic levels is the case of polar bears *Ursus maritimus* and their primary prey, the ringed seals *Phoca hispida* (Stirling and Parkinson 2006). Advances in the spring breakup of sea ice are believed to reduce the ability of polar bears to consume ringed seal pups during a time when this resource is especially critical to the polar bears (Stirling and Derocher 1993). This is particularly problematic for polar bears living in western Hudson Bay, near the southern limit of the species, where impacts of global change are expected to be felt more immediately (Skinner et al. 1998). Recent analyses of polar bears in that region have reported declines in the body condition, reproductive success, survival and population size that coincide with an advance in spring sea ice breakup (Stirling et al. 1999, Regehr et al. 2007).

Ironically, the same climate-based shift and mismatch that is potentially depriving polar bears of their ability to hunt ringed seals on the sea ice is also bringing polar bears ashore on the Cape Churchill Peninsula, near Churchill, Manitoba, at a time when a large population of lesser snow geese Chen caerulescens caerulescens (henceforth snow geese) is incubating its eggs (Rockwell and Gormezano 2009). Polar bears have increasingly been observed eating snow goose eggs when their onshore arrival overlaps the incubation period. Similar goose egg predations have been observed on Southampton and Coats Islands (Smith et al. 2010), Akimiski Island in southern James Bay (K. F. Abraham pers. comm.) and on Svalbard (Madsen et al. 1998, Drent and Prop 2008). Although this new match to a different prey species could provide a substantial nutritional resource to at least part of the local polar bear population, the situation is so new that neither the extent of future predation nor its impact on the nesting snow goose population are yet known. While polar bears have also been observed capturing and consuming flightless goslings and adults after the incubation period (Rockwell et al. unpubl.), we chose to focus on the impact of their nest predation given the comparatively low energy expenditure and high caloric reward associated with their eating eggs (Rockwell and Gormezano 2009).

Madsen et al. (1998) and Drent and Prop (2008) report that polar bear egg predation on Svalbard is sufficient that it is negatively impacting the resident goose populations. If egg predation in the Cape Churchill Peninsula region leads to a similar decline in the nesting population of snow geese, it would add a second irony to this climatebased 'mismatch becomes new match' situation. The midcontinent population of snow geese has grown to such an extent that it is severely degrading much of the Hudson Bay Lowlands (Jefferies et al. 2003). While the Canadian and US governments initiated a management program in 1997 to reduce the numbers of snow geese, those attempts have not yet been successful (Alisauskas et al. 2010). Increased climate-driven polar bear predation could actually aid in attempts to lower snow goose abundance and reduce local habitat damage.

Although the extent of egg predation and its impact on the snow goose population depends to some degree on the foraging behavior of polar bears and the reaction of snow geese to that predation, they ultimately depend on the dynamics of temporal overlap between polar bears and incubating snow geese. The processes underlying overlap - onshore arrival of polar bears and timing of snow goose incubation - are stochastic, partially independent and driven by autocorrelated climatic factors (e.g. the sea ice-albedo climate feedback mechanism: Curry et al. 1995). While deterministic linear analyses indicate the processes are advancing at different rates and suggest that overlap will increase (Rockwell and Gormezano 2009), such analyses may not accurately capture the joint dynamics of stochastic processes that are also influenced by feedbacks, time lags and increasing variability in the physical processes underlying climate change (Salinger 2005, Cryer and Chan 2008).

In this paper we examine the potential impact of increased polar bear egg predation on the Cape Churchill Peninsula population of snow geese. We first estimate advances in the incubation period of nesting snow geese and spring sea ice breakup (a surrogate for onshore arrival of polar bears, Stirling et al. 1999) using a series of models that account for autocorrelation and stochasticity in the underlying processes. We then use parameter estimates and stochastic projections from those analyses in combination with matrix population models to examine the increasing overlap and potential impact of polar bear egg predation on the nesting population of snow geese. Being mindful of the international management goal to reduce numbers of snow geese, we focus initially on models incorporating catastrophic levels of egg predation and evaluate its maximum potential impact. Since many factors related to both polar bears and snow geese could change this maximum potential impact (Discussion), we also examine the sensitivity of snow goose population dynamics under a complete range of constant and changing egg predation intensities.

We show that under the advances in overlap anticipated from global climate change, the abundance of snow geese in the Cape Churchill Peninsula will decline under all but near-trivial predation rates. However, even under the most extreme rate of predation, the snow goose colony on the Cape Churchill Peninsula should persist in the near term (25 year time span) and, as such, could continue to provide a nutritional subsidy for a portion of the local population of polar bears. Interestingly, the impact of polar bears on geese is less severe when stochastic variation in the underlying processes is accounted for than when it is ignored, as when using deterministic projections. We examine our findings in light of what is known about the interacting behaviors of polar bears and snow geese. Finally, we discuss the importance of our findings to management and conservation of snow geese and polar bears, and to general considerations of the impact of climate change and variation on trophic interactions and ecosystem stability.

Methods

Study site

This study makes use of data on snow geese and polar bears found in and around Wapusk National Park, approximately 30 km east of Churchill, Manitoba, Canada (Fig. 1). The snow geese are part of the mid-continent population (Abraham and Jefferies 1997) and the polar bears are part of the Western Hudson Bay (WH) population (Aars et al. 2006). Nesting snow geese are associated with more than 150 km of coastline on the Cape Churchill Peninsula and can be found up to 15 km inland although most occur within 5 km of the coast (Rockwell and Gormezano 2009).

Polar bears also occupy this nesting area as they move onshore in response to the breakup of sea ice in Hudson Bay (Rockwell and Gormezano 2009). During the ice-free period they occupy all of Wapusk National Park and much of the adjacent land to the west (Derocher and Stirling 1990). The advance of sea ice breakup in the spring will increasingly lead to the two species occurring in the same area at the same time. This joint use has already begun and has led to increasing predation of snow goose nests by polar bears (Rockwell and Gormezano 2009).

Data

Assessing the dynamics of temporal overlap between polar bears and incubating snow geese and projecting the potential impact of any resulting egg predation on the snow goose population requires annual timing data on both the snow goose incubation period and the on-shore arrival of polar bears. Clearly, the more years of overlap, the better are the chances of correctly capturing and projecting any joint effects. Data on lesser snow goose nesting phenology have been collected since 1968 as part of a comprehensive, long-term study on the Cape Churchill Peninsula. Methodological details are given in Cooke et al. (1995) and a preliminary deterministic linear analysis of those data, using mean hatching date as an indicator for the incubation period, is presented in Rockwell and Gormezano (2009).

The date of sea-ice breakup in the portions of Hudson Bay that are relevant to the WH polar bear population has



Figure 1. Snow geese nest in coastal and near-coastal habitat of Wapusk National Park. As sea ice breaks up in the spring, the onshore movement of polar bears takes them into the nesting habitat of snow geese. During the ice-free period, polar bears are found throughout the Park and the areas north and west towards the Churchill River. Coastal concentrations of polar bears are high from Cape Churchill to Rupert Creek with the highest concentrations usually located north of the Broad River.

been used as a surrogate for the onshore arrival date of WH polar bears (Stirling and Parkinson 2006). Four studies have used deterministic linear analyses to examine the advance in sea ice breakup and its potential effect on polar bears of the WH population (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007) and deterministic linear analyses of the data produced comparable estimates for the advance in the date of breakup (Rockwell and Gormezano 2009). More recently, Lunn (2008, Lunn pers. comm.) summarized a long continuous data series of sea ice breakup dates that extends those reported in Stirling et al. (1999). They are also based on Etkin's (1991) 50% ice cover criteria and are estimated with methods detailed in Stirling et al. (1999). Because those data cover nearly the same time span as our data on snow goose nesting phenology, we have used the Lunn (2008) data to model potential changes in the onshore arrival of polar bears. These two data sets are depicted in Fig. 2.

Statistical analysis of advancement in nesting phenology and sea ice breakup

While deterministic linear analyses demonstrated advances in both the incubation period of snow geese and the onshore arrival of polar bears (Rockwell and Gormezano 2009), failure to account for autocorrelation in time series data could lead to biased estimates of trend and stochastic variation associated with the underlying processes (Cryer and Chan 2008); parameters that are central to the rest of our analyses. To accomplish this with both snow goose nesting and sea ice breakup data, we first examined plots of the sample (partial) autocorrelation functions ('acf' and 'pacf' procedures in the TSA package of R 2.8.1). This provided some insight into plausible degrees of auto-regressive (AR) and moving-average (MA) signals in the data.

We then developed a set of stochastic regression models with AR and MA orders between 0 and 5 ('arima' procedure



Figure 2. Time series for the mean Julian dates of lesser snow goose hatch in the Cape Churchill region (\Box), and Julian dates of sea ice breakup in the portions of Hudson Bay that are relevant to the WH polar bear population (\blacksquare) (after Lunn 2008).

in the TSA package of R 2.8.1 and, henceforth ARMA models). Because time series data often exhibit high-order ARMA signals without displaying significant low-order signals, we also developed models with high-order ARMA terms and fixed the parameters for some low-order terms to 0 (i.e. the low-order terms were not estimated; Cryer and Chan 2008). In addition to the ARMA parameters, each stochastic regression model contained parameters for non-stationary trends in the respective time series (intercept and slope parameters, as opposed to differencing) and stochastic variation (i.e. 'white noise'; Cryer and Chan 2008).

Thus, the general form of our stochastic regression model was:

$$Y_{t} = \text{trend model} + \phi_{1}Y_{t-1} + \dots + \phi_{5}Y_{t-5} + e_{t} \\ + \theta_{1}e_{t-1} + \dots + \theta_{5}e_{t-5}$$
(1)

where Y denotes the response variable (date of snow goose hatching or onshore arrival of polar bears), e is a standard normal deviation from the deterministic component of the model, and φ and θ denote the AR and MA parameters respectively.

We used Akaike's information criterion adjusted for sample size (AIC_c; Akaike 1973) to determine which model(s) served as the best approximation(s) to the data (Burnham and Anderson 2002). Precision of estimated model parameters was assessed based on standard errors and the extent to which 95% confidence intervals overlapped zero (Graybill and Iyer 1994).

Projections of the advancement of snow goose incubation period and polar bear onshore arrival

We used our best stochastic regression models for dates of sea ice breakup and hatching, along with their associated parameter estimates (including variance), to project both snow goose incubation period and polar bear onshore arrival for 25 years into the future. Projections based on global circulation models were not used to model advances in sea ice breakup because they do a poor job of predicting localized phenomena, especially in the regions of Hudson Bay relevant to the WH population of polar bears (Gough and Wolfe 2001, Gagnon and Gough 2005). We believe 25 year projections provide insight into future dynamics but serve as a reasonable near-term time horizon for projections that do not overstep the length of the observed non-stationary time series (Fig. 2). Values of e_t (Eq. 1) were drawn from a normally distributed random variable $e \sim N(0,\sigma^2)$, where σ^2 denotes the estimated stochastic variation (i.e. white noise) in the time series attained from the focal model. We generated 1000 random realizations of the 25 year projections to obtain a representative sample for each of the two stochastic processes (hatching date and onshore arrival date) using R. These are referred to throughout as the ARMA projection set.

Because we were also interested in examining the possible effect of increasing levels of stochastic variance on the overlap of polar bears with the incubation period and its potential impact on the nesting snow goose population, we generated three additional projection sets using 25%, 50% and 100% inflation of the stochastic variance in the best ARMA models. These are referred to throughout as the 'added variance series', and serve as a numerical sensitivity analysis to increased temporal stochasticity.

For comparison with past studies that did not account for AR, MA or stochasticity in these two time series (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), we also evaluated our data with simple linear regression models and evaluated their support with AIC_c (Appendix 1).

Projecting the overlap of polar bears and the snow goose incubation period

Nest initiation by snow geese on the Cape Churchill Peninsula spans a 7-day period with an average of 0.06, 0.11, 0.18, 0.30, 0.18, 0.11 and 0.06 of the females initiating on day one through seven (Cooke et al. 1995, Rockwell unpubl.). Eggs are laid one per day, and given a 24 day incubation period from the time the modal clutch of four is laid, the total incubation period averages 33 days (from the time the earliest initiating geese lay their first egg until the latest initiating females hatch their eggs; Rockwell and Gormezano 2009). We assumed that all nests being actively incubated when polar bears arrived onshore were available for predation and we measured the extent of that potential by the overlap of onshore arrival with the incubation period. We estimated the overlap as match = last incubation date – arrival date + 1 and computed its change over our 25 year projection intervals.

We computed the match for each of the 25 years in the 1000 realizations of model projections; then linearly scaled the match values such that the mean match value across the 1000 realizations for year = 1 was match = 2. This corresponds to the best mean empirical estimate we have for current overlap of the end of the incubation period (Julian 175) and first onshore arrival of polar bears (Julian 174) in the Cape Churchill Peninsula (Rockwell and Gormezano 2009). To provide a point of reference for these stochastic models, we also projected the match for 25 years using a deterministic linear model in which the value increased annually from match = 2 by 0.426 days year⁻¹, the difference between our best deterministic estimates of annual advances in the snow goose incubation period (0.145 days year⁻¹).

Projecting the snow goose population in the face of overlap and potential predation

We used a baseline projection model modified from the one originally developed by Rockwell et al. (1997) for management of the mid-continent population of snow geese. The basic demography of the Cape Churchill Peninsula population is summarized by the 5-stage (1, 2, 3, 4 and 5+ age class categories), pre-breeding census, Lefkovitch projection matrix **A**, parameterized from data in Rockwell et al. (1997) and updated from Dufour et al. (2010) as:

The first row of the matrix provides stage-specific measures of reproductive success (including breeding propensity and juvenile survival) while the remaining elements correspond to adult survival. Estimates of adult survival incorporate the minor impact that conservation-order harvest regulations have had since 1998 (Alisauskas et al. 2010), whereas estimates of reproductive success were made prior to any evidence of polar bear predation on nests and include a nest failure rate of 0.085 resulting from predation primarily by arctic foxes Vulpes lagopus, herring gulls Larus argentatus and parasitic jaegers Stercorarius parasiticus (Cooke et al. 1995). Given these vital rates, the projected population growth rate is much greater ($\lambda = 1.003$) than the management goal (0.85 to 0.95 per year, Rockwell et al. 1997). The associated stable stage distribution is $w = [0.169 \ 0.141 \ 0.117 \ 0.097]$ 0.477]. We used our most recent estimate of population size, distributed according to w, to initiate all projections and this included 58 798 females of which 48 855 were nesting birds of at least age class 2 (Rockwell unpubl.).

When snow goose numbers in a localized area of the Cape Churchill Peninsula increase in numbers and degrade that habitat, they disperse to adjacent, more intact habitat and thus avoid density-dependent population regulation (Cooch et al. 2001, Jefferies et al. 2003). In similar fashion, analyses have failed to detect any evidence of negative density-dependent effects on adult survival and, in fact, increases in adult survival are the most likely cause of increases in snow goose abundance (Alisauskas et al. 2010). Densitydependent effects are also lacking for both survival and reproductive success of the closely related greater snow goose C. c. atlanticus (Menu et al. 2002, Morrissette et al. 2010). As such, our projections of overall snow goose abundance were independent of population density and pertain to the Cape Churchill region rather than specific locations that geese have moved into or away from.

In projecting the snow goose population under stochastic egg predation by polar bears, we had to account for the proportion of the nesting colony that would still be incubating when the polar bears arrived onshore. We determined this from our match value (estimated from the joint stochastic projection sets described above) and from the staggered initiation distribution of nesting birds, also given above. When match = 1, 94% of the nesting birds would have hatched their clutches, leaving only the 0.06 proportion of the population that initiated latest available for potential predation. When match = 2, the proportion available would be 0.06 +0.11 = 0.17, etc., through match = 7 or higher, when the entire nesting population would be available. Clearly, when match = 0 or less, none of the nests are available for egg predation. The proportion of the population available for predation is termed p. We use the terminology 'total match' for situations when match \geq 7, 'partial match' when 0 < match < 7 and 'mismatch' when match ≤ 0 .

For simplicity we kept adult survival and reproductive success variables not related to egg predation constant because previous studies have found the population's dynamics are robust to environmental variability and that low levels of stochasticity in these variables have little effect on projected population dynamics (Rockwell et al. 2010).

The Cape Churchill Peninsula snow goose population was represented by the five age class vector \mathbf{n} and was projected as:

$$\mathbf{n}_{t+1} = \mathbf{A} \times (1-\mathbf{p}_t) \times \mathbf{n}_t + \mathbf{A}_{0,t} \times \mathbf{p}_t \times \mathbf{n}_t$$
(3)

where $\mathbf{A}_{0,t}$ is a modification of \mathbf{A} wherein the baseline nesting success (1 - 0.085) is reduced by a scalar ranging from 0 for catastrophic, worst-case (maximum) predation by polar bears to 0.9 for low level predation. We examined the entire range of possible constant annual predation rates $(\mathbf{A}_{0,t} = \mathbf{A}_{0,t+1})$ on snow goose dynamics to establish both the worst case potential impact and to evaluate what level of predation would lead to a decline of any sort in the nesting population. These model realizations assume that a sufficient number of polar bears are ashore to achieve the specified predation rate, independent of their numbers (Rockwell and Gormezano 2009).

To provide a point of reference for the stochastic models, we projected the population under constant annual predation rates using the deterministic linear model for advancement of 'match' explained above. We also projected the population under the maximum predation rate using the 'increasing variance series' amidst ARMA processes to examine the sensitivity of snow goose population dynamics to increasing stochasticity.

Finally, because it is possible that predation rates may change (either increasing or decreasing) over the 25 year projection period, we explored the effects of monotonic annual increases or decreases in the predation rates leading to $A_{0,t} \neq$ $\mathbf{A}_{0,t+1}$. We used a range of increasing and decreasing changes in the annual rates of predation but since the results were qualitatively the same, we report only those based on the projected annual decline in the polar bear population (Regehr et al. 2007), as it is the most realistic potential value of which we are aware. Assuming, for example, that predation rate is simply proportional to the size of the WH population, one could anticipate an annual decline in the predation rate of 0.986. Symmetrically, we used the compliment of this rate, 1.015, as an exemplar of the various scenarios that could lead to an increase in annual predation. Although we examined the effects of annual decreases and increases for the entire range of initial predation rates, we report only those for the maximum, medium and minimum initial rates.

All population projections were conducted using MAT-LAB 7.1.0.246 (R14).

Results

Advancement in nesting phenology and sea ice breakup

Our best stochastic regression model for snow goose nesting phenology (Table A1a) indicated a small but statistically significant advance in the mean date of snow goose hatch (and thus the incubation period) over the 41 years of study ($\beta_0 =$ 177.92, SE = 1.75; $\beta_1 = -0.16$, SE = 0.07). In addition, hatch date displayed a negative autoregressive pattern with lag 3 ($\phi_3 = -0.32$, SE = 0.17), and deviates from the linear advancement exhibited a substantial amount of stochastic variation ($\sigma^2 = 18.06$) as well as a positive moving average with lag 5 ($\theta_5 = 0.86$, SE = 0.29). Positive ARMA terms in a stochastic regression model imply that, independent of the deterministic trend, previous values (AR) or deviations (MA; Eq. 1) are carried over and remembered by the system. Negative ARMA terms, however, indicate a tendency for the time series to oscillate around the deterministic trend with values above the trend followed by values below the trend with a lag-order of x (Cryer and Chan 2008). Thus, on top of the linear advancement over time (β_1) and substantial random variation (σ^2), variation in snow goose nesting phenology also displayed a complex autoregressive-moving average pattern (a 3rd-order oscillatory signal and a 5th-order memory in the deviates). The next-best model also fit the data well $(\Delta AIC_{c} = 0.69)$; however, these two models differed by only one AR parameter, and substantially out-performed all other candidate models including the simple linear regression model (equivalent to the one reported by Rockwell and Gormezano 2009; details in Table A1).

Our best stochastic regression model for sea ice chronology over 38 years (Table A1b) indicated that although snow geese and polar bears did not overlap very often in the past ($\beta_0 = 196.79$, SE = 1.02), the advancement in date of WH ice breakup (and thus onshore arrival of polar bears) has occurred 3.7 times more rapidly than the advancement in snow goose nesting phenology ($\beta_1 = -0.59$, SE = 0.05). Deviates from this trend exhibited a large amount of stochastic variation ($\sigma^2 = 70.26$) as well as a negative moving average with 2nd and 3rd order lags ($\theta_2 =$ -0.51, SE = 0.13; $\theta_3 = -0.47$, SE = 0.12). Thus, dates of WH ice breakup have advanced rapidly but are also highly stochastic and somewhat oscillatory (Fig. 2). This model was a much better fit to the data than the next-best model $(\Delta AIC_c = 2.76)$, which differed by only one MA parameter (Table A1b). Relative to the simple linear regression model that has been used in the past (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), the top-ranking stochastic regression model for WH sea ice with MA parameters was superior (Table A1b).

Projections of future overlap between polar bears and the snow goose incubation period

Starting from the recent two-day 'match' between first polar bears and the snow goose incubation period in the Cape Churchill Peninsula region (Methods), we used the best stochastic regression models (ARMA) described above to simulate 1000 projections of future joint advancement in snow goose nesting phenology and WH ice breakup (and thus onshore arrival of polar bears). These simulations indicate that, on average, the number of match days should increase to approximately 12 in 25 years because of the more rapid advancement in breakup of the WH icepack (~0.59 days per year) relative to the timing of snow goose nest initiation and hatch (~0.16 days per year) (Fig. 3, Table 1a). Phenologies of goose nesting and onshore arrival of polar bears are nevertheless highly stochastic (Fig. 2), and thus so is the projected degree of overlap between polar bears and nesting snow geese (Fig. 3). Now and in the near future, there will still be years when snow goose nests are not exposed to polar bear predation. Yet, the chance of such a mismatch will become smaller as climate change progresses and match years become more common (Fig. 3). Projections made with added temporal stochasticity and a deterministic model produced very similar 'mean match' results, but estimates of variance differed greatly (Table 1a).

Projections of the snow goose population in the face of overlap and potential predation

For the most severe predation scenario possible, we assumed all of the nests available when polar bears arrive onshore would be consumed annually – 91.5% by the bears and the remaining 8.5% by other, more traditional predators. We modeled the snow goose population's dynamics under this maximum predation scenario using our best-fitting, stochastic ARMA projection set. Twenty realizations of the model are depicted in Fig. 4a and the mean along with upper and lower 2.5 percentiles of 1000 such ARMA realizations are presented in Fig. 4b. The result for the deterministic projection of the same maximum predation scenario is included



Figure 3. The extent of onshore overlap of polar bears and incubating snow geese is expected to increase over time given projections from our best fitting models for nesting phenology and advancement of sea ice breakup (and thus the arrival of bears on shore). The fine lines depict 20 realizations of the joint projections while the squares (\blacksquare) and triangles (\blacktriangle) depict the mean and upper and lower 2.5 percentiles of 1000 such realizations, respectively.

in Fig. 4b for comparison. Both the deterministic and stochastic projections begin with match = 2 when only 17% of the nesting population would be available for predation. The deterministic projection remains in this partial match state until year 12. During that time period, increasing proportions of the population are still incubating when polar bears

Table 1. The (a) extent of overlap (match) expected between the onshore arrival of polar bears and the snow goose incubation period at 25 years based on projections of the best stochastic regression models (ARMA), and (b) the estimated annual growth rate from 25 year projections of the snow goose population. For the stochastic projections the means and lower and upper 2.5 percentiles of 1000 independent trials are given. The added variance series examines the effect of increased stochastic variance in the joint ARMA projections on population growth rate, and the linear deterministic model serves as a baseline for comparison. (See text for additional details.)

(a)

	Days of match at t = 25						
Models used for projection	lower	mean	upper	variance			
ARMA stochastic	-10.9048	12.1526	34.1390	141.60			
Added variance series							
ARMA stochastic + 25%	-14.2245	12.2572	40.5758	179.4664			
ARMA stochastic + 50%	-15.5873	12.3421	41.8071	210.0555			
ARMA stochastic + 100%	-20.9797	12.1343	43.2671	287.3697			
Linear deterministic		12.2240		0			

(b)

		Lambda	
Models used for projection	lower	Mean	upper
ARMA stochastic Added variance series	0.8824	0.9058	0.9293
ARMA Stochastic + 25%	0.8827	0.9069	0.9289
ARMA stochastic + 50%	0.8862	0.9095	0.9321
ARMA stochastic + 100%	0.8882	0.9122	0.9349
Linear deterministic		0.8633	

arrive onshore. After year 12, match \geq 7 and the entire nesting population is available annually for predation. From that point on, the rate of population decline due to egg predation in the deterministic model is maximized.

