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Comments in response to “Estimating the energetic contribution of polar bear (*Ursus maritimus*) summer diets to the total energy budget” by Dyck and Kebreab (2009)

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Dyck and Kebreab (2009) analyzed the required summer intake of arctic char, ringed seal blubber, and berries that polar bears must consume to maintain their body mass during a summer ice-free period. Their calculations of required intake were based on the amount of body mass lost by fasting bears in western Hudson Bay. However, fasting polar bears are in a low metabolic state with energetic requirements less than those of an active, feeding bear. Estimates of energy consumed by captive brown bears were 4–4.5 times higher than the estimates used by Dyck and Kebreab for similar diets. Furthermore, the authors' portrayal of the availability of these resources is misleading because they do not acknowledge limited accessibility of arctic char due to their limited anadromy and predominant occurrence in streams too deep to facilitate efficient capture by polar bears; effects of large interannual fluctuations in the availability of berries or competition with other frugivores; high energetic requirements associated with lengthy foraging times required to locate and consume sufficient fruit; and data from southern Hudson Bay, western Hudson Bay, and the southern Beaufort Sea that document continued declines in several biological indices over the past several decades despite the authors' suggested availability of terrestrially based food resources. Based on current information, arctic char, berries, and ringed seals in open water do not appear to be food sources with the potential to offset the nutritional consequences of an extended ice-free period. DOI: 10.1644/09-MAMM-A-399.1.

Key words: fasting, food intake, polar bears, sea ice, terrestrial foraging

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Dyck and Kebreab (2009) estimated the amount of 4 alternative food resources, crowberry (*Empetrum nigrum*), blueberry (*Vaccinium uliginosum*), arctic char (*Salvelinus alpinus*), and ringed seals (*Pusa hispida*) captured in open water, that would be required for polar bears (*Ursus maritimus*) to maintain their body mass during an extended summer–fall ice-free period when they lack a platform (ice) from which to hunt their primary prey item, ice-associated seals. They suggested that consumption of these food resources could offset the potential negative nutritional consequences of an increase in the duration of the ice-free period. Although their analyses appropriately consider a

variety of physiological and morphological features that could limit use of these food items by a bear, the authors underestimate the maintenance energy requirements of an actively feeding bear. Furthermore, their depiction of the availability of these resources is misleading because they do not adequately portray the low frequency of occurrence of these foods in the circumpolar Arctic distribution of the polar bear, or the large degree of interannual variation in the



abundance of these resources throughout much of the range of polar bears.

The authors concluded in the 1st sentence of their discussion that “The results presented in this paper indicate that polar bears can either maintain their body mass or minimize their DBML [daily body mass loss] during the fasting period, should they resort to alternative food items if climate change continues to lengthen the ice-free period” (Dyck and Kebreab 2009:589). The authors further stated that these “food resources containing energy are readily available,” suggesting that polar bears, as yet, have not taken advantage of these resources (Dyck and Kebreab 2009:590). They do not explain why polar bear populations in western Hudson Bay, which are experiencing significant declines in body condition because the average date of ice breakup is now 3 weeks earlier than it was only 30 years ago (Stirling et al. 1999; Stirling and Parkinson 2006; Obbard et al. 2006; Rode et al. 2010), resulting in declines in natality, survival, and population size (Regehr et al. 2007, 2010; Stirling et al. 1999), do not already make large and widespread use of these alternate food sources if they are as readily available as suggested. The authors’ conclusion is based on analyzing the intake of ringed seal, arctic char, blueberry, and crowberry that must be consumed to equal the estimated energetic content of lost body mass observed for polar bears in western Hudson Bay.

We propose several lines of evidence that indicate that maintenance energy requirements were underestimated by Dyck and Kebreab (2009) and that the availability or accessibility, or both, of the food resources they identified are limited during the ice-free period (or period of minimal sea-ice extent) within the range of polar bears to the extent that they currently are not, and in the future are unlikely to be, consumed at levels sufficient to offset any reduced foraging opportunities associated with sea-ice loss.

