



Plasticity in physiological condition of female brown bears across diverse ecosystems

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Abstract

Variation in life history strategies facilitates the near global distribution of mammals by expanding realized niche width. We investigated physiological plasticity in the spring body composition of adult female brown bears (*Ursus arctos*) across 4 diverse Alaskan ecosystems. Brown bears are a highly intelligent omnivore with a historic range spanning much of North America, Europe, and Asia. We hypothesized that body mass, fat mass, lean mass, and total caloric content would increase across populations with increasing food resource availability. Throughout their range, brown bears enter a period of torpor during winter months, decreasing their metabolic rate as an adaptation to this period of reduced food availability. They also give birth to and nourish offspring during this time. Due to this specific life history strategy, we further hypothesized that proportional body fat and the proportion of total calories derived from fat would be consistent across populations. Our results supported our first hypothesis: body, fat, and lean masses, and caloric content of bears across populations increased with the quality and abundance of available food. However, the proportional body fat content and proportion of calories from fat differed across populations indicating population-specific strategies to meet the demands of reduced seasonal food availability, offspring production and rearing, and climate as well as some plasticity to respond to environmental change or ecosystem perturbations. Investigations of body condition and energetics benefit from combined assessments of absolute, proportional, and caloric metrics to understand the nuances of brown bear physiological dynamics across and within populations.

Keywords Body composition · Brown bear · Energy · Plasticity · *Ursus arctos*

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Introduction

Mammals have a nearly global distribution and range in size from a few grams to over 150,000 kg with lifespans ranging from less than 3 years to over 200 years. Both physiological and behavioral adaptations have facilitated the distribution of mammals across a wide range of climates, ecosystems, and species assemblages. One such adaptation employed by a variety of mammal species is the storage and depletion of body reserves to (1) respond to seasonal variation in food availability, (2) meet the demands of producing and nourishing offspring, and/or (3) survive austere environments. Phenotypic plasticity can expand the geographic range and niche width of both species and taxa and enhance resiliency to natural or human-caused ecosystem perturbations. Ultimately, niche width and the degree of variation seen in individuals, populations, and species can profoundly impact population stability, capacity to diversify, and overall fitness (Bolnick et al. 2003).

Nutrient deposition strategies in mammals often reflect patterns of seasonal food abundance and individuals can respond to changes in relative food availability. Wild Przewalski horses (*Equus ferus przewalskii*) deposited energy reserves prior to reduced forage quality in winter (Kuntz et al. 2006). Gray wolves (*Canis lupus*) carried greater fat reserves during late winter and spring likely to meet both thermal demands and to buffer times of reduced prey availability (Hilderbrand and Golden 2013). Annual deposition and catabolism of energy and protein reserves in northern ungulates, such as muskoxen (*Ovibos moschatus*) and caribou (*Rangifer tarandus*), reflect large swings in nutrient availability that are typical of Arctic systems (Barboza and Parker 2008; Gustine et al. 2010). Differences in relative food abundance and availability can interact with population density of sea otters (*Enhydra lutris*) to impact body condition of individuals within and across populations (Monson et al. 2000). Additionally, nutrient dynamics and partitioning also occur in conjunction with a concomitant reduction in metabolic costs and/or increase in thermogenesis. This often occurs during times of both cold weather and food shortage in a variety of species, such as white (*Cynomys leucurus*) and black-tailed prairie dogs (*C. ludovicianus*) (Harlow 1997), red-backed voles (*Myodes rutilus*) (Zuercher et al. 1999), and Arctic ground squirrels (*Urocitellus parryi*) (Buck and Barnes 1999). In mule deer (*Odocoileus hemionus*) (Monteith et al. 2013) and white-tailed deer (*O. virginianus*) (Lesage et al. 2001), however, dynamics of stored nutrients ultimately reflect the trade-offs between seasonal differences in nutrient intake, reproductive costs, maintenance demands, investment in offspring, investment in body growth, and adult survival.

