In vivo Digestibility Trials of a Captive Polar Bear (*Ursus maritimus*) Feeding on Harp Seal (*Pagophilus groenlandicus*) and Arctic Charr (*Salvelinus alpinus*)

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        Abstract.- Energetic requirements of free-ranging polar bears are still poorly understood due to the limited information available. The need for such data is emphasized through imminent climatic changes impacting wild populations, and the recent development of energy-based population forecast models that are data-limited. We therefore conducted four feeding trials with a captive polar bear to investigate how 2 novel untested diets such as Arctic charr (*Salvelinus alpinus*) and harp seal meat/fat (*Pagophilus groenlandicus*) are digested and energetically utilized. Energy content, proximate nutrient values, digestive efficiency, metabolizable energy (ME) requirements, and body mass change associated with these 2 diets were quantified. The seal meat/fat diet (1:1 ratio) had a 1.5 times greater digestible energy content (kg DM basis) than the charr diet. Digestibility coefficients for nutrients (organic matter, crude protein, fat) of both diets were high (> 0.960), which corresponds well with other carnivores, and other fatty polar bear diets. Body mass increased significantly over the course of the feeding trials, consuming an average of 403 and 1149 kJ/kg BM$^{0.75}$ of ME per day of charr and seal meat/fat, respectively. It was discovered that daily energy requirements of our adult, non-reproducing polar bear was lower than previously estimated (~ 1.4 instead of 2 times basic metabolic rate). Despite our limitations, we provide baseline data that should be evaluated during further feeding trials.

        Keywords: Energetics, feeding trials, metabolizable energy, nutrition, polar bear.

INTRODUCTION

Although much is known about free-ranging polar bear (*Ursus maritimus*) population dynamics and their basic ecology, aspects on how efficiently certain food is used energetically (*e.g*., for growth, maintenance, mass gain, etc.) are very sparse. Quantifying such animal energetics in the field with free-ranging individuals is challenging, both financially and logistically. Nevertheless, such studies are relevant and important especially during times where climatic changes are projected to have drastic effects on the world's polar bear populations (Stirling and Derocher, 1993; Stirling *et al*., 1999; Derocher *et al*., 2004; Stirling and Parkinson, 2006). In order to gain detailed insights about their energy balance and to improve existing models with these newly acquired data (Molnár *et al*., 2010), studies using captive animals become invaluable.

Free-ranging polar bears feed primarily on various seal species across their range in the presence of sea-ice (Iverson *et al*., 2006; Thiemann *et al*., 2008). In areas of the Arctic where the summer sea-ice melts more or less completely polar bears are forced on shore. Here they mainly live off their stored adipose tissue (Watts and Hansen, 1987; Ramsay and Stirling, 1988), and opportunistically feed on various marine or terrestrial-based diets (Russell, 1975; Lunn and Stirling, 1985; Derocher *et al*., 1993; Donaldson *et al*., 1995; Ovsyanikov, 1996; Derocher *et al*., 2000; Dyck, 2001; Stempniewicz, 2006; Rockwell and Gormezano, 2008). Some of these diets, such as berries or vegetation, have been suggested to be energetically unimportant (Ramsay and Hobson, 1991; Hobson and Stirling, 1997; Hobson *et al*., 2009). Other diet items like fish, however, could be energetically significant, although currently this is only speculative (Dyck and Romberg, 2007; Dyck and Kebreab, 2009). Recent studies also indicated that temporal shifts in polar bear diets occurred (Iverson *et al*., 2006; Thiemann *et al*., 2008; McKinney *et al*., 2009), rendering the harp seal potentially an important prey species where available. However, it

is unclear whether differences in digestibility and energy use between seal species exist by polar bears.

