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ESTIMATING THE ENERGETIC CONTRIBUTION OF POLAR BEAR (*URSUS MARITIMUS*) SUMMER DIETS TO THE TOTAL ENERGY BUDGET

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Polar bears (*Ursus maritimus*) are faced with potential drastic changes to their ice habitat in the near future. Climate models predict that the ice-covered period during which bears use the sea ice to hunt seals is getting shorter, and that the ice-free season will become extended. Bears will not have enough ice time to accumulate the necessary body fat reserves they need to live off when stranded on land during summers. However, polar bears have been observed making use of several food sources while on land, although the energetic contributions of these diets to the bears' energy budget were considered to be minor. We examine mathematically whether observed diets (i.e., arctic charr [*Salvelinus alpinus*], ringed seal [*Pusa hispida*] blubber, and berry diets) can contribute sufficient energy to offset the daily body mass loss. We then estimate the amount or mass of the diet that must be consumed to achieve a balanced daily energy loss, and whether this is possible, given specific constraints on feeding. The analysis indicated that it is possible for polar bears to maintain their body mass while on shore by feeding on arctic charr and seal blubber. Polar bears of body masses up to 280 kg could gain sufficient energy from blueberries to match the daily energy loss. The question that arises is how many bears of a population would resort to such strategies? To better understand how polar bears will adapt to a warming climate, we recommend continued examination of polar bear diets in the field, and controlled feeding trials with captive polar bears.

Key words: alternative summer diet, climate change, energy balance, polar bears, *Ursus maritimus*

Polar bears (*Ursus maritimus*) use the sea-ice platform to hunt their prey, primarily ringed seals (*Pusa hispida*) and bearded seals (*Erignathus barbatus*—Derocher et al. 2002; Smith 1980; Stirling and Archibald 1977). During spring, when the sea ice and naïve seal pups are abundant, bears are hyperphagic. In areas where the sea ice disappears during summers and seals generally become unavailable to hunt, bears progress through a fasting stage where they can spend up to several months on shore (e.g., Aars et al. 2006; Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2008; Derocher and Stirling 1990). Here they either live off their stored fat reserves (Ramsay and Stirling 1988; Watts and Hansen 1987), or when fat deposits are likely to be insufficient they have been known to resort to several alternative food sources on an opportunistic basis. For example, polar bears have been observed hunting and stalking caribou (*Rangifer tarandus*—Brook and Richardson 2002; Derocher et al. 2000) and muskox (*Ovibos moschatus*—Ovsyanikov 1996), and even devouring conspecifics (e.g., Dyck and Daley 2002). Other food items that are opportunistically consumed range from arctic charr (*Salvelinus alpinus*) and ringed seals (Dyck and Romberg 2007; Furnell and Oolooyuk 1980), to various bird species, eggs, and human garbage (e.g., Derocher et al. 1993; Donaldson et al. 1995; Dyck 2001; Lunn and Stirling 1985; Russell 1975; Stempniewicz 2006). In addition, polar bears also have been known to consume berries (e.g., blueberries [*Vaccinium uliginosum*], crowberries [*Empetrum nigrum*], bearberries [*Arctous*], cranberries [*Vaccinium macrocarpon*], and soapberries [*Shepherdia canadensis*]—Derocher et al. 1993; Dyck 2001; Russell 1975) and kelp (*Laminaria* and *Rhodymenia*—Dyck 2001; Russell 1975) in various quantities. Although these feeding behaviors of polar bears have been observed repeatedly, the significance of the latter terrestrial food components to the overall energy budget of polar bears was considered to be minor (Hobson and Stirling 1997; Lunn and Stirling 1985; Ramsay and Hobson 1991).

Polar bears face uncertain times (e.g., Derocher et al. 2004) where increasing evidence suggests that the Arctic sea ice is

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shrinking (Arctic Climate Impact Assessment 2005; Intergovernmental Panel on Climate Change 2006). In addition, where the sea-ice platform melts earlier during summer and freezes later during fall, polar bears have presumably less time to accumulate the necessary amounts of body fat to sustain themselves throughout the summer months on shore while fasting (Stirling et al. 1999). As a result, some polar bear populations exhibit decreases in recruitment and cub survival rates, as well as reductions in body masses (i.e., poorer body condition with less accumulated adipose tissue) of individual bears (Stirling and Derocher 1993; Stirling et al. 1999; Stirling and Parkinson 2006).