Across taxa, mammal reproduction often relies on the accumulation and utilization of fat and/or protein reserves to meet the nutritional demands of offspring production and lactation (Oftedal 2000). In marine mammals, female body mass is positively related to pup growth rate, mass at weaning, and survival. For example, harbor seals (*Phoca vitulina*) use fat stores to provide 97% of the energy lost in support of lactation (Bowen et al. 2001), while gray seals (*Halichoerus grypus*) appear to use muscle stores as a labile store for reproduction (Mellish et al. 1999). Similarly some ruminants, such as muskoxen and wild sheep (*Ovis* spp.), rely almost exclusively on stored energy reserves to produce and rear offspring in early reproduction (Gustine et al. 2010). Big brown bats (*Eptesicus fuscus*) mobilize stored reserves to meet nutritional demands early in lactation but are able to rapidly recover these depleted stores in a matter of weeks (Hood et al. 2006), whereas red fox (*Vulpes vulpes*) reach their annual peak and minima of body reserves during gestation and weaning, respectively (Winstanley et al. 1999).

Brown bears (*Ursus arctos*) are a long-lived omnivorous mammal ranging from 20°N to the Arctic Ocean in parts

of North America, Europe, and Asia (Pasitschniak–Arts 1993). Body mass varies two to three fold across the species range, largely due to differences in available dietary meat (Hilderbrand et al. 1999b). While the ecosystems brown bears occupy vary widely (Servheen 1999), all female brown bears give birth in mid-winter during a period of decreased metabolic costs due to torpor (a much reduced heart rate and reduced body temperature), which often coincides with seasonal patterns of reduced food availability. Dynamics of body reserves (energy and lean mass) in female brown bears are characterized by seasonal, annual, and multi-annual patterns tied to food availability, costs of cub production and rearing, fat storage during an autumn hyperphagic period, and nutrient catabolism during winter dormancy (Hilderbrand et al. 2000; López-Alfaro et al. 2013; Hertel et al. 2017).

Body reserves in spring are critical to females as they transition from denning to the active period, incur the costs of lactation, and await seasonally available resources (e.g., spring green up of vegetation, moose (*Alces alces*) and caribou calves, and/or early summer salmon (*Oncorhynchus* spp.) runs (Farley and Robbins 1995; López-Alfaro et al. 2013). Spring body composition is a product of food availability and quality, as well as foraging efficiency, the prior year (Rode and Robbins 2000; Felicetti et al. 2003; Robbins et al. 2007; Erlenbach et al. 2014). In addition, nutrient partitioning strategies in spring can be shaped by needs for and anticipated availability of key nutrients including digestible carbohydrates and, especially, protein which comprises much of the overwinter mass loss in bears and is critical to reproductive success (Hilderbrand et al. 2000; López-Alfaro et al. 2013).

From 2014 to 2017, we assessed the nutritional ecology of brown bears in 4 distinct Alaskan ecosystems which varied in population densities, salmon availability, and climate (Fig. 1). These studies provided the opportunity to compare spring body composition across multiple populations of the same species to assess plasticity in this critical stage of life history. We determined 1) adult female spring body mass, lean mass, fat mass, and caloric content, and 2) the proportional allocation of nutritional resources between energy (fat) and body protein (as indicated by lean mass) of adult females. We hypothesized that adult female brown bears would 1) differ in absolute spring body mass (kg), body fat (kg), lean mass (kg), and total caloric content (kcal) across populations based on relative salmon abundance and availability but, 2) not differ in their proportional body composition (percent body fat and percent of total calories from fat) across populations due to species-specific similarities in reproductive and metabolic life history costs and strategies.