The objective of this study was to quantify nutrient digestibility of two novel diets (*i.e.*, Arctic charr (*Salvelinus alpinus*) and harp seal (*Pagophilus groenlandicus*) fed to a captive polar bear. To our knowledge, only one digestive feeding trial with a captive polar bear has been documented in the scientific literature (Best, 1985; but see Kaduce *et al.*, 1981; Kaduce and Folk, 2002) that examined energy content and digestibility coefficients of diets that are actually consumed by wild polar bears. By using current available (summer) diets of free-ranging polar bears, and by performing proximate analyses on these diets, more detailed data about polar bear energetics and food assimilation become available in order to understand energetic requirements. Based on Best (1985) and Dyck and Kebreab (2009), we predicted that our study animal would increase in body mass on the seal diet, and at least maintain its body mass while being fed the Arctic charr. Although digestibility trials with harp seal fat/meat have not been conducted, we hypothesized that digestibility for fat and protein would compare to those of a ringed seal diet.

MATERIALS AND METHODS

General information

In the hopes to be able to increase the sample size, the senior author initially contacted all major facilities in the United States and Canada that house captive polar bears within a 700km radius of Ottawa, Ontario, Canada, and the Bear Taxon Advisory Group of the Association of Zoos and Aquariums. All contacted institutions unfortunately declined participation, and therefore we were only able to secure access to one captive animal in Canada. Nevertheless, other feeding trial studies on bears used also relatively small sample sizes (Bunnell and Hamilton, 1983; Best, 1985; Jansen *et al.*, 2003), and data garnered from this study serve as a baseline for future work. The Polar Bear Habitat and Heritage Village (PBH and HV) at Cochrane, Ontario, selected their adult male (28 years, ~ 393 kg) to be a participant in the feeding trial study.

During most feeding trial studies of terrestrial mammals, animals usually are housed individually in small pens or crates that allow easier collection of feces and/or urine (Pritchard and Robbins, 1990; Rode *et al.*, 2001; Felicetti *et al.*, 2003; Robbins *et al.*, 2007). This, however, does not allow the animals to exhibit a broader spectrum of behaviours which they more likely would display if in a larger enclosure or in the wild (*e.g.,* digging, walking, swimming, "playing" with inanimate objects, resting). In addition, results of energy use of such confined animals are likely biased and confound a comparison to free-ranging animals that are more active. For example, during the ice-free period in the Arctic free-ranging polar bears are mostly inactive in order to conserve energy while living off their stored adipose tissue (Knudsen, 1978; Watts and Hansen, 1987; Dyck, 2001), but they are not sedentary. They are generally in a negative energy budget (*i.e.*, they can lose approximately 1 kg·d^{-1} of body mass while fasting; Derocher and Stirling, 1995; Polischuk *et al.*, 2002), but they also move slowly along shore lines, search for food, feed on various food items, dig day beds and rest, or swim occasionally. We aimed to simulate feeding trials under as natural conditions (*i.e.*, displaying common behaviours) as possible where we allowed the polar bear access to a pool, 2 large outdoor and several smaller indoor enclosures.

Diets and preparation

Harp seals and Arctic charr were harvested in Frobisher Bay, Nunavut, by Inuit and shipped frozen to the PBH and HV. These food items were stored frozen at -15°C to -20°C until used in potential feeding trials. Prior to feeding, polar bears usually strip the skin off a seal's carcass before primarily consuming the blubber, and then the meat (Smith, 1980). We therefore skinned the carcass after slight thawing so that as little as possible of the blubber remained on the carcass, which also allowed us to control the blubber and meat mass that was provisioned during each feeding trial. Flippers, head, and viscera were removed and discarded. The remaining carcass was cut into approximately 3.5 kg portions consisting roughly equally of meat and bone. The blubber was separated from the skin with a knife and cut into approximately 510 cm^3 (~ 500

g) cubes (*i.e.*, 13 cm L x 13 cm W x 3 cm thickness). All diets for the feeding trials were defrosted about 20-24 hrs before being fed to the bear, either at room temperature or at 4°C in a refrigerator.