MAINTENANCE ENERGY COSTS— THE DIFFERENCE BETWEEN FASTING AND ACTIVELY FEEDING POLAR BEARS

Polar bears, when fasting or consuming minimal amounts of food, are in a low metabolic state similar to that of denning black bears (*Ursus americanus*—Derocher et al. 1990; Nelson et al. 1983). This state is characterized by lower maintenance energy requirements and efficient protein conservation (Derocher et al. 1990; Lohuis et al. 2005; Nelson et al. 1983). In all ursids, however, the proximate trigger for this shift in metabolic state is food shortage and either complete fasting or minimal food intake (Derocher et al. 1990; Hellgren 1998; Hellgren et al. 1990; Lohuis et al. 2005; Nelson et al. 1983; Ramsay et al. 1985, 1991). For example, in captive brown bears (*Ursus arctos*) physiological winter torpor is achieved by removing access to food (Farley and Robbins 1995; C. T. Robbins, Washington State University, pers. comm.). Once a bear resumes food intake, winter torpor and its associated lower energy requirements ends. In polar bears Derocher et al. (1990) documented rapid increases in urea and creatinine ratios within 3 days of feeding, suggesting that once

a polar bear starts feeding it no longer is in a lower metabolic, protein-conserving state. These results suggest that polar bears that pursue and consume ringed seals or arctic char or forage on berries 8–12 h/day during the ice-free period, as suggested by Dyck and Kebreab (2009), would not be in a low metabolic state and therefore would have higher energy requirements to maintain body mass than a fasting bear.

Hilderbrand et al. (1999) determined that maintenance of body mass in captive brown bears consuming Pacific salmon (*Oncorhynchus tshawytscha*) requires 41.9 g digestible dry matter $\text{kg}^{-0.75} \text{day}^{-1}$. At a dry matter digestibility of 89.8%, dry matter content of 25% (based on cutthroat trout [*Oncorhynchus clarkii*]—Pritchard and Robbins 1990), and a digestible energy content of 1.49 kcal/g fresh mass (6.2 kJ/g, using 1.58 kJ/g fresh mass for salmon [Hilderbrand 1999], and digestible energy of 94.5% [Pritchard and Robbins 1990]), total digestible energy intake of bears in the study by Hilderbrand et al. was >4 times higher than the maintenance energy costs estimated from the energetic content of lost muscle and fat during fasting used by Dyck and Kebreab (2009). Similarly, digestible energy required to maintain body mass in brown and black bears consuming fruit diets (apples and blueberries) was 4.5 times higher than the maintenance energy costs estimated by Dyck and Kebreab (80 g digestible dry matter $\text{kg}^{-0.75} \text{day}^{-1}$ and 72.2% dry matter digestibility [Rode and Robbins 2000; Welch et al. 1997] or 18.71 kJ/g dry matter and 62.7% digestible energy [Pritchard and Robbins 1990]). The discrepancy between energy requirements estimated from these captive studies and those estimated by Dyck and Kebreab (2009) could be a result of differences in the energetic requirements of fasting and actively feeding animals or different physiological processes being involved in the use of body tissue (with associated energetic costs) to meet maintenance energetic requirements versus the digestion and metabolism of ingested food.

Although the captive feeding trials outlined above were conducted on brown bears, both brown bears and polar bears have a simple, short gastrointestinal tract characteristic of carnivores (Pritchard and Robbins 1990); thus, dietary digestibility is expected to be similar for these 2 species. Furthermore, polar bears apparently have the ability to move quickly into and out of a state of reduced metabolism (Derocher et al. 1990), but no evidence exists to suggest that these closely related species (Lindqvist et al. 2010) differ in their metabolism when actively feeding.

