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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