Feeding trials

Similar to other studies, captive feeding trials lasted a minimum of 9 days and consisted of a 4 – 7 day pre-trial acclimation period and a 5 day collection period (Bunnell and Hamilton, 1983; Best, 1985; Pritchard and Robbins, 1990) with constant food intake. During the collection period, all feces were collected in the outdoor or indoor enclosures every morning, and weighed (either frozen or as wet weight). All collected feces were kept frozen at -15°C until subsequent chemical and nutritional analyses. Urine was not collected during feeding trials.

Diets were administered randomly. Ideally before the start of each trial the bear underwent a 24 hr fasting period to ensure that his guts were emptied of previously consumed food (Pritchard and Robbins, 1990). However, that was not possible for all trials. We weighed the bear to the nearest 0.1 kg with an electronic low-profile floor scale (Interweigh Systems Inc., Quebec, Model ISI-99-7236) at the beginning and end of each diet-type trial. During trials, body mass was recorded every morning opportunistically before feeding commenced. Body composition of the bear could not be estimated because that would have required repeated immobilizations (*e.g.*, Hilderbrand *et al*., 1999; Felicetti *et al*., 2003). Food was provided on average 2 – 4 times daily according to usual feeding regimes. The largest portions were provided in the morning (0600-0730) and afternoon (1500-1730). The bear had access to water *ad libitum*, as well as grass which is part of the enclosures. To simulate free-ranging conditions, he was able to move and rest freely during all trials.

We used ~ 6 kg·day^{-1} of food (wet mass) for each trial. This amount was based on a) a previous captive polar bear trial with similar diets (*e.g.*, Best, 1985), and b) hypothetical scenarios (Dyck and Kebreab, 2009) linking body mass maintenance and diet mass consumption. Each provision was weighed before and after feeding (seal to the nearest 10 g; charr to the nearest 2 g) to determine the daily amount of consumed food. The seal diet was divided into approximately 2.5 kg·day^{-1} blubber and 3.5 kg·day^{-1} meat (attached to bones). Arctic charr were fed either cut in half or whole. We randomly sampled two whole Arctic charr, and several pieces of seal meat and fat of one harp seal for nutritional testing.

Because the bear was viewed by visitors on a daily basis, some "treats" were required to be fed: only the energy-rich items (*e.g.*, herring) were recorded by mass (or caloric value), whereas low-energy items (*e.g.*, lettuce, water melon) were neglected due to high water content and the small caloric contribution to the bears' daily energetic requirements. We mostly substituted treats during visitation times with portions of the prescribed trial diets, which were weighed and recorded. All environmental enrichment food caloric values were recorded where available. High shipping costs of the diets from the Arctic prevented us from performing more than two trials per diet, or to increase the length of the trials.

Analyses

Subsamples of diets and collected feces were analysed by an analytical food laboratory (Central Testing Labs, Inc., Winnipeg, Manitoba), following AOAC standards (AOAC, 1995). Each sample was run in duplicates. The whole fish were homogenized, and 2 random sub-samples were chosen for analyses. The seal fat/meat diet was consumed in an approximately 1:1 ratio, and rather than using individual analytical data for seal fat and meat, data for a 1:1 ratio of a homogenized mixture were applied for all calculations.

Food and fecal samples were analysed for moisture, dry matter (DM), crude protein (CP), crude fibre (CF), ash, minerals (calcium, phosphorus, magnesium, potassium, copper, sodium, zinc, manganese, and iron), acid detergent fibre (ADF), neutral detergent fibre (NDF), starch, total sugar (as glucose), and gross energy (GE). Other micronutrients and fatty acids of our used diets were reported by others (Hoppner *et al*., 1978; Shahidi *et al*., 1993; Shahidi and Synowiecki, 1996; Kuhnlein *et al*., 2002; Brunborg *et al*., 2006; CINE, 2010). Crude protein was determined according to