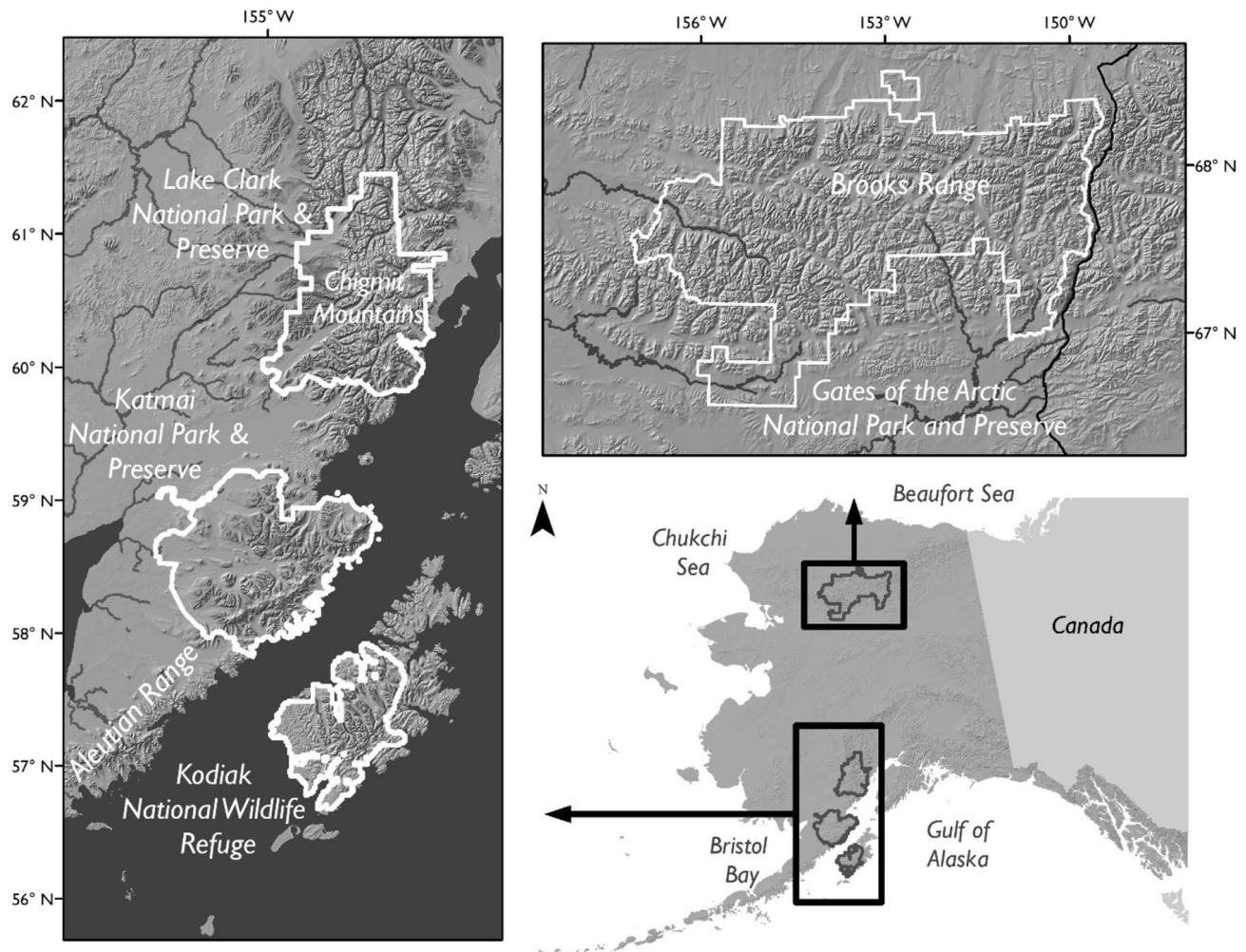


Fig. 1 Four Alaskan brown bear study areas, 2014–2016

Methods

We conducted our studies in Kodiak National Wildlife Refuge (Kodiak, 2014), Gates of the Arctic National Park and Preserve (Gates, 2014–2016), Katmai National Park and Preserve (Katmai, 2015–2017), and Lake Clark National Park and Preserve (Lake Clark, 2015–2016) (Fig. 1). Kodiak is part of the Kodiak Archipelago and home to black-tailed deer, mountain goats (*Oreamnos americanus*), small mammals, dense vegetation, numerous berry species and abundant salmon [Jun–Sep; chum salmon (*O. keta*), Chinook salmon (*O. tshawytscha*), sockeye salmon (*O. nerka*), coho salmon (*O. kisutch*), and pink salmon (*O. gorbuscha*); Deacy et al. 2016]. Gates is an interior Arctic ecosystem characterized by mountainous terrain of the Brooks Range, spruce forests (*Picea* spp.), and lowland riparian areas (Wilson et al. 2014). Primary food resources include moose, caribou, Dall’s sheep (*Ovis dalli*), small mammals, berries and herbaceous vegetation. Gates has

