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**Polar bear use of terrestrial foods**

**An old-growth concept for grasslands**

**Conservation organizations and global change**

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# Can polar bears use terrestrial foods to offset lost ice-based hunting opportunities?

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**Increased land use by polar bears (*Ursus maritimus*) due to climate-change-induced reduction of their sea-ice habitat illustrates the impact of climate change on species distributions and the difficulty of conserving a large, highly specialized carnivore in the face of this global threat. Some authors have suggested that terrestrial food consumption by polar bears will help them withstand sea-ice loss as they are forced to spend increasing amounts of time on land. Here, we evaluate the nutritional needs of polar bears as well as the physiological and environmental constraints that shape their use of terrestrial ecosystems. Only small numbers of polar bears have been documented consuming terrestrial foods even in modest quantities. Over much of the polar bear's range, limited terrestrial food availability supports only low densities of much smaller, resident brown bears (*Ursus arctos*), which use low-quality resources more efficiently and may compete with polar bears in these areas. Where consumption of terrestrial foods has been documented, polar bear body condition and survival rates have declined even as land use has increased. Thus far, observed consumption of terrestrial food by polar bears has been insufficient to offset lost ice-based hunting opportunities but can have ecological consequences for other species. Warming-induced loss of sea ice remains the primary threat faced by polar bears.**

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The effects of climate change are more evident in the Arctic than anywhere else on Earth. The disproportional rise in surface air temperatures suggests an amplification of climate-change effects in this region (Serreze and Barry 2011). Thus, the changes in species and ecosystems in the Arctic provide some of the first case studies of climate-change effects. Altered distribution (Chen *et al.* 2011) is a primary manifestation of species response to climate change. This is currently exemplified by increased use of terrestrial habitats by polar bears (*Ursus maritimus*) as the spatiotemporal extent of sea ice has declined. This distributional change has the potential to alter ecological relationships at the marine–terrestrial interface, including interspecies interactions, pathogen transmission, and human–wildlife conflict (Stirling and Derocher 2012). For instance, in western Hudson Bay, polar bears increasingly have been reported preying on birds and their eggs. Farther north, in Foxe Basin and Hudson Strait, documented increases in polar bear predation led to catastrophic effects on seabird reproduction (Iverson *et al.* 2014). These examples illustrate how changing species distributions in response to climate change could have broad, cascading ecosystem effects. However, studies on terrestrial habitat use by polar bears are limited. In this review, we assess the potential for terrestrial Arctic ecosystems to sustain polar bears as they are forced to spend more time on land.

Polar bears have become an iconic symbol of global warming (Manzo 2010). This symbolism is supported by the fact that polar bears depend on sea ice for foraging, traveling, and mating. The media attention that polar bears have received has led to increased public and scientific interest in their responses to global warming. Viewpoint articles (Dyck *et al.* 2007) and hypotheses questioning the link between global warming and polar bear persistence create the appearance of debate within the scientific community. Whether a debate is valid must be evaluated in the context of assumptions, extrapolations, and data quality (Stirling *et al.* 2008). Such evalua-

### In a nutshell:

- Polar bears, the largest and most carnivorous of all ursids, have evolved to hunt lipid-rich marine mammals on sea ice, but reports of terrestrial feeding have increased in recent years
- We evaluate the importance of terrestrial foraging to polar bears based on physiological, environmental, and nutritional constraints
- Fewer than 30 polar bears within populations ranging from 900 to 2500 individuals have been observed consuming energy-dense terrestrial foods, such as bird eggs, and no study has documented a meaningful contribution of terrestrial foods to individual bear nutrition
- The terrestrial habitats that polar bears retreat to during sea-ice minimums provide only limited or low-quality food resources, just sufficient to support low densities of much smaller, omnivorous brown bears
- Available data suggest that terrestrial foods cannot prevent declines in polar bear body condition and survival associated with sea-ice loss caused by global warming, although such foods may minimally supplement marine food for individual polar bears in some populations

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tions can differentiate between unsupported hypotheses and those that are borne out by the available data.