AOAC (1995) using a Leco nitrogen/protein determinator (Model FP-42, Leco Instruments). Fat concentrations were determined by acid hydrolysis (AACC, 1983) and followed by ether extraction using a 50/50 solvent mixture of petroleum ether and di-ethyl ether. Organic matter (OM) was calculated as DM minus ash. Gross energy (kJ or MJ) was calculated as (17.16 x CP) + (39.34 x fat) + (17.16 x carbohydrates). Digestible carbohydrates were calculated using the formula 100 – (CP + fat + CF + ash + moisture). ADF, NDF and CF were analyzed using an ANKOM A2000 automated fibre analyzer (an AOAC-approved ANKOM Technology method). Feces and diets were first dried for 48 h at 75°C, ground, and placed again in a drying oven for 48 h at 75°C – a method that prevents nutrient break-down.

Digestibility coefficients (DCs) were calculated by expressing the weight of nutrients digested (*i.e.*, food intake less feces) as proportion of the weight consumed (McDonald *et al*., 2002). Apparent digestible energy (ADE) (or digestive efficiency; White *et al*., 2007) was calculated as the GE content of food less the GE content of the feces (Lavigne *et al*., 1982). The apparent digestibility of energy was calculated by dividing the difference of the energy content of the daily DM food intake ($MJ \cdot d^{-1}$) and the energy content of the daily produced feces by the energy content of the daily DM food intake ($MJ \cdot d^{-1}$). The digestible energy (DE) content of each fed diet ($MJ \cdot kg^{-1}$) was determined by multiplying the apparent digestibility of energy by the energy content of 1 kg of diet ($MJ \cdot kg^{-1}$). Metabolizable energy was considered to be 95% of DE (Best, 1985).

Since there are only 2 trials per diet, results per diets were pooled, and descriptive statistics are provided with the mean ± standard deviation (SD), unless otherwise specified. Regressions were applied to examine trends in body mass change where trial dates were transformed into Julian Dates. Statistical analyses were considered significant at α = 0.05.

RESULTS

Diet characteristics

The harp seal fat/meat and the wild Arctic charr diets varied in nutrient composition (Table I). The harp seal diet contained the greatest proportion of fat, and Arctic charr contained greater quantities of most analyzed minerals (on a DM-basis) as compared to the seal diet, except for copper; zinc and manganese where similarly present in both diets (Table I).

Table I.-   Nutrient composition and energy content of wild Arctic charr and harp seal meat/fat (1:1 ratio) fed to a captive polar bear.

Nutrients	Wild Arctic charr		Harp seal meat/fat	
	As fed	Dry matter	As fed	Dry matter
Moisture (%)	71.82		37.54	
Dry Matter (%)	28.18		62.46	
Crude Protein (%)	18.87	66.97	12.95	20.73
Crude Fibre (%)	0.33	1.16	0.92	1.47
Fat (%)	7.33	25.99	46.72	74.81
Ash (%)	2.45	8.69	0.84	1.35
Calcium (%)	1.02	3.59	0.02	0.02
Phosphorus (%)	1.12	3.95	0.11	0.17
Magnesium (%)	0.10	0.34	0.02	0.02
Potassium (%)	1.00	3.58	0.17	0.27
Copper (mg/kg)	4.02	14.23	22.59	36.17
Sodium (%)	0.35	1.24	0.06	0.10
Zinc (mg/kg)	12.52	44.50	27.41	43.87
Manganese (mg/kg)	3.013	10.66	7.34	11.75
Iron (mg/kg)	20.78	73.82	0.01	0.02
Starch (Acid Hydrolysis) (%)	0	0	0	0
Acid Detergent Fibre (%)	0.09	0.34	3.34	5.35
Total Sugar (as Glucose) (%)	0	0	0	0
Neutral Detergent Fibre (%)	2.71	9.62	7.22	11.55
Gross energy (kJ/100g)		2161.77		3296.72