Differences in activity level between captive and wild bears would contribute further to higher maintenance energy requirements of wild bears than those estimated by Dyck and Kebreab (2009) and seen from feeding trials with captive bears. Because captive bears did not expend the energy a wild bear would use to acquire these food resources (Hilderbrand et al. 1999), we would expect the energetic requirements of a wild, feeding polar bear to be greater than those estimated in the 2 captive brown bear studies. Quantitative behavioral observations of fasting polar bears showed that inactivity accounted for 70% to >90% of the activity budget (Knudsen

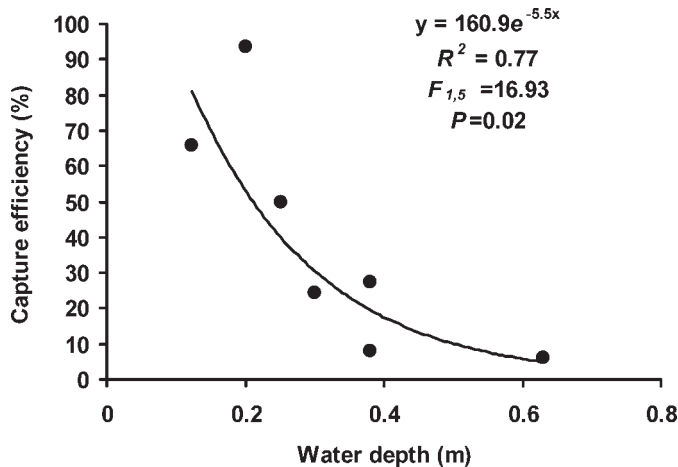


FIG. 1.—Relationship between the efficiency with which brown bears (*Ursus arctos*) capture Pacific salmon and stream water depth for 6 locations across south-central and southeastern Alaska. Observational data were collected by K. Rode between 2000 and 2004. For more information on methods and study sites see Rode et al. (2006).

1978; Latour 1981; Lunn and Stirling 1985). This level of activity contrasts starkly with the activity levels that would be required to search for and consume sufficient amounts of berries, arctic char, or ringed seal identified by Dyck and Kebreab (2009). Therefore, our calculations suggest that maintenance energy requirements used by Dyck and Kebreab (2009), which were based on mass loss during fasting, underestimated the actual energetic requirements of an actively feeding bear by at least 4- to 4.5-fold.

DISTRIBUTION AND AVAILABILITY OF ARCTIC CHAR AND OTHER ANADROMOUS FISH

Capture efficiency.—Dyck and Kebreab (2009) examined the energetic content of Arctic char and suggest that this species is an available food resource because its range overlaps that of polar bears in the eastern Canadian Arctic. They suggested that polar bears might be able to capture char in shallow streams (<0.5-m depth). However, most rivers with anadromous char populations are large (basins > 1,000 km²—Power et al. 2008) and are >1.5 m deep (Dempson and Green 1985). Arctic char also prefer pools and deeper water for habitat (Heggenes and Saltveit 2007). Although the difference in water depth might seem negligible, it is well documented that the efficiency with which brown bears capture salmon is affected significantly by water depth and is very low at depths >0.5 m (Gende et al. 2001; Fig. 1).

Geographic distribution of char.—Although arctic char occur throughout the Canadian Arctic, they are abundant only locally. Furthermore, their life histories vary such that resident lake populations are common and anadromy is not universal (Power et al. 2008). For example, in Cumberland Sound of eastern Baffin Island only 25 of several hundred rivers support anadromous char (Moore and Moore 1974). West of the Mackenzie Delta in western Canada arctic char are replaced

by anadromous Dolly Varden (*Salvelinus malma*). That black and brown bears throughout this area of the Arctic consume primarily terrestrial food resources that include vegetation, ground squirrels, and caribou (Gau et al. 2002; McLoughlin et al. 2002), are small in stature, and occur at low density (Hilderbrand et al. 1999) is strong evidence that arctic char and other anadromous fish are, at best, minimally available to bears in Arctic coastal environments. Consumption of anadromous fish by grizzly bears in the Arctic is typically limited to small numbers consumed by a few individuals (Barker and Derocher 2009). Populations of brown bears in northern Alaska and northwestern Canada acquire <2% of their diet from marine food sources, despite overlap in their ranges with populations of anadromous fish (Hilderbrand et al. 1999).