The population's dynamics under the ARMA stochastic projection are quite different. Early in the 25 year time span, some realizations include total matches (Fig. 3) and the entire nesting population would be exposed to predation. As a result, the initial mean rate of decline is greater than that found for the deterministic projection (Fig. 4b). Midway through the 25 year time span the situation changes. Unlike the case with the deterministic projection, both partial matches and mismatches are still possible after year 12 under stochastic ARMA projections (Fig. 3). As such, predation is periodically reduced or even absent in some realizations and the mean rate of population decline is lower than that expected under the deterministic projection (Fig. 4b).

Because of these differences, the overall annual growth rate of the snow goose population, estimated across the 25 years using the Heyde-Cohen equation (Caswell 2001), is higher under the stochastic ARMA projection than under the deterministic projection (Table 1b) and the anticipated population size at year 25 is more than three times higher (Fig. 4b). With stochasticity, there are periodic years of partial match and mismatch after year 12 that allow the snow goose population to successfully reproduce and rebound to some extent. The relationship between stochasticity in the match of polar bears and snow geese and the growth rate of the nesting colony is clearly seen in the added variance series of projections (Table 1). Increasing the stochastic variance of both the snow goose incubation period and polar bear onshore arrival under ARMA projection resulted in no change in the mean overlap at 25 years but substantially increased its variance (Table 1a). Increasing variance in the match raises the likelihood of periodic mismatches later in the projection period that, in turn, increasingly allows the snow geese to periodically reproduce and offset to some extent the cumulative effects of predation (Table 1b).



Figure 4. The nesting population of snow geese is expected to decline under growing polar bear egg predation stemming from increased overlap of the two species on the Cape Churchill Peninsula. The upper panel (a) depicts 20 realizations of stochastic projections using our best fitting models for advancement of nesting phenology and onshore arrival of the bears and the worst-case scenario of maximum polar bear nest predation. The lower panel (b) depicts the mean as well as upper and lower 2.5 percentiles of 1000 such realizations and also includes a deterministic projection based on a model using the mean rate of increasing overlap and maximum predation. Stochastic variation in the overlap process leads to a less severe rate of decline of nesting snow geese over the 25 years. At 25 years, the stochastic model projects 4939 nests while the deterministic model projects only 1489 nests, a more than three-fold difference.

Under the most severe predation scenario and projections of our best fitting stochastic models, the Cape Churchill Peninsula population of nesting snow geese is expected to decline to 4939 nesting pairs in 25 years, a nearly 90% reduction. Not surprisingly, as the rate of constant annual predation is reduced, reproductive output is increased and the nesting snow goose population does not decline as rapidly (Fig. 5). Importantly, however, the population would still decline as long as polar bears annually predated at least an additional 2.7% of the available nests during the climate driven increase in overlap of the two species. The number of nesting pairs at the 25 year mark would range from 4939 (at the absolute maximum predation rate) to 42 753 (at the minimum predation rate depicted in Fig. 5). In all cases, 25 year population sizes and growth rates were higher under stochastic than deterministic projections.

While projections using constant annual predation rates set the boundaries for the potential impact of polar bear

predation on the nesting snow goose population, projections involving annual changes in those rates may provide a more realistic depiction of population dynamics of the nesting snow geese. Annual changes in the initial predation rates alter snow goose population dynamics in anticipated directions and displace the projected 25 year population size and growth rate to extents that depend on both the initial predation rate and the rate of annual change (Fig. 5). For example, a 1.4% annual decline in the maximum predation rate slowed the snow goose population decline by 2.1% while a 1.4% annual increase in the minimum predation rate depicted increased the snow goose decline by less than 0.3%. Annual 1.4% changes in the medium predation rate changed the population's growth rate by 0.9% and 1.3% (for decline and increase respectively). More extreme annual changes in the initial predation rate lead to greater impacts but follow the same pattern. None of the annual changes in predation rates examined (ranging



Figure 5. The number of snow goose nests on the Cape Churchill Peninsula is projected to decline under all but trivial levels of polar bear predation. Projections assuming a constant rate of predation (solid symbols (\blacklozenge , \blacktriangle , \blacksquare) set the boundaries of possible outcomes. Projections allowing increases (+) or decreases (-) in the initial predation rate over the projection interval lead to enhanced or reduced rates of decline. (Increases in the maximum initial rate and consistent decreases in the minimum initial rate are not possible). The projected rates of increase (1.015) or decrease (0.986) are based on estimates of decline in the WH polar bear population from Regehr et al. (2007). For clarity, only the means of sets of 1000 realizations are presented. The depiction for the 'maximum predation rate' is the same as shown as the mean of the stochastic projection in Fig. 4b. Its upper and lower 2.5 percentiles are the same as depicted there and those of the other means depicted in Fig. 5 are of similar magnitude. See text for details.

from the 1.4% depicted to 10%) resulted in 25 year population sizes that were outside the boundaries set by the constant annual rate projections depicted in Fig. 5. Importantly, and consistent with the constant annual predation scenario, the anticipated annual growth rates and 25 year population sizes were higher under stochastic than deterministic projections.

Discussion

Assuming global climate change continues as anticipated, polar bears will increasingly overlap the incubation period of lesser snow geese on the Cape Churchill Peninsula. At anything higher than trivial rates, polar bear nest predation should result in a decline of the nesting snow goose colony. However, even the most catastrophic predation rate is not expected to eliminate the local nesting population in the near term because climate driven mismatches in onshore polar bear arrival and snow goose incubation will allow for periodic years of low predation and temporary increases in nesting snow goose abundance. Eggs of the persisting snow geese would serve as a supplemental terrestrial food source for a portion of the local population of polar bears that could offset spring nutritional shortfalls during the ice-free season. In the following, we discuss our findings in greater detail and relate them to climate change and the limited information currently available on interactions between polar bears and geese. We end by examining how our work relates to general issues of climate-based matches and mismatches in the phenology of species occupying different trophic levels.

Stochastic ARMA models clearly provide better fit to changes in the snow goose incubation period and the spring disappearance of sea ice (the surrogate for onshore arrival of polar bears) than do simple linear regression models (Table A1). Like those models, they also predict that onshore polar bear arrival will increasingly overlap the incubation period of snow geese on the Cape Churchill Peninsula, setting the stage for increased nest predation. Our analyses reveal the presence of autocorrelation in both processes although they do not identify underlying causes. For snow geese, such autocorrelation is likely related to the fact that the geese are long-lived and as such, the same individuals or cohorts, perhaps with similar nesting tendencies and reactions to autocorrelated climate conditions, may predominate for short strings of years (Stenseth et al. 2002). For sea ice breakup, the "sea ice-albedo climate feedback mechanism" (Curry et al. 1995) suggests a positive momentum in breakup and as such the autocorrelation we detected may actually increase over time.

The stochastic ARMA models provide not only a more accurate projection basis for the joint processes underlying the increasing overlap but also generate different population dynamics for nesting snow geese than do deterministic linear models, and this is true for all rates and patterns of predation. Theory suggests that environmental stochasticity has a negative impact on population growth (Lewontin and Cohen 1969) but this is not necessarily true for inhomogeneous systems (Caswell 2001) or when species interactions are considered (Chesson 2000). As shown in detail for the maximum rate of predation, snow geese fare better under stochasticity because mismatches allow periodic annual growth spurts to augment population abundance. Similar effects of stochasticity have been shown in maintaining coexistence in competitive systems (Adler and Drake 2008), arctic fox interactions with rodents (Henden et al. 2008), and in modifying the recovery potential of threatened species (Jenouvrier et al. 2009).

The beneficial effect of stochasticity on snow goose dynamics appears to be enhanced when the variance in mismatches is higher (Table 1). This suggests that if environmental stochasticity affecting the underlying processes increases, the snow goose decline should be less than projected. This is especially interesting in light of Salinger (2005) who indicates that environmental variation will increase as global change progresses. Combined with the work of Rockwell and Gormezano (2009), this suggests that while the climate-change-based advance in sea ice breakup leads to a new match and gives an advantage to polar bears over the snow geese, a related climate-change-based increase in environmental variation driving mismatches should diminish the edge.

The projected decline in numbers of snow geese nesting on the Cape Churchill Peninsula depends on not just overlap but also on the rate of predation by the increasingly matching polar bears. This, in turn, depends on factors related both to the numbers, arrival patterns and foraging behavior of polar bears and to the reaction of snow geese to the bears and their predation. Since the consumption of goose and other migratory waterfowl eggs is a relatively new phenomenon, information on these factors is quite limited and we summarize what is available and discuss its potential impact on our projections in the following.

Given an opportunity to forage on waterfowl eggs, polar bears will often consume large numbers of them (Madsen et al. 1998, Drent and Prop 2008, Rockwell and Gormezano 2009). Individual polar bears and their offspring have shown fidelity to new and abundant land-based food sources in the Churchill region where, for example, the same individual bears and their offspring were observed annually foraging near the Churchill landfill (Lunn and Stirling 1985). Similar habitual behavior has developed in polar bears foraging on goose and eider eggs on Svalbard where polar bears were also observed eating eggs while seals were still available on the ice, perhaps even advancing their annual onshore arrival to do so (Madsen et al. 1998, Drent and Prop 2008). Given these types of behaviors, it is possible that as individual bears begin foraging on eggs, their efficiency and rate of predation in subsequent years will increase as they become more familiar with snow goose nests, the nesting area and nesting phenology.

The spring onshore movement of polar bears is a gradual process in which the numbers of bears ashore increases as sea ice continues to disappear. As the date of breakup advances in response to climate change and the extent of overlap with the snow goose incubation period increases, larger numbers of bears, that may be more nutritionally stressed, are expected to be found on the nesting colony while there are eggs. Combined with the potentially changing foraging behaviors discussed above, these factors suggest that the average rate of polar bear egg predation could increase over time. Our projections of increasing annual predation rate (Fig. 5) show that although this would reduce the numbers of nesting geese more rapidly, it could not exceed the decline associated with the maximum constant predation rate indicated in Fig. 5 that projects a lower bound of 4939 pairs of nesting snow geese in 25 years.

At the same time, there is evidence from Regehr et al. (2007) that the number of WH polar bears is declining at an average of $\lambda = 0.986$. If that rate of polar bear decline remained constant for 25 years, the current WH population would be reduced to 653 polar bears. Assuming that nest predation is simply dependent on the number of bears and that we began at the maximum predation rate (the worstcase scenario), 25 years of decline in the numbers of available bears would only lead to a 2.1% reduction in the average rate of annual snow goose population decline from 0.909 to 0.928 (Fig. 5). However, Rockwell and Gormezano (2009) reported that a single polar bear consumed the eggs of 206 common eider nests (with clutch and egg size nearly identical to those of snow geese) in 96 h before being chased away as a safety precaution. At such a consumption rate, it would take only 237 bears to consume the eggs from all the nests of the current 48 855 pairs of snow geese (in 96 h) and, of course, fewer each subsequent year as the snow goose population declined. While a reduction in the decline of snow geese due to declines in the local polar bear population is possible, we feel it is unlikely.

It is not yet known how snow geese will react to polar bear predation, especially if they are annually exposed to increasing levels of it. It is possible, for example, that snow geese might shift nesting sites away from core areas and this could reduce the effective rate of polar bear predation. However, studies of dark-bellied brent and greater snow geese, Branta bernicla bernicla and C. c. atlanticus, indicate that continued nesting at the same site did occur in years following heavy predation by arctic foxes (Spaans et al. 1998, Bêty et al. 2002). Further, Madsen et al. (1998) found that light-bellied brent geese B. b. hrota on Svalbard continued nesting annually at the same sites despite periodic polar bear predation that led to total nesting failure for a large portion of the colony and substantially reduced overall reproductive success of the entire colony. It is important to note, though, that geese can shift in response to some environmental pressure as evidenced by the initiation of two new southern nesting colonies of barnacle geese B. leucopsis (van der Jeugd et al. 2009).

On the Cape Churchill Peninsula, there was complete reproductive failure in 2009 resulting in part from heavy predation by a variety of predators including polar bears. Nesting density in 2010 was unchanged from its previous five year average suggesting that a single year's failure does not result in mass exodus (Rockwell unpubl.). A pilot study of marked snow geese at La Pérouse Bay showed that more than half of females whose nests were totally predated by arctic foxes and/or herring gulls changed their nest location in the subsequent year by up to 15 km (Rockwell unpubl.). Such a local geographic shift is well within the range over which polar bears are known to move and forage (D. Hedman pers. comm.) so it is unlikely that regional movement within the Cape Churchill Peninsula would substantially reduce the impact of polar bears. Two such scenarios, starting at the maximum and a medium initial predation rate are depicted in Fig. 5. In both cases, the impact of 1.4% annual reductions in predation rates is not substantial. Unless the reaction of the geese virtually eliminated polar bear predation on the Cape Churchill Peninsula, the local snow goose population is expected to decline under global climate change.

The eggs of snow geese nesting on the Cape Churchill Peninsula are a nutrient resource that can be used by arriving polar bears to offset energy shortfalls related to earlier sea ice breakup and onshore arrival (Rockwell and Gormezano 2009). As the nesting population declines under increased overlap and predation, it might be expected that the available nutrient resource would also decline. However, since overlap and predation would occur earlier during the incubation period, a larger proportion of nests would still be available and the nutritional value of their eggs would be higher (Rockwell and Gormezano 2009). As a point of reference, our best data indicate there is currently a two day overlap between arriving polar bears and incubating snow geese. The eggs of the 17% of the snow goose population still incubating would provide 4.34×10^6 kilocalories of energy (Rockwell and Gormezano 2009).

Under anticipated climate change, the overlap of polar bears and the snow goose incubation period increases to a projected 12 day overlap in 25 years. On average, the entire nesting population (rather than just 17%) would still be incubating eggs and those eggs would have a 49% higher average caloric value than the near-hatching embryos encountered with the current two-day match (Rockwell and Gormezano 2009). In 25 years under the maximum predation rate (0.915), the expected 4,939 nests would provide 3.77 \times 10⁶ kilocalories. Under a medium predation rate (0.458), the expected 18 110 nests would provide 13.81×10^6 kilocalories. And under the minimum polar bear predation rate depicted in Fig. 5 (0.092), the expected 42 753 nests would provide 32.61×10^6 kilocalories. Except for near-maximum predation rates, the anticipated energy reserve from snow goose eggs after 25 years of predation is actually higher than what is currently available. This simply reflects the facts that earlier arriving bears would encounter a higher proportion of the nesting population and that the eggs of those geese would be more nutritionally valuable.

These energy reserves must be viewed as supplements that could be used by a portion of the population to offset deficits accrued through lost seal hunting opportunities related to climate change. Since increased overlap in arrival and incubation period would result from earlier sea ice breakup, that deficit could be larger unless polar bear foraging behavior prior to onshore arrival changed (e.g. increasing their daily rate of seal capture prior to or during breakup, Rockwell and Gormezano 2009). Such behavioral changes along with nutrient supplements from snow geese and other terrestrial and open-water sources (Dyck and Kebreab 2009, L. J. Gormezano unpubl.) are necessary if the region's polar bears are to maintain their current energy intake in the face of projected climate-mediated decreases in spring seal hunting opportunities. Research will be needed to document how polar bear foraging behavior changes as the climate warms.

The snow geese both nesting and rearing their young on the Cape Churchill Peninsula are partly responsible for the extreme habitat degradation of both coastal and near-coastal marshes since the mid 1980s (Jefferies and Rockwell 2002). The explosive growth of the local and mid-continent population of snow geese was in part a response to an increased nutrient subsidy across linked ecosystems that reduced potential bottom-up regulation of the herbivores in their summer habitat and helped initiate an apparent trophic cascade that continues to threaten the region (Jefferies et al. 2003, Abraham et al. 2005). Increased polar bear predation of snow goose eggs would serve as a novel form of 'topdown' regulation, operating to reduce the local snow goose population. As shown here, nearly any level of increased polar bear predation would begin reducing the numbers of nesting snow geese on the Cape Churchill Peninsula. Preliminary work (Rockwell unpubl.) suggests that if snow goose numbers were reduced there would be some recovery of some types of degraded habitat (e.g. fresh water sedge fen meadows). Such a situation represents a case where differential changes in phenologies across trophic levels (a greater advance in polar bear arrival than snow goose incubation period) lead to something other than destabilization of an ecosystem (cf. Visser and Both 2005).

The standard pattern to emerge when climate change affects phenologies differentially across trophic levels is that the mismatch reduces the success of one or both of the focal species (Both et al. 2009). We agree fully with Visser and Both (2005) that studies of the differential impacts of climate change on phenologies should address the extent of such mismatch and develop a yardstick to measure its effects. However, while the mismatch of polar bears and ringed seals, forced by advancing sea ice breakup, appears to be negatively impacting the polar bears, the new match with nesting snow geese may offset some of those losses. As such, the work here suggests that the valid quest for a mismatch yardstick needs to span a larger portion of single or linked ecosystems than just historically interacting species and traditional prey.

The work here also suggests that mismatches are not all 'bad'. In the short term, while periodic mismatches between polar bear arrival and snow goose incubation may restrict the nutrient supplement for bears in a single year, the same mismatch helps the geese by allowing periodic reproductive success and promoting pulses of population growth. In the longer term, such mismatches, especially when affected by stochasticity in the underlying climatic drivers, lead to a more persistent population of geese and a more sustained energy resource for the polar bears. Continuing the previous theme, the yardstick measuring the impact of mismatches must also integrate both near- and long-term dynamics with potentially increasing environmental stochasticity.

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Appendix 1

To compare our stochastic regression approach to past studies of the advancement in snow goose nesting and onshore arrival of polar bears that used simple, linear correlation or regression and did not account for autoregressive moving averages or stochasticity in these two time series (Stirling et al. 1999, 2004, Stirling and Parkinson 2006, Regehr et al. 2007, Rockwell and Gormezano 2009), we also evaluated our data with simple linear regression models and evaluated their support with AIC_c following Burnham and Anderson (2002) (Table A1). Because the top-performing stochastic regression (ARMA) models were a better fit to the time series data than simple linear regression models ($\Delta AIC_c > 2$), we focused on the ARMA models in the main text.

Nevertheless, we also projected future dates of snow goose hatch, onshore arrival of polar bears, and the match between the two processes using the simple linear regression models with and without a variance (σ^2) component (referred to as the linear projection sets). These provide for comparison to past studies but with updated data. Both the ARMA and linear projections assumed that dates of snow goose hatch and onshore arrival of polar bears vary independently over time. While there is some evidence that land- and marine-based climate processes are coupled (Gagnon and Gough 2005, Varvus 2007), there are also physical processes and evidence suggesting that any such coupling will likely not be

complete (Curry et al. 1995, Skinner et al. 1998). The data used here have a Pearson product-moment correlation of r =0.46 between dates of hatching and sea ice breakup. Such a correlation could reflect some common ecological drivers for annual changes in the dates or could be spurious, resulting from both time series having a negative non-stationary trend. To include the possibility that the correlation is meaningful in our evaluations, we generated projections for incubation period and onshore arrival under both ARMA and linear models using a multivariate random normal distribution that incorporated the observed estimate of correlation. These are referred to as the correlated ARMA and correlated linear projection sets. Details of the projections were conducted as described in the main text.

Estimates of 'mean match' were similar across the various projection sets, but estimates of variance differed greatly (Table A2). Higher levels of variance in the dynamics of overlapping phenologies provide periodic relief to the snow goose population and the resulting snow goose population growth rate is higher than other projections with lower variance (Table A3).

Given that the ARMA models were a much better fit to the data (Table A1), near-term projections made with these models should be more accurate than those made without parameters accounting for underlying autoregressive movingaverage signals in the data (e.g. linear projections; Burnham and Anderson 2002). Table A1. The best approximating stochastic regression models for the time series of (a) lesser snow goose hatch dates in the Cape Churchill region and (b) WH ice breakup based on Akaike's information criterion adjusted for sample size relative to that of the top model (ΔAIC_c). Each of these models contain an intercept and linear slope parameter (found to be a superior fit relative to nonlinear models), as well as a parameter for stochastic variation (white noise); the auto-regressive (AR) and moving average (MA) order of each model is denoted with an X. K denotes the total number of estimated parameters in each model, and the last model indicated is a simple linear regression model that does not account for temporal autocorrelation and is equivalent to the deterministic one reported in Rockwell and Gormezano (2009). Other models were considered but only those performing better than the linear regression model (last model in the list) are reported. Weight of evidence for a model is inversely related to its ΔAIC_c with $\Delta AIC_c = 0$ having the best fit. (a) Snow goose hatch dates

Table A3. The estimated annual growth rate from 25 year projections of the snow goose population using our four stochastic projection sets and a linear deterministic model (under the worst-case scenario of polar bear nest predation). For the stochastic projections the means and lower and upper 2.5 percentiles of 1000 independent trials are given.

	Lambda					
Models used for projection	lower	Mean	upper			
ARMA stochastic	0.8824	0.9058	0.9293			
Linear stochastic	0.8730	0.9059	0.9372			
Correlated ARMA stochastic	0.8798	0.9042	0.9275			
Correlated linear stochastic	0.8735	0.9027	0.9334			
Linear deterministic		0.8633				

Model

AR1	AR2	AR3	AR4	MA1	MA2	MA3	MA4	MA5	Κ	ΔAIC_{c}
		Х						Х	5	0.00
								Х	4	0.69
				Х	Х	Х	Х	Х	8	9.40
				Х	Х	Х			6	9.68
Х	Х	Х	Х	Х	Х				9	9.77
Х	Х			Х	Х	Х			8	9.81
Х	Х	Х		Х	Х				8	9.88
Х				Х					5	10.15
									3	11.48

(b) WH ice breakup

Model									
AR1	AR2	AR3	MA1	MA2	MA3	MA4	К	ΔAIC_{c}	
				Х	Х		5	0.00	
			Х	Х	Х		6	2.76	
Х	Х						5	4.30	
Х			Х	Х			6	4.95	
Х			Х	Х	Х		7	5.61	
			Х	Х	Х	Х	7	5.64	
							3	6.01	

Table A2. The extent of overlap (match) expected between the onshore arrival of polar bears and the snow goose incubation period at 25 years under our four stochastic projection sets and a linear deterministic model. For the stochastic projections the means, lower and upper 2.5 percentiles and variances of 1000 independent trials are given.

	Days of match at t = 25					
Models used for projection	lower	mean	upper	variance		
ARMA stochastic	-10.9048	12.1526	34.1390	141.60		
Linear stochastic	-12.0850	11.8139	34.0789	137.84		
Correlated ARMA stochastic	-6.9960	11.8992	31.3447	97.45		
Correlated linear stochastic Linear deterministic	-5.8567	11.6247 12.2240	29.6552	79.63 0		

SHORT NOTE

Terrestrial predation by polar bears: not just a wild goose chase

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Abstract Behavioral predictions based on optimal foraging models that assume an energy-maximizing strategy have been challenged on both theoretical and empirical grounds. Although polar bears (*Ursus maritimus*) are specialist predators of seal pups on the Arctic ice pack, the use of terrestrial food sources during the ice-free period has received increased attention in recent years in light of climate predictions. Across a 10-day period of observation, we documented between four and six individual polar bears successfully capture at least nine flightless lesser snow geese (*Chen caerulescens caerulescens*) and engage in at least eight high-speed pursuits of geese. The observed predatory behaviors of polar bears do not support predictions made by energy-optimizing foraging models and suggest that polar bears may frequently engage in energy

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R. F. Rockwell e-mail: rfr@amnh.org inefficient pursuits of terrestrial prey. Further study of the nutritional needs and foraging behaviors of polar bears during the ice-free period is warranted, given that polar bears are predicted to spend more time on land as climate change advances.

Keywords Optimal foraging · Diet choice · Predation · Energy budget · *Chen caerulescens · Ursus maritimus*

Introduction

Models used to predict predator foraging behaviors are often premised on balancing energy intake (Schoener 1971) with the handling time and energetic costs to the predator of capturing and processing prey (Sih and Christensen 2001). To accurately predict costs associated with predation events, models must account for intraspecific differences among predators, such as body mass (e.g., Brose 2010), physical condition (e.g., Donnelly and Sullivan 1998), hunting ability (e.g., Bevelhimer and Adams 1993), sex, and age (e.g., Clark 1980). However, these models are of limited use when pursuit of prey is motivated by reasons other than optimizing energy intake (Pyke 1984). For example, when consuming a mixed diet, pursuit of novel prey may enhance digestion or post-digestive utilization of nutrients (Hailey et al. 1998; Singer and Bernays 2003), satisfy vitamin/mineral requirements (Belovsky 1978; Hailey et al. 1998), allow sampling of available foods to assess quality for potential switching (Westoby 1978), dilute toxins (Hailey et al. 1998), or minimize intraspecific predation risk (Singer and Bernays 2003). Together, these considerations may explain the divergence of observed foraging behaviors from those predicted by models based on strict energy optimization.