Body mass changes

The polar bear's body mass increased significantly during both seal trials (trial 1: F = 79.55, P = 0.0001, r^2 = 0.93; trial 2: F = 68.15, P = 0.0001, r^2 = 0.88), and the Arctic charr trial 2 (F = 8.83, P = 0.018, r^2 = 0.53). Charr trial 1 did not have sufficient weight measurements for further analyses. Body mass increase for both seal trials are best described by a curvilinear function (Fig. 1). In general, body mass fluctuated on a daily basis but overall resulted in a net gain. Daily mass gains on the harp seal fat/meat diet were about 5.5 to 6.5 greater than on the Arctic charr diet. Whether the gain was accumulated as muscle or adipose tissue mass could unfortunately not be investigated.
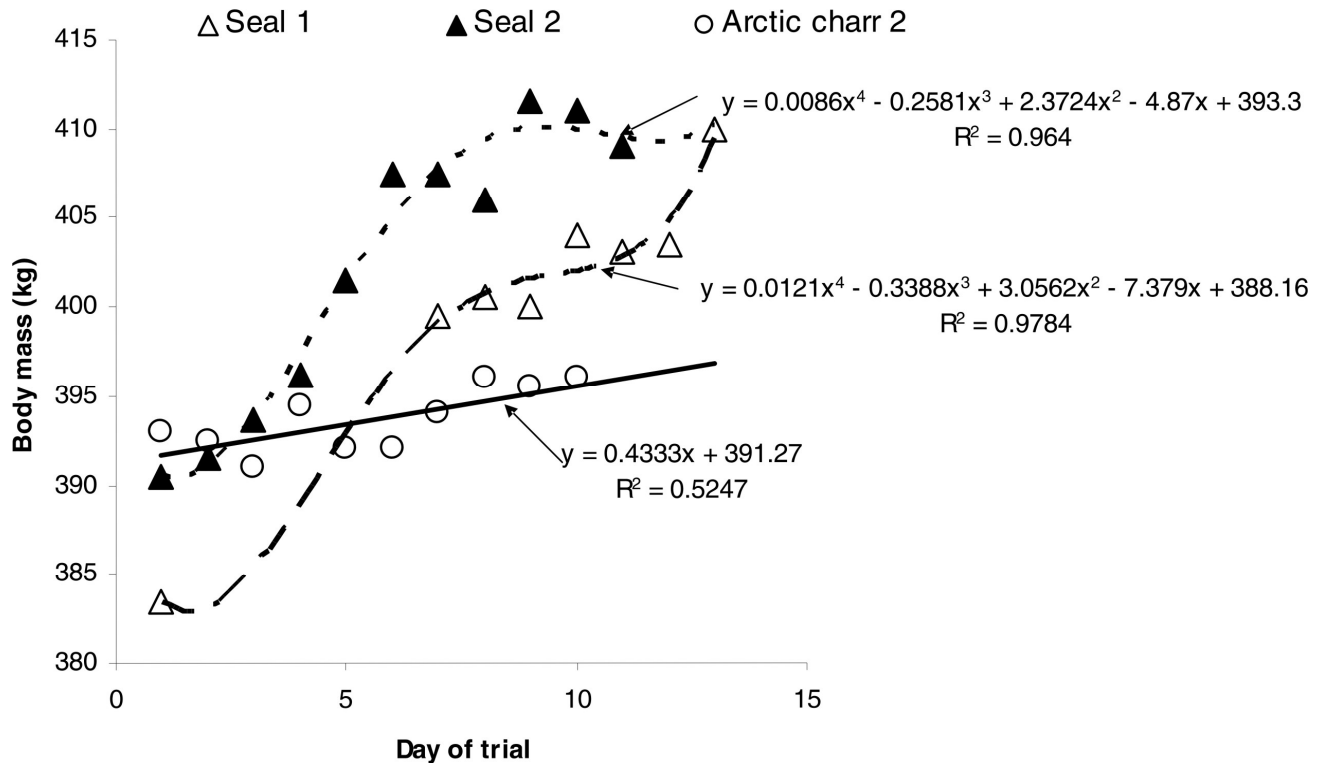
Fig. 1. Body mass changes of a captive polar bear fed Arctic charr and harp seal fat/meat diets. Arctic charr trial 1 not shown due to missing body mass data.