Energetic costs of fishing.—Dyck and Kebreab (2009) assume that “swimming and diving for char is perhaps energetically less expensive than walking (or searching for berries) because of buoyancy.” Although snorkeling and diving for fish might not be as energetically costly as other forms of fishing, migrating anadromous fish typically are captured by both black and brown bears by “standing, running, and plunging,” as the authors acknowledge. Furthermore, arctic char are iteroparous (Power et al. 2008) and do not deteriorate in condition to the extent that Pacific salmon do as they move upstream to spawning habitats. Sockeye salmon lose 55–61% of their protein reserves and 90% of their fat reserves moving upstream, where they ultimately die (Burgner 1991). This deterioration is likely to make Pacific salmon slower and easier to capture than arctic char that are in better condition.

Although specific data comparing the energetic expenditure of bears in various activities are not available, Rode et al. (2006) documented that free-ranging brown bears weighing approximately 200 kg consumed 13 kg/day of wild, anadromous salmon—more than 6 times the amount estimated by Dyck and Kebreab (2009) to maintain body mass of a polar bear of similar size consuming arctic char. If we assumed that the extra intake was used to gain mass, bears in the study by Rode et al. (2006) would have gained 2.5 kg/day (assuming 25% dry matter and 89.8% digestibility—Pritchard and Robbins 1990), an increase not typical of wild bears (Hilderbrand et al. 1999) and well above the maximum mass gain of 0.7 kg/day observed for the brown bears in the study of Rode et al. (2006; K. D. Rode, pers. obs.). The high intake of salmon by wild brown bears likely replaces, in part, the energy expended while chasing and successfully capturing anadromous fish.

Observations of polar bear fishing behavior.—Observations of polar bears consuming arctic char or other anadromous fish are rare. Dyck and Romberg (2007) suggest that this is due to low human presence within areas where fishing might occur, but in many areas long-term studies of anadromous fish and polar bears have occurred with no observations of polar bear foraging (Moore 1974). Despite extensive research on polar bears in the Arctic over the past 35 years (often involving 1- to

3-month-long aerial surveys and capture programs), in all areas of the eastern Canadian Arctic during the ice-free period, no published reports of polar bears fishing exist. Although a few historic observations of fish eating have been reported, none of these accounts support consistent use of anadromous fish by polar bears throughout a population or any intake of consequence by individual bears. For example, Russell (1975) reported trace amounts of fish in the scat of a polar bear collected during the summer–fall in Hudson Bay. Smith et al. (1975) reported an observation made in 1778 of 32 polar bears foraging on Atlantic salmon (*Salmo salar*) in the Eagle River in Labrador. No other observations of this behavior have been reported.

Perhaps most significantly, Inuit who have lived nomadically throughout the Arctic and at fish-drying camps at rivers with anadromous fishes only occasionally report opportunistic catching of char by polar bears (Igloolik Oral History Database 2009; McDonald et al. 1997). In a study focused specifically on documenting bear use of arctic char, Dyck and Romberg (2007) observed only 1 of 8 bears successfully capturing arctic char, by diving and snorkeling.

Considering the lack of evidence of fishing by polar bears, little support exists for the hypothesis that fish could become a significant energetic resource for polar bears. Due to limited availability and accessibility of arctic char throughout much of the range of polar bears, and the limited use of this resource by both polar bears and other ursids, little evidence can be found to support consumption of arctic char as a strategy to offset body-mass loss during the ice-free period beyond perhaps a few individuals in restricted geographic areas.

LIMITATIONS TO BERRY AVAILABILITY AND USE

Dyck and Kebreab (2009:590) stated that at berry densities observed in Nunavut and Labrador “sufficient amounts of berries can be easily ingested by polar bears while ashore in order to offset their daily energetic requirements.” No biomass measurements were provided to support this statement. Furthermore, a number of factors that constrain the ability of bears to ingest sufficient berries, taken cumulatively, provide an explanation of why polar bears continue to exhibit declining body condition despite access to berries and apparent berry consumption in several populations in some years.