A reduction in a polar bear's body mass (body fat) could mean that less stored energy is available for times of food shortage (i.e., fasting—Pond et al. 1992). However, these fat deposits are important for females and their reproductive success because maternal fat deposits are positively related to offspring body weight and survival (Atkinson and Ramsay 1995). Moreover, a continued reduction in body mass of pregnant females below a certain threshold may make it impossible to rear viable offspring in the future (Derocher et al. 2004). As the ice-free season becomes more extended, which results in less time for polar bears to hunt, an increased feeding on alternative summer diets may become more pronounced. This could enable polar bears to minimize the rate of their daily body mass or energy loss, and to increase their probability for reproduction and survival.

Polar bears, like other ursid species, have adapted to periods of food shortage by accumulating large fat deposits when food is abundant. However, because of different hunting skills or experience (Stirling 1974; Stirling and Latour 1978), every bear in a population will not be equally successful in accumulating fat stores and therefore the body condition of bears coming ashore once the sea ice melts will be different (Obbard et al. 2006; Stirling et al. 2008). Consequently, bears in poorer condition are more likely to feed on alternative summer diets. Moreover, as less seal hunting time on the sea ice becomes available to maximize fat reserves for the fasting period, and as the ice-free period becomes extended (e.g., Stirling et al. 1999), the proportion of polar bears in a population exhibiting poorer body conditions also is expected to increase. Therefore, it is probable that polar bears, in an attempt to reduce their daily rate of energy loss, will expend energy in order to find existing alternative food resources during their summer of adaptive fasting.

Although polar bears were observed feeding on alternative summer diets, estimating the energetic contributions of these diets and whether they could play a part in the reduction of weight (or energy) loss while restricted to land (e.g., Derocher et al. 1993) has not been attempted thus far, in part due to the logistical constraints. Therefore, we attempted to provide a hypothetical mathematical solution to this question, and in order to establish a base comparison between diets, we calculated the energy required (in kJ) to meet daily body mass loss (DBML). The reader should be aware that, with this paper, we are not attempting to claim that polar bears will be able to survive as a species in a world without an ice platform from which they hunt their prey species. Rather, we intend to demonstrate that polar bears could increase their probability of survival and reproduction during an extended ice-free period should they utilize available food sources.

The objectives of this study were to summarize energetic content of 4 selected summer (or alternative) polar bear diets from existing literature; to examine whether these diets hypothetically can contribute sufficient energy to reduce DBML of polar bears while on land; to provide example calculations for bears of selected body masses that allow comparisons between the different diets and their masses required to cover DBML; and to explore possible behavioral and physical limitations to feeding on these diets.

Materials and Methods

In order to investigate possible energetic contributions of alternative summer diets to the energy budget of polar bears of different body masses while restricted to land, DBML (MJ), most likely diets, digestible energy (DE) of these diets, and the relationship between mass of diet and energetic content were determined. For sake of simplicity, no mixed diets were assumed. The study focused on independent (i.e., adults including females with offspring, and subadults) polar bears because dependent young receive the majority of their required energy from their mother (Arnould 1990).

Daily body mass loss of polar bears during fasting.—Independent polar bears of both genders lose between 0.8 and 0.9 kg of body mass per day (Derocher and Stirling 1995; Polischuk et al. 2002), with the majority of this DBML being accounted for by the loss of body fat (Atkinson et al. 1996; Polischuk et al. 2002). This DBML accrues to (286 kJ of body energy) (kg of body mass$^{0.75}$)$^{-1}$ (Atkinson et al. 1996), which we used for our calculations. Although small in sample size, the study of Atkinson et al. (1996) obtained similar results for DBML for polar bears as compared to other studies (i.e., Derocher and Stirling 1995; Polischuk et al. 2002), which makes the use of their energy equivalent a valid starting point for our calculations. In addition, this value also allows a more realistic approach to our DBML calculations because recapture rates for polar bears in these studies ranged between 41 and 79 days (Atkinson et al. 1996; Derocher and Stirling 1995), which incorporates any activity behavior of bears that would mean an expenditure of energy (e.g., resting, walking, searching for food, etc.).