Polar bear use of terrestrial foods has been reported since the 1400s (Derocher 2012). Numerous recent scientific papers have documented the consumption of terrestrial and freshwater foods by polar bears and suggest that such use is increasing (Rockwell and Gormezano 2009; Smith *et al.* 2010; Iversen *et al.* 2013; Iverson *et al.* 2014). Some authors hypothesize that such observations are evidence that terrestrial foraging will play a major role in polar bear adaptation to global warming (Gormezano and Rockwell 2013a), and will allow them to withstand increasingly ice-free conditions (Dyck and Kebreab 2009; Rockwell and Gormezano 2009). This scenario, which implies a changing role for polar bears in the Arctic ecosystem, has been described in several journal articles and has received considerable media coverage. Here, we revisit the question of whether, and to what extent, polar bears may benefit from terrestrial foraging. We consider the importance of terrestrial foraging at three scales: (1) across polar bears' circumpolar range relative to the availability and abundance of terrestrial foods, as well as to the potential limitations of competing with brown bears (*Ursus arctos*) for these resources; (2) at the population level; and (3) at the individual level relative to meeting energy and nutrient requirements. Finally, we provide recommendations for needed research, including the limitations of various methodological approaches.

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***Figure 1.*** *A polar bear family on the sea ice in the Chukchi Sea. Often remaining on sea ice year-round, polar bears hunt for ringed seals and bearded seals (*Erignathus barbatus*), which require sea ice for hauling out, molting, and pupping.*

## Polar bear distribution and evolutionary history

Polar bears currently only inhabit areas covered by Arctic sea ice for much of the year. They are divided into 19 recognized subpopulations within four identified ecoregions (based on annual sea-ice dynamics; Amstrup *et al.* 2008). Over most of their range (ie in three of the four ecoregions), entire populations have historically remained on sea ice year-round, where they hunt marine mammals (Figure 1), with only pregnant females regularly venturing onto land to occupy maternal dens. In the fourth, seasonal ice ecoregion, there has been no multi-year or perennial ice throughout the human historical record. Here, polar bears actively prey on marine mammals from seasonally available sea ice. After foraging on the ice and accumulating large amounts of fat, they then spend an extended period on land, metabolizing their accumulated stores of fat and muscle (Atkinson *et al.* 1996).

Because global warming has reduced the spatiotemporal availability of sea ice, polar bears are spending more time on land – in both seasonal (Stirling *et al.* 1999) and historically perennial sea-ice habitats (Figure 2; Schliebe *et al.* 2008). In seasonal ice habitats, such as western Hudson Bay, increased duration of the ice-free period has coincided with declines in polar bear body mass, condition, cub survival (Stirling *et al.* 1999; Rode *et al.* 2010), and population

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***Figure 2.*** *An adult female polar bear and her yearling onshore in the southern Beaufort Sea during the annual sea-ice minimum. An increasing proportion of the southern Beaufort Sea population has come onshore in recent years (Schliebe* et al. *2008; USGS unpublished data).*

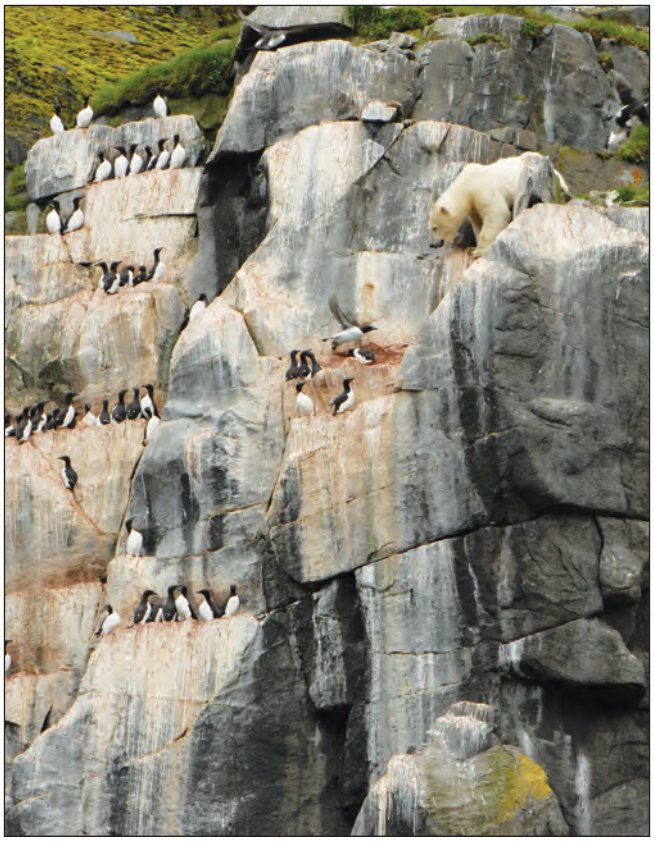

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***Figure 3.*** *A polar bear foraging for thick-billed murre (*Uria lomvia*) eggs in Alkefillet, Svalbard, in July 2013. Although reports of polar bears feeding on land-based foods have increased, few bears have been documented exhibiting such behavior, making it unlikely to contribute to the health of the overall population.*