Polar bears (Ursus maritimus), like other arctic predators, will opportunistically consume a variety of foods on land and ice in addition to their primary prey, ringed seals (Phoca hispida) (Russell 1975; Dyck and Romberg 2007). As the sea ice melts completely in summer, polar bears in the southwestern Hudson Bay population are forced on land where they are thought to survive primarily off stored fat reserves acquired from consuming seal pups in spring (Stirling and McEwan 1975). With warming temperatures reducing ice extent and duration in Arctic regions, access to these energy rich seals is becoming limited (Stirling and Parkinson 2006), and the loss of this food source has been associated with declines in body condition, reproductive success, and sub-adult survival (Stirling et al. 1999; Regehr et al. 2007). As a result, there has been an increased focus on examining the energetic value of terrestrial foods as a means to offset potential nutritional deficits related to lost seal hunting opportunities (e.g., Hobson et al. 2009). Many terrestrial foods that polar bears commonly consume, such as berries, grass, and eggs (Gormezano and Rockwell, in review) provide few calories per unit compared to seal but require little energy to obtain (Rockwell and Gormezano 2009).

In contrast, catching small but higher caloric prey such as flightless water birds may necessitate more energy intensive pursuits (e.g., running or climbing; Stempniewicz 2006; Smith et al. 2010). Lunn and Stirling (1985) estimated that a 320 kg polar bear would have to catch an adult lesser snow goose (Chen caerulescens caerulescens, henceforth snow goose) in <12 s to accrue a net gain in energy. Nevertheless, polar bears have been observed displaying predatory behavior toward post-hatching water birds including barnacle geese (Branta leucopsis: Stempniewicz 2006), little auks (Alle alle: Stempniewicz 1993), and thick-billed murres (Uria lomvia: Smith et al. 2010). In addition, Russell (1975) documented that a surprisingly high percentage (>50 %) of terrestrial polar bear scats in southern Hudson Bay contained post-hatching water birds in 1968 and 1969, and recent fecal analysis from the Cape Churchill Peninsula suggests that the occurrence of water birds in terrestrial polar bear diets is high (Gormezano and Rockwell, in review). Predatory interactions between polar bears and flightless waterfowl in western Hudson Bay have been observed since the early 1980's (Rockwell, pers. obs.), but have not been rigorously documented.

To better understand the relationship between polar bear foraging behavior and the predicted energy gains and time constraints for flightless snow geese estimated by Lunn and Stirling (1985), we rigorously documented and analyzed predatory interactions between polar bears and snow geese on the Cape Churchill Peninsula of western Hudson Bay. In this note, we describe six independent predation events occurring over the last 11 days of July 2011, involving at least four distinct bears of multiple age classes (sub-adult and adult polar bears as well as a sow with cub). We describe the foraging behaviors used by polar bears to capture flightless snow geese, the numbers and age classes of geese caught, and the duration of each predation event. We discuss the lack of concordance between observed pursuit times and those expected if energy gains are being optimally balanced with energetic costs. For the first time, we also provide supplementary video and digital images that document several of these events in detail.

Materials and methods

Following onshore arrival of polar bears in late July 2011, we monitored and documented terrestrial polar bear behavior along the coast of Hudson Bay in Manitoba, Canada, between La Pérouse Bay (58°43'N, 93°24'W) and Cape Churchill (58°46'N, 93°14'W). Observations were primarily made within the vicinity of our long-term research camp and near snow goose study areas. The Cape Churchill Peninsula and surrounding coastal marshes support a breeding population of over 100,000 lesser snow geese, which has been studied annually since the late 1960's from a long-term research camp located on the western coast of La Pérouse Bay (Rockwell and Gormezano 2009; Rockwell et al. 2011). Approximately 2-3 weeks after the hatch of goslings (but before fledging), adult geese molt their primary flight feathers and remain flightless for several weeks. Since snow geese initiate nesting (and subsequently hatch nests) relatively synchronously, nearly the entire population of adults, goslings, and molt-migrants is flightless, and thus more vulnerable to predation for this period of time.

All predatory behavior and interactions between polar bears and flightless geese were recorded (as they were opportunistically observed) from July 20 to July 30, 2011. Photographs and video were captured with a hand-held Canon Power Shot SX30 camera with \times 35 optical zoom, which limited video quality. We noted the duration of each predation event, predatory behaviors employed by polar bears, the stage classes of bears and geese involved in each event, and the number of prey items caught.

Results

The estimated mean hatch date for snow geese in western Hudson Bay in 2011 was 20 June, 3 days earlier than the long-term average (RF Rockwell, *unpublished data*). The mean flightless period of adult geese in 2011 was estimated to extend from approximately July 8 to August 1. Mean summer (July–August) air temperature was 11.6 °C

(1.3 °C warmer than the long-term average calculated between 1971 and 2011), suggesting that sea ice breakup in 2011 was earlier than average (formal calculation of the date of sea ice breakup is delayed by 2–3 years; Galbraith and Larouche 2011). Consistent with earlier breakup, the overall number of polar bear encounters during this period was above the long-term average (RF Rockwell, *unpublished data*). Summary data regarding polar bear predation on flightless snow geese in 2011 at La Pérouse Bay are presented in Table 1 included in Online Resource 1. Descriptions of the 6 events are detailed below.

Event 1

Our first documentation of polar bear predation on flightless snow geese occurred on July 20, 2011. At 15:05, \sim 350 m northwest of our permanent research camp in La Pérouse Bay, we spotted a sub-adult (based on structural size) polar bear walking from west to east through the braided Mast River delta that flows into Hudson Bay. Given the proximity of the bear to the camp, all camp members climbed to the roof of our main building (part of safety protocol-http://research.amnh.org/users/rfr/ our hbp/bearsafe.pdf), the spot from which most of our beargoose observations were made in 2011. The bear raised its nose in the air and oriented itself toward a nearby flock of snow geese (henceforth "scenting"). The bear then ran for approximately 30 s before capturing a flightless adult snow goose (Fig. 1). After pausing briefly to drop the first prey item, a 15-s chase resulted in the capture of at least one additional gosling (Online Resource 2; note that video length was limited by journal specifications). Both prey items were retrieved and consumed by the bear over the course of several minutes. The next day we located one gosling and one adult carcass at the location of where the event occurred. Unfortunately, scavenging, primarily by herring gulls (Larus smithsonianus), prevented us from determining the parts of carcass that were consumed by the bear.

Event 2

We observed another predation event during banding efforts for mark-recapture studies of snow geese. During these operations, large flocks of gosling and adult snow geese are temporarily rounded up in mesh banding pens and subsequently released with leg bands. Polar bears sometimes approach the study area during banding, presumably drawn by sounds of large numbers of geese, and are deterred for safety reasons with cracker shells if sufficiently close to study areas. On 22 July at ~12:15, we observed a distant adult polar bear (~700 m away; a safe distance and thus the bear was not deterred with cracker

shells) chase and consume a snow goose gosling that was not part of our captured sample. Observations of trophic interactions during banding operations may be biased because of the noise attraction, but nevertheless provide further evidence that bears will opportunistically utilize terrestrial food sources during the ice-free season.

Event 3

On 25 July at 12:45, we noted a polar bear sow with cub ~ 1 km northeast of our camp. After scenting and avoiding our camp, the sow continued walking northwest through a series of shallow lagoons sometimes occupied by flocks of flightless snow geese. At ~13:15, after scenting a small flock of snow geese ~ 400 m in front of her, the sow began moving at a faster pace in the same direction, leaving the cub behind. As the sow approached the lagoon (now at a slower pace), the flock quickly ran and then swam to the opposite shore of an adjacent pond, reaching a distance of \sim 500 m from the bear. The sow continued approaching the flock through several hundred meters of shallow water by crouching low and walking slowly through the lagoon. The nearby cub appeared to imitate the sow, walking while maintaining a low profile in the water. Allowing only her head to protrude from the surface, the sow periodically lifted her nose to scent the flock of geese, which now appeared to be unaware of her approach. At a distance of \sim 150 m from the bear, the geese were loafing and fanning their wings, apparently unaware that the sow was continuing her stalk. After slowly circling the geese and placing them between her and the lagoon, the sow ran toward the flock, chasing the geese into deep water and considerably slowing their escape. The sow isolated a single gosling from the flock, captured it, and carried it to a nearby island to be consumed by both bears. The total length of the highspeed chase was approximately 45 s.

Event 4

A sow and cub pair (likely the same as event 3) was spotted approximately 8 h later at 22:12, ~ 250 m south of camp, after we heard distress sounds of nearby snow geese and heavy splashing in the river. We observed the sow carrying an adult snow goose to a nearby island for consumption 15 min later, and the family pair walked toward a distant flock of snow geese before becoming obstructed from view by high willows.

Event 5

On 28 July at 10:05, we observed a small, likely sub-adult (based on structural size) polar bear walk past our research camp, scenting a large flock of adult snow geese near a



Fig. 1 Screenshot of supplementary video in Online Resource 2. On 20 July at 15:15, a sub-adult polar bear with a captured adult blue-phase snow goose in its mouth charges toward the remainder of the flock before capturing a second snow goose gosling in the same predation event

large lagoon of the Mast River. The bear approached the snow geese (~ 400 m away) from down-wind, through thick patches of willow (Salix spp.) and dwarf-birch (Betula glandulosa). While circling the large flock of adult geese, the bear came upon a second small flock of geese approximately 50 m away in a patch of willows. After spotting this new flock, the bear turned and chased the flock (Fig. 2; Online Resource 3) for 12 s before capturing an adult blue-phase snow goose. We observed the bear slowly consuming the goose and loafing on a nearby island for nearly 45 min, before walking north toward another flock of snow geese (while scenting periodically). After spotting the flock ~ 350 m away, the bear began a second chase, charging toward the flock for 50 s before capturing another adult snow goose, which was then dropped to pursue an additional goose in a chase lasting 10 s. Unsuccessful in capturing the last prey item, the initially captured goose was eaten on a nearby island. After an additional 15 min of loafing and eating, the bear began approaching another flock of nearby snow geese, approximately 150 m away. The bear stopped to watch the flock of geese walk directly past it, and after pausing for a minute, the bear engaged in its third chase of the day. During its charge, the bear split the flock in two and captured its third flightless adult snow goose after a 30 s pursuit. The goose was taken to a nearby island and consumed slowly over the course of 15 min.

Event 6

On 30 July at $\sim 20:00$, we observed a sub-adult polar bear (possibly the same individual observed in event 5) 250 m west of camp, carrying a fresh adult snow goose in its mouth into a stand of dwarf-willow (Fig. 3). The bear spent approximately 20 min eating the prey, before leaving the area.

Discussion

Following on-shore arrival of polar bears in 2011, we observed six predation events in which a total of at least nine flightless snow geese were captured and consumed. Since we could not distinguish individual bears (except for the lone adult and the sow and cub pair), we conclude that these events involved between four and six distinct bears in multiple demographic stage classes (one adult, one to three sub-adults, and a sow with a cub). We emphasize that these events occurred over an 11-day period and were opportunistically documented for the short duration in which our research overlapped terrestrial polar bear activity. Furthermore, our research camp (from which the majority of observations were made) is located in an area where the densities of polar bears and snow geese are currently lower than other portions of the Cape


Fig. 2 Screenshot of supplementary video in Online Resource 3. On 28 July at 10:20, a sub-adult polar bear chases a flock of snow geese before capturing an adult blue-phase snow goose



Fig. 3 On 30 July at 20:00, a sub-adult polar bear carries an adult white phase snow goose onto a nearby island before consuming it

Churchill Peninsula. Thus, estimates of bear-goose interaction rates derived from our observations would likely be conservative. We are developing a systematic

approach to monitoring predatory interactions across a gradient of snow goose densities that will allow us to accurately estimate encounter rates.

All but one of the chases we observed occurred in shallow water, and in several cases, polar bears appeared to be intentionally chasing flightless geese into coastal lagoons. Since flightless geese move more slowly in water than on land, chasing them into water may reduce the chase duration for polar bears. In addition, it may reduce hyperthermia caused by increased metabolic heat generated during chases (Lunn and Stirling 1985). In one case, the sow appeared to fully submerge herself in the water, possibly as a means of increasing heat loss, to avoid detection by nearby geese, or a combination of the two.

We observed at least five chases lasting longer than 15 s, and the average chase duration per prey captured (for known duration chases) was approximately 25 s. This is longer than the 12 s "inefficiency" threshold estimated by Lunn and Stirling (1985). This threshold was estimated using an energetic model developed by Hurst et al. (1982a) that allowed combining the oxygen consumption of a 320 kg polar bear running at 20 km/h with the average body composition of female snow geese. However, the caloric value of female snow geese increases after the incubation period (Ankney and MacInnes 1978). Since the exact caloric value of female snow geese used in Lunn and Stirling's (1985) calculations is not provided, we independently estimated the caloric value of adult female snow geese during our observational time frame using goose body composition estimates from Ankney (1979), while correcting for energy conversion and digestibility (see Rockwell and Gormezano 2009). We estimated that the energy available from the average adult female during the time period of our observations is 625.29 kcal. Following Lunn and Stirling (1985), we combined this value with the Hurst et al. (1982a) oxygen uptake model and estimated that the inefficiency threshold for a 320 kg bear running at 20 km/h would be 11.19 s. From this, a large fraction of the behaviors we observed appear to be energetically inefficient.

There are several non-mutually exclusive explanations for the number of energetically inefficient but successful pursuits we observed. The exact mass of the bears we observed is unknown, but four of the five "prolonged chases" (>12 s) involved sub-adult bears that likely weighed less than 320 kg. Scaling the Hurst et al. (1982a) model used by Lunn and Stirling (1985) suggests a higher inefficiency threshold for smaller bears. However, such estimation actually requires the use of mass-specific models of oxygen consumption (Hurst et al. 1982b). While such evaluations are complex and beyond the scope of this paper, preliminary analyses suggest that many of the successful predation events we observed were likely energetically inefficient (Gormezano and Rockwell, *in preparation*).

There is little doubt that the performance of predators improves with experience and practice (e.g., Estes et al. 2003). This has been shown for polar bears hunting seals (Stirling 1974) and suggested for polar bears catching fish (Dyck and Romberg 2007). It may well be that individuals such as those described here will gain speed and handling ability to a point where their successful pursuits become energy efficient. It is noteworthy that the individuals with the longest pursuit times were sub-adults and a sow with a cub. The sow's foraging may have been fettered by the cub's behavior or its learning attempts (Stirling 1974). If maturation and experience do lead to energy efficient predation events, then the occurrence of inefficient predation events for inexperienced individuals may be explicable in terms of future energetic payoffs.

Importantly, if there are non-energetic nutritional constraints on diet, then assumptions of simple energy balance can lead to incorrect projections of foraging behavior (Pulliam 1975; Simpson et al. 2004). In fact, it is possible that using energy as the currency to predict foraging behavior is not always valid (e.g., Pyke 1984). Energy inefficient foods may fulfill important micronutrient requirements that are otherwise absent from highly specialized diets and their consumption may not be predicted when energy alone is the optimization criterion (e.g., Belovsky 1978; Hailey et al. 1998). Lack of concordance between the optimal behavior predicted from an energetic model and observed field behavior suggests that further studies are required to understand the relationships between the energetic and nutritional needs of polar bears and their foraging behaviors during the ice-free period.

An accurate evaluation of the potential consequences of these interactions for both polar bear and snow goose populations will require a combination of long-term, systematic observational field studies to estimate interaction frequency, a more complete understanding of the changing nutritional requirements of polar bears, as well as rigorous modeling efforts to project future demographic structure and predator-prey dynamics. Several studies have begun investigating these issues, paying particular attention to predation of nests and resulting energetic benefits of eggs to the bears (e.g., Rockwell and Gormezano 2009; Rockwell et al. 2011). However, since polar bears are expected to spend more time on land as climate change advances (e.g., Regehr et al. 2007; Rockwell et al. 2011), a complete evaluation of predation on all life stages of snow geese is warranted as it will provide a better assessment of the overall potential of snow geese to offset nutritional deficits experienced by polar bears as a result of climate change.

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What to eat now? Shifts in polar bear diet during the ice-free season in western Hudson Bay

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Introduction

Polar bears (*Ursus maritimus*) are the most carnivorous of the Ursids, feeding primarily on ringed seals (*Phoca hispida*) and less frequently on bearded seals (*Erignathus barbatus*) and other marine mammals while sea ice is available for hunting (Stirling and Archibald 1977; Thiemann et al. 2008). Most of this foraging occurs in spring when polar bears accrete the majority of their fat reserves from ringed seals and their newborn pups (Stirling and Øritsland 1995). The ice in western Hudson Bay melts completely by mid- to late July forcing the bears ashore without easy access to their primary prey until freeze-up in the following

Abstract

Under current climate trends, spring ice breakup in Hudson Bay is advancing rapidly, leaving polar bears (Ursus maritimus) less time to hunt seals during the spring when they accumulate the majority of their annual fat reserves. For this reason, foods that polar bears consume during the ice-free season may become increasingly important in alleviating nutritional stress from lost seal hunting opportunities. Defining how the terrestrial diet might have changed since the onset of rapid climate change is an important step in understanding how polar bears may be reacting to climate change. We characterized the current terrestrial diet of polar bears in western Hudson Bay by evaluating the contents of passively sampled scat and comparing it to a similar study conducted 40 years ago. While the two terrestrial diets broadly overlap, polar bears currently appear to be exploiting increasingly abundant resources such as caribou (Rangifer tarandus) and snow geese (Chen caerulescens caerulescens) and newly available resources such as eggs. This opportunistic shift is similar to the diet mixing strategy common among other Arctic predators and bear species. We discuss whether the observed diet shift is solely a response to a nutritional stress or is an expression of plastic foraging behavior.

> fall (Gagnon and Gough 2005). While ashore, polar bears are in a negative energy balance (Derocher et al. 1993), reportedly surviving primarily on their fat reserves, although supplementary, terrestrial foods are also consumed when available (e.g., Lunn and Stirling 1985; Derocher et al. 2013). This period onshore is projected to increase as warming trends keep Hudson Bay ice free for progressively longer periods each year (e.g., Stirling and Parkinson 2006). Surviving these extended periods on land without access to seals is believed to be critical to the persistence of polar bears in western Hudson Bay (Molnár et al. 2010).

> Polar bears are known to consume various types of terrestrial and marine foods during the ice-free period

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(hereafter terrestrial or land-based foods). Items reported include marine algae (Harrington 1965), grasses (Koettlitz 1898), berries (Russell 1975), fish (Dyck and Romberg 2007), small mammals (Pedersen 1966; Russell 1975), caribou (*Rangifer tarandus*) (Derocher et al. 2000), seals (Russell 1975), various species of waterfowl and their eggs (e.g., Stempniewicz 1993; Drent and Prop 2008; Rockwell and Gormezano 2009), and willow ptarmigan (*Lagopus lagopus*) (Miller and Woolridge 1983).

Despite these observations, some of which date back to the late 1800s (Koettlitz 1898), polar bears are often referred to as "fasting" while ashore (e.g., Amstrup et al. 2007; Molnár et al. 2010; Robbins et al. 2012). Although the term may apply to some polar bears, extension to the majority of the western Hudson Bay population seems inappropriate given multiple observations to the contrary (see above), and the inherent limitations of behavioral and physiological studies (Knudsen 1978; Latour 1981; Ramsay and Hobson 1991; Hobson et al. 2009) that are often used to justify the term's use. For example, observational studies may only offer a snapshot of behavior for discrete periods (Knudsen 1978; Latour 1981) and coastal or inland sampling may preclude certain demographic groups because they tend to spatially segregate once ashore (Latour 1981; Derocher and Stirling 1990). Physiological studies, such as stable carbon isotopes and fatty acid signatures offer a more integrated assessment of the diet but are fraught with inconsistencies. For example, stable carbon isotopes can give variable results depending on the tissue examined (Ramsay and Hobson 1991; Hobson et al. 2009) and the mixing of marine and terrestrial signatures of foods polar bears commonly consume on land (e.g., marine algae, waterfowl feeding in salt marshes; McMillan et al. 1980; Hobson et al. 2011). Fatty acid signatures can vary by individual depending on differential accumulations and deficits (Pond et al. 1992; Grahl-Nielsen et al. 2003).

The direct analysis of passively sampled scat offers several advantages for determining dietary details on the extent and pattern of land-based foraging by polar bears. Scats deposited reflect foods consumed over longer spans (i.e., spring, summer, or fall), through various diurnal cycles, and during weather changes in which periods of active foraging may fluctuate. Although exact numbers and sexes of polar bears sampled cannot be assessed from scat in the absence of genetic analyses, collection of scats over a large geographic extent increases the chances of sampling from different sex and age groups and from different individual polar bears given their tendency to move relatively little once ashore (Derocher and Stirling 1990; Parks et al. 2006). While exploring the nutritional and energetic value of terrestrial food is beyond the scope of this study, we use scat analysis to examine the land-based diet of polar bears

across a large portion of the terrestrial habitat used during the ice-free period in western Hudson Bay.

Reports of polar bears exploiting land-based prey have become more common in recent years (e.g., Derocher et al. 2000; Drent and Prop 2008; Rockwell and Gormezano 2009; Iles et al. 2013). For example, consumption of eggs and young from nesting colonies of waterfowl across the Arctic is increasingly pervasive, and predation on larger land mammals, such as caribou, had been reported (Derocher et al. 2000). Although categorized as specialists that primarily hunt seals on the ice (Derocher et al. 2004; Amstrup et al. 2007), polar bears have been observed walking, running, and even climbing cliffs (Smith et al. 2010) on land to pursue alternate prey. Like other bear species, polar bears may well be opportunists, pursuing the most readily available food source (Lunn and Stirling 1985; Beckmann and Berger 2003; Thiemann et al. 2008). It remains unclear whether exploiting these alternate foods (behavioral shifts) is mainly a response to nutritional stress or simply a typical Ursid response to a changing food supply.

To better understand how polar bears may be reacting to climate change or other environmental factors, we first created a comprehensive inventory of the current polar bear diet across their terrestrial range in western Hudson Bay by analyzing passively collected scat. Second, to identify any dietary shifts during the ice-free season that may have occurred since the recent onset of rapid climate changes we compared our data to a similar scat-based diet study performed in the Hudson Bay Lowlands 40 years earlier by Russell (1975). In parallel with this comparison, we compared the average 50% breakup dates during this and Russell's diet study as an index of climate-related environmental change between the two time periods. Finally, we explore other possible bases for the observed shifts in landbased foraging we document and discuss the implications they have for polar bears' ability to persist in the face of reduced ice conditions that limit their time to hunt seals.

Material and Methods

Study area

Scat sampling occurred along 160 km of coastline and adjacent inland areas of what is now termed the Cape Churchill Peninsula (Rockwell et al. 2011) where polar bears are known to occur during the ice-free period in western Hudson Bay (Derocher and Stirling 1990). Coastal areas within the study area extended from the town of Churchill, Manitoba (58°46'N, 94°12'W), east to Cape Churchill (58°47'N, 93°15'W) and south to Rupert Creek (57°50'N, 92°44'W). We also collected samples from six separate denning areas southeast of Churchill and inland of the coastline to 93°51W' (Fig. 1). By



Figure 1. Polar bear scat was collected along the coast of western Hudson Bay from the town of Churchill, Manitoba, to Rupert Creek. Scat was also collected near maternity dens at six inland sites. Collections were made from 2006 through 2008.

including both coastal and inland denning habitat we can provide a more complete inventory of the land-based diet of all demographic groups that differentially use this region (Latour 1981; Derocher and Stirling 1990).

The coastline south of Cape Churchill is largely flat with poor drainage, characterized by salt marsh interspersed, as one moves inland, with successively older relict beach ridges that run parallel to the coast (Dredge 1992). The vegetation along that section of coastline, as well as the better drained coastline from Churchill to Cape Churchill, is dominated by sedges (i.e., *Carex* spp.), grasses (e.g., *Puccinellia phryganodes, Dupontia fisheri*), and herbs (e.g., *Primula egaliksensis, Parnassia palustris*) with interspersed woody shrubs including willow (*Salix* spp.), birch (*Betula glandulosa*), and *Rhododendron lapponicum* (Ritchie 1960).