Because there are no data that indicate a significant difference between adult and subadult male bears (Atkinson et al. 1996), or male and female bears (Derocher and Stirling 1995), our suggested results are independent of sex. Using the above equation, a 400-kg bear, for example, would lose approximately 25.6 MJ per day while fasting. For the purpose of this paper, we calculated DBML for bears between 100 and 650 kg of body mass.

Selected alternative summer diets for calculations.—We chose food items that are easily accessible, occur throughout most of the range of Canadian polar bears, and that have been previously reported to be part of the diet of polar bears. In order to compute energy gain by these various diets, digestibility of food items needed to be assessed. This was mostly only possible by using published data from brown bears (*Ursus arctos*) or black bears (*U. americanus*) because feed trial data of these diets from captive polar bears do not exist. However, using digestibility values of similar brown and black bear diets is appropriate because polar bears and brown bears are closely related evolutionarily (Kurtén 1964); the digestive capabilities of the polar bear differ little when compared to the closest relative, the brown bear (Bunnell and Hamilton 1983); and no significant differences in digestibility between brown and black bears were detected in feeding trials (Pritchard and Robbins 1990). In addition to raw ringed seal blubber (diet 1), we chose raw arctic charr (diet 2), raw blueberries (diet 3), and raw crowberries (diet 4).

Energy content of diets.—Values of energetic content (per 100 g; generally determined via proximate analysis) of diets 1, 3, and 4 were directly taken either from published literature (i.e., Kuhnlein 1989; Kuhnlein et al. 2002; Kuhnlein and Soueida 1992) or nutritional Web sites (i.e., Centre for Indigenous Peoples' Nutrition and Environment [CINE] 2007). Kuhnlein et al. (2002) and Kuhnlein and Soueida (1992) also provided energy content of arctic charr (diet 2); however, a relationship between energy content, body mass, and fork length of the sampled charr was not obvious from their data sets.

Arctic charr fluctuate in their energy content, depending on reproductive class and size (Dutil 1984, 1986). In order to account for these variabilities, and to obtain a representative energy content per 100 g of charr, we 1st averaged the mean weights of charr of 600-mm fork length across the 6 reproductive classes listed by Dutil (1984). The energy contents across the same reproductive classes for the same fork length were then averaged. This resulted in a mean weight and energy content of 2,144 g and 17,361 kJ, respectively, or 810 kJ/100 g of charr. We chose a fork length of 600 mm because this size is quite common across Nunavut (Read 2000), and we have observed polar bears to devour charr often of even greater fork lengths. A summary of the energetic content for diets 1–4 is provided in Table 1.

Digestible energy (DE) of food items.—Other than the digestibility of ringed seal (diet 1), very little information exists on the caloric value of food items consumed by polar bears during the ice-free period (Best 1985). The DE values found in the literature for the same or comparable diets provided to captive brown and black bears (i.e., Pritchard and Robbins 1990; Welch et al. 1997) were used for the purpose of our calculations (i.e., diet 2). The DE values for brown and black bears listed by Pritchard and Robbins (1990) were averaged for diet 2 because the authors did not detect significant differences between these 2 ursids. The DE values for diets 3 and 4 were directly taken from Welch et al. (1997). Based on these values, the DE available to a polar bear from each diet was calculated as the product of the gross energy of the diet and its digestibility.

Relationship between DE and mass of food items consumed.—A question of interest was how much (in kg) of a particular diet a polar bear of a particular body mass (in kg) would need to consume in order to gain sufficient energy to achieve a DBML of 0 kJ. To answer this question, the mass of each diet needed to match the DBML was calculated based on the DE content per 100 g of diet, for polar bears weighing 100–650 kg. In order to examine whether these diet masses could be obtained behaviorally (i.e., through feeding), the number of individual food items (i.e., fish or berries) that need to be eaten by bears to obtain a DBML of 0 kJ were estimated. Mean charr body mass was used as described earlier. Berry masses were taken from Dyck (2001), where the average of 20 hand-picked fresh berries at Churchill, Manitoba, Canada, was used for calculations. Individual masses for blueberries and crowberries were 0.227 g and 0.278 g, respectively.