size (Regehr *et al.* 2007). More frequent land use by polar bears is projected to occur as sea ice declines (Derocher *et al.* 2004; Stirling and Derocher 2012).

The evolutionary history of polar bears and their close relative, the brown bear, suggests potential limitations on the ability of polar bears to exploit terrestrial foods while onshore. Polar bears separated from a common ancestor with brown bears as recently as 500 000 years ago (Liu *et al.* 2014; Welch *et al.* 2014). By the late Pleistocene, they had evolved dentition and conformational differences from brown bears that are consistent with a primarily carnivorous diet and specialization for preying on seals and other marine mammals from a sea-ice platform (Ingolfsson and Wiig 2008). Several recent studies have begun to identify the genetic differences between polar bears and brown bears and have attempted to tease apart the differing physiologies of these two species (Liu *et al.* 2014; Welch *et al.* 2014). Five of the top 20 candidate genes for positive selection in polar bears, but not brown bears, are associated with lipid metabolism, suggesting that one of the ways polar bears have diverged physiologically from other ursids is through the development of metabolism specific to a diet rich in fat (Table 1). The degree to which polar bears have adapted to a carnivorous, lipid-rich diet, as discussed more specifically below, has important negative implications for their ability to effectively use lipid-poor terrestrial foods, and therefore for their ability to compete with sympatric brown bears.

## Range-wide trends in use and availability of terrestrial food resources

Across the circumpolar Arctic range, reports of increased use of terrestrially available foods by polar bears have mostly come from Hudson Bay and Foxe Basin. In these seasonal ice habitats, consumption of a wide variety of terrestrial and freshwater foods has been documented, including berries (eg *Vaccinium uliginosum*, *Empetrum nigrum*, and *Ribes oxyacanthoides*), vegetation (eg *Palmaria palmata*, *Equisetum* spp, and sedges), mammals (eg *Rangifer* spp, *Ovibos moschatus*, *Urocitellus parryii*, and *Lemmus* spp), birds and bird eggs (*Branta* spp, *Somateria* spp, *Anser caerulescens*, *Uria lomvia*, and *Larus* spp), fish (*Salvelinus alpinus*, *Boreogadus saida*, and *Salmo salar*), and others (Russell 1975; Derocher *et al.* 1993; Dyck and Romberg 2007; Ovsyanikov and Menyushina 2010; Gormezano and Rockwell 2013a). Consumption of terrestrial foods, including hunting of muskox (*O moschatus*) and lesser snow geese (*Chen caerulescens caerulescens*), has also been reported in perennial sea-ice ecoregions, but to a lesser extent (eg Wrangel Island [Ovsyanikov and Menyushina 2010] and in Svalbard [Iversen *et al.* 2013]). Derocher (2012) provided an appendix listing 66 foods eaten by polar bears in terrestrial environments. These foods are typically consumed during a short but growing portion of the year when polar bears are on land.

There are few long-term, systematic observations that allow evaluation of trends in the contribution of terrestrial foods to individual bear diets or the numbers of polar bears consuming terrestrial foods. In some areas, polar bears appear to be eating more eggs of colonial nesting birds (eg common eider, *Somateria mollissima*; thick-billed murre, *U lomvia*) (Figure 3; Smith *et al.* 2010; Iverson *et al.* 2014). However, in most cases it is unclear whether terrestrial foraging by polar bears has become more com-

**Table 1. Five genes of lipid metabolism that demonstrate positive selection in polar bears but not brown bears**

| Gene | Lipid metabolism related functions | HKA test P value | |
|---|---|---|---|
| | | Polar bear | Brown bear |
| ***APOB*** | Production of apolipoprotein B | <0.0001 | 0.52 |
| ***SH3PXD2B*** | Adipocyte differentiation | <0.0001 | 0.34 |
| ***EHD3*** | Cholesterol and sphingolipid transport | <0.002 | 0.91 |
| ***ARID5B*** | Transcription of genes involved in adipogenesis | 0.013 | 0.75 |
| ***POLR1A*** | Kidney growth and purine metabolism | 0.019 | 0.66 |

**Notes:** Modified from Liu *et al.* (2014). HKA test = Hudson-Kreitman-Aguadé test.

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mon, and nowhere has it been documented that terrestrial foods are becoming a more important component of polar bear diets.