The inland denning sites and the more inland areas near Churchill, Manitoba, are in the ecotone between boreal forest and low Arctic tundra. The area is a mosaic of vegetation communities including open canopies of white spruce (*Picea glauca*), black spruce (*P. mariana*), and tamarack (*Larix laricina*). Forested areas are interspersed with sedge meadows (primarily *Carex aquatilis*), upland lichen-heaths bogs with *Vaccinium uliginosum*, *Cladina rangiferina*, and *Sphagnum* spp., and fens with shrubby vegetation such as willow and birch (Ritchie 1960). Polar bear dens are often dug into frozen peat banks of rivers or lakes at the base of black spruce trees or beneath permafrost hummocks (Clark et al. 1997).

Onshore movement of polar bears in western Hudson Bay coincides with the breakup of sea ice, and an algorithm based on 50% spring ice cover has often been used as a reliable predictor of arrival date (Stirling and Parkinson 2006). Using this approach, Lunn (2008) predicted that polar bears arrived onshore shortly after 24 June, 22 June, and 28 June in 2006, 2007, and 2008, respectively. We used 24 June, the mean breakup date, as an index of current environmental conditions and compared it to the mean breakup date during Russell's (1975) study as a means to compare dietary differences coincident with changes in environmental conditions. From Lunn (2008) we used the earliest 5-year period in that data set (1971–1975) and projected the mean breakup date for 1968–1969 using a linear relationship previously developed by Rockwell and Gormezano (2009).

Fecal collection

Fecal piles were found using a trained detection dog along 31 linear coastal transects and in the vicinity of inland dens in the six denning areas from 2006 through 2008. The numbers of scats collected each year was not fixed a priori. Transects were 1-3 kilometers long and were parallel to the coastline. Coastal transects between the town of Churchill, Manitoba, and the White Whale River were walked between 25 May and 7 August, and coastal transects from Cape Churchill to Rupert Creek were walked between 14 July and 11 August. Upland habitat in the vicinity of inland dens was searched between 30 May and 17 June. The collection team was transported to and from all collecting sites by helicopter (except those accessible by truck near Churchill) and the team consisted of the coauthors, the detection dog, and, when possible, an additional armed polar bear warden.

Intact scat piles were placed in plastic bags and stored frozen at -20° C until analyzed. Date, geographic coordinates, substrate, and relative freshness were recorded for each sample. Intact piles of all ages were collected. Scat piles were often found to be clumped along a transect or near a denning site. To reduce potential bias resulting from multiple scat piles being deposited by a single individual, we did not use all the samples collected from clumped points along each of our 31 transects for these diet analyses. We also subsampled across the entire collection so that the scat piles analyzed for diet were representative of the relative frequencies and geographic extent of the sampled areas. Although the actual number of polar bears depositing the sampled scats remains unknown, we assume from the size and geographic extent of our sampling and the facts that once ashore polar bears segregate and move little once ashore (Derocher and Stirling 1990; Parks et al. 2006) that our samples are representative of the land-based diet of those polar bears that do forage on the Cape Churchill Peninsula during the ice-free period.

Fecal analysis

Entire scats were defrosted, broken apart, and examined for plant and animal remains using flame-sterilized forceps. To preserve specimens for future genetic tests to identify individual bears, we did not use washing techniques (e.g., Russell 1971; Hewitt and Robbins 1996). Multiple bone, hair, and feather samples believed to represent individual prey animals were removed from each pile. These specimens were cleaned by soaking and gently rubbing in a bowl with water and mild soap and assigned to species or the finest taxonomic level possible. Taxonomic determinations were made independently from each hair, bone, and feather specimen in the same pile to minimize assignment bias because animals of different species were often found in the same pile. Unique plant items were removed from scats and also identified to the lowest taxonomic level. Garbage constituted all items from anthropogenic sources (e.g., plastic, paper, apples). We considered food items (other than polar bear, see below) to occur in a scat if any amount of that food item, regardless of volume, was present. For consistency, all analyses were performed by the lead author.

Based on the morphology of bone fragments, the type and source taxa were identified using museum skeletons, reference keys (Wolniewicz 2001, 2004; Post 2005), and expert opinion (N. Duncan and A. Rodriguez, pers. comm.). If specimens could not be identified beyond "bird" or "mammal," they were marked as "indeterminable" and only included in statistical analyses where the pooled, higher taxonomic groups (i.e., birds, mammals) were used. Bones classified no finer than "animal" were only included in summary statistics of major food categories (e.g., vegetation, animals).

Hairs were identified where possible by comparison to a reference collection (obtained from harvested animals in the study area) using morphological features such as color, pattern, length, and texture. Hairs that could not be identified this way were mounted on $3 \times 1''$ glass slides with Flo-Texx[®] mounting medium (Lerner Laboratories, Delray Beach, FL), covered with 22-mm glass slide covers and examined under 10, 20, and $40 \times$ magnification with a compound light microscope. Cuticle-scale patterns and the shape and presence of the medulla were compared to the reference collection, museum specimens, and a key

(Brunner and Coman 1974). Lack of observable structural differences for some samples limited identification to genus (e.g., *Lepus* spp.), family (e.g., Phocidae, Cricetidae), or order (e.g., Cetacea). Unidentifiable hairs were classified as belonging to "indeterminable mammals." Most scats contained polar bear hair which was likely ingested during grooming. Evidence of cannibalism, however, was distinguished from grooming by the larger volume of hair, presence of flesh, bone, and a distinct smell.

Bird feathers from scat were identified by comparing shape, size, and color patterns with museum specimens. We also used barbule node patterns of feathers of unknown birds, in comparison with reference slides and published guides, to make taxonomic identification (Dove and Agreda 2007; C. Dove, pers. comm.). Downy barbs from the plumulaceous region were removed from both sides of the vanes with forceps, elongated and mounted in a similar manner to hairs. The presence, position, and density of nodes on barbules viewed at $10-40 \times$ magnification using a compound light microscope were used to identify birds to the lowest taxonomic level.

In addition to these morphological characteristics, we used knowledge of which birds overlap polar bears onshore in western Hudson Bay in making some final taxonomic determinations (Rockwell et al. 2009). For example, individual feathers and node patterns of Brant and Canada Geese (*Branta bernicla* and *B. canadensis*, respectively) appear similar, but only Canada Geese nest and molt in the region when polar bears are present and at a time when they are most vulnerable to predation. Consequently, feathers with a morphological match to both species were classified as Canada geese.

Plants and fungi from scats were identified using keys (Johnson 1987; Marles et al. 2000); however, due to the variety encountered and time constraints, we pooled occurrences of samples into broad taxonomic groups. These included marine algae (e.g., Fucus spp., Laminaria spp.), berries (e.g., Vaccinium uliginosum, Empetrum nigrum), lichens (e.g., Cladina stellaris), mosses (e.g., Sphagnum fuscum), and mushrooms (Lycoperdon and Bovista spp.). Due to the high occurrence of Lyme grass (Leymus arenarius) shafts and their protein-rich seed heads (Facciola 1998) in scat and observations of bears targeting just seed heads (Gormezano and Rockwell, in review) that emerge in July (Johnson 1987), we separated "Lyme grass" (shafts and/or seed heads) and "seed heads" (only seed heads, no shafts) into different categories for some analyses. We pooled all other grass species, such as Festuca brachyphylla, into "other grasses." Leaves and stems of shrubs and woody plants (e.g., Salix planifolia, B. glandulosa) were not quantified in our study because they consistently comprised <1% of individual scat piles and we

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assumed that they were either accidentally ingested or picked up from the substrate during collection.

We compared the contents of polar bear scats to those reported in Russell (1971), who used different techniques to identify food items. These included soaking previously dried scats, washing them through a series of screens and examining the contents using both macroscopic and microscopic techniques (Russell 1971). Russell's method of washing entire piles may have resulted in identification of more food items, thus findings of lower frequencies in the current diet may be due to lower consumption of those foods or missing those foods during examination. Conversely, finding more items in the current diet would support higher consumption of those foods and be less likely the result of sampling error. Furthermore, we took advantage of more recent advances in microscopic techniques to identify bird remains that were not available during Russell's study (e.g., Dove and Agreda 2007) and which may have contributed to differences in the number of specific taxa identified between the two studies.

It is worth noting that scat analysis has inherent advantages and limitations that affected both studies (Reynolds and Aebischer 1991). For example, although scat collections were noninvasive, eliminating impacts of capture and handling, exact information on individual animals and times of deposition could only be inferred. Furthermore, due to differential digestion, foods possessing less digestible parts (e.g., fibrous plants, fur, bone) were easier to identify, and thus may be overly represented compared to highly digestible foods (e.g., seal and whale blubber, fish; Best 1985; Hewitt and Robbins 1996).

Statistical analysis

We examined the diet of polar bears using 14 inclusive groups of food items with each group having at least five occurrences of all the included taxa. These groups were polar bear, seal, caribou, rodents (i.e., muskrats [Ondatra zibethicus], meadow voles [Microtus pennsylvanicus], collared or bog lemmings [Dicrostonyx richardsoni and Synaptomys cooperi]), birds, eggs, Lyme grass shafts, Lyme grass seed heads, other grasses, marine algae, berries, mosses, mushrooms, and garbage. Although the seed heads of Lyme grass originate from the same plant as the shafts, their occurrences within scat piles are independent (see below).

Both the (1) raw frequencies (number of times each food item was found) and (2) scat occurrences (the number of scats with a food item) were used in statistical analyses. We use the percentages of these (relative to their appropriate sum) for ease of presentation in some cases. The raw frequencies and the number of scat occurrences are the same value unless multiple items from the same category occur in a scat pile (i.e., two birds in one scat pile). Multiple items were only counted for animals when evidence was conclusive (e.g., three bird feet) and were not counted for plants and fungi. Depending on the analysis, we conflated food items into inclusive taxonomic groups (e.g., birds vs. mammals, animals vs. plants), which allowed us either to reduce problems of small numbers within group sample sizes or to address broader and more general questions. Because we did not determine digestibility of different foods, we did not include volumetric measures to infer the energetic contribution of different foods in the polar bear diet (Reynolds and Aebischer 1991).

Piles of scat often contained more than one food item, reflecting that bears may eat more than one item at a time or one scat pile may represent multiple feeding sessions. Because we were interested in the individual items consumed, we used the raw frequencies of items instead of the scat occurrences as the unit of measure in statistical analyses. To justify this approach, however, we first needed to determine whether food items occurred independently across scat piles. Using occurrences of pairs of food items in scat (co-occurrences), we conducted multiple 2×2 log-likelihood chi-square tests (Zar 1999) to evaluate whether the frequencies of individual food items occur independently from all others across scat piles. Significance of these pairwise and subsequent multiple comparison tests was evaluated using a sequential Bonferroni approach (Holm 1979) to reduce inflation of our overall alpha error rate.

Comparison of diet changes over time

We compared the distribution of food items found in our 642 scat piles sampled from 2006 to 2008 to those found from 1968 to 1969 in 212 scat piles collected in three areas along the west and south coast of Hudson Bay (Cape Churchill, West Pen Island and Cape Henrietta Maria) by Russell (1971, 1975). He pooled the data on food items found in the scat over the three areas and 41% of his samples were from the Cape Churchill area, which is common with our study. Although the exact extent of his sampling in the Cape Churchill area is not clear, it is known that most researchers worked out of the "Cape Churchill camp" (now referred to as Nester 1), located 14 km south of Cape Churchill. Sampling from the camp typically covered a 76 km range from the Cape (58°47'N, 93°15'W) to the Broad River (58°07'N, 92°51'W; L. Vergnano, pers. comm.). His other sites are south and east. The difference in geographic coverage leads to an asymmetrical problem for inferences from comparisons between the two studies. If we fail to find one of the food items he reported or find that an item has decreased in frequency, we can draw inferences regarding changes in food use only by assuming that his pooled proportions for particular food items are

representative of the Cape Churchill area. By contrast, however, if we find a new food item or an increase in the proportion of an item, we can reasonably conclude that the item is now being used or being used more in the Cape Churchill area since the 1960s.

We used raw frequencies from both studies in our statistical analyses and percent frequencies and percent scat occurrences in depicting the results. Raw frequencies for each of Russell's food items were obtained from Table 7 (p. 30) in Russell (1971) and pooled across volume categories. Because Russell's sample sizes were smaller, we combined food items into nine inclusive groups with each group having at least five occurrences of all included taxa. The groups were mammals, birds (including eggs), Lyme grass, other grasses, marine algae, berries, mosses, mushrooms, and garbage (referred to as "debris" by Russell). Russell did not separate out parts of the Lyme grass plant so all references to "Lyme grass" include a composite of shafts and/or seed heads, as it does in our study. Other food items, such as cetaceans, lagomorphs, insects, marine invertebrates, fish, lichens, club mosses, horsetails, rushes, and sedges, were found in very low frequencies or not specifically classified in either study so were excluded from chi-square tests. The data from Russell (1971, 1975) were collected from coastal areas, whereas our data were from both coastal and inland areas. Before the comparison with Russell's data, we used 2×9 log-likelihood chisquare test to evaluate differences in the frequencies of nine major food items between coast and inland areas during our study. Based on the results, we excluded our inland data from all statistical comparisons with Russell's data.

Pooling major food groups, we used a 2×3 loglikelihood chi-square test to evaluate whether there was a difference in the proportions of animals, vegetation, or garbage consumed by polar bears between the late 1960s and present. We then compared the proportions and 95% confidence limits to determine which category was responsible for the observed differences. On the basis of the relationship between the binomial and F distributions, we calculated exact 95% upper and lower confidence limits for each proportion and used single and double harmonic interpolation to calculate F critical values for large values of n (Zar 1999). To determine if there were shifts in the types of foods consumed within these broader categories, we used a 2×9 log-likelihood chisquare test to evaluate whether there were differences in the frequencies of nine inclusive food groups (described above) consumed between time periods. On the basis of the results of this test, we compared the proportions and 95% confidence limits of food item frequencies to assess which individual groups differed. For this comparison, we further broke down the "mammal" category into polar bears, seals, rodents, and caribou and "birds" was separated into birds and eggs.

Using all animal taxa identified to the finest level possible in either study (including those excluded from the chi-square analyses, see above) along with the major plant categories described above (with the addition of lichens), we used a Mann–Whitney test to further compare the two diets. The Mann–Whitney test is a nonparametric test that uses the degree of variability or dispersion between two groups to evaluate whether the rank order of the observed frequencies of food items is derived from the same diet (Zar 1999).

Results

We collected a total of 1262 scats and analyzed 642 of them; 219, 248, and 175 in 2006, 2007, and 2008, respectively (Table 1). Of these, 593 scats were collected from coastal areas and 49 from inland areas. Nearly one-third (29.0%) of all scats contained bird and/or egg remains, the majority of which were snow geese (43.1% of bird remains) and Canada Geese (9.7% of bird remains). Eggs occurred in 4.4% of scats. The most common mammals were caribou (10.1%), seal (most likely P. hispida) (6.5%), and polar bear (from cannibalism, not grooming) (5.1%), with small mammals (i.e., rodents, Arctic or snow-shoe hares [Lepus arcticus and L. americanus]) occurring in lower frequencies (<1.0%). Grasses (61.7%; mainly Lyme grass, 57.0%) and various species of marine algae (46.1%) were the primary forms of vegetation. Other common food items include mosses, puffball mushrooms, and berries, occurring in 13.6%, 8.9%, and 8.7% of scats, respectively.

No pairs of food items in scat piles showed significant patterns of co-occurrence at our adjusted alpha error level, and we therefore consider food items to occur independently in scats. This lack of co-occurrence justifies the use of the raw frequencies of food items as a unit of measure in subsequent statistical tests rather than the number of scats containing each item. Perhaps not surprisingly, marine algae and berries were observed together less often than expected (G = 6.31, df = 1, P = 0.013), although the result did not reach the adjusted alpha level (14 tests; $\alpha = 0.0035$) required to avoid error inflation.

Comparison of diet changes over time

We compared 593 scats (1237 occurrences) of our coastal data with 212 scats (528 occurrences) from Russell's study to examine polar bear diet changes over time. We found a shift in the frequencies of major food categories (animals, vegetation, garbage) (G = 25.54, df = 2, P < 0.0001). This result was due to a larger proportion of animals

 Table 1. The frequencies of food items in 642 polar bear scats from western Hudson Bay 2006-2008.

	Raw fr	equencies*	Scat occurrences	
Таха	n	%	%	
Birds				
Aves, indeterminable	45	3.3	7.0	
Anatidae, indeterminable	14	1.0	2.2	
Anserinae, indeterminable	6	0.4	0.9	
Anser caerulescens	80	5.9	12.5	
caerulescens				
Branta Canadensis	18	1.3	2.8	
Anatinae, indeterminable	2	0.1	0.3	
Anas rubripes	1	0.1	0.2	
Anas crecca	1	0.1	0.2	
Anas acuta	1	0.1	0.2	
Merginae				
Mergus serrator	3	0.2	0.5	
Somateria mollissima	2	0.1	0.3	
Melanitta perspicillata	1	0.1	0.2	
Galliformes, Lagopus lagopus	3	0.2	0.5	
Passeriformes, <i>Plectrophenax</i>	1	0.1	0.2	
nivalis				
Charadriiformes, indeterminable	1	0.1	0.2	
Limnodromus ariseus	1	0.1	0.2	
Egg shell/hatching membrane	28	2.1	4.4	
Aves – total	208	15.3	29.0	
Mammals				
Mammalia, indeterminable	6	0.4	0.9	
Phocidae	42	3.1	6.5	
Ursidae. Ursus maritimus	33	2.4	5.1	
Cervidae. Rangifer tarandus	65	4.8	10.1	
Cricetidae, indeterminable	3	0.2	0.5	
Ondatra zibethicus	3	0.2	0.5	
Microtus pennsylvanicus	1	0.1	0.2	
Lemmini	1	0.1	0.2	
Cetacea	1	0.1	0.2	
Lagomorpha, Lepus spp.	2	0.1	0.3	
Mammalia – total	157	11.6	22.0	
Animal (Mammal or Bird).	11	0.8	1.7	
indeterminable				
Marine invertebrates				
Asteroidea (sea stars)	1	0.1	0.2	
Bivalvia. <i>Mvtilus edulis</i>	4	0.3	0.6	
Fish	2	0.1	0.3	
Insects	3	0.2	0.5	
Grasses	-			
Levmus arenarius	366	27.0	57.0	
(43 had seed heads)				
Other grasses	67	4.9	10.4	
Grasses – total	433	31.9	61.7	
Mushrooms				
Lycoperdon pvriforme or	57	4.2	8.9	
L. perlatum				
Marine algae	296	21.8	46.1	
Mosses	87	6.4	13.6	
Berries	56	4.1	8.7	
			(Continued)	

Table 1. C	Continued
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	Raw fre	Scat occurrences		
Таха	n	%	%	
Lichens Garbage**	1 41	0.1 3.0	0.2 6.4	

Data are presented as (1) the number of times each food item was found (raw frequencies), (2) raw frequencies/total frequencies (n = 1357) of all food items (percent frequencies), and (3) the number of scats with a food item/total number of scats (percent scat occurrences).

*the number of scat occurrences is excluded because it is the same value as the raw frequencies for all food items except birds. We were able to identify multiple birds in seven of 180 (3.9%) scats with birds. **includes apple peel, aluminum foil, cantaloupe seed, cardboard, corn kernel, chicken bone, cigarette butt, duct tape, foam rubber, glass, paint chips, paper, plastic, string, tomato seed, watch band, and wood chips/sticks.

 $(\hat{p} = 27.32, \text{ CI} = 25.13-29.18 \text{ vs. } \hat{p} = 23.48, \text{ CI} = 20.00-27.16)$ and less garbage $(\hat{p} = 3.23, \text{ CI} = 2.11-4.61 \text{ vs.} \hat{p} = 9.09, \text{ CI} = 6.05-12.58)$ in scats in our study compared to Russell's study (Fig. 2A). Within these major food categories, there were differences in the frequencies of nine major food items (birds, mammals, Lyme grass, other grasses, marine algae, berries, mushrooms, moss, and garbage; G = 130.31, df = 8, P < 0.0001). The two diets (historic vs. current) also differ in the rank order of items (Mann–Whitney test: U = 317; P = 0.015).

Among animals, rodents occurred considerably more frequently in Russell's study ($\hat{p} = 7.95$, CI = 5.80–10.59) than in ours ($\hat{p} = 0.65$, CI = 0.28–1.27), but we observed more polar bear remains ($\hat{p} = 2.59$, CI = 1.48–3.63 vs. $\hat{p} = 0.38$, CI = 0.05–1.36). Russell did not detect any caribou, whereas caribou was the most common mammal found in our study ($\hat{p} = 4.69$, CI = 3.58–6.02). There was no significant difference in the frequencies of seals or birds, but we found eggs in scats ($\hat{p} = 2.18$, CI = 1.44–3.16), whereas Russell did not (Fig. 2B).

Observed differences in vegetation were due to higher proportions of Lyme grass ($\hat{p} = 28.54$, CI = 26.35–30.40 vs. $\hat{p} = 16.48$, CI = 13.46–19.90) and mushrooms ($\hat{p} = 4.53$, CI = 3.44–5.85 vs. $\hat{p} = 0.76$, CI = 0.21–1.93), but lower proportions of other grasses ($\hat{p} = 4.61$, CI = 3.51–5.93 vs. $\hat{p} = 15.72$, CI = 12.75–19.09) and marine algae ($\hat{p} = 23.77$, CI = 21.57–25.59 vs. $\hat{p} = 28.41$, CI = 24.70–32.18) were observed in our study. There were no significant differences in the proportions of berries and mosses (Fig. 2C). These data are summarized as both percent frequencies and percent scat occurrences for comparison in Table 2.

Coincident with these dietary changes, we estimated the mean breakup date during Russell's study (1968–1968) to



have been 17 July, which is 22 days later than the mean breakup date for this study (2006–2008).

Discussion

If the trend toward earlier spring ice breakup in Hudson Bay continues, polar bears will spend more

Figure 2. The percent frequencies of some food items found in scat along the coast of western Hudson Bay differed between collections made in 1968–1969 and 2006–2008. Analytical 95% confidence intervals are indicated for each. Note the *y*-axis scale differences in the depictions for (A) pooled categories (animals, vegetation, and garbage) and individual (B) animal and (C) plant, fungi, and garbage food items.

time onshore during summer, making any foods consumed during this period increasingly important for the bears' persistence. Their current land-based diet is diverse, consisting of many plants and animals, often consumed together in various combinations. Numerous scats were collected across the entire Cape Churchill Peninsula, from both coastal and inland areas. Given Table 2. Comparison of food items in polar bear scats from coastal areas of western Hudson Bay, Manitoba, (2006-2008) and Cape Churchill, Cape Henrietta Maria, and the west Pen Island (1968-1969).

	Gormezano & Rockwell (2006-2008)			Russell (1968-1969)		
	Raw freq	uencies	Scat occurrences	Raw freq	luencies	Scat occurrences
Таха	n	%	%	n	%	%
Birds						
Aves	122	9.9	18.0	4	0.8	1.9
Aves – unidentified	43	3.5	7.3	52	9.8	24.5
Egg shell/hatching membrane	27	2.2	4.6	0	0.0	0.0
Aves total + eggs	192	15.5	28.8	56	10.6	26.4
Mammals						
Phocidae	42	3.4	7.1	20	3.8	9.4
Ursidae, Ursus maritimus	32	2.6	5.4	2	0.4	0.9
Cervidae, Rangifer tarandus	58	4.7	9.8	0	0.0	0.0
Cricetidae	8	0.6	1.3	42	8.0	21.7
Mammalia – unidentified	6	0.5	1.0	4	0.7	1.9
Mammalia – total	146	11.8	24.6	68	12.9	32.1
Grasses						
Leymus arenarius	353	28.5	59.5	87	16.5	41.0
Other grasses	57	4.6	9.6	83	15.7	39.2
Grasses – total	410	33.1	63.1	170	32.2	80.2
Marine algae	294	23.8	49.6	150	28.4	70.8
Berries	21	1.7	3.5	6	1.1	2.8
Mushrooms	56	4.5	9.4	4	0.8	1.9
Mosses	78	6.3	13.2	26	4.9	12.3
Garbage	40	3.2	6.7	48	9.1	17.0

Data are presented as the percent frequencies of all food items (n = 1237, n = 528) and the percent scat occurrences (n = 593, n = 212) for the current and past polar bear diets, respectively.

the spatial extent of our sampling, and the propensity for bears to segregate (Latour 1981; Derocher and Stirling 1990) and to move relatively little once ashore (Parks et al. 2006), we assume our results reasonably reflect the land-based diet of those polar bears that do forage on the Cape Churchill Peninsula during the icefree period. However, consistent with behavioral observations we have made (Iles et al. 2013; Gormezano and Rockwell, in review) and foraging reports by others (e.g., Dyck and Romberg 2007; Smith et al. 2010), it appears that a number of polar bears do not abstain from eating during the ice-free period. Continued use of the term fasting to describe the behavior of polar bears in general during this period (e.g., Stirling and Derocher 2012) seems rather misleading.