In order to determine how much mass (kg) of each diet was required to match the DBML, we simply summed each diet's DE until it equaled DBML. Each diet's energy value (i.e., intake diet energy value = DBML) was then expressed as mass (kg).

Example calculations and constraints.—The limit to how much a bear can eat is its stomach capacity, which was assumed to be 17% of polar bear body mass (Best 1977). Intake rate is another constraint that must be considered, especially when bears feed on berries (Welch et al. 1997). Welch et al. (1997) observed maximum intake rates of 30 g/min for 0.5-g berries, and maximum feeding times on berries

Table 1.—Summer diets of polar bears (*Ursus maritimus*), their gross energy content (kJ/100 g), digestibility (%), and digestible energy (kJ/100 g).

Diet	Food item	Gross energy content (kJ/100 g)	Digestibility (%)	Digestible energy (kJ/100 g)
1	Ringed seal blubber, raw	3,443[a]	95.0[b]	3,271
2	Arctic charr	810[c]	93.4[d]	757
3	Blueberry, raw	290[e]	72.2[f]	209
4	Crowberry, raw	145[g]	49.2[f]	71

[a] Kuhnlein and Soueida (1992).
[b] Best (1985).
[c] As calculated from Dutil (1984).
[d] Pritchard and Robbins (1990).
[e] Kuhnlein et al. (2002).
[f] Welch et al. (1997).
[g] CINE (2007).

of 12 h/day. To estimate whether polar bears would be able to ingest sufficient berries during a 12-h feeding bout, and whether stomach capacity was adequate to hold the berry masses, we calculated a proportional intake rate based on our berry masses and the reported intake rate by Welch et al. (1997; i.e., intake berry mass [g] = [30 g/min × individual berry mass]/0.5 g). The calculated intake rates per minute for blueberries and crowberries were 13.6 g and 16.7 g, respectively. A 12-h feeding bout then resulted in a blueberry and crowberry intake of 9.80 kg and 12.02 kg, respectively.

Some example calculations were performed to demonstrate the difference of food or diet intake required to achieve a DBML of 0 kJ among independent polar bears of differing body masses (Table 2). Body masses of polar bears from Cattet et al. (1997) and Derocher and Wiig (2002) were used in the calculations.

A limitation of this study might be that the cost of searching for food was not estimated. Lunn and Stirling (1985) estimated that energetic costs are high when bears are running down prey. Energetic costs, at least for berry diets, are already incorporated into our calculations by using the energy equivalents reported by Atkinson et al. (1996). As previously pointed out, these authors used bears that were captured and recaptured in intervals of up to 79 days, and the bears' behavior during that time was not confined to being only sedentary. Polar bears are inefficient walkers (Hurst et al. 1982), and swimming and diving for charr is perhaps energetically less expensive than walking (or searching for berries) because of buoyancy.

RESULTS

Ringed seal blubber and arctic charr contained between 12–24 times and about 3–5 times more gross energy than any of the 2 berry diets, respectively (Table 1). By consuming 0.3–1.2 kg of blubber or 1.0–4.9 kg of charr, respectively, polar bears of body masses ranging between 100 and 650 kg would be able to obtain sufficient energy to balance their DBML. Alternatively, a bear of the same body masses would need to consume 4.3–17.6 kg of blueberries or 12.7–51.8 kg of crowberries. Stomach capacity for these berry masses is not a constraint (Table 2).