An important consideration is the range-wide availability of terrestrial food resources in Arctic polar bear habitats. Dyck and Kebreab (2009) suggested that Arctic char (*S alpinus*), ringed seal (*Pusa hispida*), bog blueberry (*V uliginosum*), and crowberry (*E nigrum*) could be important foods for offsetting lost ice-based foraging opportunities. In response to Dyck and Kebreab (2009), Rode *et al.* (2010) cited data showing that availability of *S alpinus* is limited across the Arctic due to a lack of streams shallow enough to allow the bears to catch them. Moreover, not all char are anadromous (migrating up rivers to spawn) nor are they semelparous (going through a single reproductive cycle during their lifetime), and even brown bears make little use of fish in the Arctic (Barker and Derocher 2009). Because there is very little evidence that polar bears can capture ringed seals in open water, consumption of this prey species during the ice-free season is likely very rare. Estimates of their contribution to polar bear energy budgets are therefore misleading. Similarly, large interannual fluctuations in berry availability and competition with other frugivores limit the availability of this resource in some years (review in Rode *et al.* 2010).

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***Figure 4.*** *A polar bear and a brown bear feeding at the remains of a bowhead whale (*Balaena mysticetus*) carcass harvested by human subsistence hunters in the southern Beaufort Sea. Over much of the polar bear's range, terrestrial habitats are occupied by brown bears, which consume many of the available terrestrial food resources and, as in this case, compete for marine-mammal carcasses.*

The population ecology of brown bears in terrestrial Arctic landscapes offers some of the best evidence that these habitats are unlikely to provide substantial food resources for polar bears, even over short time periods. In Arctic landscapes, brown bears occur at very low densities (Miller *et al.* 1997) and are among the smallest of their species (Hilderbrand *et al.* 1999). Food availability was determined to be the most important factor limiting a brown bear population in the Canadian Arctic (McLoughlin *et al.* 2002). Food limitations would be particularly problematic for the much larger polar bears, which often have a body mass double that of Arctic brown bears. Observations suggest that brown bears, which occur on land adjacent to much of the polar bear's circumpolar sea-ice habitat, can displace polar bears from feeding sites (Figure 4; S Miller pers comm). Furthermore, brown bears already occupy Arctic coastal terrestrial habitats throughout much of the polar bears' range and consume terrestrial food resources. For example, in 2013, two to three brown bears and associated avian predators consumed eggs from >90% of about 2000 black brant (*Branta bernicla nigricans*) and lesser snow goose nests on the southern Beaufort Sea coast (J Hupp and D Ward pers comm). Polar bears forced onto land due to sea-ice loss will have to compete with brown bears where their ranges overlap. Further research is needed to understand habitat and food-resource use when and where these two species are sympatric.

## Population-level use of terrestrial food resources

The importance of terrestrial foods for polar bears depends on a sufficient population segment having access to and using those resources. Derocher *et al.* (1993) estimated that 10–63% of polar bears in the western Hudson Bay population were feeding on vegetation – primarily berries. In Svalbard, 33% of polar bear scat samples contained terrestrial plants and lichens, but 71% contained seal remains (Iversen *et al.* 2013). Rockwell and Gormezano (2009) observed six bears feeding on goose eggs, while more recently, Iverson *et al.* (2014) observed 22 polar bears – including four cubs over 3 years of age – feeding on eider eggs, although evidence other than direct observations was also detected. Iles *et al.* (2013) and Smith *et al.* (2010) documented four to six individual bears feeding on adult lesser snow geese. Gormezano and Rockwell (2013a) examined terrestrial foods in polar bear scat in western Hudson Bay and compared its composition to earlier studies, but the proportion of the population represented was unknown, as was the energetic contribution of these foods to individual requirements. Such studies suggest that, so far, only very small numbers of polar bears are eating birds and bird eggs. More widely available terrestrial foods, such as berries, are more commonly consumed, but the nutritional value of many of these foods is much lower than birds and bird eggs (see next section).