Table II.- Averages of 2 digestibility trials in which a captive polar bear was fed Arctic charr (*Salvelinus alpinus*).

	Dry matter (DM)	Organic matter	Crude protein	Fat
Analyses (g/kg DM)				
Arctic charr	-	925.6	669.8	259.9
Feces	-	509.1	229.6	31.7
Nutrients (kg/d)				
Consumed	1.771	1.617	1.186	0.460
Excreted	0.098	0.049	0.023	0.003
Digested	1.673	1.568	1.163	0.457
Digestibility coefficients	0.945	0.969	0.981	0.993
Digestible nutrients (g/kg DM)	-	897.04	657.09	258.15

Feed intake, digestibility, and energy

    There was a significant difference in daily feed intake between the trials (F = 111.75, P<0.0001), but not between the feeding trials of the same diet (P for feeding trials of the same diet >0.0083). The daily mean DM intake of Arctic charr was lower than the intake of seal fat/meat. Food intake for seal with 37 g DM intake/kg BM^{075} was almost twice as high as charr intake (20 g DM intake/kg BM^{075}). Crude protein intake per kg BM^{075} was about twice as much while feeding on charr as compared to the seal diet; fat intake during the seal trials with 27.7 g/ kg BM^{075} was 5 times greater than during the charr trials (Tables II, III).

    Digestibility coefficients for OM, CP, and fat (DM) were all high, with fat having the highest (> 99%) in both trial diets (Tables II and III). Apparent digestibility of energy for the seal diet was 0.990, whereas that for the charr was somewhat lower (0.978). Digestible energy (DE) content of the seal diet with 32.63 MJ/kg DM was greater than that of the charr diet (21.14 MJ/kg DM). Given the daily DM intake and the DE content (DM) of both diets, our study bear had a mean daily DE intake of

106.79 MJ (1209.4 kJ/[kg $BM^{0.75}$ d]) and 37.44 MJ (424 kJ/[kg $BM^{0.75}$ d]) when feeding on seal or charr, respectively.

Table III.- **Averages of 2 digestibility trials in which a captive polar bear was fed a 1:1 mixture of harp seal (*Pagophilus groenlandicus*) fat and meat.**

	Dry matter (DM)	Organic matter	Crude protein	Fat
Analyses (g/kg DM)				
Harp seal fat/meat (1:1 ratio)	-	986.5	207.3	748.0
Feces	-	973.0	251.0	87.7
Nutrients (kg/d)				
Consumed	3.272	3.228	0.678	2.448
Excreted	0.083	0.060	0.021	0.007
Digested	3.189	3.168	0.657	2.441
Digestibility coefficients	0.975	0.981	0.969	0.997
Digestible nutrients (g/kg DM)	-	968.1	200.9	745.8

DISCUSSION

Protein and fat are the food constituents that contain the greatest energy content with fat (lipids) being the most concentrated source of energy (Blaxter, 1989; Lawson *et al*., 1997). Both provided diet items are fed upon by free-ranging polar bears (Iverson *et al*., 2006; Dyck and Romberg, 2007; Thiemann *et al*., 2008), and contain high CP and fat contents to cover a bear's daily energy requirement (DER). In addition, both of these diets are also rich in macronutrients, minerals, and fatty acids (Shahidi *et al*., 1993; Shahidi and Synowiecki, 1996; Kuhnlein *et al*., 2002; Brunborg *et al*., 2006; CINE, 2010) required for growth and maintenance.

