Worth the dip? Polar bear predation on swimming flightless greater snow geese and estimation of energetic efficiency

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Abstract

As sea-ice cover is shrinking, polar bears (*Ursus maritimus*, Phipps, 1774) face decreased access to seals, their primary prey, resulting in a greater dependence on terrestrial food sources. Whether polar bears can benefit from these terrestrial food sources, however, depends on their ability to find and capture prey items without expending more energy than is acquired. Here, we report one of the northernmost observations of polar bear predation on adult birds. The bear used a dive-hunting technique, which consisted of submerging itself, approaching underwater, and catching flightless greater snow geese (*Anser caerulescens caerulescens* (Linnaeus, 1758)) from beneath the surface of a tundra pond. After evaluating energy expenditures during swimming and energy intakes from consuming geese, we estimated that this rarely documented dive-hunting technique could be energetically profitable for a certain range of pursuit durations. This observation highlights the behavioral plasticity that polar bears can deploy to punctually exploit land-based food sources.

Key words: Climate change, *Ursus maritimus,* Foraging tactics, Energy uptake, *Anser caerulescens*, Arctic lakes and ponds

Introduction

Polar bears hunt seals on the sea ice and rely on the accumulated energy reserves to survive the ice-free season (Watts and Hansen 1987; Atkinson et al. 1996; Polischuk et al. 2001). During this period, they were documented to make use of a variety of land-based or near-shore resource items (Russell 1975; Rode et al. 2010, 2015; Gormezano and Rockwell 2013a, 2013b; Gormezano et al. 2017; Bourque et al. 2020), which usually contain less energy and fat than seals, their preferred prey (Stirling and Øritsland 1995; Gormezano and Rockwell 2015; Rode et al. 2015). Models predict that climate change and shrinking sea ice will increase the occurrence of polar bear starvation (Molnár et al. 2010, 2020; Stirling and Derocher 2012; Regehr et al. 2016), and even though the use of land-based resources could sustain a few individuals (Gormezano and Rockwell 2015), the impact of such behavior is unlikely to be reflected at the population level (Rode et al. 2015). On land, polar bears face the double challenge of finding unevenly distributed fat-rich resources (Rode et al. 2015, 2021) and of displaying foraging techniques that minimize energy expenditure (Gormezano and Rockwell 2015). For example, on-land pursuits of waterfowl by bears may only be profitable when short distances are covered at a relatively low running speed (Gormezano et al. 2016). Moreover, egg consumption was shown to provide energetic surpluses only at the beginning of the nesting season, when the density of this resource is at its peak (Jagielski et al. 2021). As energetic gains are uncertain when foraging on land, documenting land-based hunting techniques used by bears and assessing their energetic efficiency will help understand polar bear resilience to environmental changes.

In the Arctic and sub-arctic, polar bears have been observed preying on adult birds on land using various techniques, either chasing (Iles et al. 2013), ambushing (Gormezano et al. 2017), or stalking (Miller and Wooldridge 1983; Gormezano et al. 2017) birds during their nesting and brood-rearing periods. Near the shore, bears were seen swimming underwater until they were close enough to attack birds from underneath, as seen on various alcid species (Russell 1975; Stempniewicz et al. 2014; Obbard et al. 2022).

In this paper, we report on an undocumented situation of a polar bear catching flightless greater snow geese using a rarely observed dive-hunting technique in tundra ponds and lakes (see illustration of the technique in Fig. 1).

Fig. 1. Illustration of the dive-hunting strategy used by the bear to stalk and catch the snow geese by surprise.
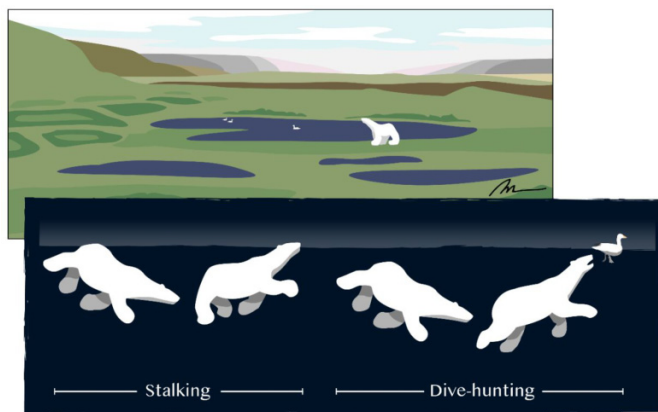
Study area