runs of chum and Chinook salmon from mid-July to early September (Alaska Department of Fish and Game Anadromous Waters Catalog <https://www.adfg.alaska.gov/sf/SARR/AWC/Catalog>). The coastal portion of Katmai, where our study was focused, is bounded by the Aleutian Range to the west and the Gulf of Alaska to the east. Brown bears consume marine mammals, marine invertebrates, salmon [May–Oct; chum salmon, Chinook salmon, sockeye salmon, and coho salmon], flounder (*Platichthys stellatus*), meadows of sedge (*Carex* spp.) and goose tongue (*Plantago maritima*), and berries. Lake Clark includes the Chignik Mountains, lowland spruce forests, riparian areas and sub-Arctic tundra (Stanek et al. 2017). Moose, caribou, Dall’s sheep, small mammals, berries, and Bristol Bay salmon (May–Oct) are important foods for Lake Clark brown bears. Salmon are more abundant and widely distributed in Kodiak, Katmai, and Lake Clark than in Gates. Further, more salmon species are present in Lake Clark, Kodiak, and Katmai than Gates (Alaska Department

of Fish and Game Anadromous Waters Catalog <https://www.adfg.alaska.gov/sf/SARR/AWC/Catalog>.

Adult female brown bears ($n = 70$) were captured across study areas and years (Kodiak $n = 14$, 2014; Gates $n = 27$, 2014–2016; Katmai $n = 18$, 2015–2017; Lake Clark $n = 11$, 2015–2016) with a mean capture date of 29 May $\pm$ 13.9 days (range = 28 Apr–23 Jun). The timing of capture in each study area targeted the period between den emergence and leaf out and was thus phenologically similar across study areas. All bears were anesthetized via darting from a helicopter using a 1:1 mixture of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Fort Dodge Laboratories, Fort Dodge, Iowa, USA) at a dose rate of 10–12 mg/kg (Taylor et al. 1989). Each bear was weighed using an electronic load cell (± 0.5 kg; MSI-7200; Measurement Systems International, Seattle, Washington, USA) and body composition was determined by bioelectric impedance analyses (RJL Systems, Clinton Township, Michigan, USA) (Farley and Robbins 1994; Hilderbrand et al. 1998). Bear age was estimated based on tooth wear, with an accuracy of 0.26 ± 2.74 (1 SD) years (Hilderbrand et al. in press). Each bear was classified into reproductive classes at the time of capture as either alone, with cubs of the year, with yearlings, or with older cubs. Capture and handling procedures were approved by the Institutional Animal Care and Use Committees of the National Park Service (AKR_KATM_Hilderbrand_Brown-Bear_2014, AKR_LACL_Mangipane_BrownBear_2014, AKR_GAAR_Gustine_GrizzlyBear_2014), the U.S. Geological Survey, Alaska Science Center (2014-01, 2015-04, 2015-06), and the U. S. Fish and Wildlife Service-Kodiak National Wildlife Refuge (ADFG ACUC 07-08, USFWS IACUC Permit 2012008, USFWS IACUC Permit 2012008 Renewal, USFWS IACUC Permit 2015-001).

For comparisons across populations, we included only adult bears in our analyses and individuals were included only once in cases of multiple year sampling areas. We defined adult bears as individuals ≥ 8 years of age because both males and females across the populations in our study achieved the majority of their maximum skull size (range 88.3–96.8%) and body length (86.3–96.5%) by age 8 (Hilderbrand et al. in press). For calculations of total calories, we assumed lean mass was 22% protein (4.1 kcal/g) and fat mass was 96% lipid (9.1 kcal/g) (Robbins 2001). Spring adult female body mass, composition (lean mass and fat mass), and calorie content (both absolute values and as percentages of the body total) were each compared across populations using a one-way analyses of variance (ANOVA) (Zar 1999). Pairwise comparisons between populations followed the Holm-Sidak method (Sidak 1967; Holm 1979). Fat content (percent and as a percent of total body energy) was compared across reproductive classes pooled across study areas using ANOVA. Year effects within each study area where captures spanned multiple years were assessed

for each metric using ANOVA (Gates, Katmai, and Lake Clark). We assumed statistical significance at $\alpha < 0.05$. All statistical tests were run in Sigma Plot 12 (Systat Software, Inc., San Jose, CA, USA). All data that support the findings of this publication can be found in Hilderbrand (2017).