Significant interannual variation in berry production.—Berry production, as the authors mention, exhibits temporal variation. This interannual variation is pronounced and can result in biomass varying 2- to 3-fold from one year to the next (Norment and Fuller 1997; Rode et al. 2006; Wallenius 1999). This level of variation observed in berry-producing species has been linked to effects on the survival, growth, and reproductive success of black bears that rely heavily on berries as a main food source (Rogers 1976). Brown and black bears that consume berries complement a berry diet with a variety of other foods that buffer the effects of interannual variation in berry abundance (Eagle and Pelton 1983; Rode et al. 2006)

and maintain protein levels to minimize maintenance energy requirements (Rode and Robbins 2000). Although berries may help reduce mass loss during the ice-free period (or period of minimal sea-ice extent) in polar bears, this potential benefit varies significantly across years and is not reliable.

Foraging times and maintenance of a low metabolic state.—Dyck and Kebreab (2009) calculated that bears weighing <280 kg could not meet their maintenance energy requirements by consuming berries. But even smaller bears between 150 and 280 kg, the typical size of adult females (Derocher and Stirling 1994), would need to forage 8–12 h/day to maintain their body mass. Examination of data on the physiology of polar bears suggests that this level of foraging activity and food intake would not coincide with a low metabolic, hibernation-like state. The basis for the occurrence of a low metabolic state in polar bears is low food intake, lethargy, and low activity levels (Derocher et al. 1990; Nelson et al. 1983). This would not be the physiological state of a bear that was foraging 8–12 h/day.

Protein content of fruit and maintenance energy requirements.—Brown and black bears rarely, if ever, consume 100% of their diet as berries because of high maintenance energy requirements associated with a fruit-only, low-protein diet (Rode and Robbins 2000). Dyck and Kebreab (2009) suggest that because brown bears in these studies were attempting to gain body mass, protein requirements were higher than would be expected for polar bears. However, brown bears consume berries in the fall when they are accumulating body fat in preparation for hibernation; thus, the protein required during this time period is largely to maintain lean body mass, similar to what would be required of a polar bear during the ice-free period. Unless polar bears can forage up to 8–12 h and simultaneously maintain protein conservation typical of fasting physiology, it is likely that requirements for maintenance energy would be elevated, as observed in brown bears, when consuming a fruit-only diet.

Competition with other frugivores.—Arctic geese increasingly consume berries in late summer and fall as they switch from grazing on graminoids to foods with higher soluble carbohydrate content (Sedinger and Bollinger 1987; Sedinger and Raveling 1984). At Izembek National Wildlife Refuge in Alaska approximately 34–77% of the crowberry berry crop was removed by frugivores in September and October, with geese accounting for approximately 50% of berries consumed during that period (Hupp et al. 2003). Given dramatic increases in snow goose (*Chen caerulescens*) and Ross’s goose (*Chen rossii*) populations and some Canada goose (*Branta canadensis*) populations in coastal areas of the Arctic (including western Hudson Bay) over the past 3 decades (United States Fish and Wildlife Service 2009) polar bears likely would face substantial interspecific competition for berry resources.

Spatial variation in crowberry and blueberry distribution.—Areas dominated by berry-producing dwarf shrubs are less common in coastal areas with the exception of western Hudson Bay, southern Hudson Bay, Davis Strait, Canada, and

parts of western Russia (Hulten 1968; Walker et al. 2009). Arctic coastal areas are dominated more commonly by vegetative communities containing mixtures of dwarf shrubs and sedges (Walker et al. 2009), which results in lower berry densities. Specific data on berry density and production throughout coastal areas are lacking, but mixed vegetation communities would result in lower foraging efficiency.