When berry intake was based on a 12-h feeding bout, sufficient energy to match the DBML could be obtained from blueberries (9.8 kg or 43,172 blueberries = 20.4 MJ) for bears up to 280 kg. Alternatively, only bears up to about 100 kg would gain sufficient energy to match DBML when feeding on crowberries for 12 h (12.0 kg or 43,165 crowberries =

TABLE 2.—Examples for polar bears (*Ursus maritimus*) of selected body masses, their daily body mass loss (MJ), and mass of consumed diet required to achieve daily energy loss of 0 kJ.[a]

Body mass (kg)	Stomach capacity (kg)	Daily body mass loss (MJ)	Mass (kg) of diet required to cover daily energy loss	Diet[b]	Individual berries or charr
100	17.0	9.0	0.28	1	—
			1.19	2	0.56
			4.31	3	18,987
			12.68	4	45,612
170	28.9	13.6	0.41	1	—
			1.78	2	0.83
			6.44	3	28,370
			19.00	4	68,345
200	34.0	15.2	0.47	1	—
			2.01	2	0.9
			7.28	3	32,070
			21.42	4	77,050
280	47.8	19.6	0.60	1	—
			2.60	2	1.2
			9.37	3	41,278
			27.57	4	99,173
400	68.0	25.6	0.78	1	—
			3.40	2	1.58
			12.24	3	53,921
			36.00	4	129,496
500	85.0	30.2	0.92	1	—
			4.00	2	1.87
			14.47	3	63,745
			42.60	4	153,237
650	110.5	36.8	1.13	1	—
			4.86	2	2.27
			17.62	3	77,621
			51.86	4	186,547

[a] Each selected body mass provides a comparison among the 4 different diets as to how much of each diet (in kg or in individual food items) must be consumed in order to balance the daily body mass loss of that particular body mass.

[b] Diet 1 = raw ringed seal blubber; diet 2 = arctic charr; diet 3 = blueberry; diet 4 = crowberry.

8.5 MJ). Feeding bout length is at least 1 limiting factor when feeding on a berry diet alone. However, even with realization of a 12-h feeding bout, DBML can be reduced between 50% and 80% for bears >280 kg when feeding on blueberries, and between 23% and 62% for bears >100 kg when feeding on crowberries.

DISCUSSION

The results presented in this paper indicate that polar bears can either maintain their body mass, or minimize their DBML during the fasting period, should they resort to alternative food items if climate change continues to lengthen the ice-free period. Based on the 4 diets examined, seal blubber and arctic charr are the most likely food sources that contribute maximally to a polar bear's daily energy budget or requirements while on land. Seals are most easily caught on the sea ice (Derocher et al. 2002; Stirling 1974; Stirling and Latour 1978), but isolated occurrences from different polar bear populations where seals are caught successfully during the ice-free period also are known (from Foxe Basin [Furnell and Oolooyuk 1980] and from western Hudson Bay and Davis Strait [M. G. Dyck, pers. obs.]). However, it is more a question of how many polar bears of a population can acquire this skill in order to survive and reproduce, which some authors doubt might occur (Derocher et al. 2004).

Polar bears hunt seals in open water through stalking, where a bear could be mistaken for an ice floe by a seal (Furnell and Oolooyuk 1980). When a seal basks atop a small ice floe, or swims in the open water, polar bears can approach their prey within short distances, and lunge for the kill. This hunting technique is very likely learned by young bears through observation and practice (Stirling 1974; Stirling and Latour 1978) and could increase in frequency within a population. How and if polar bears and seals coevolve their predator–prey relationship (e.g., morphologically and behaviorally) in a world completely void of ice is speculative at this point.