The Bylot Island Migratory Bird Sanctuary (73°08′N, 80°00′W; see Lepage et al. (1996) for more details on the study area) harbors the largest known greater snow goose breeding colony. Around 20,000 pairs nest in a 70 km^2 area from mid-June to mid-July (Fig. 2a; Reed et al. 2002). After hatching, goose families journey from the nesting area to the main rearing area 30 km NW (Qalikturvik Valley, Fig. 2a; Mainguy et al. 2006) to molt and prepare for their southward migration in late August. As adults are molting and flightless during brood-rearing, broods form groups of 50–500 individuals and stay close to ponds to escape predation by arctic foxes (*Vulpes lagopus* (Linnaeus, 1758)), their main predator (Bety et al. 2002; Reed et al. 2003). The brood-rearing habitats used by geese in the Qalikturvik valley are dominated by freshwater wetland polygon fens where grasses and sedges, preferred by geese, are abundant (e.g., *Dupontia fisheri* R. Br., *Eriophorum scheuchzeri* Hoppe). This area is located on an extensive ice-wedge polygon terrace near a proglacial river connected to the Navy Board Inlet (Department of Energy, Mines and Resources 1969) and is studded with shallow lakes and ponds with a few deeper glacial lakes (maximum depth of 12 m). Sea ice usually breaks up in late July, after which more polar bears are observed inland, often following the dry and uniform coast of Navy Board Inlet or in a directional movement (no feeding behavior) from the inlet to the mountains at the head of the Qalikturvik valley (Fig. 2a). Over the last 14 years of incidental observations across the study area, between zero and three bears were spotted each year (exception of seven in 2013), with an average of 1.14. The events we report in this note are the first record of bear predating on adult birds in our study site.

Field research permit

Fieldwork on the Bylot Island Migratory Bird Sanctuary was approved by the Mittimatalik Hunter and Trapper Organization and Parks Canada (permit # SIR-2021–39399).

Description of observations

The observations took place on 8 August 2021, in the main snow goose brood rearing area (Qalikturvik Valley, Fig. 2a), 6 km inland from the Navy Board Inlet. The bear was first spotted around 13:00, approaching from the northwest while walking in the large, shallow river near the research camp. Four people then walked to the top of the hill adjacent to the research camp (Fig. 2b) with a spotting scope (Kowa TSN-883) to monitor its activity. The dive-hunting behavior (Fig. 1) was first observed 45 min after the bear was first spotted. The bear walked towards a pond (Point A, Fig. 2b), in which a group of approximately 30 geese had taken refuge (Fig. 3a). By the time the bear reached the pond, all the geese had exited on the opposite side of the pond except for one adult. The bear entered the pond and swam toward the goose and dove, but emerged too far from the bird to catch it. The bear repeated its dive-hunting maneuver a few times, always initiating its dive ~30 m from the goose. Meanwhile, the goose remained in the pond and stopped swimming away from the bear as soon as the bear dove underwater. The bear finally caught the goose on its fourth attempt, at 14:00, after 15 min of swimming and diving. The bear then brought it to shore and ate it until 14:50 (Fig. 3b). At 17:17, after spending a few hours sleeping, eating, and manipulating the goose carcass, the bear went into a larger pond nearby (Point B, Fig. 2b). It was observed swimming and walking in the pond but was not seen diving. Several groups of geese were in the pond, and the bear followed them, changing targets from time to time. Despite numerous attempts, the snow geese evaded. The bear came out of the pond at 17:50 and went to a third pond at 18:30 (Point C, Fig. 2b). Using the same diving-hunting technique, it caught a juvenile snow goose on its second dive, with the whole interaction lasting less than 10 min. The bear made no other predation attempt and left the Qalikturvik Valley, walking toward Navy Board Inlet at 20:30.

Foraging efficiency

To evaluate whether the observed behavior could be energetically profitable for a bear, we determined, for a range of bear masses, the pursuit durations for which the energy gained from catching the prey equaled the energetic costs of the chase (i.e., gains − costs = 0). These efficiency thresholds (ETs), defined as the pursuit duration under which a chase is energetically profitable, are calculated as

$$\mathrm{ET} = \frac{\mathrm{Gains}}{(V_{O_2} \times \mathrm{bear\,mass} \times K)}$$

where Gains are the caloric value associated with the consumption of an adult greater snow goose (913.3 kcal); V_{O_2} is the metabolic rate (L g^{-1} min^{-1}) of swimming polar bears; and $K = 4.735$, the standard conversion of 1 L of oxygen to kilocalories. The caloric value of a goose was derived from Gormezano et al. (2016) for a 1.9 kg post-hatch adult lesser snow goose (*Anser caerulescens atlanticus* (Kennard, 1927)) and scaled to the mass of a post-hatch adult greater snow goose (2.6 kg, Gauthier (unpublished data); scaling factor = 1.37).