Rockwell and Gormezano (2009) calculated that goose eggs available in their western Hudson Bay study area

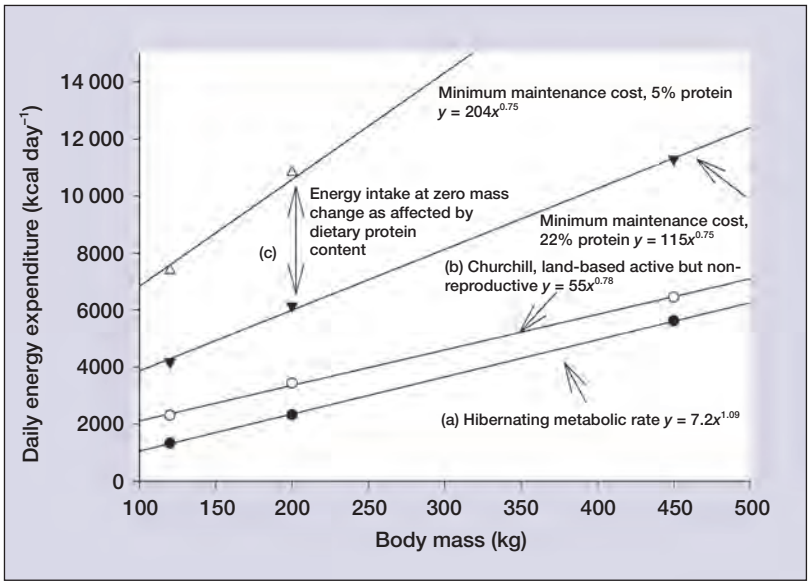


***Figure 5.*** *Comparison of the (a) estimated energy expenditure of polar bears, brown bears, and black bears when hibernating; (b) energy expenditure of land-based male polar bears at Churchill, Manitoba (western Hudson Bay) during ice-free times; and (c) metabolizable energy intakes by captive brown bears at various dietary protein contents that are necessary to maintain their starting mass (ie maintenance; Robbins* et al. *2012; Erlenbach* et al. *2014). Minimum maintenance costs are metabolizable energy estimated as digestible energy times 0.95 (Pritchard and Robbins 1990) and are therefore equivalent to the heat loss estimates described by the other statistical regressions. Maintenance energy intakes of captive bears should be viewed as minimums, in that all food was provided and so there were no foraging costs, which could dramatically increase energy expenditure. The necessary energy intakes when consuming higher-protein, meat-based diets fall within the two extremes shown.*

could offset the nutrition that a polar bear would acquire during 1438 days of foraging for seals on the ice. Theoretically, therefore, each of the ~900 polar bears in the western Hudson Bay population (Regehr *et al.* 2007) could offset about a day and a half of lost sea-ice foraging by consuming all of the available goose eggs in the region. To date, few bears have been documented exploiting this resource, but use could increase if polar bears continue to come onshore earlier in the year than they have in the past (Stirling *et al.* 1999). Although it may help some individuals to meet their energy needs, availability of birds and their eggs is insufficient to support all the polar bears in this population when their time on land is increasing by weeks (Stirling *et al.* 1999; Regehr *et al.* 2007), and the localized, catastrophic effect on bird populations (Smith *et al.* 2010; Rockwell *et al.* 2011; Iverson *et al.* 2014) means a polar bear focus on such resources is unsustainable.

Despite evidence of increased use of terrestrial food resources by polar bears, any potential benefit of terrestrial foraging has yet to be reflected in polar bear demography, which is the ultimate indicator of nutritional value. In western Hudson Bay, where high-quality terrestrial foods (birds, bird eggs, and caribou [*Rangifer tarandus*]) may be more readily available than in most other Arctic landscapes, survival rates and population size have declined with increasing time spent on land (Regehr *et al.* 2007), despite well-documented terrestrial foraging (Rockwell and Gormezano 2009; Smith *et al.* 2010; Gormezano and Rockwell 2013a, b).