The energy content of seal blubber is very high (CINE 2007; Stirling and McEwan 1975), and therefore not much volume is required to gain high energetic contributions (Table 1). For example, a 500-kg polar bear need only consume 1 kg of seal blubber per day to maintain its body mass. Arctic charr also is energy-rich food (Dutil 1984, 1986). A typical 500-kg polar bear would need to consume about 2 fish (or 4 kg) per day to maintain its body mass. The fish masses used in this study underestimate body masses of some arctic charr from different Nunavut regions, where most of the world's polar bears exist (Aars et al. 2006). For example, arctic charr masses are estimated to be >3 kg at Creswell Bay, Somerset Island, Nunavut, where a subadult male bear caught and consumed arctic charr (Dyck and Romberg 2007). Hilderbrand et al. (1999) reported that captive brown bears consumed an average of 10.8 kg of fish/day during summer and fall which would be equal to 81.4 MJ and any polar bear up to 650 kg would have an energy surplus, and could gain body mass under these conditions. Salmon (*Oncorhynchus*) contribute much needed energy to brown bears for hibernation, gestation, and lactation (Gende and Quinn 2004; Gende et al. 2001; Hilderbrand et al. 2004; Ruggerone et al. 2000), and consumption of arctic charr also can contribute significantly to the energy budget of polar bears. The question that arises is how realistic is it that polar bears catch fish? Most recently, this behavior has only been observed or recorded from Creswell Bay (Dyck and Romberg 2007) and Cumberland Sound, Nunavut (S. Sowdlooapik, Government of Nunavut, Department of Environment, pers. comm.), and Labrador (M. G. Dyck, pers. obs.; Smith et al. 1975). Where spawning rivers are shallow (i.e., <0.5 m—Gende et al. 2001; Quinn and Kinnison 1999), charr can be caught like salmon by brown bears through standing, running, or plunging (Klinka and Reimchen 2002). Alternatively, while charr congregate in estuaries before their upstream spawning run, and densities are high, charr can be captured through diving (Dyck and Romberg 2007).

Our calculations indicate that a pure blueberry diet could contribute enough energy to balance the DBML for polar bears up to 280 kg. Berries also have been shown to be an important food source for brown bears during times of hyperphagia (Felicetti et al. 2003; Gau et al. 2002; MacHutchon and Wellwood 2003). However, for brown bears to accumulate sufficient body mass (lean body mass and body fat) during spring and fall to sustain themselves through hibernation, a protein-containing diet is necessary (Felicetti et al. 2003; Rode et al. 2001). In contrast, polar bears feed primarily on seal during spring, maximizing their fat and protein intake to obtain optimum body mass and fat reserves for their fasting period during late summer when brown bears still continue to maximize their body mass. It is therefore possible that polar bears may not require any protein intake during fasting because they are in a state of hibernation with reduced metabolic activity (Nelson et al. 1983). Because of low protein content of berries, the limiting nutrient for growth is more likely to be protein than energy, which means the animals need to consume more food than is necessary to maintain their energetic balance. Alternatively, polar bears could reduce their body mass loss if glucose, a berry constituent (CINE 2007), is used as simple energy source, instead of the more complex fatty acid molecules from adipose tissue. Polar bears do not necessarily need glucose to produce energy from their fat stores through metabolic pathways (Cattet 2000), but will very likely use it if it is part of a diet (i.e., berries) in order to maintain their stored fat for periods when energy is required again.

Availability of diets suggested in this study may be limited throughout the range of most Canadian polar bears. However, anadromous arctic charr are abundant in the Canadian Arctic, and the distribution is similar to that of the polar bear (Canadian Circumpolar Institute 1992; COSEWIC 2008; Johnson 1980; Read 2000). There are more than 200 recognized charr stocks, with many more stocks unknown in Nunavut (R. Tallman, Department of Fisheries and Oceans Canada, Freshwater Institute, Winnipeg, Manitoba, Canada, pers. comm.). Estimated stock sizes range from 1,000s to several hundreds of thousands (Kristofferson et al. 1991; McGowan 1990; McGowan and Low 1992; Read 2003). Charr migrate from freshwater to salt water to feed as soon as rivers break open (Johnson 1980). Spawning migrations and upstream runs occur from mid-July to late September (Gulseth and Nilssen 2000; Hunter 1976; Johnson 1980) and at this time polar bears have easy access to charr. Nunavut is rich in arctic charr resources (e.g., Priest and Usher 2004; Read 2000), and many rivers and bays could provide alternative feeding opportunities for polar bears.