We obtained the metabolic rates for swimming polar bears from Griffen (2018) and Pagano et al. (2019), which used dif-

Fig. 2. (*a*) Location of the main study site (Qalikturvik Valley—black rectangle; and the average contour of the Greater snow goose colony—black polygon) on the Southwest Plain of Bylot Island, Nunavut, Canada. Turquoise and orange asterisks mark research camps. The Qalikturvik Valley is the predominant brood-rearing area. (*b*) Aerial view of the bear–goose predation area. Observations were made from a vantage point (yellow cross) near the research camp (turquoise asterisk). We show the main locations of the bear dive-hunting attempts (red letters) and its trajectory between these locations (orange hatched line). Ponds are covered with ice, as the satellite image dates from 2 July 2020. Boundaries and hydrological features were retrieved from the Government of Canada open data (Governement of Canada 2016-2022). The satellite base map was acquired from ©2020 Maxar Technologies. Maps are in WGS 84 and UTM 17 N. Media may publish or use these images with the cutline photo credit "satellite image ©2020 Maxar Technologies".
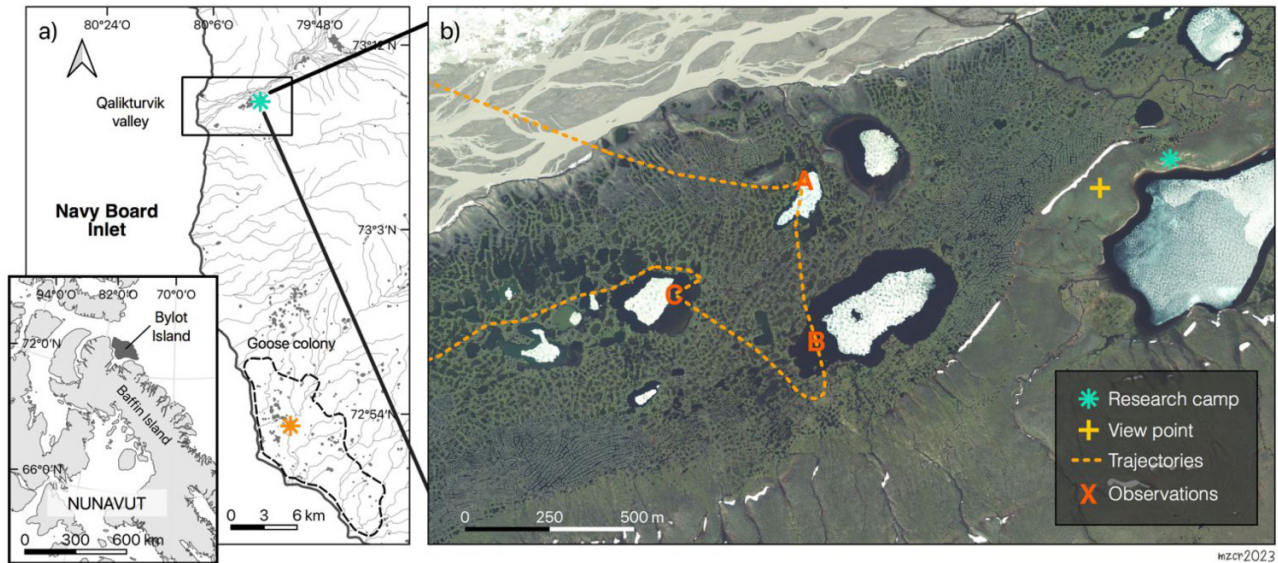
ferent methods in different contexts. Griffen (2018) estimated the metabolic costs of two wild seafaring, long-distance swimming bears using data on internal and external temperature combined with mathematical modeling of heat production and conduction to the surrounding water. Pagano et al. (2019) measured the oxygen consumption of a sub-adult captive bear swimming in a low-current tank of warm water. The metabolic rate (0.59 O_2 g^{-1} h^{-1}) of Pagano et al. (2019) was thus used to determine the minimal energetic cost of swimming. As the swimming metabolic rates reported by Griffen (2018) are higher and much more variable (1.24–3.95 O_2 g^{-1} h^{-1}), we used the 2.5th and 97.5th percentiles of the metabolic rate distribution provided in Fig. 1 of Griffen (2018), as well as the mean, to calculate ETs along a range of realistic polar bear mass values (125–425 kg). The ETs delineate the pursuit durations under which a chase could be profitable if swimming energetic costs are minimal (the costs of in-tank paddling polar bears, 0.59 O_2 g^{-1} h^{-1}; Pagano et al. (2019)), low, high, or maximal, which are, respectively, the 2.5th percentile, the mean, and the 97.5th percentile derived from Griffen (2018) (1.71, 2.75, and 3.70 O_2 g^{-1} h^{-1}).