Results

All the body metrics we assessed differed across populations (Table 1). Adult female brown bear body mass (kg) was least in Gates, intermediate in Lake Clark and greatest in Kodiak and Katmai (Table 2). Lean mass (kg) followed the same pattern as body mass; however, fat mass (kg) was the same across Lake Clark, Katmai, and Kodiak (Tables 2 and 3). Fat mass of Gates bears was about 40% that of bears from the other study areas (Table 2). Proportionally, Lake Clark bears were fatter than bears in Gates while all other comparisons showed no significant difference (Table 3).

The total energy and fat energy content (kcal) of bears was less in Gates than the other three study areas, which did not differ statistically from each other (Table 3). The energy content of lean mass followed the same pattern as body mass with Katmai and Kodiak bears being the highest followed by Lake Clark and then Gates (Tables 2). The proportion of total body energy derived from body fat (%) differed between Lake Clark and Gates but not in other comparisons across populations (Table 3).

While females with cubs of the year had less proportional body fat than all other classes (Fig. 2), the differences were not significant for percent body fat ($F_{(3,60)} = 2.143$, $p = 0.104$) or percent fat of total body calories ($F_{(3,60)} = 1.424$, $p = 0.245$). There was no difference across years in any study area for any metric: body mass (Gates $F_{(2,24)} = 0.203$, $p = 0.818$; Katmai $F_{(2,15)} = 0.859$, $p = 0.443$;

Table 1 Results of one-way ANOVA comparisons of spring body composition of adult female brown bears across 4 Alaskan brown bear populations (Kodiak National Wildlife Refuge, 2014; Gates of the Arctic National Park and Preserve, 2014–2016; Katmai National Park, 2015–2017; Lake Clark National Park and Preserve, 2015–2016)

	df	F	p
Body Mass (kg)	3, 66	54.467	< 0.001
Fat Mass (kg)	3, 60	9.204	< 0.001
Lean Mass (kg)	3, 60	45.091	< 0.001
Body Fat (%)	3, 60	3.432	0.002
Calories (cal)	3, 60	17.156	< 0.001
Fat calories (%)	3, 60	2.906	0.042

The sample sizes for body mass and all other metrics are 27 and 26 for Gates, 11 and 10 for Lake Clark, 14 and 10 for Kodiak, and 18 and 18 for Katmai, respectively. Data are available at <http://dx.doi.org/10.5066/F7CZ35ND>

Table 2 Spring body composition of adult female brown bears from Kodiak National Wildlife Refuge (Kodiak, 2014), Gates of the Arctic National Park and Preserve (Gates, 2014–2016), Katmai NationalPark and Preserve (Katmai, 2015–2017), and Lake Clark National Park and Preserve (L. Clark, 2015–2016) reported as the mean $\pm$ 1 SD

Study area	Body mass (kg)	Lean mass (kg)	Fat mass (kg)	Fat mass (%)	Energy (kcal)	Fat energy (%)
Kodiak (14, 10)	183.1 $\pm$ 28.3	145.7 $\pm$ 21.6	26.6 $\pm$ 9.7	15.6 $\pm$ 5.9	364.9 $\pm$ 77.6	61.7 $\pm$ 11.3
Gates (27, 26)	91.5 $\pm$ 15.2	80.6 $\pm$ 13.8	10.7 $\pm$ 7.3	11.6 $\pm$ 7.0	167.0 $\pm$ 64.6	49.9 $\pm$ 21.1
Katmai (18, 18)	165.5 $\pm$ 31.1	144.7 $\pm$ 26.2	20.8 $\pm$ 13.6	12.2 $\pm$ 6.7	313.4 $\pm$ 124.2	51.7 $\pm$ 22.0
L. Clark (11, 10)	129.3 $\pm$ 28.0	107.3 $\pm$ 22.0	24.8 $\pm$ 8.0	18.6 $\pm$ 4.0	314.2 $\pm$ 84.0	68.0 $\pm$ 5.5