Blueberries and crowberries have a wide northern arctic–alpine distribution (Johnson 1987; Mallory and Aiken 2004), where spatial and temporal variation in availability is common (Chapin and Shaver 1985, 1996; Kudo and Suzuki 2003; Press et al. 1998; Shevtsova et al. 1995). Both berry types are commonly found in Arctic tundra. They ripen in late July–early August, and provide nourishment even the following spring after snowmelt. Their combined densities and biomass can reach between 300 and 1,000 berries/m^2 and 35 and 213 g/m^2 in Nunavut and Labrador (E. Lévesque, Université du Québec à Trois-Rivières, and L. Hermanutz, Memorial University of Newfoundland, pers. comm.). At these densities, sufficient amounts of berries can be easily ingested by polar bears while ashore in order to offset their daily energetic requirements, thereby minimizing the reliance on stored fat resources. The only published observations of polar bears feeding on berries come from the Hudson Bay area (Derocher et al. 1993; Dyck 2001; Russell 1975); however, feeding on berries also was noted during a population inventory of the Davis Strait polar bear population in 2006 and 2007 (M. G. Dyck, pers. obs.). The fact that ''significant'' amounts of berries are consumed (Derocher et al. 1993) indicates the importance of berries to the energy budget of polar bears even when energy is expended during searching for food. When lactating females with offspring from western Hudson Bay were captured several kilometers inland during August and recaptured during September–October, their body mass clearly indicated that fat reserves were not used to the maximum (i.e., usually an estimated body mass loss of about 1 kg/day—Derocher and Stirling 1995; Polischuk et al. 2002). Some females even gained body mass by feeding on berries, which was verified from feces and stains on the fur and teeth (S. Atkinson, formerly with Government of Nunavut, Department of Sustainable Development, pers. comm.). It is therefore very plausible that berries, if present in sufficient densities, contribute positively to a polar bear's energy budget to meet daily maintenance energy requirements.

We demonstrated that it is possible for polar bears to minimize their DBML, if these diets are available. What does this mean for polar bears in a changing climate? Polar bears have evolved to deal with food shortage (i.e., being on land during the ice-free period) via accumulation of fat storage as energy for the fasting period (Pond et al. 1992; Watts and Hansen 1987), so fasting is a normal occurrence. However, if the ice-free period becomes extended where bears cannot build up the necessary fat reserves to sustain themselves while on land, additional energy sources are available that can be utilized to minimize DBML. By coming onshore with less body mass than historically observed, bears could maintain a threshold-level body mass (Derocher et. al. 2004) that would be necessary for reproduction or survival. It is therefore very likely that polar bears will use additional alternative summer food sources (e.g., eggs, molting birds, and berries) in greater quantities should climatic change become more pronounced, and body condition of polar bears deteriorates. How polar bears would fare without any sea ice and access to seals in the spring over the long-term is beyond the scope of this paper.

One consideration when examining these energetic contributions of alternative summer diets is the potential for behavioral plasticity of polar bears. Data on activity patterns of Canadian polar bears during the ice-free period are sparse, dated, and restricted to only 1 regional location (i.e., Hudson Bay area—Dyck 2001; Knudsen 1978; Lunn and Stirling 1985). Without current behavioral data it is difficult to assess whether feeding behavior of polar bears during the summer has changed between the early 1970s (Knudsen 1978) and now, given that climatic effects were suggested to have affected these polar bears since the early 1990s (Stirling and Derocher 1993; Stirling et al. 1999; but see Dyck et al. 2007, 2008). Polar bears spend only about 3% of their time feeding, as was suggested by Knudsen (1978). However, a more recent study estimated that some bears feed up to 24% of their time during fall (Dyck 2001). Without the examination of daily activity or feeding patterns, or both, of polar bears from areas other than Hudson Bay, a clearer picture of possible adaptation to climatic change cannot be presented.

It should be recognized that the methods presented in this paper only elaborate on theoretical, mathematical concepts, and that the outcome (i.e., bears consuming alternative food sources) is contingent on the behavior of polar bears. The food sources containing the energy are readily available. However, in order to examine the true DE value of the diets used in this study, feeding trials with captive polar bears should be conducted. Moreover, behavioral and physiological studies that record whether summer feeding occurs, either via direct observations or by other means, are encouraged. A reexamination of terrestrial feeding of western Hudson Bay polar bears is recommended because previous studies used samples collected between 1986 and 1991, which was before any changes in polar bear ecology at western Hudson Bay were detected. Repeating the studies with post-1990 samples would aid in the current understanding of the importance of terrestrial food sources of polar bears, and the bears' possible adaptation to a changing environment.

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