Many foods polar bears are consuming have not changed since the 1960s on the Cape Churchill Peninsula, but we did find new foods and marked changes in the frequency of others. The overall proportion of animals in the diet has increased, whereas the proportion of vegetation has not changed. Caribou and eggs are now present in the diet, the proportion of polar bear remains has increased and that of small mammals has decreased. We also identified more species of birds (11 vs. 1), the majority of which were lesser snow geese. Most scats contained at least one type of vegetation and there were only minor shifts in the types consumed. We also found less garbage in scats than was found in the 1960s (Russell 1975). In the following, we discuss various habitat and environmental changes that occurred during the ensuing 40 years coincident with observed diet changes, including a 22-day advance in the date of sea ice breakup and the closing of the Churchill dump.

Russell did not report caribou or snow geese in polar bear fecal samples collected along the coast of the Hudson Bay Lowlands. In the 1960s, fewer than a hundred caribou were estimated for the population north of the Nelson River (C. Jonkel, S. Kearney, pers. comm.) and sparse groups of <50 animals were counted further south (Abraham and Thompson 1998). Caribou numbers have been increasing steadily (30- to 50-fold) since (Williams and Heard 1986; C. Jonkel, S. Kearney, and R. Brook, pers. comm.), while the animals are also expanding their summer range toward the coast (Abraham and Thompson 1998), thus increasing potential interactions with arriving bears (Fig. 3). Similarly, snow goose abundance has increased 5- to 20-fold across the region since the 1960s



Figure 3. A polar bear looks up from the recently killed caribou it was eating at Keyask Island (58.16958°N 92.85194°W) on July 26, 2010. Photograph by R. F. Rockwell.

(Hanson et al. 1972; Kerbes et al. 2006; Alisauskas et al. 2011), with highest increase and geographic expansion being on the Cape Churchill Peninsula (Rockwell et al. 2009).

Although the scarcity of snow geese in the region during the 1960s likely explains their absence in Russell's study, it is important to note that considerably more (96.2%) of his bird remains were left unidentified compared to our study (21.6%). This may have been due, in part, to our use of more stringent bird identification techniques (see Material and Methods). However, all of Russell's unidentified bird remains comprised "trace to 5.0%" amounts by volume, whereas only 16.2% of our snow goose remains occurred in "trace to 5.0%" amounts. The remaining 83.8% of our scats with snow goose comprised an average of 65.0% of a scat pile by volume, with nearly 40% comprising >90% of a pile. Given the size of lesser snow geese and direct observations of how polar bears consume them (Iles et al. 2013), these larger volumes seem reasonable and their absence in Russell's study further suggest that the unidentified bird remains were likely not snow geese.

Polar bears seem to have taken advantage of the substantial increase in availability of both caribou and snow geese (Table 1). During the summer months, when the two species are raising their offspring, polar bears arriving onshore now regularly overlap herds of caribou and flocks of geese as the bears travel along the coast and move inland (Iles et al. 2013; L. J. Gormezano and R. F. Rockwell, unpubl. obs.). The increased co-occurrence of polar bears and the now plentiful caribou and snow geese facilitate opportunities for both predation as well as scavenging of kills made by other predators (e.g., wolves, *Canis lupus*, [Brook and Richardson 2002]; grizzly bears, *Ursus arctos*, [Rockwell et al. 2008]). Predation events on other waterfowl species during incubation or brood rearing on our study area (Table 1) and elsewhere (e.g., Madsen et al. 1998; Drent and Prop 2008) suggest that other avian species are similarly vulnerable.

Egg remains occurred in 4.6% of scats we collected along the coast, contrasting with Russell's study that reported no eggs (Russell 1975). Earlier observations had documented polar bears eating eggs as part of a varied diet (e.g., Harrington 1965; Pedersen 1966) or had reported them in the stomachs of harvested bears (pers. comm. to R. H. Russell 1975). Russell (1975) found egg remains in 5.0% of scats on the Twin Islands in James Bay, Ontario, but concluded that foraging on eggs was likely uncommon because polar bears were on the ice during the peak periods of hatch. With breakup occurring on average 22 days earlier, however, polar bears are arriving onshore sooner and are overlapping the incubation period of snow geese, common eiders, and other species of waterfowl (Rockwell and Gormezano 2009). Reports of polar bears consuming eggs of nesting waterfowl have increased across the polar bears' range (see Drent and Prop 2008; Smith et al. 2010). We also observed polar bears capturing adult birds (e.g., snow geese, Canada geese, common eiders) guarding their nests in addition to consuming their eggs. Consistent with our observations, we found that 25% of the scats with egg remains occurred in the same pile as the remains of adult snow geese.

Although the overall proportion of mammals in our scats has not changed substantially from Russell's study (24.6% vs. 32.1% of scats, respectively), we found caribou (above), more polar bear remains, and fewer rodent remains in our samples (Table 2). Assuming the rodent estimates in Russell (1975) are typical for the Cape Churchill area, the difference in rodents may be due either to our sampling occurring during 3- to 5-year cyclic fluctuations (Krebs and Myers 1974) or to declines in peak lemming abundance thought to be associated with warmer temperatures during fall freeze-up and subsequent high levels of precipitation into early winter that drive lemmings to higher ground where they are less protected through the harsh winter (Scott 1993).

The increased number of scats with polar bear remains relative to the 1960s (Table 2) is consistent with reported higher rates of cannibalism (i.e., intraspecific predation and/or scavenging). Several authors have speculated that because of earlier breakup of ice, nutritional stress could lead to increased intraspecific aggression and cannibalism (e.g., Taylor et al. 1985; Amstrup et al. 2006; Stirling et al. 2008). Recent observations of intraspecific attacks initiated by polar bears in poor condition support this suggestion (Lunn and Stenhouse 1985; Taylor et al. 1985), but many instances of healthy polar bears initiating similar attacks have also been reported (Taylor et al. 1985; Derocher and Wiig 1999; Dyck and Daley 2001; Stirling and Ross 2011). Furthermore, not all polar bears that are killed are consumed, suggesting that there may be other reasons for this behavior (Taylor et al. 1985; Derocher and Wiig 1999).

Different types of vegetation, particularly grasses and marine algae, were pervasive; occurring in 84.9% of polar bear scat piles and this is similar to observations across the circumpolar range of polar bears (Koettlitz 1898; Pedersen 1966; Russell 1975). Although the overall proportion of vegetation items has not changed since the 1960s (67% and 69%), the proportion of Lyme grass has increased while other grasses have decreased (Table 2). Like other predatory mammals, polar bears might consume vegetative roughage (e.g., grass stalks, marine algae, moss) as part of self-medicative efforts to reduce loads of worm parasites (Huffman 2003), to acquire a source of fiber to facilitate bowel movement (McKeown 1996) or to acquire nutrients that are lacking from animal sources. For example, polar bears preferentially consume the spikes of Lyme grass (Russell 1975; Lunn and Stirling 1985) that have protein-rich seed heads in early July through late August (Johnson 1987). Lyme grass has occurred along the entire coast of western Hudson Bay for many years (Jefferies et al. 2006) and unless polar bears are recently targeting it to fulfill a protein or other dietary need we can offer no firm explanation of its increased consumption. However, preliminary analyses of plant phenology on the Cape Churchill Peninsula (C. P. H. Mulder and R. F. Rockwell, unpubl. ms.) suggest that flowering and seed set is advancing although not as fast as sea ice dissolution. It is thus possible that polar bears are increasingly overlapping the seed heads much as snow goose eggs.

We also found a higher proportion of scats with mushrooms along the coastal portions of our study area than Russell (1975) found in the 1960s (Table 2). The two species we identified, Lycoperdon pyriforme and L. perlatum, occur from July through November along the entire western Hudson Bay coastline and thrive on driftwood that litters the coastline, fallen trees further inland, and soil substrates across the landscape (McKnight and McKnight 1998). Although Russell (1975) commented that mushrooms were typically found in low volumes (5-10%) with crowberries and suggested that they were consumed together at the same site, we found no patterns of co-occurrence of mushrooms with any other foods. Mushrooms were typically found in volumes of 10% or less, but we also found many (28.1% of scats with mushrooms) where mushrooms comprised 50% or more of a scat pile. There were four scats that contained only mushrooms, indicating that polar bears may consume them in large quantities when available, perhaps in attempt to acquire limiting micronutrients (e.g., Iversen et al. 2013).

The decrease in proportion of garbage in scats in the current diet may be due to marked changes in the availability of garbage both near the town of Churchill and in areas further east along the Hudson Bay coast. In 2005, the town of Churchill closed the landfill, which previously attracted numerous polar bears (Lunn and Stirling 1985). Garbage was subsequently secured from bears prior to recycling or removal from the area. Also, rules governing the securing and removal of waste from research camps, including Nester 1, from which Russell's Cape Churchill collections were based, became more stringent with the establishment of Wapusk National Park in 1996 (R. F. Rockwell, pers. obs.). Stored garbage depots were systematically removed from areas south of Cape Churchill and more effectively secured from polar bears in subsequent field seasons.

General considerations

Our data indicate that polar bears are now foraging on increasingly abundant terrestrial prey such as caribou and snow geese and utilizing novel resources like eggs that have become newly available through climate-induced shifts in their onshore arrival. These observations combined with those of other studies and the diverse patterns of different foods in scats (Gormezano and Rockwell, in review) suggest that some polar bears are opportunistic omnivores. If this observed foraging renders some present or future benefit, it may be an example of "diet mixing" (ingestion of multiple species over an animal's lifetime or life cycle that differ qualitatively to the consumer) (Singer and Bernays 2003), a foraging strategy shared by many predators in Arctic ecosystems (Samelius and Alisauskas 1999; Elmhagen et al. 2000). This mode of foraging is similar to that observed in other bear species that are known to shift their diet regularly to exploit both seasonally (e.g., Persson et al. 2001) and newly available resources (Beckmann and Berger 2003) to meet their nutritional needs. In the closely related brown bear, dramatic differences in diet have been observed in response to local prey and vegetation abundance (e.g., Hilderbrand et al. 1999), competition (e.g., Gende and Quinn 2004), and environmental change (e.g., Rodríguez et al. 2007).

It is generally agreed that polar bears diverged from brown bears at least 600,000 years ago and evolved to survive in the specialized Arctic environment (Hailer et al. 2012; Cahill et al. 2013; Weber et al. 2013). One or more hybridization events have likely occurred since then, evidenced by brown bear mitochondrial DNA having introgressed into polar bear lines (Hailer et al. 2012). It has been suggested that such events may have helped polar bears persist through multiple interglacial warm phases (Edwards et al. 2011; Hailer et al. 2012). We suggest that the wide range of foraging behaviors observed for polar bears, like those present in brown bears, may reflect an inherent plasticity and shared genetic legacy that was likely retained over time (e.g., Agosta and Klemens 2008; Miller et al. 2012; Weber et al. 2013). Among those polar bears foraging, the shifts in the diet that have occurred (and are occurring) since Russell's (1975) study may be an innate plastic response to changing prey availability and exemplify the type of foraging behavior that these polar bears are capable of as climate change reduces their opportunities to hunt seals. Pending the outcome of current genetic analyses, however, it is yet unclear how many polar bears are exhibiting this behavior and thus the extent of any benefits that may be gleaned from it.

There is evidence that body mass and survival of at least some demographic classes of polar bears has declined coincident with the advancing date of breakup of Hudson Bay sea ice (e.g., Stirling and Parkinson 2006; Regehr et al. 2007). It is suggested that the declines are the result of the bears becoming increasingly nutritionally stressed and that this may, in turn, lead them to seek alternative food sources (Stirling and Parkinson 2006; Regehr et al. 2007). While possible, this seems unlikely to be the only cause of such terrestrial foraging because land-based hunting, scavenging, and grazing actually predate recorded climaterelated changes (e.g., Pedersen 1966; Russell 1975).

Also, polar bears have switched between major prey items in the past when nutritional stress was likely not a causative factor. For example, Thiemann et al. (2008) found that polar bears switched their primary consumption from bearded to ringed seals when the abundance of the two species changed in western Hudson Bay. The switch was independent of the date of ice breakup and they concluded that polar bears are "... capable of opportunistically altering their foraging to take advantage of locally abundant prey, or to some degree compensating for a decline in a dominant prey species." (Thiemann et al. 2008). Our observations on consumption of increasingly abundant caribou, snow geese, and their eggs are consistent with this assessment. Observations of polar bears coming ashore seeking eggs even while seals were still available on the ice (Madsen et al. 1998; Drent and Prop 2008) lend additional support to their prey switching abilities and general plasticity in foraging.

Current threats to the persistence of polar bears in western Hudson Bay are clear as the ice-free season expands, limiting polar bear access to seals on the ice (e.g., Stirling and Derocher 2012). However, with a history of adaptive foraging behavior and pursuit of novel prey across their Arctic habitat (e.g., Dyck and Romberg 2007; Smith et al.

2010), it is unlikely that polar bears will abstain from exploiting new terrestrial resources solely because they were ignored in the past in favor of more easily accessible marine prey. Some polar bears currently eat a variety of terrestrial animals and plants during the ice-free period, taking opportunistic advantage of abundant species. We suggest that research now focus on determining both the number of polar bears making this shift and the nutritional and energetic gains associated with this shifting terrestrial diet. Furthermore, these gains must be considered when modeling future polar bear survival. Shifts in diet composition, even for what may comprise a small fraction of the annual nutritional and energy budget may become increasingly important for some individuals in the population as ice conditions worsen (e.g., Dyck and Kebreab 2009; Rockwell and Gormezano 2009).

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Conflict of Interest

None declared.

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Dietary composition and spatial patterns of polar bear foraging on land in western Hudson Bay

Gormezano and Rockwell



RESEARCH ARTICLE



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Dietary composition and spatial patterns of polar bear foraging on land in western Hudson Bay

Linda J Gormezano^{*} and Robert F Rockwell

Abstract

Background: Flexible foraging strategies, such as prey switching, omnivory and food mixing, are key to surviving in a labile and changing environment. Polar bears (*Ursus maritimus*) in western Hudson Bay are versatile predators that use all of these strategies as they seasonally exploit resources across trophic levels. Climate warming is reducing availability of their ice habitat, especially in spring when polar bears gain most of their annual fat reserves by consuming seal pups before coming ashore in summer. How polar bears combine these flexible foraging strategies to obtain and utilize terrestrial food will become increasingly important in compensating for energy deficits from lost seal hunting opportunities. We evaluated patterns in the composition of foods in scat to characterize the foraging behaviors that underpin the diet mixing and omnivory observed in polar bears on land in western Hudson Bay. Specifically, we measured diet richness, proportions of plant and animal foods, patterns in co-occurrence of foods, spatial composition and an index of temporal composition.

Results: Scats contained between 1 and 6 foods, with an average of 2.11 (*SE* = 0.04). Most scats (84.9%) contained at least one type of plant, but animals (35.4% of scats) and both plants and animals occurring together (34.4% of scats) were also common. Certain foods, such as Lyme grass seed heads (*Leymus arenarius*), berries and marine algae, were consumed in relatively higher proportions, sometimes to the exclusion of others, both where and when they occurred most abundantly. The predominance of localized vegetation in scats suggests little movement among habitat types between feeding sessions. Unlike the case for plants, no spatial patterns were found for animal remains, likely due the animals' more vagile and ubiquitous distribution.

Conclusions: Our results suggest that polar bears are foraging opportunistically in a manner consistent with maximizing intake while minimizing energy expenditure associated with movement. The frequent mixing of plant-based carbohydrate and animal-based protein could suggest use of a strategy that other Ursids employ to maximize weight gain. Further, consuming high rates of certain vegetation and land-based animals that may yield immediate energetic gains could, instead, provide other benefits such as fulfilling vitamin/mineral requirements, diluting toxins and assessing new foods for potential switching.

Background

Flexibility in foraging is key to persisting in a labile and changing environment (e.g., [1-4]). Three common strategies are used by predators to exploit available food in such situations: prey switching, omnivory and food mixing [5-7]. Prey switching involves shifting between ecologically diverse prey, seasonally or over an animal's lifetime in response to the availability or quality of the prey [2,7,8]. Omnivory is defined as foraging on both animal and plant material and can benefit species that are primarily carnivorous by

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providing an alternate source of nutrition when preferred animal-based food is in short supply or not easily obtained [6,9,10]. Food mixing involves ingesting material from different species either simultaneously or over various intervals of an animal's lifetime that differ qualitatively to the consumer [11]. For example, brown bears (*Ursus arctos*) and Speck's hinge back tortoises (*Kinixys spekii*) consume specific combinations of different foods to obtain optimal proportions of macronutrients [6,12].

Polar bears (*Ursus maritimus*), especially those that spend portions of the year on land, are versatile predators and appear to use all of these strategies, as they seasonally exploit food across trophic levels (e.g., [13-16]). Although



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the more southern populations of Hudson Bay are pagophilic (ice-loving) for much of the year, they move to land for a minimum of 4–5 months as the sea ice melts completely by summer [17]. While on the sea ice, they are mostly carnivorous, feeding primarily on ringed seals (*Phoca hispida*) but periodically consuming bearded seals (*Erignathus barbatus*), harbor seals (*Phoca vitulina*) and other marine mammals (e.g., [18]). As these "southern" polar bears move to land, they adopt a more omnivorous and mixed diet including fruit and other vegetation as well as different varieties of animals (e.g., [14,16,19]).

Climate change is causing Hudson Bay sea ice to melt earlier in the spring and this increasingly limits the time polar bears have to hunt seal pups, from which they historically have gained the majority of their annual fat reserves [17]. These reduced hunting opportunities are believed to have resulted in nutritional deficits that have been linked to decreases in survival and reproductive output of some demographic groups [20,21]. Ironically, the earlier melting of sea ice that has resulted in a mismatch with their traditional spring prey has also produced a new match with land-based prey on the Cape Churchill Peninsula of western Hudson Bay [22]. Earlier onshore arriving polar bears are now taking advantage of lesser snow geese (Chen caerulescens caerulescens) and their eggs as well as caribou (Rangifer tarandus) from the increasing populations of both species [16,23].

It is possible that, once ashore, switching to these new land-based prey could offset some of the nutritional deficits incurred by earlier arriving polar bears and mitigate some of the reductions in survival and reproductive success [16,22,23]. It is more likely, however, that those deficits could be offset if these resources are combined with other readily available plant and animal land-based resources these polar bears consume during the ice-free period [23,24]. Such food mixing and omnivory can result in synergisms that lead to otherwise unexpected nutritional gains (e.g., [12]). Unfortunately, little is known about the basic foraging patterns that might underpin omnivory and food mixing in polar bears during the ice-free period [24] and that behavioral perspective is crucial to understanding the potential utility of these strategies [11]. For example, what foods are consumed over similar time frames and how is that consumption related to the spatial distribution of those foods?

The range of terrestrial foods sought by polar bears suggests a high level of plasticity in their foraging behavior which may have always been present (e.g., [25]), but actually might be increasing over time in response to changing ecological conditions [26]. For example, polar bears have been observed chasing and capturing lesser snow geese on land [27], climbing rocky outcrops to eat thick-billed murres (*Uria lomvia*) and their eggs [28], leaving the ice to consume eggs on land [29,30] and traveling to land or further inland to consume lower quality vegetation (compared to animals) such as graminoids and berries [31,32]. Again, however, what is not well known is how regularly these foods occur together in the diet of polar bears, especially during the ice-free period when the benefits of omnivory and food mixing could offset nutritional deficits [24].

In this paper, we use data from a large-scale polar bear scat collection on the Cape Churchill Peninsula of western Hudson Bay to examine patterns in dietary composition and richness within and between feeding sessions (as defined by the foods present in a scat pile) and how these vary across the landscape to more fully understand the extent and potential utility of omnivory and food mixing behaviors on land. Specifically, we examine (1) diet richness to evaluate how many items polar bears generally consume within foraging sessions; (2) food-specific co-occurrence to see if certain foods are consumed with fewer accompanying foods compared to other items; (3) *degree of omnivory* to determine to what degree polar bears are consuming different food types (e.g., vegetation, animals) alone or in combinations; (4) spatial composition to see if polar bears are depositing scats (and likely consuming foods) where they are most available; and (5) spatial food-specific co-occurrence to see if polar bears consume fewer accompanying foods when consuming certain foods that occur relatively more frequently in scats in a particular area. In addition, we use a rough temporal index to compare composition and food-specific co-occurrence rates in scats collected fresh in mid-summer compared to older "unknown" age scats to examine foraging patterns limited to that time period.

Methods

Study area

Scat was collected along 160 km of coastline and inland areas within the Cape Churchill Peninsula [22] where polar bears are known to occur during the ice-free period in Manitoba, Canada [33]. The sampling area extended from the town of Churchill, Manitoba (58°46'N, 94°12'W), east to Cape Churchill (58°47'N, 93°15'W) and south to Rupert Creek (57°50'N, 92°44'W). Samples collected from 6 denning areas southeast of Churchill extended inland of the coastline to 93°51'W (Additional file 1: Figure S1). For site description details, see Gormezano and Rockwell [16]. During the sampling period, polar bears were predicted to arrive on land shortly after 24 June, 22 June and 28 June in 2006, 2007 and 2008, respectively, based on standard calculations for 50% sea ice breakup [34,35].

Scat collection and analysis

We used a trained detection dog to find scats along 1-3 kilometer linear coastal transects (parallel to the coastline) and in the vicinity of inland dens from 2006 through 2008.

Coastal transects from the town of Churchill and Rupert Creek were walked between 25 May and 11 August. Upland habitat in the vicinity of inland dens was searched between 30 May and 17 June when they were likely to be vacant. For all scats collected, we recorded the date, geographic coordinates, substrate and relative freshness. Samples were categorized as either "fresh" (from the current season) or "unknown age" (from the current or previous season) based on smell, color and presence of insect larvae. Intact scats of all ages were collected and foods were identified from entire piles. Samples collected prior to the arrival of polar bears in a given year (see above) were all from a previous season (old) whereas those collected after that date were a mixture of fresh and old scats. Because freshness of scats was dependent, in part, on time of collection, we use the composition of "fresh" samples collected after the bears' arrival only to identify foods definitely consumed in mid to late summer (and not previously). All collection protocols were approved by the Institutional Animal Care and Use Committee of the American Museum of Natural History (Reference Number: 11-1025-2005).

Scats were often found to be clumped along a transect line or near a denning site. To minimize potential bias resulting from multiple scats being deposited by a single individual, we did not use all of the samples collected from clumped points along each of our 31 transects for these diet analyses. We randomly selected approximately 50% of the scats collected from each transect for analysis so that they would be representative of the relative frequencies and geographic extent of the sampled areas. Though the actual number of polar bears depositing the sampled scats is unknown, we assume from the size and geographic extent of our sampling and other studies suggesting that polar bears segregate and move little once ashore [33] that our samples are representative of the land-based diet of those polar bears that do forage on the Cape Churchill Peninsula.

Animal remains were identified from entire scats using a combination of microscopy, reference keys [36-39] and expert opinion (N. Duncan, A. Rodriguez, C. Dove). Plant and fungi were identified using keys [40,41] but most were subsequently pooled into broad taxonomic categories due to the variety encountered and time constraints. Identification techniques are described in detail in Gormezano and Rockwell [16]. Bones, hairs and feathers were identified to the lowest taxonomic level possible but if they could not be identified beyond 'bird' or 'mammal' they were only included in statistical analyses where pooled, higher taxonomic groups (i.e., birds, mammals) were used. Bones classified no finer than 'animal' were only included in summary statistics of major food categories (e.g., vegetation, animals).

Polar bear hair was found in most scats and was likely ingested during grooming. We distinguished evidence of

cannibalism from grooming by the larger volume of hair, presence of flesh, bone and a distinct smell. All food items (other than polar bear) were considered present if they were identified in a scat pile, regardless of volume.