Samples sizes for body mass and all other metrics are listed following each study area. Data are available at <http://dx.doi.org/10.5066/F7CZ35ND>

Table 3 Pairwise comparisons following one-way ANOVAs of spring body composition of adult female brown bears from Kodiak National Wildlife Refuge (KOD, 2014), Gates of the Arctic National Park and Preserve (GA, 2014–2016), Katmai National Park (KAT, 2015–

2017), and Lake Clark National Park and Preserve (LC, 2015–2016) (Holm-Sidek method). Fat cal (%) is the proportional contribution of fat calories to total calories

	Body mass	Fat mass	Lean mass	Fat (%)	Calories	Fat cal (%)
LC v G	< 0.001	0.002	0.002	0.029	< 0.001	0.066
GA v KAT	< 0.001	0.006	< 0.001	0.763	< 0.001	0.757
GA v KOD	< 0.001	< 0.001	< 0.001	0.351	< 0.001	0.322
LC v KOD	< 0.001	0.686	< 0.001	0.508	0.379	0.702
LC v KAT	< 0.001	0.525	< 0.001	0.070	0.980	0.141
KAT v KOD	0.051	0.371	0.908	0.466	0.388	0.440

The sample sizes for body mass and all other metrics are 27 and 26 for GA, 11 and 10 for LC, 14 and 10 for KOD, and 18 and 18 for KAT, respectively. Data are available at <http://dx.doi.org/10.5066/F7CZ35ND>

Lake Clark $F_{(1,9)} = 0.768$, $p = 0.404$), fat mass (Gates $F_{(2,23)} = 0.559$, $p = 0.580$; Katmai $F_{(2,15)} = 2.917$, $p = 0.085$; Lake Clark $F_{(1,8)} = 0.003$, $p = 0.958$), lean mass (Gates $F_{(2,23)} = 0.020$, $p = 0.981$; Katmai $F_{(2,15)} = 0.086$, $p = 0.918$; Lake Clark $F_{(1,8)} = 0.434$, $p = 0.529$), percent body fat (Gates $F_{(2,23)} = 0.451$, $p = 0.642$; Katmai $F_{(2,15)} = 1.993$, $p = 0.171$; Lake Clark $F_{(1,8)} = 0.249$, $p = 0.631$), total calories (Gates $F_{(2,23)} = 0.585$, $p = 0.565$; Katmai $F_{(2,15)} = 2.872$, $p = 0.088$; Lake Clark $F_{(1,8)} = 0.039$, $p = 0.848$), or percent of total calories from fat (Gates $F_{(2,23)} = 0.858$, $p = 0.437$; Katmai $F_{(2,15)} = 1.999$, $p = 0.170$; Lake Clark $F_{(1,8)} = 0.083$, $p = 0.781$).

Discussion

We have conducted the first comparative assessment of absolute and relative spring body composition across multiple wild bear populations. On average, adult female brown bears in Kodiak had more than twice the mass of Gates bears, while Katmai and Lake Clark bears were 85 and 41% heavier than Gates bears, respectively. The proportion of meat in the diet of brown bears is known to positively impact body size, individual productivity, and population density (Hilderbrand et al. 1999b). The results of our study support these prior findings and our hypothesis that spring body mass, body fat,

lean mass, and energy content generally increase with the relative quantity and quality of available nutritional resources. Coastal bears in Kodiak and Katmai have access to substantial marine meat resources, especially salmon, throughout much of their active period as various runs start in May and continue through October. Lake Clark bears also have access to summer and fall runs of Bristol Bay salmon, especially sockeye salmon, while some bears in Gates use smaller runs of chum salmon and Chinook salmon in the Noatak, Kobuk, and Koyukuk River drainages. The spatial and temporal distribution, number of salmon species, and general run abundance are less in Gates than the other study areas (Alaska Department of Fish and Game Anadromous Waters Catalog <https://www.adfg.alaska.gov/sf/SARR/AWC/Catalog>).