Due to the high CP and fat content of both administered diets, it was not surprising to see a body mass increase during the feeding trials. More than the daily required energy during the charr and seal trials was consumed (see below) hence the increase in body mass. We believe that the body mass increase on the charr diet is somewhat reduced because our charr were harvested just at the early onset of fat accumulation, and perhaps were on the lower end of their GE. Normally, polar bears attempt to catch charr during late summer when individual fish are energy-richer from greater accumulation of fat/oil and eggs, anticipating their migration to their spawning sites (Dyck and Romberg, 2007). A wild polar bear can easily catch 2 charr (or about 6 kg wet weight of food) within less than 30 min (Dyck and Romberg, 2007) to cover DER.

Polar bears have adapted to a fatty diet and therefore have high DCs for lipids. Our DCs for fat were similar to what was reported by Best (1985) and Jansen *et al*. (2003), however, values for CP and DM were somewhat higher in this study. Our bear was not confined to a chamber, and was exposed to different ambient temperatures, which could have affected the digestive efficiency. Nevertheless, overall our values are in general agreement with results compiled by Clauss *et al*. (2010) for various carnivores.

Digestibility of food can be affected by food composition and passage rate where a faster rate reduces digestion (McDonald *et al*., 2002). We did not quantify defecation rate or gastrointestinal transit time per se, so were unable to determine whether there were differences between the two seal trials. Subjectively, we did not detect any difference in defecation because feces were located every morning in the enclosure after our rounds. It is unclear whether a difference in the mean ambient temperature (a 25°C difference between both trials) could also have affected DCs for CP during both seal trials. Apparent digestibility for the charr DM was somewhat lower than for the seal. This most likely can be explained by the presence of bones in the fish. While on the seal diet, the bear commonly cleaned bones rather than consuming them.

It is interesting to note that our bear's DER was lower as previously reported during other feeding trials (Best, 1985). Kleiber (1975) estimated the DER as being between 2.0 and 2.6 times the basal metabolic rate (BMR; with BMR = 70 $m_b^{0.75}$ in kcal/d where $m_b^{0.75}$ is the metabolic body mass), which equals between 140 (586 kJ) and 182 kcal (762 kJ) of metabolizable energy/kg^{075} for a bear of similar body mass as was used in this study (*i.e.*,

393 kg). Further, it was also assumed that an active bear under normal thermoneutral conditions would require 12 000 (50,226 kJ) to 16,000 kcal/d (66,968 kJ) (Best, 1985). During the charr trials our bear consumed on average 403 kJ/kg $BM^{0.75}$ of ME (96.3 kcal) of charr per day at a mean temperature of -7.3±0.3°C, and while being active. Using the previous formula and assumptions, the calculated BMR for our bear is 25 870 kJ/d of ME with a DER ranging between 51,741 and 67,263 kJ/d. Mean daily ME intake during the charr trial was 35,563 kJ, which is about 1.4 x BMR. Given that our bear was a) not restricted in his movements (*i.e.*, he walked, swam, searched for food, dug a den, and played with inanimate objects) and b) gained body mass during the trial even while daily temperatures varied greatly, it is likely that the DER for a moderately active or resting adult polar bear is somewhat <1.4 x BMR, and a more active bear would require perhaps about 2 x BMR (~ 52,000 kJ/d). This would approximate the field metabolic rate for all mammals (~ 61,565 kJ/d) as described by Nagy *et al*. (1999).

We could not address individual variation in our study, nor were we able to establish a species-specific inference regarding DER. However, we demonstrated that a diet such as Arctic charr can cover DER, at least in our case. Data on energetics and DER of polar bears are likely needed in light of climatic changes and diet shifts, especially if one attempts to predict wild polar bear population persistence from an energetic point of view (Molnár *et al*., 2010), rather than sea-ice modeling (Amstrup *et al*., 2007; Durner *et al*., 2009). Important information like the one presented here can only be gathered through captive animals and the cooperation between institutions that house these bears and researchers.

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