## Individuals and terrestrial foraging: energetics of foraging on land

The potential energetic contribution of terrestrial foods has been estimated (Dyck and Kebreab 2009; Rockwell and Gormezano 2009), but no study has empirically quantified caloric intake by polar bears based on terrestrial foods. Dyck and Kebreab (2009) concluded that polar bears could ingest enough energy to maintain body mass (ie balance daily energy loss) while on land if feeding on Arctic char and ringed seals, and smaller bears (up to 280 kg) could maintain their body mass through berry consumption. However, these conclusions assumed that feeding polar bears expend energy at the same rate as fasting, less active polar bears. Even in captivity, actively feeding brown and American black bears (*Ursus americanus*) required four times the energy as compared with fasting wild polar bears (Rode *et al.* 2010). More recent studies suggest that the additional demands of searching for, consuming, and metabolizing large amounts of food would increase energy expenditure twofold to eightfold (Figure 5). Although the estimates in Figure 5c are based on studies that examined the effect of varying dietary composition of protein, carbohydrate, and fat in captive brown bears (Erlenbach *et al.* 2014), the only polar bear study looking at these questions – that of Dyck and Morin (2011) – produced similar results. Thus, food intake levels would have to be much higher than those calculated by Dyck and Kebreab (2009), and studies of captive bears indicate such intake levels are likely to be limited by foraging efficiency and food availability.

Large-bodied brown bears cannot meet their energy requirements by consuming berries or herbaceous vegetation even in captivity, where such foods were provided in abundance (Welch *et al.* 1997; Rode *et al.* 2001). Two studies attempted to use stable isotopes to determine whether polar bears are consuming meaningful amounts of terrestrial foods in western Hudson Bay and found no evidence of substantial consumption (Ramsay and Hobson 1991; Hobson *et al.* 2009). Hobson *et al.* (2009) noted that the isotopic composition of breath expelled by fasting bears and by berry-eating bears was consistent with metabolism reflecting fasting and mobilization of lipids derived from seals. Despite uncertainties in correction factors by

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which stable isotope studies account for digestive and metabolic processes affecting tissue isotope concentration, if a large proportion of the population were compensating for lost marine foraging opportunities by consuming terrestrial foods, survival rates should not continue to decline as sea-ice extent decreases and land use increases.

Polar bears are the largest extant ursid, and like other large bears face a foraging dilemma when there is a mismatch between the rates of energy expenditure and energy intake. Because of their lower energy requirement, smaller bears may be able to successfully balance energy expenditure with energy intake when consuming berries, vegetation, or foods requiring greater foraging effort relative to the energetic reward (Welch *et al.* 1997; Rode *et al.* 2001). Some observations support the hypothesis that terrestrial food resources, particularly those in which the foraging cost is high relative to the energetic return, are consumed in greater quantities by smaller polar bears. Derocher *et al.* (1993) found berry-eating to be least prevalent among adult male polar bears. Three of six bears observed chasing live birds were sub-adults (Smith *et al.* 2010), and egg consumption was most common among sub-adult bears (Rockwell and Gormezano 2009). However, to date, no study has demonstrated a sizeable nutritional benefit from terrestrial foraging, even among sub-adults.

Studies of polar bear activity patterns while onshore in Hudson Bay suggest that these animals have adopted an energy conservation strategy as opposed to an active foraging strategy. Field observations revealed that land-based polar bears in James Bay and western Hudson Bay spent 87% and 73–79%, respectively, of their time resting, and only 2% of their time foraging (Knudsen 1978; Lunn and Stirling 1985). Updated data on sex- and age-specific activity patterns would inform whether bears are devoting more time to foraging.

## Nutritional value of terrestrially based foods

Some authors suggest that polar bears may benefit from consuming vegetation and land-based animals to fulfill vitamin and mineral requirements (Derocher 2012; Gormezano and Rockwell 2013b). However, if terrestrial foraging is essential for trace element intake, bears in all populations would historically have spent time foraging in terrestrial habitats; yet this has not been the case. Omnivores and herbivores are more likely to select foods based on micronutrient composition (McDowell 1992), but the diets of carnivores such as polar bears are complete in essential micronutrients if they consume organs and bones in addition to meat and fat (Robbins 1993). Polar bears do consume foods for which the nutritional value is unclear, such as seaweed (Lønø 1970), but mineral deficiencies in wild, carnivorous populations are rare (Robbins 1993) and have not been documented in polar bears.