We used these thresholds to assess the energetic benefits of each pursuit event as well as the overall energetic benefit when considering all three pursuits together. The first and third pursuits were likely energetically efficient for bears of all weights if swimming metabolic costs were minimal or low, yet only for light bears if costs were high or maximal (Fig. 4). When considering the overall time spent actively hunting, in-
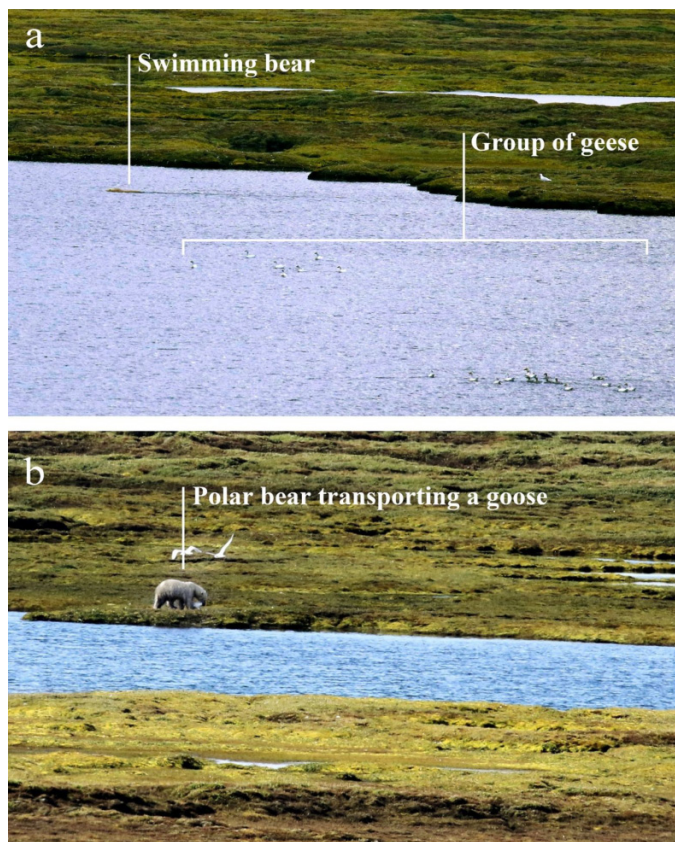
cluding the failed attempt (58 min), the capture of two geese was energetically efficient only for light bears if swimming metabolic costs were low or for all bears if costs were minimal (overall interaction on Fig. 4).

Discussion

As polar bears' access to sea ice is declining, they are increasingly using terrestrial food sources, including nesting birds (Iverson et al. 2014). While terrestrial food resources are most likely insufficient to compensate for the impact of climate change on polar bear populations (Rode et al. 2015), land-based energy-conservative hunting techniques could provide some relief to individuals (Gormezano and Rockwell 2015). Here, we report one of the first documentations of a polar bear dive-hunting in an inland waterbody to access terrestrial prey. Our results suggest that this scarcely documented technique may opportunistically be energetically profitable, especially for smaller individuals.

Our observation supports the idea that polar bears can transfer ice-based hunting strategies and adapt them to exploit terrestrial food sources (Gormezano et al. 2017). The dive-hunting technique, where a bear swims underwater toward its prey until it is close enough to launch an attack, is used to approach seals resting on ice (Stirling 1974) or on rocks (Stirling 2011; Bajzak et al. 2013). Similar dive-hunting events have been reported on alcids in open water (Russell 1975; Stempniewicz et al. 2014; Obbard et al. 2022). We ob-
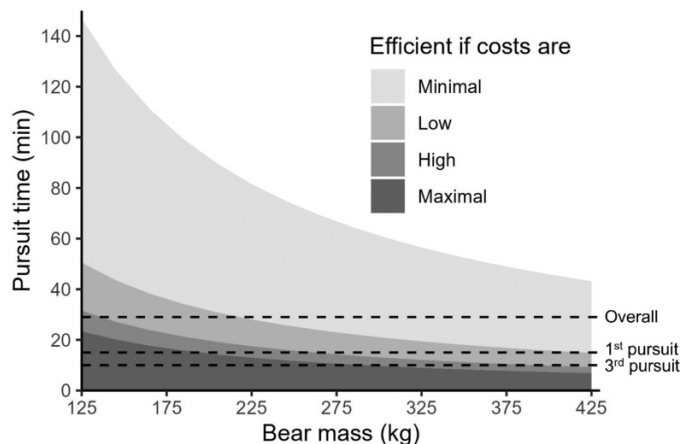
Fig. 3. (*a*) The polar bear is swimming in a pond near a flock of greater snow geese before its first predation attempt. (*b*) The bear walks with the adult geese caught using the dive-hunting technique.