Statistical analysis

We examined the diet of polar bears using the: (1) raw frequencies (number of times each food item was found) and (2) scat occurrences (the number of scats with a food item). We use the percentages of these (relative to their appropriate sum) for ease of presentation in some cases. Raw frequencies of individual food items were found to occur independently in scats, justifying their use in statistical analyses [16]. The raw frequencies and the scat occurrences are the same value unless multiple items from the same category occur in a scat pile (i.e., 2 birds in one scat). Multiple items were only counted for animals when evidence was conclusive (e.g., 3 bird feet) and was not counted for plants and fungi.

Most analyses of spatial and compositional patterns in diet were done using 14 inclusive groups of food items with each group having at least 5 occurrences of all included taxa. These groups were polar bear, seal (e.g., Phoca hispida), caribou (Rangifer tarandus), rodents (i.e., muskrats (Ondatra zibethicus), meadow voles (Microtus pennsylvanicus), collared or bog lemmings (Dicrostonyx richardsoni and Synaptomys cooperi)), birds, eggs, Lyme grass (Leymus arenarius; shafts and/ or seed heads), Lyme grass seed heads (seed heads only), other grasses (e.g., Festuca brachyphylla), marine algae (e.g., Fucus spp., Laminaria spp.), berries (e.g., Vaccinium uliginosum, Empetrum nigrum), mosses (e.g., Sphagnum fuscum), mushrooms (Lycoperdon and Bovista spp.) and garbage. Although the Lyme grass seed heads and shafts come from the same plant, their raw frequencies within scats are independent and they are treated as separate food items [16].

We tabulated the percent scat occurrences that included at least one food item that was: vegetation, animal (mammals, birds or eggs) and land-based animal (*LBA*; i.e., birds, eggs, caribou, rodents) across all piles. As an index of the complexity of the diet of individual bears, we also calculated the number of scats containing both vegetation and animal, >1 animal and >1 *LBA*.

As an additional index of diet complexity, we calculated the minimum, maximum and mean number of food types per pile using scat occurrences as the unit of measure. Because the "Lyme grass" category includes both the shafts and/or seed heads, including "Lyme grass seed heads" as a separate category when scat occurrences are the unit of measure is redundant. For this reason, "Lyme grass seed heads" was excluded from this analysis (13 groups used). To examine whether complexity differed depending on the presence of a particular food type, we quantified the scat occurrences of co-occurring food items in each scat for each of the 14 food categories and plotted their distribution and mean (with standard error) across all scats. Different animal and plant matter pass through the digestive tract of bears at different rates [42], so we assumed that the observed combinations reflect foods consumed within a single feeding session, not necessarily at the same time. We define a 'feeding session' as the period between ingesting and defecating the undigested remains, which can vary between 6.2 and 19.0 hours based on minimum digestive rates for vegetation (by grizzly bears) [43] and maximum digestion rates for meat (by polar bears) [44], respectively.

To examine potential effects of spatial differences in topography, vegetation and local prey abundance that might affect diet composition, raw frequencies of different food items were compared across 5 different sections of the study area. Although polar bears are capable of traversing long distances, they are known to move relatively little on land compared to on the ice [33,45]. We therefore hypothesized that scats collected from areas with distinct landscape characteristics, such as anthropogenic land use (e.g., the town of Churchill, tundra vehicle based tourism), concentrations of known nesting bird colonies, and distinct vegetation clines [46], would contain food items specific to the areas from which they were collected. For example, we expected to see more garbage where people reside, more berries inland and more birds in scats in the vicinity of the historical lesser snow goose (Anser caerulescens caerulescens, henceforth snow goose) and common eider (Somateria mollissima) colonies near La Pérouse Bay.

Using the raw frequencies of items from the 14 inclusive food groups, we pooled items to major categories (animal, vegetation or garbage). To evaluate if there was an overall difference in the proportions of these categories among areas, we used a 5×3 log-likelihood chi-square test. For this test, the 3 food categories were cross-classified against the 5 areas and expectations computed under the independence assumption as the product of the proportion of scats containing the food category and the proportion of scats in the area times the total number of scats. The log-likelihood chisquare was used rather than the chi-square because it is less affected by low cell frequencies [47]. Expectations for subsequent log-likelihood chi-square analyses were computed in a similar fashion. Because this overall test was significant (G = 100.27, DF = 8, P < 0.0001), indicating a difference in proportions, we performed 5×2 loglikelihood chi-square tests for each food category to identify in which category items varied.

We performed a similar test evaluating differences in the proportions of individual foods (from the 14 inclusive groups) across the study area using a 5×14 loglikelihood chi-square test. Because the overall test was highly significant (G = 376.14, DF = 52, P < 0.0001), indicating differences among the 5 sections of the study area, we performed 2×14 log-likelihood chi-square tests for each of the 5 sections to identify which had food items that varied. Significance of these pair-wise tests was evaluated using a sequential Bonferroni approach [48] to reduce inflation of our overall α -error rate. For the sections in which items differed, we then compared the proportions and 95% confidence limits of the frequencies of each food item to identify which ones differed the most.

To test the hypothesis that polar bears would consume certain foods more frequently in a particular area to the exclusion of others, whether because of preference or availability, we compared the means and 95% confidence intervals of scat occurrences of co-occurring foods in areas where foods were consumed more frequently with those from all other areas. We hypothesized that if other foods were being excluded the mean number of co-occurring foods in those areas would be less than (and outside the confidence interval of) all other areas. We illustrate our results by plotting the differences between mean number of co-occurring items among scats containing foods consumed relatively more often in a particular area and the mean number of co-occurring foods in scats containing these same items in all other areas. Because we use mean differences, a value of zero equals no difference. Pooled estimates of variance are used in derivation of confidence limits [47].

Although we could not assign exact age to most scats, it was possible to identify those deposited in the current season. Because our sampling occurred just as polar bears were arriving ashore, we assumed that these scats contained foods consumed either on the ice (just before coming ashore) or shortly after arriving. Using raw frequencies as the unit of measure, we performed a 2×3 log-likelihood chi-square to evaluate whether there were differences in the proportions of major food categories (animals, vegetation and garbage) between fresh and unknown age scats. We then performed a 2×14 loglikelihood chi-square test to assess whether the frequencies of individual foods (within these broad categories) differed in fresh and unknown age scats. Because the overall test was highly significant (G = 36.79, DF = 13, P = 0.0004), indicating differences between foods in fresh and unknown age scats, we compared the proportions and 95% confidence limits of the frequencies of food items to identify which ones were being consumed and deposited in scat more or less often when polar bears first come ashore.

To evaluate whether polar bears were consuming certain foods at relatively higher rates to the exclusion of others in mid-summer, we also compared the mean number and 95% confidence interval of scat occurrences of co-occurring foods for new and unknown age scats with more frequently consumed items. Results are illustrated using differences and 95% confidence intervals of mean numbers of cooccurring items in fresh scats containing the more frequently consumed items and the mean numbers of co-occurring items in unknown age scats containing these same items.

Results

We evaluated 642 scats (of 1,262 collected); 219, 248 and 175 in 2006, 2007 and 2008, respectively. 593 scats were collected from coastal areas and 49 from inland sites. Vegetation and land-based animals occurred in 84.9% and 35.4% of all scats, respectively. Polar bears that consumed animals (either land- or marine-based; 45.8% of scats) did not appear to specialize on that particular resource because we also observed a high co-occurrence of animal and vegetation (34.3%) and multiple animal taxa (9.3%) in the same scat (Table 1).

There were between 1 and 6 different foods in each scat, with an average of 2.11 (SE = 0.04) items. The mean number of co-occurring items ranged from 1.21 (SE = 0.19) for Lyme grass seed heads to 2.61 (SE = 0.26) for eggs (Figure 1). The percentage of scats that were found with 0, 1, 2, 3, 4 and >4 accompanying items is also illustrated for each of the 14 food items in Figure 1.

The overall proportions of food categories (animals, vegetation and garbage) differed across the study area (G = 100.27, DF = 8, P < 0.0001), but this difference was only due to differences in the proportions of vegetation (G = 39.25, DF = 4, P < 0.0001) and garbage (G = 82.27, DF = 4, P < 0.0001). The proportions of animals (G = 11.14, DF = 4, P < 0.025) did not significantly differ at our adjusted alpha level ($\alpha = 0.0167$). Individual food items significantly differed across the study area (G = 376.14, DF = 52,

Table 1 The number and percentage of polar bear scats (n = 642) containing 'vegetation', 'animal', 'land-based' food items

	Scats containing food item		
	#	%	
Food type (≥ 1)			
Vegetation	545	84.9	
Animal	294	45.8	
Land-based food	605	94.2	
Land-based animal	227	35.4	
Food combinations			
Animal + Vegetation	220	34.3	
> 1 Animal	60	9.3	
> 1 Land-based animal	42	6.5	

'Vegetation' includes grasses, marine algae, mosses, mushrooms and berries; 'Animal' includes identified and unidentified birds, mammals and eggs; 'Land-based food' includes any food item except seal or polar bear (which could have been consumed on the ice); 'Land-based animal' includes caribou, birds, eggs and rodents. P < 0.0001). More specifically, area #1 (G = 95.62, DF = 13, P < 0.0001, n = 69 scats), area #2 (G = 55.45, DF = 13, P < 0.0001, n = 71), area #4 (G = 149.49, DF = 13, P < 0.0001, n = 369) and area #5 (G = 180.58, DF = 13, P < 0.0001, n = 49) each had food items that occurred in different proportions than expected given total occurrences in all other areas. The proportions for area #3 (G = 25.30, DF = 13, P = 0.021, n = 84) were not significantly different using our adjusted alpha level ($\alpha = 0.01$).

Within and adjacent to the town of Churchill (area #1, Figure 2), we found scats with more eggs and garbage. Further east, along the tundra vehicle route, which runs between two temporary camps set up by tundra vehicle tour operators in the fall (area #2), we found a higher proportion of marine algae and garbage (more than areas #3, 4 and 5, but less than area #1). In the stretch of coast south of Cape Churchill to just north of Rupert Creek (area #4), we found a higher proportion of scats with Lyme grass shafts and Lyme grass seed heads. Inland areas near dens (area #5) had significantly more berries, other grasses and less marine algae. No significant differences in proportions were detected along the coast near La Pérouse Bay (area #3). Proportions of food item frequencies in each area with confidence limits are summarized in Table 2.

Four of the food items that were found to be spatially in excess of expectation also occurred with fewer accompanying food items compared to other areas, suggesting the bears consumed foods at higher rates in these areas and to the exclusion of other foods. This was the case with marine algae ($\bar{x} = 2.02 \pm 0.27$ vs. $\bar{x} = 2.61 \pm 0.14$) in area #2, Lyme grass ($\bar{x} = 2.31 \pm 0.14$ vs. $\bar{x} = 2.75 \pm 0.25$) and Lyme grass seed heads ($\bar{x} = 2.05 \pm 0.38$ vs. $\bar{x} = 3.6 \pm 1.42$) in area #4, and berries ($\bar{x} = 2.11 \pm 0.34$ vs. $\bar{x} = 4.00 \pm 1.07$) in area #5 (Figure 3a).

A total of 125 fresh scats with a total of 262 occurrences of food items was collected, all found along the coast. The proportions of foods from major categories (animals, vegetation and garbage) were significantly different (G = 6.30, DF = 2, P = 0.043) between fresh and unknown age scats due to an increase in the proportion of animals in fresh scats (G = 4.52, DF = 1, P = 0.0335). The frequencies of individual food items significantly differed (*G* = 36.79, *DF* = 13, *P* = 0.0004). More specifically, we found a higher proportion of Lyme grass seed heads ($\hat{p} = 7.25$, CI = 4.42-11.12 vs. $\hat{p} = 2.16$, CI = 1.39-3.20) and lower proportions of marine algae ($\hat{p} = 14.12$, CI = 10.14-18.92 vs. $\hat{p} = 23.35$, CI = 20.95-25.36) and berries ($\hat{p} = 1.91$, CI = 0.62-4.40 vs. $\hat{p} = 4.60$, CI = 3.44-6.02) in fresh scats. Of these foods, only marine algae occurred in piles with significantly fewer accompanying foods in unknown age scats ($\hat{p} = 1.69$, CI = 1.56-1.83) than in fresh scats ($\hat{p} = 2.84$, *CI* = 2.45-3.23); and thus were consumed at higher rates to the exclusion of others later in the season (Figure 3b).



diet complexity. For each food item on the x-axis, each section of the vertical bars is the percent frequency of the number of co-occurring food items. For example, seed heads occurred alone in 39.5% of scats, with one other food item in 23.3% of scats, etc. The diamond points connected by the black line are the mean number of co-occurring foods (right y-axis) with associated standard errors for each food item.



			Site #		
Food item:	1	2	3	4	5
	20.43	19.96	27.46	13.26	24.70
Birds	14.01	12.98	20.97	10.89	15.79
	9.00	9.07	15.35	8.84	9.09
	18.23	2.78	6.16	2.46	5.73
Eggs	12.98*	0.00	2.69	1.38	1.05
	9.52	0.00	0.88	0.69	0.03
	8.09	8.30	4.96	7.17	14.63
Caribou	3.82	3.82	2.15	5.38	7.37
	1.42	1.25	0.59	3.93	3.01
	7.25	1.49	4.64	4.45	5.73
Polar bears	3.18	0.00	1.61	3.00	1.05
	1.04	0.00	0.33	1.93	0.03
	636	3 10	2.96	1 28	3.81
Rodents	2 55	0.76	0.54	0.50	0.00
	0.70	0.02	0.01	0.14	0.00
	8.09	8.70	8.30	4.29	3.81
Seals	3.82	3.82	4.30	2.88	0.00
	1.42	1.25	1.87	1.83	0.00
	20.43	31.84	29.88	34.81	22.24
Lyme grass	14.01	23.66	23.12	32.04*	13.68
	9.00	16.71	17.28	31.03	7.51
	4 5 1	1 4 9	4 64	646	3.81
Lyme grass seed heads	1.27	0.00	1.61	4.76*	0.00
	0.15	0.00	0.33	3.38	0.00
	8.00	7.64	6.88	6.89	18 5 1
Other grasses	3.87	3.05	3 23	5 13	10.51*
other grasses	1.42	0.84	1.19	3.71	5.16
	26.16	<i>4</i> 7 10	27.15	23.50	7 20
Marine algae	19 11	38 17*	25 27	20.09 20.78	7.J9 7.11
	13 21	20.76	10.21	18.02	2.11

Table 2 The proportions and upper and lower 95% confidence limits of the frequencies of food items in 5 different areas across the study area

Table 2 The proportions and upper and lower 95%confidence limits of the frequencies of food items in 5different areas across the study area (Continued)

	8.09	3.10	4.96	2.30	47.29
Berries	3.82	0.76	2.15	1.25	36.84*
	1.42	0.02	0.59	0.60	27.16
	7.25	3.10	9.66	6.61	5.73
Mushrooms	3.18	0.76	5.38	4.88	1.05
	1.04	0.02	2.60	3.49	0.03
	8.98	10.71	9.66	13.20	17.27
Moss	4.46	5.34	5.38	6.76	9.47
	1.81	1.77	2.60	5.12	4.42
	22.58	12.64	4.64	1.10	5.73
Garbage	15.92*	6.87	1.61	0.38	1.05
	10.59	4.82	0.33	0.08	0.03

Proportions (in bold) with confidence limits that do not overlap the proportions of another value are considered significantly different (*) from other values.

Discussion

Climate-driven environmental changes are forcing polar bears to spend extended periods on land with smaller sealbased fat reserves. As such, land-based food consumed during this ice-free period may become increasingly important for survival and reproductive success [16,22]. The compositional and spatial patterns of these land-based foods can inform the extent to which terrestrial foraging may alleviate nutritional deficits associated with lost seal hunting opportunities. Currently, the polar bear diet on land is diverse, consisting of many plants and animals, often consumed together in various combinations. Even though they are consuming a mixed diet, polar bears consume higher rates of specific foods, sometimes to the exclusion of others, (e. g., Lyme grass seed heads, berries and marine algae) and often deposit these scats in areas where these foods occur most abundantly, suggesting little movement among habitat types between feeding sessions. The remains of animal prey were found often in scat but unlike plant material there was no obvious spatial pattern to their occurrence. In the following, we discuss possible reasons for the observed dietary patterns, how they may differ between sex and age groups and suggest potential benefits to polar bears consuming a mixed, omnivorous diet on land.

Foraging on vegetation was pervasive across the study area and certain plants were consumed more often, especially in areas where they predominated and where polar bears spent substantial time once they were ashore. Lyme grass, for example, occurs on primary

Figure 3 Foods consumed at relatively higher rates by polar bears to the exclusion of other foods (a) across the study area and (b) between fresh and unknown age scats. Black dots in (a) represent the differences between mean number of items co-occurring with foods consumed more often in a particular area and the mean number of co-occurring foods with these same items collected from all other areas. Black dots in (b) represent differences between mean numbers of items co-occurring with foods found more often in fresh scats and the mean number of co-occurring foods with these same items collected from unknown age scats. Values above the zero (the dotted line) indicate that more foods co-occurred with the more frequently consumed items, whereas those below indicate fewer co-occurred (or were excluded). Foods with 95% confidence limits that do not overlap zero (zero = no difference) indicate that polar bears consumed these foods at a relatively higher rate with significantly fewer (or more) co-occurring foods.

(fewer co-occurring)

2.00 Differences between mean #s of food items per scat 1.00 eggs (site #1) other grasses (site #5) 0.00 garbage (site #1) lyme grass (site #4) marine algae (site #2) -1.00 seed heads (site #4) berries (site #5) -2.00



-1

-1.5



and secondary beach ridges along most of the coast south of Cape Churchill to the Owl River (Figure 2, area #4) and is used extensively for temporary beds by arriving polar bears ([33,49], unpublished observations). While lying in these beds, polar bears consume the entire Lyme grass plant (above ground parts), but will often preferentially consume just the seed heads [14,49] that mature in early to late July and remain available until late August [40].

The bears have also been seen walking through these stands of Lyme grass eating just the mature seed heads (unpublished observations). The relatively high gross energy yield (compared to other grains) [50], relatively high protein content [51] and convenient access would make these seed heads an attractive food source to arriving polar bears. It could also explain why many (44.1%) of the "fresh" scats contained seed heads and occurred with fewer accompanying foods where they were most abundant along the coast (area #4, Figure 2). They also comprised entire scats more often than any other food we recorded (39.5%; Figure 1).

Berries and marine algae were, similarly, found in scats more often where they predominated, but were likely consumed later in summer or early fall. Consistent with an earlier study [52], berry remains in scats were concentrated further inland, where mainly adult females with and without cubs as well as some subadults occur [53]. Berries were consumed more often and to the exclusion of other items, likely in late summer and early fall when commonly consumed species, such as "blueberries" (alpine bilberry, Vaccinium uliginosum) and black crowberry (Empetrum nigrum), ripen. During early fall, many polar bears congregate along the coast east of Churchill, where the landscape is dominated by Larch Fen and Bogs (area #2, Figure 2) [54], waiting for the ice to refreeze. Here, marine algae are more common than other vegetation and therefore may be more convenient to consume. Polar bears may also consume these plants at higher rates later in the season (and not when they first arrive onshore) to consume more desirable parts that become available in fall [55]. Also, shoreline piles of decaying marine algae often contain high concentrations of tipulid (cranefly) larvae (unpublished observations), which may attract polar bears to the plants later in the season when the insect larvae reach maximum size [56]. Reports of polar bears consuming marine algae in other regions, even when seals were available, have also been documented [57-60].

Animals, occurring in 45.8% of scats, are commonly consumed by polar bears during the ice-free period, however, we found no spatial patterns in scats containing them. One reason for this could be that because passage rates are longer for animals than plants [43,44], so they are moving between habitat types faster than the time required to defecate animal remains. Although given the small difference in passage rates (6–12 hours) and limited movements of polar bears on land [33,45], we feel it is more likely due to the widespread occurrence and/or mobile nature of the land-based animals that polar bears consume. For example, most of the birds consumed are various species of flightless waterfowl, the most common of which is Lesser snow geese, occurring in 12.5% of scats [16]. Since the 1960s, the population of snow geese in the Cape Churchill Peninsula has grown nearly 20-fold and expanded its nesting and brood rearing range from the La Pérouse Bay area to the entire Cape Churchill Peninsula as far south as Rupert Creek [23,61].

Earlier arriving polar bears have begun to overlap the incubation period of snow geese (and other waterfowl species) [23], but at present more commonly arrive while young and adult geese are flightless and dispersing along the coast to forage on graminoids. Similarly, the bears co-occur with caribou, whose numbers have increased substantially since the 1960s and that have expanded their summer range closer toward the coast [62], where interactions with arriving polar bears are common (unpublished observation). Other prey, such as rodents, are less mobile but are common in upland habitat, occurring within 5 km from the coast in years when they are abundant [63,64].

Seal, being a preferred food, often occurred alone in scats and with fewer accompanying items. Although it is unclear whether seals were captured on the sea ice or from land (predation or as carrion), we observed multiple seal carcass remains on shore while sampling (unpublished observations). Further, when consumed with other foods, 57.1% of those were either land-based vegetation (i.e., grasses, moss, mushrooms; 21 of 42 scats) or land-based animals (i.e., birds, eggs; 9 of 42 scats). Others have similarly reported polar bears consuming seals and land-based food together through inspection of stomach contents, scat and direct observation [14,16,31,32,60,65]. The purpose of this diet mixing is unclear but could serve to dilute toxins accumulated in the flesh of seals [6,66-69]. Though capture of seals from the shore (e.g., seals resting on rocks) or in open water is considered rare [57], it does occur (Figure 4) ([70], C.J. Jonkel pers. comm.) and may be responsible for some of the seal remains found in our study.

The spatial and compositional patterns in foods consumed suggest that polar bears are foraging on individual foods opportunistically. That is, they are consuming vegetation where and when it is most abundant and in random combinations with other foods (i.e., their occurrences are statistically independent) [16]. Despite the fact that polar bears are known to move little while on land [33,45], animal consumption appears to have no spatial component, likely because the animals are ubiquitously distributed and mobile. It is unclear whether foraging, in and of itself, is opportunistic or coincident with other observed behaviors. For example, is the intense foraging on Lyme grass



coincident with resting on it once ashore or do they rest on Lyme grass after seeking it for consumption? Do certain demographic groups travel inland to consume more berries or are they consuming them coincident with being inland (where berries are more abundant) to avoid the threat of intraspecific predation along the coast?

Though the propensity to forage may differ between individuals, when it does occur, polar bears likely employ foraging tactics that minimize travel to conserve fat reserves. Polar bear locomotion on land is inefficient with costs of travel increasing with decreasing size [71,72]. As a result, search costs would be expensive, making it beneficial for polar bears to partake in large volumes of readily available food and include a large range of possible choices [5]. The generally high species richness and varied composition in scat that we observed, as well as apparent high consumption of locally abundant vegetation supports this. We also found that polar bears often consume more than one type of vegetation in a single feeding session (42.4% of scats). Switching between different types of plants may help maintain both high search efficiencies and bite rates, perhaps making longer bouts of foraging (with increased movements) energetically profitable [24,73].

Adopting a mixed diet of both animal-based protein and plant-based carbohydrates, which occurred frequently in our study (34.3% of scats), may allow polar bears to overcome some of the nutritional constraints associated with large body mass and inclusion of low quality forage in their diet. Other bear species are known to seasonally specialize on certain types of vegetation [73,74] but simultaneously consume animal-based protein and fat sources in limited amounts to maximize mass gain [9,12]. Robbins et al. [12] postulated that brown bears consumed an optimal combination of protein and carbohydrates that minimized the costs associated with protein digestion (deaminating and excreting excess nitrogen) while maximizing digestible energy intake. As a result, bears in the study gained disproportionately more mass on the optimal diet, than they would have gained from the same calories of each macronutrient alone. Polar bears on the Cape Churchill Peninsula may be optimizing their macronutrient intake during the ice-free season in a similar fashion.

Diet food mixing also has the potential to yield nutritional benefits beyond immediate mass gain. For example, various types of vegetation may provide vitamins and minerals absent from their primary diet [6,75]. Iversen [60], for example, describes specific vitamins and minerals in marine algae that are lacking in seal blubber, that might explain why polar bears of all sex and age classes (including adult males) consume this and terrestrial vegetation in Svalbard even when seals are still available to hunt. This may also explain observations of polar bears expending energy to dive, then selectively eating only specific parts of marine algae plants (C.J. Jonkel pers. comm., [14,57,58]).

