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

Received: 22 February 2008 / Revised: 30 September 2008 / Accepted: 1 November 2008 © Springer-Verlag 2008

**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

Division of Vertebrate Zoology,

The American Museum of Natural History,

Central Park West at 79th Street, New York, NY 10024, USA e-mail: rfr@amnh.org

#### 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

R. F. Rockwell (🖂) · L. J. Gormezano

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<sup>-1</sup> with a few stretches (<5 km each), where density averages <1 nest ha<sup>-1</sup>. 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

**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<sup>-1</sup>, 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

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<sup>-1</sup> 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<sup>-1</sup>, 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  $4.24 \times 10^6$  to  $17.02 \times 10^6$  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  $32.25 \times 10^6$ 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.

Acknowledgments This work benefited greatly from discussions with George Barrowclough, Dave Koons, Scott McWilliams and the

late Malcolm Ramsay. Bob Jefferies, Dave Koons, Maarten Loonen and Scott McWilliams provided suggestions that improved the manuscript. This work was supported through funds and resources provided by the Hudson Bay Project and the American Museum of Natural History. The research reported complies with all relevant Canadian laws.

# References

- Aars J, Lunn NJ, Derocher AE (2006) Polar bears: proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group. IUCN, Gland, Switzerland, and Cambridge, UK
- Abraham KF, Jefferies RL (1997) High goose populations: causes, impacts and implications. In: Batt B (ed) Arctic ecosystems in peril: report of the Arctic Goose Habitat Working Group. Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, and US Fish and Wildlife Service, Washington, DC, pp 7–72. ISBN 0-9617279-3-4
- Abraham KF, Mineau P, Cooke F (1977) Unusual predators of snow goose eggs. Can Field Nat 91:317–318
- Amstrup SC (1986) Polar bear. In: DiSilvestro RL (ed) Audubon wildlife report. National Audubon Society, New York, pp 790–804
- Amstrup SC, Nielsen CA (1989) Acute gastric dilation and volvulus in a free-living polar bear. J Wildl Dis 25:601–604
- Badzinski SS, Ankney CD, Leafloor JO, Abraham KF (2001) Composition of eggs and neonates of Canada Geese and Lesser Snow Geese. Auk 118:687–697
- Beckmann JP, Berger J (2003) Rapid ecological and behavioral changes in carnivores: responses of black bears (*Ursus americanus*) to altered food. J Zool (Lond) 261:207–212. doi:10.1017/ S0952836903004126
- Best RC (1977) Ecological energetics of the polar bear (Ursus maritimus). In: Phillips RL, Jonkel C (eds) Proceedings of the 1975 predator symposium. University of Montana Press, Missoula, pp 203–211
- Best RC (1985) Digestibility of ringed seals by the polar bear. Can J Zool 63:1033–1036
- Carlens H, Lydersen C, Krafft BA, Kovacs KM (2006) Spring haul-out behavior of ringed seals (*Pusa hispida*) in Kongsfjorden, Svalbard. Mar Mamm Sci 22:379–393. doi:10.1111/j.1748-7692. 2006.00034.x
- Cooke F, Rockwell RF, Lank DB (1995) The snow geese of La Pérouse Bay: natural selection in the wild. Oxford University Press, Oxford, 289 pp
- Cury JA, Schramm JL (1995) Sea ice-albedo climate feedback mechanism. J Clim 8:240–247
- Derocher AE, Stirling I (1990) Distribution of polar bears (*Ursus maritimus*) during the ice-free period in western Hudson Bay. Can J Zool 68:1395–1403
- Derocher AE, Andriashek D, Stirling I (1993) Terrestrial foraging by polar bears during the ice-free period in western Hudson Bay. Arctic 46:251–254
- Derocher AE, Wiig Ø, Bangjord G (2000) Predation of Svalbard reindeer by polar bears. Polar Biol 23:675–678
- Derocher AE, Lunn NJ, Stirling I (2004) Polar bears in a warming climate. Integr Comp Biol 44:163–176. doi:10.1093/icb/44.2.163
- Drent RH, Prop J (2008) Barnacle goose *Branta leucopsis* surveys on Nordenskiöldkysten, west Spitzbergen 1975–2007; breeding in relation to carrying capacity and predator impact. Circumpolar Stud 4:59–83
- Dyck MG, Romberg S (2007) Observations of a wild polar bear (*Ursus maritimus*) successfully fishing Arctic char (*Salvelinus alpinus*) and Fourhorn sculpin (*Myoxocephalus quadricornis*). Polar Biol 30:1625–1628. doi:10.1007/s00300-007-0338-3