a
Swimming bear
Group of geese

b
Polar bear transporting a goose

Fig. 4. Energetic efficiency thresholds for polar bears feeding on adult greater snow goose based on pursuit duration and bear mass. Shaded areas represent the pursuit durations for which a chase can be profitable for a bear of a given mass, with each area descending to 0 and being shown as overlayed. Minimal costs represent calm water paddling (Pagano et al. 2019). Low, high, and maximal cost areas are all relative to seafaring bears and represent the 2.5th percentile, mean, and 97.5th percentile of metabolic costs observed by Griffen (2018). Pursuit durations observed on Bylot Island are presented in minutes/goose caught (dotted lines). The overall pursuit includes the second pursuit, which lasted 33 min but in which no goose was caught, as well as the successful first and third pursuits. The efficiency thresholds (pursuit duration over which the energetic gains are equal to the costs) were calculated as $ET = gains/(Vo_2 * mass * K)$, where gains are 913.3 kcal (derived from Gormezano et al. (2016) and scaled for a greater snow goose), Vo_2 is the energetic costs of swimming in mL g^{-1} min^{-1} derived from Pagano et al. (2019) and Griffen (2018), and $K = 4.735$, the standard conversion of 1 L of oxygen to kilocalories. The caloric value of a goose used in our calculations is conservative since it assumes that geese have negligible amounts of fat reserves at that time of the year (Ankney and MacInnes 1978).

served what seems to be the same dive-hunting technique but in an environment where it is still undocumented, namely an inland tundra pond.

An issue with the consumption of land-based resources by polar bears is whether the calories they provide outweigh their acquisition costs. Our calculations suggest that the dive-hunting technique can be energetically efficient when aiming for large birds such as greater snow geese and when pursuit durations are short (<15 min) and swimming costs are low or minimal. Swimming metabolic costs experienced by the bear we observed are likely comparable with the minimal costs used in our calculations. Indeed, low, high, and maximal swimming metabolic costs were derived from polar bears swimming continuously in the open sea (Griffen 2018) at speeds higher than reported in other studies (2.0 km h^{-1}, Pagano et al. 2012; 2.0 km h^{-1}, Pilfold et al. 2017), whereas the individual we observed was intermittently paddling in a calm tundra pond, resembling the in-tank captive situation from which the minimal swimming metabolic costs were obtained (Pagano et al. 2019). Moreover, the actual capture sequence, which includes the bear approaching, diving, and resurfacing under the goose, lasted less than a minute. An experienced bear directly catching the goose could potentially shorten the pursuit duration, increasing the energetic efficiency of the chase. On the other hand, the overall interaction may not be

profitable when considering the energy lost during the unsuccessful chase. During 7.5 h of observation, the bear captured only two adult geese and swam for a total of 58 min (i.e., 29 min per bird caught on average), a cost–benefit ratio that is less likely to be efficient (Fig. 4). In sum, the calories gained by opportunistically dive-hunting geese may at times outweigh the associated swimming costs, especially for light bears or experienced individuals, but the overall benefit seems lower when considering the bear's entire energy budget.

Despite the additional calories individual bears may acquire when opportunistically hunting flightless snow geese in ponds, the added food resource is likely negligible at the population level and is not expected to compensate for the decline in seal-hunting opportunities caused by climate change (Rode et al. 2015). Polar bear diet is mainly based on fat, and the overconsumption of protein decreases their net energy intake because of the need to metabolize and excrete

excess nitrogen (Rode et al. 2021). The fat content of molting snow geese is much lower than seals and may not align with the macronutrient requirements of polar bears. In addition, the availability of this food item is low; the temporal overlap between flightless snow geese and land-roaming bears only last 3–4 weeks (Marmillot et al. 2016), plus their spatial overlap is compromised by the geese patchy distribution. Polar bears foraging on land might also have lower access to prey due to competition with other terrestrial predators (Barnas et al. 2020).

As for the greater snow goose colony of Bylot Island, such predation events by polar bears in refuge ponds are unlikely to affect its population dynamics. Sea-ice extent is usually still large during the goose nesting period, and polar bears are hence rarely observed inland, preventing them from wreaking havoc as observed in some eider, gull, and other goose species colonies (Drent and Prop 2008; Smith et al. 2010; Iverson et al. 2014; Prop et al. 2015; Dey et al. 2017, 2018; Jagielski et al. 2021). Also, as stated above, the overlap between on-land polar bears and the availability of vulnerable and flightless geese is narrow. The observed interaction reported in this paper should thus have little ecological consequence on the snow goose population.