Another non-energetic benefit of consuming a mixed diet is to allow sampling of available food to assess quality for potential switching or adding of new foods [5]. Traveling to new patches and the effort associated with capturing new prey (e.g., trial and error) are costly and may not yield an immediate energetic gain, however, greater familiarity with various food patches and improvement in efficiency of capturing prey may yield a net energy profit over an animal's lifetime or that of its offspring [27,76,77]. A possible example of this would be the pursuit and capture of flightless waterfowl on land by polar bears. Although some report that consuming a goose after a long pursuit can not be energetically profitable [49], multiple observations of such behavior and the frequent occurrence of waterfowl remains in scat (28.0%; 180 of 642 scats) indicates successful captures occur often ([27], unpublished observations). Given that geese are still a relatively new resource in western Hudson Bay [16] polar bears probably possess varying levels of expertise in capturing them. It may be that only until they have optimized their hunting technique will polar bears glean an energetic benefit from pursuing them.

The sex of polar bears consuming different foods can not be determined from our data without further genetic analyses, however, based on the tendency for different sex/age classes to segregate once ashore and move little on land [33,45,53], general inferences can be made. For example, females with cubs and sub-adults tend to move further inland, whereas adult males tend to predominate along the coast [53], which could lead to some partitioning of resources, as peak availability of certain foods (e.g., berries) might be more accessible to certain demographic groups. Derocher et al. [52] similarly noted the importance of broad spatial (and temporal) sampling in assessing the importance of terrestrial plants in the diet due to observations of berries being primarily consumed by adult females and sub-adults further inland. Although we found no spatial patterns in animal remains in scat, it is conceivable that travel to inland areas might increase interactions with more mobile prey, such as nesting waterfowl. Edwards et al. [4] reported that the degree of carnivory among female grizzly bears increased linearly with movement rate in the Mackenzie Delta region.

Conclusions

Our results support previous findings and Traditional Knowledge that polar bears are opportunistic foragers that exploit a wide variety of plants and animals (e.g., [14,19]). There are clear spatial patterns of food use, especially among plants, and ample evidence that multiple different foods are consumed during single feeding sessions. These foraging patterns define food mixing and omnivory strategies on relatively small spatial and temporal scales. They would permit the bears to maximize calorie intake while minimizing energy expenditures associated with movement [12]. Non-energetic benefits, such as fulfilling vitamin/mineral requirements, diluting toxins, assessing new resources and learning processes, may also motivate seemingly unprofitable foraging behaviors [5,67,76,77].

We suggest that future research include genetic analyses to allow definition of the diet compositions of individuals of known identity and gender. That research should also establish the energetic costs of foraging to obtain mixed and omnivorous land-based diets as well as the energetic gains, including those obtained through food synergism, from those diets. Such information will allow the development of more realistic models of the effect of climate change on survival and reproductive success than current models that assume no nutritional input during the increasing ice-free period (e.g., [78,79]). Finally, future research should continue to monitor changes in polar bear foraging that may result from the bears responding to their changing environment.

Additional file

Additional file 1: Figure S1. Polar bear scat collection areas. Polar bear scat was collected along the coast of western Hudson Bay from the town of Churchill, Manitoba, to Rupert Creek. Scat was also collected near maternity dens at 6 inland sites. Collections were made from 2006 through 2008.

Authors' contributions

Both LJG and RFR participated in the design of the study. LJG collected the data, identified and analyzed items in scat, performed statistical analyses and wrote the manuscript. RFR participated in the collection of data, assisted in the analysis of scat contents and statistical analysis, and edited drafts of this manuscript. Both authors read and approved the final manuscript.

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RESEARCH ARTICLE

The Energetic Value of Land-Based Foods in Western Hudson Bay and Their Potential to Alleviate Energy Deficits of Starving Adult Male Polar Bears

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Abstract

Climate change is predicted to expand the ice-free season in western Hudson Bay and when it grows to 180 days, 28-48% of adult male polar bears are projected to starve unless nutritional deficits can be offset by foods consumed on land. We updated a dynamic energy budget model developed by Molnar et al. to allow influx of additional energy from novel terrestrial foods (lesser snow geese, eggs, caribou) that polar bears currently consume as part of a mixed diet while on land. We calculated the units of each prey, alone and in combination, needed to alleviate these lethal energy deficits under conditions of resting or limited movement (2 km d⁻¹) prior to starvation. We further considered the total energy available from each sex and age class of each animal prey over the period they would overlap landbound polar bears and calculated the maximum number of starving adult males that could be sustained on each food during the ice-free season. Our results suggest that the net energy from land-based food, after subtracting costs of limited movement to obtain it, could eliminate all projected nutritional deficits of starving adult male polar bears and likely other demographic groups as well. The hunting tactics employed, success rates as well as behavior and abundance of each prey will determine the realized energetic values for individual polar bears. Although climate change may cause a phenological mismatch between polar bears and their historical ice-based prey, it may simultaneously yield a new match with certain land-based foods. If polar bears can transition their foraging behavior to effectively exploit these resources, predictions for starvation-related mortality may be overestimated for western Hudson Bay. We also discuss potential complications with stable-carbon isotope studies to evaluate utilization of land-based foods by polar bears including metabolic effects of capture-related stress and consuming a mixed diet.

Introduction

Climate change is causing the sea ice in arctic regions to melt earlier in spring (e.g., [1,2]), leading to a trophic mismatch between polar bears and their primary spring prey, the pups of ringed seals (*Phoca hispida*) [3]. The bears acquire the majority of their annual energy reserves from hunting seals on the ice, especially during the spring when they capture pups in their snow lairs [4]. In western Hudson Bay, polar bears have historically relied on the energy from hunting these seal pups to sustain them through the ice-free period on land until the ice reforms in fall [5,6]. Assuming that polar bear survival is dependent on access to seals during this critical period, many predict declines in polar bear survival and abundance coincident with the advance of sea ice breakup as polar bears will be forced ashore with smaller fat reserves for longer periods (e.g., [3,7,8]).

Molnár et al. [8] used a mechanistic approach to predict polar bear survival that involved establishing a relationship between physical measures (size and structure) and body composition to determine how energy stores are incrementally depleted as polar bears spend longer periods on land during the ice-free season. The model was parameterized with measurements of captured polar bears in western Hudson Bay and daily maintenance costs that are based on past patterns of average daily weight loss experienced by the bears until they returned to the ice [9,10]. Molnár et al. [8] used the model to predict the proportions of adult males that would starve to death as the ice-free season expands to 180 days, a scenario predicted as ice conditions worsen in response to climate change. The model takes into account somatic maintenance costs and the effects of limited movements (2 km d⁻¹) but does not allow for energy influx into the system from consuming additional food on land.

Molnár et al. [8] justified not including a food intake parameter with the assertion that there is no "energetically meaningful" food available for polar bears to eat. They cite Hobson et al. [11] who found that polar bears only utilize fat accumulated from hunting seals prior to coming ashore for energy based on "marine" (as opposed to "terrestrial") stable carbon isotope signatures in exhaled CO_2 of polar bears captured on land. Because energy utilization pathways can change under conditions of extreme stress (which polar bears may experience when captured [12]) and since land-based foods, such as geese and marine algae, can possess a marine signature [13,14,15] their assertions may not be valid.

Polar bears are opportunists (e.g., [16,17]) and have been documented consuming various types and combinations of land-based food since the earliest natural history records (e.g., [18,19, 20,21]). While subadults and family groups have been most often observed pursuing terrestrial animal prey [22,23] and eating plants such as berries [16], the spatial distribution of polar bear scats and personal observations (L.J. Gormezano and R.F. Rockwell), suggest that at least some adult males currently consume plants and animals during the ice-free period [21]. In the absence of genetic analyses, the proportion of adult males using land-based resources is not yet known, but it is reasonably assumed that if such foraging occurs and yields some energetic benefit it will increase in frequency (e.g., through social learning) as the needs intensify [24,25].

In this paper, we reconstruct Molnár et al.'s [8] model to predict future survival of adult male polar bears as the ice-free season expands to 180 days, but consider a scenario in which nutritionally stressed bears seek additional terrestrial food when available. Because polar bears have always consumed food on land and such feeding is already incorporated into daily weight loss patterns used to build the original model, we only include novel animal foods (caribou, *Rangifer tarandus*, eggs and Lesser snow geese, hereafter snow geese or LSGO, *Chen caerules-cens caerulescens*) that have more recently been identified in the land-based diet [13]. The recent population increases of snow geese and caribou (i.e., 1980s, 1990s) have made them more

available to arriving bears, which coincides with the onset of advance in spring ice-breakup [13]. Arriving polar bears now spatially overlap nesting snow goose colonies (see Figure 1 in [26]) as well as local caribou herds which extend across the Cape Churchill Peninsula, south to the Nelson River [13]. Furthermore, as polar bears come ashore earlier they will overlap more of both the incubation periods of snow geese and calving of caribou, potentially creating a new trophic match on land to compensate for the growing mismatch with seals on the earlier disappearing ice.

To evaluate the potential effectiveness of each food toward fulfilling daily energy requirements of adult males projected to starve while on land for 180 days according to Molnár et al. [8], we address these questions:

- 1. How many individual or combined units of each animal sex and age class (e.g., clutch of eggs, caribou calves) would need to be consumed to prevent starvation in each adult male polar bear?
- 2. What is the total energy potentially available to polar bears each day from snow geese, eggs and caribou?
- 3. How many starving adult male polar bears could be supported by each food source?

We discuss the limitations of our derived energy calculations in light of the absence of rigorous data on certain aspects of polar bear foraging behavior such as locomotive costs associated with different foraging techniques.

Methods

Polar bear energy budget during the ice-free season

We used a 2 component, dynamic energy budget model [27] developed by Molnár et al. [8] to track daily energy expenditures and potential deficits that polar bears could accrue while on land as the ice-free season expands. Daily expenditures were presented as the change in storage energy utilizations for somatic maintenance and movement over time. Parameters such as metabolic rate and fat reserves were modeled with straight-line body length and total body mass of different sex and age classes of polar bears captured on land in western and southern Hudson Bay. Based on these relationships, daily estimates of structural volume and energy stores were generated and used to predict critical thresholds beyond which starvation occurred [8].

Application of this model is limited to adult male polar bears (\geq 7 years old) during the icefree season, so other draws on storage energy, such as thermoregulation, structural growth and reproduction are not accounted for. Because Molnár et al. [8] assume that there is no influx of energy from foods consumed during this period, the general model (Eq (2) in [8] changes solely as a function of daily expenditures, including somatic maintenance and movement:

$$\frac{dE}{dt} = \underbrace{-mLBM}_{0} \underbrace{-(aM^{b} + cM^{d}v)}_{0}$$
(1)

Somatic maintenance Movement

where somatic maintenance is assumed to be proportional to the costs associated with maintenance of lean body mass (*LBM*) and the metabolic rate (*m*) is the energy required to maintain a unit mass of lean tissue [10]. Movement costs were derived from an allometric equation describing how costs change as a function of total body mass, M [10]. The first component, postural costs, (aM^b) describes metabolic costs associated with standing and the second, cM^bv , describes how energy consumption increases linearly as a function of velocity, v [28,29]. As explained by Molnar et al. [10], Eq (1) can further be expanded and parameterized using the body composition model:

$$\frac{dE}{dt} = -m(\alpha^{-1}(1-\varphi)E + \rho_{STR}kL^3)$$

Somatic maintenance

$$-(a(a^{-1}E + \rho_{STR}kL^3)^b + c(\alpha^{-1}E + \rho_{STR}kL^3)^d\nu$$
(2)

Movement

Where α represents the energy density of storage, φ is the proportion of storage mass that is fat and $\rho_{STR}k$ is a constant to estimate structural mass from straight-line body length, *L*. Storage energy, *E*, can be expressed as a function of total body mass and straight-line body length (Eq. (1) in [10]):

$$E = \alpha (M = \rho_{STR} k L^3) \tag{3}$$

Following [10], body composition and maintenance parameters were estimated as m = 0.089 MJ kg⁻¹ d⁻¹, $\alpha = 19.50$ MJ km⁻¹, $\varphi = 0.439$, $\rho_{STR}k = 14.94$ kg m⁻³ and movement parameters were estimated as a = 0, c = 0.0214 MJ km⁻¹ and d = 0.684 [30]. Parameter *b* is not reported but we assume this is because a = 0, so postural costs must equal zero, regardless of the value of *b*.

Most adult males are reported to be inactive on land during the ice-free season [31], however, movement rates of approximately 2 km d⁻¹ have been reported [32] in western Hudson Bay. Molnár et al. [8] consider both scenarios, where v = 0 (i.e., somatic maintenance only) and $v = 2 \text{ km d}^{-1}$ for calculations of energy costs. Also, they observed little variation in straight-line body length among the adult males sampled, so a mean length (L = 2.34 m) was used in all calculations. With initial energy stores, E_0 , the time to death by starvation was computed by numerically integrating Eq.(2) and solving for time T when E(T) = 0 [8]. Two ice-free season threshold lengths were used to compare starvation rates among adult males during times of contrasting climate conditions: 120 days, typical of the 1980s, and 180 days to represent potential future conditions as warming trends progress. Using measurements for 97 adult male polar bears captured in 1989–1996, and assuming those sampled bears were representative of all adult males in the western Hudson Bay population, Molnár et al. [8] estimated that approximately 3% died of starvation at the end of a 120-day period if resting and 6% if walking 2 km d⁻ ¹. As that period expands to 180 days, 28% and 48% would die of starvation if resting or walking, respectively. For sake of reference, adult males comprise approximately 25% (234 polar bears) of the western Hudson Bay population (N = 935 in 2004) based on proportions captured during darting operations once surveys were expanded to include all age and sex classes [33].

To reproduce their results, we computed energy density values (*E/LBM*) for sequential mass values (in 1 kg intervals) using Eqs (2) and (3):

$$\frac{E}{LBM} = \frac{\alpha(M - \rho_{STR}kL^3)}{(\alpha^{-1}(1 - \varphi) * \alpha(M - \rho_{STR}kL^3) + \rho_{STR}kL^3)}$$
(4)

and matched the mass values associated with the energy densities for 97 adult male polar bears extracted from Figure 3 in Molnár et al. [8]. Using discrete numerical calculations, we reproduced the daily energy usages for each of the 97 adult male polar bears under scenarios of resting or walking and for 180 days. Under scenarios of resting and walking, we iteratively calculated the daily energy required to prevent starvation by adding the somatic maintenance and movement costs (v = 2) for the mass that the bear was on the day before energy stores

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reached zero. Movement costs were added to the new daily energy requirements regardless of whether these bears had been "moving" prior to starving because movement would be necessary to obtain food from that point forward. The daily energy requirements were summed across all remaining days within the 180-day span for each starving bear (hereafter total energy deficit) and ranked by total value. These data are illustrated by listing the number of starving polar bears with total energy deficits in sequential 50,000 kcal groupings.

Food availability during a 180-day ice-free season

Although sea ice concentration and extent have delayed freeze-up in parts of Hudson Bay [2], expansion of the ice-free season thus far has mainly been attributed to earlier breakup [1,7]. For this reason, we only consider an annual advance in spring sea-ice breakup to predict when Hudson Bay would be ice-free for 180 days and thus when polar bears would be forced ashore for that duration. We calculated this date following Rockwell and Gormezano [34] by linearly projecting a 0.72 d yr⁻¹ advance from the average breakup date observed in the 1980s (1980–1989), when an ice-free period of 120 days was typical [8]. The year when this annual advance resulted in a 60-day expansion of the ice-free period (180–120 = 60) was 2068.

To estimate snow goose arrival, breeding and molt during the 180-day ice-free season, we projected the mean hatch date in 2068 based on a $0.16 \text{ d}^{-1} \text{ yr}^{-1}$ advance from 2008 (21 June) [34]. Caribou are cued to initiate spring migration to the calving grounds based on day length and studies in other caribou populations indicate that calving date has advanced little in response to climate change [35]. We, therefore, used the 2013 estimated calving date, 1 June, for energy calculations in 2068. For sake of simplicity, we used 2013 estimates of population size for LSGO (71,068 nesting pairs) and caribou (minimum count of 3000) for energy calculations in 2068.

Energy compensation to starving polar bears

Translating energy available into energy required to prevent starvation is difficult in a species for which there is little information available on actual terrestrial foraging behaviors or the energetic costs and dynamics associated with those behaviors. In dealing with this uncertainty, we make an initial attempt at integrating the energy available with energy needed by examining maximum potentials and then computing the foraging efficiency that would be required for the translation.

We tabulated the total energy that would be available from each food in 2068 as the ice-free season expands to 180 days. We then compared these energy estimates to different deficit levels that are projected for polar bears that will be susceptible to starvation (28% of resting and 48% of walking bears) according to Molnár et al.'s [8] model. Total energy deficits for each starving bear were ranked into 5th (highest energy requirements), 25th, 50th, 75th and 95th (lowest energy requirements) percentiles with each computed from the average of all energy values falling within 2.5 percentage points (above or below) each of the aforementioned percentiles. We then calculated how many units of each food item (e.g., clutches of eggs, individual animals) could maximally compensate for the total energy deficits of starving bears in each of the 5 energy condition percentiles for bears that were either resting or walking 2 km d⁻¹ prior to starvation assuming only the added 2 km d⁻¹ movement costs (and no additional energetic cost) to procure each food item. Also, because polar bears often consume different foods together [21], we provide an example of potential combinations of foods, based on patterns observed in polar bear scat, that together compensate for total energy deficits in each percentile for resting or walking bears.

Adult male polar bears have been observed pursuing and consuming each of the food items discussed, which suggests that the behavior could become widespread through social learning and energetic need [22,25]. For this reason, we also modeled the total number of starving adult male polar bears that could be supported by each of the food items (eggs, LSGO, caribou) as the ice-free season expanded to 180 days. For each day polar bears overlapped a food source, the total available energy from each food (eggs, goslings, pre-hatch adult females, flightless adults, calves, yearlings, cows, bulls) was tabulated. For this analysis, we only considered an "average" year for gosling survival and used the minimum estimate of 3000 caribou in the Churchill area (see "Computing the potential caloric values of land-based foods"). Using Molnár et al.'s [8] proportions of 97 adult male polar bears that would starve in 180 days, we calculated the energy needed for somatic maintenance and movement costs at 2 km d⁻¹ (whether or not they had been walking previously) at the mass the day before they would starve (E(t) = 0). Because most of the starving bears depleted their energy reserves at approximately the same mass ($\bar{x} = 191.93$ kg, SD = 0.2512) the daily energy requirements (including both somatic and movement costs) did not differ much between individuals so we used the mean value (4450.28 kcal d^{-1} , SD = 5.37) in calculations. We divided the total energy value of each food item, summed across days, by the mean daily energy deficit (4450.28 kcal) multiplied by the maximum number of days that a starving polar bear would need daily energy supplementation (122 days) to obtain the minimum number of adult male polar bears coming ashore susceptible to starvation that could be supported by each food. This is a conservative estimate of supported bears because individual bears depleted their energy reserves at various points within the 180-day span depending on their arrival mass. 122 days represents the longest period over which males in the worst condition would need to supplementation (days 59 through 180); all others would require food for shorter periods of time. In accordance with Molnar et al. [8], we use the same distribution of arrival masses for calculations of adult male survival as were observed during the 1980s and 1990s. The lack of procurement costs, other than those for movement 2 km d⁻¹, in calculations of daily energy requirements may lead to overestimation of the number of bears supported by each food item so these estimates should be considered the maximum limits.

Recreation of energy profiles for individual polar bears and other computations were completed using R 3.0.1 [<u>36</u>].

Computing the potential caloric values of land-based foods

Snow Geese. In 2006, the nesting population of snow geese on the Cape Churchill Peninsula (CCP) was estimated to be 48,885 pairs [34]. In response to management actions taken to control the Mid-continent Population of snow geese, adult survival had been reduced since 1996 and the population was thought to be nearly stationary [37]. After 2006, however, adult survival increased [38] and the population has again been growing at its pre-management rate of $\lambda = 1.05$ to 1.06 (R.F. Rockwell, unpublished data). Because a complete inventory of the CCP snow geese is not scheduled until 2016, we estimated the 2013 population size by projecting the 2006 value forward with a discrete time geometric growth using the midpoint of the population growth estimate as $48,855 \times 1.055^7 = 71,068$ pairs of nesting geese.

We used the fat and protein content of newly laid snow goose eggs estimated by Badzinski et al. [39] and described the changes in caloric worth over the 24-day incubation period from patterns of decline as the yolk content is consumed by the embryo [40,41]. We projected a peak hatch date of 20 June for 2013 based on 0.16 day per year advance since 2006 (21 June) described in Rockwell and Gormezano [34]. The actual hatch date will vary over a span of 7 days each year due to asynchronous nest initiation [34]. Using the peak (or mean) hatch date

will result in a slightly different projected overlap with polar bear arrival from what was reported earlier based on annual advance rates [34]. Assuming a 1:1 sex ratio among adults [42] and all females bred, we estimated energy values for 71,068 clutches and 284,272 eggs, using a modal clutch size of 4. We calculated values for partial clutches for the 3 days after laying was initiated until day 4 when most clutches were complete (i.e., contained 4 eggs) and assumed that both eggs and adult females would be vulnerable to predation during laying and incubation. A daily nest survival rate was computed based on an overall nesting success of 91.5% over the 24-day incubation period $(0.9962 = 0.915^{(1/23 \text{ days})})$ [26].

Post-hatch gosling survival varies annually, depending, in great part, on the degree to which hatch coincides with peak emergence of wetland grasses (e.g., *Puccinellia phryganodes*) that goslings forage upon [42]. Years of closer match between hatch and peak emergence of graminoids (hereafter "good years") results in higher survival rates 30 days after hatch (e.g., 2013 s = 0.795, computed from the decline in the proportion of goslings between hatch and banding operations 30 days later when the proportion of goslings is again estimated). Years when hatch precedes graminoid emergence (hereafter "bad" years) result in lower survival during the same period (e.g., 2007, s = 0.525). The number of goslings on day 1 (260,109) was computed from the proportion of successful nests multiplied by 4 (modal clutch size). Gosling numbers from day 2 to 30 were computed using daily survival estimates for good (0.9921 = $0.795^{(1/29 \text{ days})}$), bad (0.9807 = $0.525^{(1/29 \text{ days})}$) and an average year ($0.9864 = 0.660^{(1/29 \text{ days})}$), using the midpoint of good and bad.

Fat and protein values were available for neonates [43], however only body mass and protein measures could be obtained for growing goslings (at days 31 and 43) from Akimiski Island, Nunavut [44], where snow geese are generally smaller than those nesting further north on the CCP (R.F. Rockwell pers. obs.). To establish general relationships describing increases of both protein and body mass, based on 3 measures (days 1, 31 and 43), we calculated the daily average geometric growth rates between measurements using the following equation:

Daily Growth Rate =
$$(m_{i+1}/m_i)^{1/(t_{i+1}-t_i)}$$
 (5)

where *m* is the measured content (e.g., mass, protein) in kilograms and *t* is time in days between the measurements. Between days 1 and 31 daily increases in protein and mass were 1.1164 and 1.0988 grams, respectively, and between days 32 and 43, growth slowed to 1.0175 and 1.0128 grams of protein and mass, respectively.

To relate the proportion of protein to mass of the goslings observed on Akimiski Island to the larger ones on the CCP, we first used regression to establish a general relationship of how body mass of CCP goslings changes through the growth period. Using body mass values of neonates from the McConnell River in Nunavut (i.e., similar mass to CCP neonates) [43] and those from the CCP from days 23 to 50 (R.F. Rockwell, unpublished data), we fit a power function to describe changes in body mass with time ($y = 85.479x^{0.7766}$; $R^2 = 0.99$). We then multiplied ratios of protein to body mass calculated from the Akimiski Island gosling data [44] to the masses of goslings in CCP to estimate daily protein content.

To estimate fat content of goslings, we used a lipid index model from Table 4b in Aubin et al. [45] that describes how fat reserves decrease with gosling age. We scaled the index units to known lipid values (in grams) for neonates (i.e., day 1) [39,46] and fit the data to a power function ($y = 0.562x^{-0.992}$; $R^2 = 0.74$) that predicts daily fat content and suggests a drastic drop after day 3 when the remaining yolk is exhausted by the gosling. Grams of fat and protein were converted to gross energy using standard coefficients of 9.39 and 4.30 kcal g⁻¹, respectively [47,48]. We further scaled these by the digestibilities of fat and protein for polar bears (0.97 and 0.84, respectively) provided by Best [49].