Decline in body condition of polar bears consuming berries.—Even in areas where berries appear abundant, polar bears do not appear to be able to obtain substantive nutritional value. Studies (Hobson et al. 2009; Ramsay and Hobson 1991) that used isotopic values of breath samples collected from polar bears during the fall in western Hudson Bay did not provide evidence of significant consumption of berries. Derocher et al. (1993) documented berry consumption in only 10–63% of the bears they captured in western Hudson Bay between 1986 and 1992. McKinney et al. (2009) found decreasing $\delta^{13}\text{C}$ values in polar bear tissues sampled in the fall and winter in western Hudson Bay between 1991 and 2007, which could indicate increased terrestrial foraging over that time period. However, body condition, reproduction, survival, and population size of polar bears in this population continued to decline (Regehr et al. 2007; Stirling et al. 1999), suggesting that any potential increase in berry foraging failed to offset the reduced foraging opportunities on the sea ice. Moreover, McKinney et al. (2009) found that decreased $\delta^{13}\text{C}$ values in polar bear tissues between 1991 and 2007 in western Hudson Bay were more likely indicative of a shift in diet from bottom-dwelling (e.g., bearded seals [*Erignathus barbatus*]) to pelagic-dwelling (e.g., harp seals [*Pagophilus groenlandicus*]) seals than an increase in terrestrial foraging.

Dyck and Kebreab (2009) stated that evidence of females gaining body mass by feeding on berries “was verified from feces and stains on the fur and teeth” on captured bears. However, these observations demonstrate only that bears consume berries. Without actual data on the body masses of bears before and after periods of feeding on berries, such observations do not confirm that consumption of berries is associated with maintenance of body mass during the ice-free season.

USE OF RINGED SEALS BY POLAR BEARS DURING THE ICE-FREE PERIOD

Although some use of ringed seals and other marine mammals by polar bears might occur during the ice-free period, declines in body condition and reproduction of bears in western Hudson Bay (Regehr et al. 2007; Stirling et al. 1999), southern Beaufort Sea (Regehr et al. 2010; Rode et al. 2010), and southern Hudson Bay (Obbard et al. 2006) suggest that, at least in these regions, this behavior is not common. If feeding on ringed seals in open water was a viable option, in populations in which significant sea-ice changes have occurred polar bears would have adopted this strategy. Examination of data from Davis Strait and Baffin Bay similarly indicates a decline in body condition since the

1990s (K. D. Rode and E. Peacock, pers. obs.). Ice-breakup dates became earlier during the same time period (Stirling and Parkinson 2006) as these declines, suggesting that, similar to the situation in western Hudson Bay, bears have been unable to access sufficient prey during the ice-free period.

VARIATION IN POLAR BEAR LIFE HISTORIES AND LAND USE

Only 5 of 19 polar bear populations occupy habitats that become completely ice free seasonally, resulting in entire populations coming onto land (Amstrup et al. 2008; Thiemann et al. 2008). Land use by other polar bear populations is variable, with <10% of individuals in some populations coming on land during the annual sea-ice minimum (Schliebe et al. 2008). Some polar bear populations, such as those in the Barents Sea and Canadian Archipelago, rarely spend time in terrestrial environments (Ferguson et al. 2001; Mauritzen et al. 2003; Taylor et al. 2001). Most polar bear populations, therefore, must adapt to changing sea-ice conditions through mechanisms other than terrestrial-based foraging.

CONCLUSIONS

Arctic char, berries, and ringed seals captured in open water do not appear to be food sources with the potential to offset the negative nutritional consequences for polar bears of progressively longer seasonal ice-free periods (or reduced sea-ice extent during the annual sea-ice minimum) resulting from continued climate warming. Although limited localized use of these food items might occur, arctic char and ringed seals during the ice-free period are minimally accessible to polar bears throughout their range. Moreover, examination of current data suggests that populations with access to berries and arctic char within their range have failed to use these resources sufficiently to mitigate lost foraging opportunities on the sea ice. Instead, these populations have continued to demonstrate quantified declines in body condition. For populations in areas that retain some sea ice throughout the year, mechanisms (i.e., other food sources or physiological changes that reduce energetic requirements) other than increased terrestrial foraging will be required to sustain bears through an extended period of open water. Polar bear populations whose habitat becomes seasonally ice free could be limited in their ability to mitigate foraging opportunities lost by a lengthened ice-free period.

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