We report one of the northernmost observations of a polar bear predation event on an adult bird and the first on greater snow geese in a tundra pond. This description of a dive-hunting technique in an inland waterbody adds to the mounting evidence that polar bears may transfer hunting strategies evolved on the sea ice to benefit from land-based resources (Gormezano and Rockwell 2015). Our study shows that the added calories obtained by opportunistically hunting geese in tundra ponds might at times benefit individual bears, but the population-level consequences of these interactions are likely minimal for both snow geese and bears.

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Data generated or analyzed during this study are provided in full within the published article or within the other referred articles.

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Competing interests

The authors declare there are no competing interests.

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References

Ankney, C.D., and MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. The Auk, **95**: 459–471.

Atkinson, S.N., Nelson, R.A., and Ramsay, M.A. 1996. Changes in the body composition of fasting polar bears (*Ursus maritimus*): the effect of relative fatness on protein conservation. Physiological Zoology, **69**: 304–316. doi: 10.1086/physzool.69.2.3016418610.1086/physzool.69.2.30164186.

Bajzak, C.E., Bernhardt, W., Mosnier, A., Hammill, M.O., and Stirling, I. 2013. Habitat use by harbour seals (*Phoca vitulina*) in a seasonally ice-covered region, the western Hudson Bay. Polar Biology, **36**: 477–491. doi: 10.1007/s00300-012-1274-410.1007/s00300-012-1274-4.

Barnas, A.F., Iles, D.T., Stechmann, T.J., Wampole, E.M., Koons, D.N., Rockwell, R.F., and Ellis-Felege, S.N. 2020. A phenological comparison of grizzly (*Ursus arctos*) and polar bears (*Ursus maritimus*) as waterfowl nest predators in Wapusk National Park. Polar Biology, **43**: 457–465. doi:10.1007/s00300-020-02647-w10.1007/s00300-020-02647-w.

Bety, J., Gauthier, G., Korpimaki, E., and Giroux, J.-F. 2002. Shared predators and indirect trophic interactions: Lemming cycles and Arctic-nesting geese. Journal of Animal Ecology, **71**: 88–98. doi: 10.1046/j.0021-8790.2001.00581.x10.1046/j.0021-8790.2001.00581.x.

Bourque, J., Atwood, T.C., Divoky, G.J., Stewart, C., and McKinney, M.A. 2020. Fatty acid-based diet estimates suggest ringed seal remain the main prey of southern Beaufort Sea polar bears despite recent use of onshore food resources. Ecology and Evolution, **10**: 2093–2103. doi: 10.1002/ece3.604310.1002/ece3.6043. PMID: 32128141.

Department of Energy, Mines and Resources. 1969. Inland water branch: Bylot Island glacier inventory: area 46201. Ottawa.

Dey, C.J., Richardson, E., McGeachy, D., Iverson, S.A., Gilchrist, H.G., and Semeniuk, C.A.D. 2017. Increasing nest predation will be insufficient to maintain polar bear body condition in the face of sea ice loss. Global Change Biology, **23**: 1821–1831. doi: 10.1111/gcb.1349910.1111/gcb.13499. PMID: 27614094.

Dey, C.J., Semeniuk, C.A.D., Iverson, S.A., Richardson, E., McGeachy, D., and Gilchrist, H.G. 2018. Forecasting the outcome of multiple effects of climate change on northern common eiders. Biological Conservation, **220**: 94–103. doi: 10.1016/j.biocon.2018.02.00710.1016/j.biocon.2018.02.007.

Drent, R., and Prop, J. 2008. Barnacle goose (*Branta leucopsis*) survey on Nordenskiöldkysten, west Spitsbergen 1975–2007: breeding in relation to carrying capacity and predator impact. Circumpolar Studies, **4**:59–83. doi: 10.1186/1472-6785-13-51

Gormezano, L.J., and Rockwell, R.F. 2013a. What to eat now? Shifts in polar bear diet during the ice-free season in western Hudson Bay. Ecology and Evolution, **3**: 3509–3523. doi: 10.1002/ece3.74010.1002/ece3.740. PMID: 24223286.

Gormezano, L.J., and Rockwell, R.F. 2013b. Dietary composition and spatial patterns of polar bear foraging on land in western Hudson Bay. BMC Ecology, **13**: 51 10.1186/1472-6785-13-5110.1186/1472-6785-13-51. PMID: 24359342.

Gormezano, L.J., and Rockwell, R.F. 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, **10**: e0128520. doi: 10.1371/journal.pone.012852010.1371/journal.pone.0128520. PMID: 26061693.