As expected, females with cubs of the year had the least fat mass and energy, while females with no dependent young had the greatest though the difference between reproductive classes was not significant (Fig. 2). Females with yearlings or older young had intermediate levels. Cubs of the year are completely reliant on their mother for nutrients, thus increasing the demand relative to older cubs that can gain some nutrients foraging on their own (Farley and Robbins 1995; López-Alfaro et al. 2013). Furthermore, on average, females have to support more cubs of the year than older offspring because of mortality occurring in the litter over time (Schwartz et al. 2006).

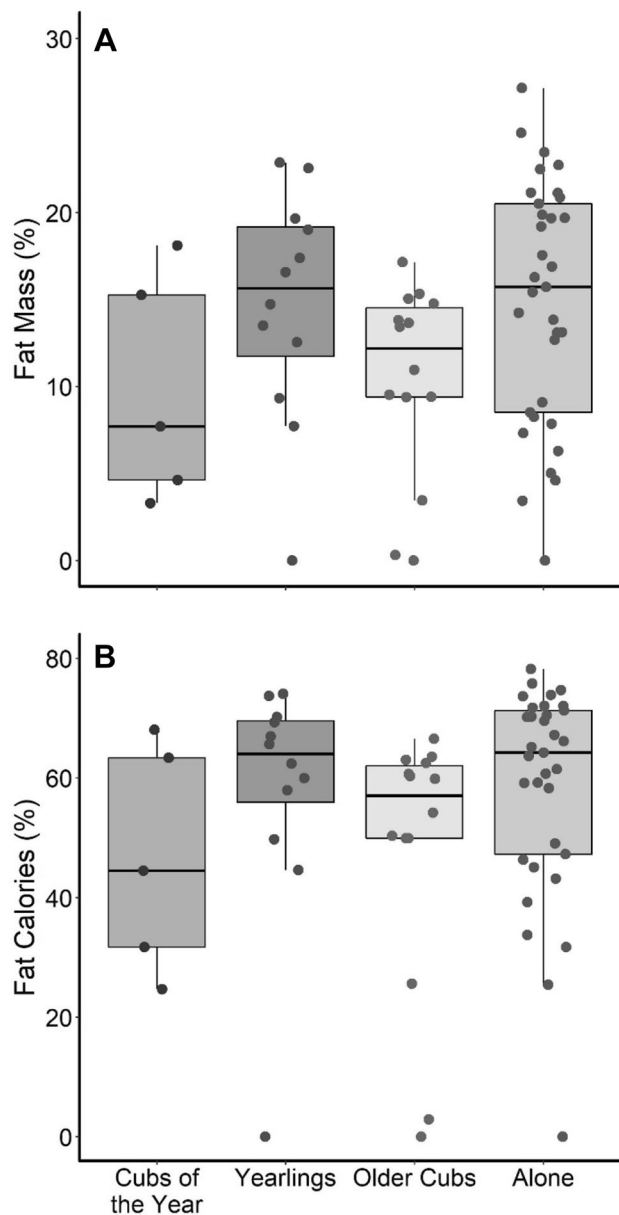


Fig. 2 Percentage of body mass from fat (A) and body energy from fat (B) of adult female brown bears grouped by reproductive class from Gates of the Arctic National Park and Preserve (2014–2016), Lake Clark National Park and Preserve (2015–2016), Kodiak National Wildlife Refuge (2014), and Katmai National Park (2015–2016). No females with cubs < 1 year of age were handled in Katmai. The bars indicate the median values, the boxes the first and third quartiles, and the whiskers 1.5* the interquartile range of each category. Data are available at <http://dx.doi.org/10.5066/F7CZ35ND>

In general, net primary productivity decreases with increased latitude (Cramer et al. 1999), so vegetative food resources are likely more limited for Gates bears than for the study areas further south. In contrast to the generalized pattern of increased body size with increased latitude described by Bergmann (1847), brown bears at more southerly

latitudes were the largest, supporting the hypothesis that nutrient availability and intake are the critical factors that influence brown bear size and density (Hilderbrand et al. 1999b; Mowat and Heard 2006).