Both adult males and females are present during incubation, however, females of both snow geese and common eiders (*Somateria mollissima*) have been observed being attacked by polar bears while guarding their nests [50]. During these attacks the females are stalked slowly then rushed by polar bears [50] suggesting that females are vulnerable to predation during this period even though capable of flight. For this reason, we include the caloric value of adult females (not males) from the initiation of laying through hatch using fat and protein values from Ankney and McInnes [51]. We fit a power function ($y = 2E+19x^{-7.31}$; $R^2 = 0.99$) to the calculated available energy (kcal) modeled with time for the laying, early and late incubation periods and predicted daily energy values from day 1 of incubation through hatch for 35,534 females.

Approximately 18 days after hatch, adults begin molting their flight feathers [52,53] and both sexes are vulnerable to predation (e.g., [22,54]). We calculated the available energy (kcal) from protein reserves (fat content is negligible) of both adult males and female during the post-hatch, early and late molt periods [51,55]. A linear regression model was fit to the average available energy of males and females with time ($y = 2E+06x^{-1.491}$; $R^2 = 0.63$) and used to predict energy values from the beginning of molt (2 July) to flying, approximately 4 weeks later (2 August). Gross energy from protein was scaled by Best's [49] estimate of digestibility (0.84).

Caribou. Unlike the case for snow geese, there is no long-term database available for the caribou of the CCP. In generating our estimates of available calories, we have relied on all information there is on this herd and information from studies of mostly nearby herds. Rigorous population surveys are lacking for the Churchill caribou herd, however recent counts (in 2005 and 2012) suggest a stable minimum population size of approximately 3000 animals (R. Brook and C. Elliott pers. comm., [56,57]). Using this value as a lower limit, we consider caloric values from a total of 3000, 4000 and 5000 individuals (D. Hedman, pers. comm., [56,57]) to reflect the uncertainty surrounding population size. The number of adults was estimated based on a sex ratio of 0.85:1, males to females [58].

Calves were most often first sighted on or around 1 June in the CCP (R.F. Rockwell, pers. comm.), so this date was chosen as day 1 to determine calf composition based on daily growth with age. This date seems reasonable since it occurs midway between peak calving in the Pen Islands herd to the south (17–28 May) [59,60] and the Qamanirjuaq herd to the north (5–15 June) [61]. Although data from collared females in the Churchill herd indicate that adult females typically migrate toward the coast in April (V. Trim, pers. comm.), we considered all age and sex classes of caribou to be vulnerable to predation by polar bears from the onset of calving (1 June) until they leave the coast by 15 October (total days = 137 days) (V. Trim, pers. comm.)

Calf survival was based on observed proportions of calves in the population and estimates of mortality during different times of the year. We used an estimate of 21.1% calves during the post-calving period (~ 1 July) based on the average of counts from 2008 (23.1%) and 2009 (16.1%) in the Pen Islands Herd [60]. We estimated calf mortality (28.6%) from birth to the post-calving period (1 July), based on average mortality estimates for the Porcupine herd in Alaska during the first month after birth (1983–1985) [62]. Using the proportion of calves present in the population on 1 July (21.1%) and calculating the average daily survival from 1 June (birth) to 1 July (0.9888 = $0.714^{(1/30 \text{ days})}$), we estimate of over-winter calf survival (14.7%) based on average calf to adult ratios (17.2:100) from late winter surveys of the Churchill herd conducted in 2012 and 2013 (V. Trim, pers. comm.) to calculate the survival rate (0.6967) from 1 July to 1 March based on the average change in proportion of calves in the population during this period. The average daily survival rate during this period was calculated in a similar fashion as above (0.9985 = $0.6967^{(1/242 \text{ days})}$).

We also used the proportion of calves in the population that survived the winter (14.7%) to estimate the proportion of yearlings available during summer. Given that 12–15% recruitment is generally considered to be the threshold for population stability in caribou populations [63] and the Churchill herd is considered relatively stable [57], an estimate of 14.7% is not unreasonable.

The fat and protein content (kg) of adult females and calves at different stages of growth were taken from Gerhart et al. [64] based on data from the Central Arctic and Porcupine herds. Gerhart et al. [64] developed a series of equations to predict fat and protein content of caribou from measurements of total body mass (kg). We used standard coefficients, 4.30 and 9.39 kcal g⁻¹, to convert predicted fat and protein, respectively, to gross energy. Available energy was calculated using digestibilities of fat and protein (0.97 and 0.84, respectively) provided by Best [49]. Energy values for adult males and yearlings were predicted using these relationships from body mass (kg) values of Svalbard reindeer (for adult males) [65] and Svalbard reindeer and caribou (for yearlings) [65,66] at various times of the year.

Daily changes in fat and protein composition for adults, yearlings and calves were calculated using Eq.(5). Daily growth rates of fat and protein in calves were calculated based on measurements obtained for 1 Jun, 27 Jun, 23 Oct., 11 Sep. 13 Oct., corresponding to days 1–134 from birth [64]. Measurements for adult females were obtained for 7 May, 7 Jul., and 3 Oct. [64]. We obtained monthly estimates of body mass for adult males and yearlings and estimated daily growth rates from the mid-point of each month, including May, Jun., Aug., Oct. (and Nov. for adult males only) [65,66].

Results

Of the 97 adult male polar bears sampled, Molnár et al. [8] predicted that 28% (27) and 48% (47) would starve if resting or walking before energy depletion, respectively. Of those bears that were resting before starving, we found that many (10) experienced energy deficits of less than 50,000 kcal. Of those bears that were walking before starving, most (28) experienced deficits less than 100,000 kcal, with most falling between 50,000 and 100,000 kcal based on our analyses (Fig 1).

Potential energy available from land-based foods

The energetic value of all stages of LSGO (eggs, goslings, adults) calculated for the 2013 population size was approximately 11,702, 10,959 or 10,334 million kcals depending on whether it was a good, average or bad gosling survival year, respectively. During an average gosling survival year, eggs, pre-hatch adult females and flightless adults comprised 11.8%, 31.2% and 16.4% of the total kcals available to polar bears. Goslings comprised 47.4%, 40.6% and 34.9% of the total available kcals in good, average and bad survival years, respectively. The number of clutches and their respective caloric values both dropped over the course of the 24-day incubation period. For example, on day 1 approximately 71,068 clutches were each worth 840.05 kcal, whereas on day 24 the number of clutches drops to 65,027 and were each worth 493.18 kcal. Goslings, available for 43 days, grew rapidly and range in value from 118.68 kcal at hatch to 1128.23 kcal shortly before flight (\bar{x} = 576.61 kcal). Pre-hatch females could provide the most energy per unit and were most valuable during laying and beginning of incubation (3394.46 kcal), then rapidly lost weight over the 27-day period, dropping to 1015.84 kcal just before hatch ($\bar{x} = 1950.04$ kcal). Flightless adults, having exhausted their fat reserves, could provide between 603.76 kcal (post-hatch) to 505.64 kcal (before flight), with an average value of 552.38 kcal over the 25 days that they were available (Fig 2).

Caribou can provide a total of 38,584, 51,445 or 64,307 million kcal for an estimated population size of 3000, 4000 and 5000, respectively. Assuming an average population size of 4000, calves, yearlings, adult females and adult males comprised 6.2%, 7.8%, 45.9% and 40.1% of the total energy available to polar bears. Adult females were each worth 70,964.09 kcal at the onset of calving and increased to 141,066.20 kcal by the middle of October ($\bar{x} = 89,835.99$ kcal).



Fig 1. The number of starving adult males that are expected to come ashore with different-sized energy deficits during a 180-day ice-free season. Calculations are based on the additional kilocalories required for daily somatic maintenance and limited movement (2 km d⁻¹) needed to prevent starvation in each bear for the entire projected 180 days ashore.

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Calves and yearlings also steadily gained mass and were each worth 4,751.22 and 34,132.37 kcal, respectively, on 1 June, and increased to 51,653.94 and 55,921.61 kcal by 15 October, averaging 29,539.02 and 50,072.52 kcals, respectively, while on the calving grounds. Individual adult males arrived at the calving grounds potentially worth 64,415.41 kcal and steadily increased in value until the onset of the rut (approx. 15 Sep.), peaking at 139,641.91 kcal, then dropping to 118,835.01 kcal over then next month, averaging 105,956.41 kcal (Fig 3).

Compensation to starving polar bears

Molnár et al. [8] used the average body lengths (2.34 m) across their sample of adult male polar bears, leaving initial body mass as the sole determinant (except for movement costs) of whether a bear would starve during an extended 180-day ice-free season and for how many days energy compensation would be needed. Assuming the current mean body length has future legitimacy, adult male polar bears (\geq 7 years old) would starve shortly after reaching 191.93 kg and would require approximately 4,450.28 kcal d⁻¹ upon reaching that threshold mass to survive.

Adult male caribou could provide the most energy per unit, with less than 5 animals per polar bear (<1 every 27 days) needed to prevent starvation for the entire 180-day ice-free period under scenarios of resting or walking. Because of the high caloric value of each caribou and the incidences of multiple polar bears feeding off a single caribou carcass (Fig 4), the exact proportions of each animal that would be required to meet the daily caloric needs may be important and are presented (Fig 5a and 5b). Calves, though considerably smaller, could still



Fig 2. The total available energy from snow geese and their eggs during the laying, incubation, post-hatch and molting stages of their life cycle that occurs in the Cape Churchill Peninsula. The mean hatch and polar bear arrival dates provided (left-most vertical dashed lines) are for 2013, however, if the ice-free season expands to 180 days, polar bears would arrive before nesting geese and thus have access to all the available energy illustrated.

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potentially support a starving walking polar bear in the 5th percentile with 15.8 units or approximately 1 calf every 8.7 days while they are available. As expected, smaller food units would require more frequent effort to obtain. For example, to sustain a starving walking bear in the 5th percentile ~26 clutches of eggs or 19 goslings would need to be consumed each day. For starving walking bears in 50th percentile, the effort would drop to 10 clutches and 7.5 goslings per day. The minimum number of units of each food required to sustain polar bears in each condition percentile are presented in Fig <u>5a</u> and <u>5b</u>.

Given the opportunistic nature of polar bears [13,21], combinations of food items may be a more realistic means to fulfill daily energy deficits, especially since availability of different age classes of each item does not necessarily overlap (e.g., LSGO, Fig 2). For example, to sustain starving walking polar bears in the 50th percentile would require consuming ~5 egg clutches every 3 days, ~1 incubating female off the nest every 3 days, ~2 goslings every 3 days, 1 flightless adult each day and 1 adult male caribou. Different food combinations for each condition percentile for walking and resting starving polar bears are presented in Fig 5a and 5b.

Maximum number of starving adult male polar bears supported by each food

Assuming a polar bear population size similar to the last estimate (935) $[\underline{33}]$ and the proportion of adult males remains constant (~25%), then the available calories from eggs, LSGO and



Fig 3. The total available energy from different sex and age classes of caribou on the summer calving grounds on the Cape Churchill Peninsula. If the ice-free season expands to 180 days, polar bears are projected to come ashore prior to the onset of calving, which is currently 1 June, and have access to all the available energy illustrated.

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caribou would each far surpass the energetic needs of adult males coming ashore at risk of starvation. To sustain 28% of resting adult males (66 = 935 * 0.25 * 0.28) for 117 days (the maximum # days that a resting starving bear would need supplementation for), the available calories would surpass total energy required to sustain the starving bears by a factor of 38 for eggs to a factor of 520 for adult female caribou. Similarly, to sustain the 48% of walking adult males (112 = 935 * 0.25 * 0.28 * 0.48) that would be susceptible to starvation for 122 days (the maximum time needed), the available calories would surpass those needed by a factor of 21 for eggs to a factor of 291 for adult female caribou. The maximum number of adult male polar bears that could be supported by LSGO for 122 days is 1,614, 5,551, 4,274 and 2,242 by eggs, goslings, pre-hatch adult females and flightless adults, respectively (Fig 6). The maximum number of adult males that could be supported by caribou is 4,378, 5,572, 32,651 and 28,464 by calves, yearlings, cows and bulls, respectively (Fig 6).

Discussion

As the ice-free season expands with earlier spring breakup, polar bears are expected to come ashore in western Hudson Bay with smaller energy stores [3] causing them to rely on terrestrial food sources to compensate for energy deficits and avoid starvation. Molnár et al. [8] predicted that, depending upon their activity while ashore, between 28 and 48% of adult male polar bears



Fig 4. Three adult male polar bears feed on the remains of a bull caribou on Keyask Island (58.1695°N 92.8519°W) on the Cape Churchill Peninsula on 8 August, 2012. This type of communal foraging illustrates the importance of how consumption of incomplete carcasses (as carrion or from predation) can contribute to daily energy requirements. Here, the bear in the poorest physical condition (top) is most likely in need of the additional calories, however, those in better condition still partake in the meal. Photograph by R.F. Rockwell.

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would starve to death unless supplemental food was consumed. By evaluating the energy value of novel foods that polar bears currently consume on land, caribou, snow geese and their eggs, we found that there are sufficient calories to compensate for daily accrued energy deficits of adult male polar bears expected to starve as the ice-free season expands to 180 days. The veracity of relying on these land-based resources, however, likely depends on a number of factors including future prey availability, polar bear foraging behavior, energy costs associated with prey procurement and physiological utilization of different macronutrients.

Although local populations of both snow geese and caribou have grown substantially since the 1960s [13], future availability is difficult to predict. Both species have displayed weak phenological shifts in response to climate change, as reproductive cycles are cued more by day length than air temperature [34,35]. As a result, mismatches with emergent vegetation at the peak of goose brood rearing and peak caribou calving as well as habitat changes have impacted both species [57,67]. Snow geese in the CCP have responded to changes in food availability (mostly due to destructive foraging) by inhabiting new areas, moving further inland from the coast and consuming alternative plant species [67]. Further, there is evidence to suggest that deficiencies from mismatches with emergent vegetation at the onset of brood rearing may, in part, be compensated for by earlier access to berries later in the season (C.P. Mulder,





Fig 5. The number of indivudal units (left) or combinations (right) of food items that could satisfy total energy deficits (numbers on arrows in center) of starving male polar bears onshore for 180 days. The levels of energy deficits vary from the lowest (95%) to the highest (5%) and are presented for scenarios in which the bears have been resting (a) or walking (b) on land prior to starving. A 2 km d⁻¹ energy cost associated with movement is depreciated from daily food value calculations. If costs to procure food items exceed this movement cost, numbers of individual food requirements may be underestimated.

unpublished data). Behavioral changes, such as range shifts, are possible with heavy predation, however, the lack of such responses from other nesting geese experiencing arctic fox and polar bear predation suggests that local snow goose populations would likely not alter their behavior substantially (see [26] and references therein). Such adaptive responses to environmental stresses and resilience in the face of rigorous management control attempts [38,68] suggests that snow geese may remain a viable future food source for polar bears on the CCP.

The resiliency of caribou in the face of progressive environmental change is less certain [57]. Although the Churchill herd is currently stable, studies in other regions have suggested that increases in variability and advances in emergence of commonly consumed plants with warming temperatures have negatively impacted calf survival [35]. Other threats have included replacement of preferred winter forage (i.e., lichen and herbaceous plants) with shrubs and grasses from forest fires, grazing and warmer temperatures [69,70,71]. Also, projected increases in precipitation would give predators, such as wolves, an advantage potentially increasing mortality [72]. These changes, however, can affect populations adapted to harsh conditions in different ways [73], so that some populations are experiencing growth while others decline [57]. Given the small number of animals required to satisfy the energetic requirements of starving polar bears, it is unclear whether even modest future declines in the Churchill herd would hinder polar bear predation efforts as long as caribou maintain their current distribution (i.e., along the coast). Caribou may occupy the coast of western Hudson Bay (where polar bears occur in high densities) for a variety of reasons including to avoid harassment by insects (e.g., [74]) so whether the increased threat of predation would cause them to shift their distribution further





Fig 6. The maximum number of adult male polar bears projected to starve as the ice-free season expands to 180 days that could be supported by the total energy pools from each food resource. Estimates are based on 2013 population sizes of each prey and take into account somatic maintenance and daily movement costs. Values may be overestimated if true procurement costs exceed those included.

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inland is unknown. Encounter rates between polar bears and caribou may decrease with declines in abundance and shifts in distribution, but the method of capture (e.g., ambush versus chase) may be more important in determining predation success [75,76].

With the paucity of knowledge regarding energy consumption rates at varying speeds of travel, especially for adult males (i.e., > 235 kg), it is difficult to fully evaluate the feasibility of the foraging scenarios suggested. However, based on past and current behavior, it is clear that polar bears are capable of successfully capturing land-based ungulates, such as caribou (R.F. Rockwell, pers. obs., [77]) and muskoxen [78] and actively pursuing them in western Hudson Bay and other regions (L.J. Gormezano, pers. obs., [23,56]). The mean digestible energy content of a seal, pooled across age classes, is 69,047 kcal [79], which is roughly equivalent to the average worth of an adult female caribou during June and July, although most of the energy is from protein rather than fat. Using surprise hunting techniques, such as stalking and ambushing, whereby landscape features (i.e., ice, water) are used to mask their approach, polar bears are able to successfully capture seals without engaging in potentially costly pursuits [80,81]. Polar bears have employed these same techniques on land, using shrubs and physiographic features as cover to surprise caribou (R.F. Rockwell, pers. obs., [56]) suggesting equivalent (seal) calories could be obtained on land without drastic changes in energy output. Further, caribou capture rates (1 every 8.7–31.1 days) required to sustain starving walking polar bears coming ashore in the worst condition, are comparable to capture rates (1 seal every 5.6–24.4 days) [4] of different aged seals by polar bears in spring and summer.

Consumption rates of snow goose eggs and goslings that would compensate starving walking bears ranged from 3 to 26 clutches of eggs and 2 to 19 goslings per day depending on daily energy deficits. High daily depredation rates of goose nests have been reported in populations around the Arctic (e.g., 108 barnacle goose nests) [82] but can vary depending on nest density and total availability [83,84]. Based on camera footage of an common eider colony in western Hudson Bay, some polar bears were consuming between 19 and 38 nests per day (D. Iles, unpublished data) suggesting that the maximum consumption rates required to support starving

be projected for 2068), they would overlap the entire incubation period, which would provide substantially more calories to arriving bears than are currently available [34]. Capture rates of goslings and adults are rarely reported [85,86] but observations of polar bears capturing and consuming up to 3 individuals per day (of various ages) have been reported for snow geese [22]. The extra skill and effort required to obtain birds (as opposed to eggs) might pose limitations on meeting daily energy requirements from birds alone, however, maximum rates suggested in the combination diet (0.2 to 1.2 goslings d⁻¹, for example) are quite reasonable. Further, anecdotal observations of flightless goslings and adult snow geese being consumed consecutively by the same bear [22] and remains of adult snow geese and eggs recorded in the same scat (25% of scats with eggs) further suggests a combination diet (Fig 5a and 5b) would be a more realistic means to satisfy daily energy requirements.

bears (26 clutches) is not unrealistic. Also, polar bears coming ashore 60 days earlier (as would

The large numbers of starving polar bears that can be supported by each food resource suggest that surpluses would be available for other age and sex classes coming ashore with energy deficits. It is important to note, however, that the actual number of bears that will come ashore with energy deficits is unknown and may increase over time as marine food resources become limited. Further, the only costs associated with procurement of prey are a 2 km d⁻¹ movement cost above somatic maintenance. Similar to lions (*Panthera leo*), polar bears are considered inefficient walkers so extended pursuits could reduce energetic returns [87]. Pursuits of geese on land rarely exceed 30 seconds (R.F. Rockwell, pers. obs., [22]), however, pursuits of caribou (running, walking and swimming) have lasted up to an hour (L.J. Gormezano, pers. obs., [23,56]) suggesting that costs associated with each capture (including failed attempts) could be substantial.

Williams and Yeates [88] calculated an efficiency ratio (benefits/costs) of 3.8 for African lions pursuing ungulates on land. Given the comparable locomotive inefficiencies between lions and polar bears (Gormezano and Rockwell, unpublished data, [87,89]) it is possible that when polar bears engage in longer distance pursuits, as opposed to more energy conserving surprise techniques, a similar efficiency ratio could apply. In a hypothetical example, we applied this ratio to the energetic returns for caribou and found that it increased capture costs (i.e., above somatic and movement) 1.7, 3.0, 5.3 and 6.3 times their previous value of approximately 4,450 kcal for calves, yearlings, adult females and adult males, respectively. Applying these increased costs to the calculation of the number of starving walking polar bears supported by 84% from 28,464 to 4,543 bears. Although the exact energetic costs of polar bears pursuing caribou using different hunting strategies remain unknown, the data presented here provide a basis to estimate them once the appropriate behavioral and energetic studies have been performed.

Previous studies have questioned the use of land-based foods to satisfy daily energy requirements while polar bears are on land [90,91]. Hobson et al. [11], for example, tested carbon dioxide exhaled by anesthetized polar bears in summer to evaluate whether a marine (seal) or terrestrial (berry) stable-carbon signature would be obtained and thus, which was supplying energy for current metabolic processes. Finding signatures that were almost identical to seals (and different from berries), they concluded that all bears were persisting solely on energy derived from oxidized fat reserves accumulated while on the ice [11].

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It is possible, however, that the metabolic states of the bears in the Hobson et al. [11] study were altered due to the biochemical effects of being captured [92]. Using the same drugs and capture protocol, Cattet [12] found that the plasma cortisol levels of polar bears after capture were extremely elevated and although they decreased 40–50% after 1 hour, he noted that the physiological effects would continue well after the plasma cortisol levels decreased. He also observed sustained concentrations of plasma glucose correlated with the cortisol surge and suggested the bears may be exhibiting insulin resistance [12]. One of the many effects of cortisol is to sensitize adipose tissue to the action of lipolytic hormones and to cause insulin resistance by decreasing the rate at which insulin activates the glucose uptake system [93]. As a result, insulin resistance leads to the disinhibition of lipolysis in humans [94]. If similar processes occur in polar bears, the use of fat as a metabolic fuel that Hobson et al. [11] observed may not represent the prevalent process, but instead, may have been temporary and triggered by the stress of capture [92].

Furthermore, certain foods that polar bears consume on land can complicate results of biochemical studies to distinguish 'marine' versus 'terrestrial' sources of expended energy using stable carbon isotopes (δ 13C) [14,95,96]. For example, marine algae (*Laminaria* spp. and *Fucus* spp.), typical C4 plants that polar bears commonly consume from land, are more enriched with carbon and have higher δ 13C values (-24 to -12‰) compared to most C3 (terrestrial) plants, although values range widely depending on plant part and time period sampled [14,95].

Similarly, waterfowl, such as snow geese, Canada geese (*Branta canadensis*) and common eiders, summering on land in western Hudson Bay can exhibit 'marine' signatures from foraging on plants and animals in brackish marshes and marine habitats [97,98]. Muscle δ 13C values for the aforementioned and other seabirds that polar bears consume can range from (-22.0 to -15.5‰) [15,97,98], which clearly overlap δ 13C values for ringed seal muscle (-19.4 to -18.1‰) [90,97] and could, therefore, lead to erroneous conclusions regarding the sources of energy used on land. Without specifically including these terrestrial foods (i.e., marine algae, birds) a priori in carbon isotope mixing models, their proportional contribution can not be accurately assessed [99], especially given the range of food combinations observed in the summer diet from scat analysis [21].

Earlier arriving bears may come ashore with greater nutritional deficits from lost seal hunting opportunities as the ice-free season expands [7] but calories necessary to prevent starvation will likely be available from land-based resources, such as caribou, snow geese and eggs. The projected earlier 60-day arrival would allow polar bears to overlap both the entire incubation and calving periods of snow geese and caribou, respectively, creating new phenological matches to compensate for the growing mismatch with seals. Using the same energy-saving, surprise hunting methods (e.g., ambush, stalk) to hunt geese and caribou that they typically use to capture seals [80,81], would provide polar bears energy compensation similar to the maximum values reported here. Until further behavioral and oxygen consumption studies are performed, however, the true costs associated with different foraging strategies and thus the total energy returns can only be approximated.

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Author Contributions

Conceived and designed the experiments: LJG RFR. Performed the experiments: LJG. Analyzed the data: LJG. Contributed reagents/materials/analysis tools: LJG RFR. Wrote the paper: LJG.

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