Gormezano, L.J., McWilliams, S.R., Iles, D.T., and Rockwell, R.F. 2016. Costs of locomotion in polar bears: when do the costs outweigh the benefits of chasing down terrestrial prey? Conservation Physiology, **4**: cow045. doi: 10.1093/conphys/cow04510.1093/conphys/cow045.

Gormezano, L.J., Ellis-Felege, S.N., Iles, D.T., Barnas, A., and Rockwell, R.F. 2017. Polar bear foraging behavior during the ice-free period in western Hudson Bay: observations, origins, and potential significance. American Museum Novitates, **3885**: 1–28. doi: 10.1206/3885.110.1206/3885.1.

Government of Canada. 2016. Provincial and territorial limits. Available from https://open.canada.ca/data/fr/dataset/a883eb14-0c0e-45c4-b8c4-b54c4a819edb [accessed March 2023].

Government of Canada. 2022. National hydro network. Available from https://open.canada.ca/data/fr/dataset/a4b190fe-e090-4e6d-881e-b87956c07977[accessed March 2023].

Griffen, B.D. 2018. Modeling the metabolic costs of swimming in polar bears (*Ursus maritimus*). Polar Biology, **41**: 491–503. doi: 10.1007/s00300-017-2209-x10.1007/s00300-017-2209-x.

Iles, D.T., Peterson, S.L., Gormezano, L.J., Koons, D.N., and Rockwell, R.F. 2013. Terrestrial predation by polar bears: not just a wild goose chase. Polar Biology, **36**: 1373–1379. doi: 10.1007/s00300-013-1341-510.1007/s00300-013-1341-5.

Iverson, S.A., Gilchrist, H.G., Smith, P.A., Gaston, A.J., and Forbes, M.R. 2014. Longer ice-free seasons increase the risk of nest depredation by polar bears for colonial breeding birds in the Canadian Arctic. Proceedings of the Royal Society B: Biological Sciences, **281**: 20133128. doi: 10.1098/rspb.2013.312810.1098/rspb.2013.3128.

Jagielski, P.M., Dey, C.J., Gilchrist, H.G., Richardson, E.S., and Semeniuk, C.A.D. 2021. Polar bear foraging on common eider eggs: estimating the energetic consequences of a climate-mediated behavioural shift. Animal Behaviour, **171**: 63–75. doi: 10.1016/j.anbehav.2020.11.00910.1016/j.anbehav.2020.11.009.

Lepage, D., Gauthier, G., and Reed, A. 1996. Breeding-site infidelity in greater snow geese: a consequence of constraints on laying date? Canadian Journal of Zoology, **74**: 1866–1875. doi: 10.1139/z96-21010.1139/z96-210.

Mainguy, J., Gauthier, G., Giroux, J.-F., and Bêty, J. 2006. Gosling growth and survival in relation to brood movements in greater snow geese (*Chen caerulescens atlantica*). The Auk, **123**: 1077–1089. doi:10.1642/0004-8038(2006)123[1077:GGASIR]2.0.CO;2

Marmillot, V., Gauthier, G., Cadieux, M.-C., and Legagneux, P. 2016. Plasticity in moult speed and timing in an Arctic-nesting goose species. Journal of Avian Biology, **47**: 650–658. doi: 10.1111/jav.0098210.1111/jav.00982.

Miller, G.D., and Wooldridge, D.R. 1983. Small game hunting behaviour of polar bears, *Ursus maritimus*. Canadian Field-Naturalist, **97**:93–94.

Molnár, P.K., Derocher, A.E., Thiemann, G.W., and Lewis, M.A. 2010. Predicting survival, reproduction and abundance of polar bears under climate change. Biological Conservation, **143**: 1612–1622. doi: 10.1016/j.biocon.2010.04.00410.1016/j.biocon.2010.04.004.

Molnár, P.K., Bitz, C.M., Holland, M.M., Kay, J.E., Penk, S.R., and Amstrup, S.C. 2020. Fasting season length sets temporal limits for global polar bear persistence. Nature Climate Change, **10**: 732–738. doi: 10.1038/s41558-020-0818-910.1038/s41558-020-0818-9.

Obbard, M.E., Corrado, C.D., Franco, J., Pimenta, R., and Wise, B. 2022. Polar bear depredation of a thick-billed murre fledgling in open water at Prince Leopold Island, Nunavut. Polar Research, **41**: 8176. doi: 10.33265/polar.v41.817610.33265/polar.v41.8176.

Pagano, A.M., Durner, G.M., Amstrup, S.C., Simac, K.S., and York, G.S. 2012. Long-distance swimming by polar bears (*Ursus maritimus*) of the southern Beaufort Sea during years of extensive open water. Canadian Journal of Zoology, **90**: 663–676. doi: 1 0.1139/z2012-03310.1139/z2012-033.