In addition to satisfying requirements for micronutrients, the marine-based diet of polar bears provides a high lipid, calorically dense food resource that minimizes total energy costs. Ringed seal bodies contain 34–76% fat (Stirling and McEwan 1975) and polar bears have been documented to consume up to 70% of their diet as lipids (Best 1985; Cherry *et al.* 2010). Recently, Erlenbach *et al.* (2014) showed that such a high fat, low protein diet minimizes the energy requirements of bears as compared with higher protein diets or high carbohydrate diets (eg berries; Figure 5). Thus, the lipid-rich, carnivorous, marine-based diet of polar bears is likely to provide all essential nutrients and is ideal for maximizing fat accumulation and minimizing energy requirements.

Few terrestrial foods are as energetically dense as marine prey. Polar bears have been observed catching snow geese at a time of year when the geese are undergoing molt, during which they often lose body mass and have reduced fat stores (Portugal *et al.* 2011). Potential ungulate prey, such as muskox and caribou, consist primarily of protein rather than fat, and are often scavenged rather than preyed upon (Derocher *et al.* 2000), which could result in consumption of animals in poor condition. Vegetation resources are primarily composed of carbohydrate and smaller amounts of protein. The terrestrial food resource that most closely matches the nutritional composition of the polar bears' marine prey is bird eggs, but, as discussed above, these are limited in availability for a substantial proportion of any polar bear population.

## Research needs

The ultimate measure of the benefit of terrestrial foraging is the degree to which it reverses the current trend of declining physical condition, reproduction, and survival rates among polar bears that are spending increasing amounts of time on land. Repeated captures could allow researchers to track mass and fat dynamics while bears are onshore (Atkinson *et al.* 1996) and to document reproductive success and survival in relation to individual feeding behaviors. Greater effort is also needed to quantify the number of bears utilizing terrestrial foods, trends in the frequency of resting and foraging behavior for bears while onshore, differences in behavior among sex and age classes, and availability and nutritional value of terrestrial foods. The primary methods used in recent reports of terrestrial foraging have been direct observation and scat analysis. These techniques can reveal only whether a bear is consuming terrestrial foods and the relative proportions of each food type. Neither scat analyses nor direct observations can assess energetic contribution to individual diets unless all scats deposited by an individual bear are collected and calculations carried out to correct for differential digestibility among dietary items (Pritchard and Robbins 1990). Stable isotope analyses offer information on the total dietary contribution over longer time periods. Both stable isotope and scat-based estimates of bear diets onshore can co-occur with genetic analyses (Waits and Paetkau 2005) to determine the number of bears consuming terrestrial foods, a metric that is lacking in most studies. Snare-based hair sampling for genetic and stable isotope

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analyses is effective in areas where polar bears congregate (Herreman and Peacock 2013). Fatty acid analysis can also be used to determine if terrestrial foods are providing a substantial proportion of fat resources in polar bear diets (Thiemann *et al.* 2008). Monitoring bear activity onshore could provide data on whether bears are increasingly active and foraging or are maintaining an energy conservation strategy. While it is tempting to publish any observations of polar bears feeding on terrestrial foods, these observations are of limited value in understanding the importance of these behaviors. More directed and focused quantitative studies, as described above, are needed.

## Conclusions

Available data do not support the conclusion that polar bears can replace lost access to marine-mammal resources with terrestrially derived foods. For terrestrial foods to stabilize declines in polar bear survival and abundance, observed behaviors in some bears must provide net energetic gain, be indicative of behavior that is or soon will be displayed by much of the rest of the population, and will become widespread throughout the entire polar bear range. Observations of polar bears feeding on bird eggs near Hudson Bay and Foxe Basin, and bears mixing meat and vegetation, represent a small proportion of the population (Smith *et al.* 2010; Gormezano and Rockwell 2013b). At best, these behaviors may offset some ice-based foraging opportunities for some individuals. However, behaviors of just a few bears can have important ecological consequences, as evidenced by the catastrophic nest failure among black brant resulting from polar bear predation (Iverson *et al.* 2014). Therefore, the role of polar bears in terrestrial ecosystems may be changing, even though evidence suggests that the nutritional contribution of terrestrial foods to polar bear diets will probably remain negligible.

More focused research and monitoring is needed to determine whether terrestrial foods could contribute appreciably to polar bear nutrition despite the physiological and nutritional limitations and low availability of most terrestrial food resources. Projections for continued substantial declines in sea-ice extent emphasize the threat of global warming to polar bears, which warrant cautious management, particularly in areas where declines in body condition, cub survival, and population size have already occurred.

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Use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

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