- Ferguson SH, Stirling I, McLoughlin P (2005) Climate change and ringed seal (*Phoca hispida*) recruitment in Western Hudson Bay. Mar Mamm Sci 21:121–135. doi:10.1111/j.1748-7692.2005. tb01212.x
- Gagnon AS, Gough WA (2005) Trends in the dates of ice freeze-up and breakup over Hudson Bay, Canada. Arctic 58:370–382
- Gende SM, Quinn TP, Willson MF (2001) Consumption choice by bears feeding on salmon. Oecologia 127:372–382. doi:10.1007/ s004420000590
- Heppell S, Caswell H, Crowder LB (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. Ecology 81:654–665
- Hilderbrand GV, Jenkins SG, Schwartz CC, Hanley TA, Robbins CT (1999) Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. Can J Zool 77:1623–1630
- Koons DN, Rockwell RF, Grand JB (2006) Population momentum: implications for wildlife management. J Wildl Manage 70:19–26
- Lunn NJ, Stirling I (1985) The significance of supplemental food to polar bears during the ice-free period of Hudson Bay. Can J Zool 83:2291–2297
- Lunn NJ, Stirling I, Nowicki SN (1997) Distribution and abundance of ringed (*Phoca hispida*) and bearded seals (*Erignathus barbatus*) in western Hudson Bay. Can J Fish Aquat Sci 54:914–921
- Madsen J, Bregnballe T, Mehlum F (1989) Study of the breeding ecology and behaviour of the Svalbard population of Light-bellied Brent Goose *Branta bernicla hrota*. Polar Res 7:1–21
- Madsen J, Bregnballe T, Frikke J, Kristensen IB (1998) Correlates of predator abundance with snow and ice conditions and their role in determining timing of nesting and breeding success in Svalbard Light-bellied Brent Geese *Branta bernicla hrota*. Nor Polarinstitutt Skrifter 200:221–234
- Murphy-Klassen H, Underwood TJ, Sealy SG, Czyrnyj AA (2005) Long-term trends in spring arrival dates of migrant birds at Delta Marsh, Manitoba in relation to climate change. Auk 122:1130– 1148. doi:10.1642/0004-8038(2005)122[1130:LTISAD]2.0.CO;2
- O'Connor R (1984) The growth and development of birds. Wiley, New York
- Overpeck J, Hughen K, Hardy D, Bradley R, Case R, Douglas M, Finney B, Gajewski K, Jacoby G, Jennings A, Lamoureux S, Lasca A, MacDonald G, Moore J, Retelle M, Smith S, Wolfe A, Zielinski G (1997) Arctic environmental change of the last four centuries. Science 278:1251–1256. doi:10.1126/science.278.5341.1251
- Ramsay MA, Stirling I (1988) Reproductive biology and ecology of female polar bears (Ursus maritimus). J Zool Soc Lond 214:601– 634
- Ramsay MA, Hobson K (1991) Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. Oecologia 86:598–600
- Randall DA, Wood RA, Bony S, Colman R, Fichefet T, Fyfe J, Kattsov V, Pitman A, Shukla J, Srinivasan J, Stouffer RJ, Sumi A, Taylor KE (2007) Climate models and their evaluation. In: Solomon S, Qin D, Manning M, Miller HL (eds) Climate change 2007: the physical science basis. Contribution of Working Group I to the 4th Assessment Report of the IPCC. Cambridge University Press, Cambridge, pp 589–662
- Rankin DJ, Bargum K, Kokko H (2007) The tragedy of the commons in evolutionary biology. Trends Ecol Evol 22:643–651. doi:10.1016/j.tree.2007.07.009
- Regehr EV, Lunn NJ, Amstrup SC, Stirling I (2007) Effects of early sea ice breakup on survival and population size of polar bears in Western Hudson Bay. J Wildl Manage 71:2673–2683. doi:10.2193/2006-180