Proportional body composition differed across study areas with adult females in Lake Clark having a greater percent body fat and percent energy from fat than the other study areas, especially Gates. This does not support our hypothesis that proportional spring body composition is consistent among bear populations due to species-specific life history strategies. While much has been learned about foraging efficiencies, diet optimization, hibernation and reproductive costs, and generalized reproductive thresholds, much of this work has been conducted on captive bears and the varied environments in which wild bears exist can further shape and constraint these idealized strategies.

On a proportional basis (percent fat and percent of calories from fat), Gates bears were essentially smaller versions of bears from Katmai and Kodiak. While bears in Lake Clark were smaller than bears from Katmai and Kodiak on an absolute basis (kg), they were the same “size” based on total energy content due to their higher proportional fat content. In Lake Clark, both the growing season length and nutrient availability generally exceed that of Gates (Monahan et al. 2016), but spring resources may be less than the diversity and quality of resources available on Kodiak and the Katmai coast, thus driving the need to “save” additional body energy stores until spring resources emerge. Gates bears do not carry the same level of fat reserves as Lake Clark bears, despite the shorter growing season length and more limited nutritional options. This may be partially explained by a longer period of hibernation and later den exit in Gates than the other study areas.

The most pronounced differences in absolute size were between Gates and the other populations. Hilderbrand et al. (in press) found that, of the 4 study areas, Gates was the only population where females reached an asymptote in lean body mass. Females from the other populations continued to grow throughout their life indicating that Gates bears, due to a combination of a shorter growing season and reduced nutrient availability (typical of low Arctic montane systems), are nutritionally restrained. In Gates, the costs of reproduction largely equal the nutrients available and females may be fully investing in reproduction and less able to store additional energy reserves or allocate resources towards growth (Hilderbrand et al. in press).

One of the only other studies of spring female body composition of Alaskan brown bears was on the Kenai Peninsula. Kenai brown bears have proportional spring body compositions (~ 19% body fat) similar to those we found for Lake Clark but their body mass (~ 155 kg) is greater than bears in Lake Clark and less than Katmai and Kodiak bears (Hilderbrand et al. 1999a). While the spatial and temporal salmon

abundance on the Kenai is similar to that of Kodiak and Katmai, access is more restricted due to human development and resource use (Suring et al. 2006) and population density may be reduced below natural carrying capacity through human-caused mortalities (Suring and Del Frate 2002). In addition, recreation, especially activities that occur near concentrated food resources such as salmon, may disturb bears and negatively impact food intake while increasing energy expenditure (Fortin et al. 2016). Collectively these factors likely constrain either Kenai bears from reaching their idealized body size and/or limit available functional habitat. Of our 4 study areas, Gates bears are likely to have the least resiliency to adapt to additional perturbations, from either natural or man-made causes, due to their sub-optimal energetics and nutrient stores.

Lafferty et al. (2015) and Mangipane et al. (2017) saw similar fall female body fat contents in brown bears in Denali (~ 26%) and Lake Clark (~ 28%), respectively, despite variation in the proportion of salmon in their diet. Their overall findings support the Niche Variation Hypothesis (NVH) that posits populations occupying wider niches should exhibit greater among-individual variation and that individual variation in dietary niche width confers an adaptive advantage (Lafferty et al. 2015). Hilderbrand et al. (in press) found that variation in body frame size and lean mass in our 4 study areas also supports the NVH. In the current study, a range of expressed phenotypic outcomes of physiological processes were evident across populations in spring body mass, lean mass, and fat mass and this largely reflected the availability of nutritional resources, which was consistent with our initial hypothesis. However, the differences we noted in proportional body composition and energetics across study areas do not support our second hypothesis that an over-arching species-specific seasonal body composition strategy exists. Rather, our findings and previous work suggest that brown bears use multiple strategies that balance trade-offs between the timing and availability of season-specific food resources, the costs of reproduction and cub-rearing, investment in body growth, and the need for energy reserves. Finally, investigations of body composition and energetics benefit from combined assessments of absolute (kg), proportional (%), and caloric (kcal) metrics to avoid missing some of the subtleties of brown bear physiological dynamics across and within populations.

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