Pagano, A.M., Cutting, A., Nicassio-Hiskey, N., Hash, A., and Williams, T.M. 2019. Energetic costs of aquatic locomotion in a subadult polar bear. Marine Mammal Science, **35**: 649–659. doi: 10.1111/mms.1255610.1111/mms.12556.

Pilfold, N.W., McCall, A., Derocher, A.E., Lunn, N.J., and Richardson, E. 2017. Migratory response of polar bears to sea ice loss: to swim or not to swim. Ecography, **40**: 189–199. doi: 10.1111/ecog.0210910.1111/ecog.02109.

Polischuk, S.C., Hobson, K.A., and Ramsay, M.A. 2001. Use of stable-carbon and -nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. Canadian Journal of Zoology, **79**: 499–511. doi: 10.1139/z01-00710.1139/z01-007.

Prop, J., Aars, J., Bårdsen, B.-J., Hanssen, S.A., Bech, C., Bourgeon, S., et al. 2015. Climate change and the increasing impact of polar bears on bird populations. Frontiers in Ecology and Evolution, **3**: 33. doi: 10.3389/fevo.2015.0003310.3389/fevo.2015.00033.

Reed, A., Hughes, R.J., and Boyd, H. 2002. Patterns of distribution and abundance of greater snow geese on Bylot Island, Nunavut, Canada 1983–1998. Wildfowl, **53**: 53–65.

Reed, E.T., Bêty, J., Mainguy, J., Gauthier, G., and Giroux, J.-F. 2003. Molt migration in relation to breeding success in greater snow geese. Arctic, **56**: 76–81. doi: 10.14430/arctic60410.14430/arctic604.

Regehr, E.V., Laidre, K.L., Akçakaya, H.R., Amstrup, S.C., Atwood, T.C., Lunn, N.J., et al. 2016. Conservation status of polar bears (*Ursus maritimus*) in relation to projected sea-ice declines. Biology Letters, **12**: 20160556. doi: 10.1098/rsbl.2016.055610.1098/rsbl.2016.0556. PMID: 27928000.

Rode, K.D., Reist, J.D., Peacock, E., and Stirling, I. 2010. Comments in response to "Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget" by Dyck and Kebreab (2009). Journal of Mammalogy, **91**: 1517–1523. doi: 10.1644/09-MAMM-A-399.110.1644/09-MAMM-A-399.1.

Rode, K.D., Robbins, C.T., Nelson, L., and Amstrup, S.C. 2015. Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities? Frontiers in Ecology and the Environment, **13**: 138–145. doi: 10.1890/14020210.1890/140202.

Rode, K.D., Robbins, C.T., Stricker, C.A., Taras, B.D., and Tollefson, T.N. 2021. Energetic and health effects of protein overconsumption constrain dietary adaptation in an apex predator. Scientific Reports, **11**: 15309. doi: 10.1038/s41598-021-94917-810.1038/s41598-021-94917-8. PMID: 34321600.

Russell, R.H. 1975. The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic, **28**: 117–129. doi: 10.14430/arctic282310.14430/arctic2823.

Smith, P.A., Elliott, K.H., Gaston, A.J., and Gilchrist, H.G. 2010. Has early ice clearance increased predation on breeding birds by polar bears? Polar Biology, **33**: 1149–1153. doi: 10.1007/s00300-010-0791-210.1007/s00300-010-0791-2.

Stempniewicz, L., Kidawa, D., Barcikowski, M., and Iliszko, L. 2014. Unusual hunting and feeding behaviour of polar bears on Spitsbergen. Polar Record, **50**: 216–219. doi: 10.1017/S003224741300005310.1017/S003224741300053.

Stirling, I. 1974. Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Canadian Journal of Zoology, **52**: 1191–1198. doi:10.1139/z74-15710.1139/z74-157.

Stirling, I., and Øritsland, N.A. 1995. Relationships between estimates of ringed seal (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. Canadian Journal of Fisheries and Aquatic Sciences, **52**: 2594–2612. doi:10.1139/f95-84910.1139/f95-849.

Stirling, I. 2011. Polar bears: the natural history of a threatened species. Fitzhenry & Whiteside, Markham, ON.

Stirling, I., and Derocher, A.E. 2012. Effects of climate warming on polar bears: a review of the evidence. Global Change Biology, **18**: 2694–2706. doi: 10.1111/j.1365-2486.2012.02753.x10.1111/j.1365-2486.2012.02753.x. PMID: 24501049.

Watts, P.D., and Hansen, S.E. 1987. Cyclic starvation as a reproductive strategy in the polar bear. Symposium of the Zoological Society of London, **57**: 305–318.