- Robbins CT (1993) Wildlife feeding and nutrition, 2nd edn. Academic Press, New York
- Robbins CT, Fortin JK, Rode KD, Farley SD, Shipley LA, Felicetti LA (2007) Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. Oikos 116:1675–1682
- Rockwell RF, Abraham KF, Witte CR, Matulonis P, Usai M, Larsen D, Cooke F, Pollak D, Jefferies RL (2009) The birds of Wapusk National Park. Parks Canada, Ottawa
- Romanoff AL (1967) Biochemistry of the avian embryo. Wiley, New York, 398 pp
- Rosing-Asvid A (2006) The influence of climate variability on polar bear (*Ursus maritimus*) and ringed seal (*Pusa hispida*) population dynamics. Can J Zool 84:357–364. doi:10.1139/Z06-001
- Ross RK, Abraham KF, Fillman D, Collins BT, Kerbes RH (2004) A helicopter-based survey method for monitoring the nesting component of snow goose colonies. Northeast Wildl 58:9–22
- Russell RH (1975) The food habits of polar bears of James Bay and southwest Hudson Bay in summer and autumn. Arctic 28:117–129
- Schmidt-Nielsen K (1997) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge
- Skinner WR, Jefferies RL, Carleton TJ, Rockwell RF, Abraham KF (1998) Prediction of reproductive success and failure in lesser snow geese based on early season climatic variables. Global Chang Biol 4:3–16
- Smith AE, Hill MRJ (1996) Polar bear, Ursus maritimus, depredation of Canada goose, Branta canadensis, nests. Can Field Nat 110:339–340
- Stirling I (1974) Midsummer observations on the behavior of wild polar bears (*Ursus maritimus*). Can J Zool 52:1191–1198
- Stirling I, Archibald WR (1977) Aspects of predation of seals by polar bears. J Fish Res Board Can 34:1126–1129
- Stirling I, Derocher AE (1993) Possible impacts of climatic warming on polar bears. Arctic 46:240–245
- Stirling I, Derocher AE (2007) Melting under pressure—the real scoop on climate warming and polar bears. Wildl Prof 1:24–27, 43
- Stirling I, Latour PB (1978) Comparative hunting ability of polar bear cubs of different ages. Can J Zool 56:1768–1772
- Stirling I, McEwan EH (1975) The caloric value of whole ringed seals (*Phoca hispida*) in relation to polar bear (*Ursus maritimus*) ecology and hunting behavior. Can J Zool 53:1021–1027
- Stirling I, Øritsland NA (1995) Relationships between estimates of ringed seals (*Phoca hispida*) and polar bear (*Ursus maritimus*) populations in the Canadian Arctic. Can J Fish Aquat Sci 52:2594–2612
- Stirling I, Parkinson CL (2006) Possible effects of climate warming on selected populations of polar bears (*Ursus maritimus*) in the Canadian Arctic. Arctic 59:261–275
- Stirling I, Lunn NJ, Iacozza J (1999) Long-term trends in the population ecology of polar bears in Western Hudson Bay in relation to climate change. Arctic 52:294–306
- Stirling I, Lunn NJ, Iacozza J, Elliott C, Obbard M (2004) Polar bear distribution and abundance on the southwestern coast of Hudson Bay during open water season in relation to population trends and annual ice patterns. Arctic 57:15–26
- Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: faster than forecast. Geophys Res Lett 34:L09501. doi:10.1029/2005GL025624
- Watts PD, Hansen SE (1987) Cyclic starvation as a reproductive strategy in the polar bear. Symp Zool Soc Lond 57:305–318
- Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River