

Body size and lean mass of brown bears across and within four diverse ecosystems

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Abstract

Variation in body size across populations of brown bears (*Ursus arctos*) is largely a function of the availability and quality of nutritional resources while plasticity within populations reflects utilized niche width with implications for population resiliency. We assessed skull size, body length, and lean mass of adult female and male brown bears in four Alaskan study areas that differed in climate, primary food resources, population density, and harvest regime. Full body-frame size, as evidenced by asymptotic skull size and body length, was achieved by 8–14 years of age across populations and sexes. Lean body mass of both sexes continued to increase throughout their life. Differences between populations existed for all morphological measures in both sexes, bears in ecosystems with abundant salmon were generally larger. Within all populations, broad variation was seen in body size measures of adults with females displaying roughly a 2-fold difference in lean mass and males showing a 3- to 4-fold difference. The high level of intraspecific variation seen across and within populations suggests the presence of multiple life-history strategies and niche variation relative to resource partitioning, risk tolerance or aversion, and competition. Furthermore, this level of variation indicates broad potential to adapt to changes within a given ecosystem and across the species' range.

Introduction

The resilience of species and viability of populations likely corresponds with niche width (Van Valen, 1965). Phenotypic plasticity and the implied capacity of individuals to adapt within dynamic systems may be of greater import for species that reside in ecosystems most vulnerable to rapid change with more pronounced climate- and human-related influences (e.g. coastal and arctic systems; Harley *et al.*, 2006; O'Neel *et al.*, 2015; Van Hemert *et al.*, 2015). Phenotypic plasticity is seen in a wide range of taxa including fish (Jeffrey *et al.*, 2017), birds (Hudin *et al.*, 2016), small mammals (Gür & Gur, 2012), ungulates (Sand, Cederlund & Danell, 1995), and carnivores (Stahler *et al.*, 2013). This plasticity is ascribed to various combinations of trade-offs between increasing competitive advantage for resources or mates, investing in reproductive costs, and responding to variation in the environment.

Brown bears (*Ursus arctos*) are circumpolar and occur in portions of North America, Europe, and Asia. They are highly intelligent, diverse in their localized food habits and habitat use, and vary greatly in individual body size and population density (Pasitschniak-Arts, 1993; Servheen, 1999; Leclerc *et al.*, 2016). Body size in brown bears is related to the quality, quantity, and availability of nutritional resources, especially protein (Hilderbrand *et al.*, 1999a), though realized diet is shaped by macronutrient optimization and energy needs (Erlenbach *et al.*, 2014) and the availability of food resources that allow for optimization (Deacy *et al.*, 2017). Despite dietary plasticity indicating broad niche variation in nutritional resource utilization, the proportional fall body composition (i.e. percent body fat) within a population has been shown to be largely consistent indicating that different strategies can lead to the same outcome relative to individual fitness (Lafferty, Belant & Phillips, 2015; Mangipane *et al.*, 2017). Larger body

size is positively associated with increased individual fitness and thus, population vigor and density (Hilderbrand *et al.*, 1999b; Zedrosser *et al.*, 2007). While large body size may offer some competitive or reproductive advantages, there are additional nutritional and physiological costs to increased growth and maintenance larger body size (Welch *et al.*, 1997; Rode, Farley & Robbins, 2006; McLellan, 2011).

Growth rates of male and female North American ursids diverge as females begin to invest substantially in reproduction and rearing offspring. Growth rates for male brown and black bears (*Ursus americanus*) tend to be steeper as they invest in larger body size to gain a competitive advantage for breeding and reproductive success, as well as access to forage (Bartareau, Cluff & Larter, 2011; Bartareau *et al.*, 2012). Rode *et al.* (2013) also reported steeper growth curves and longer periods of growth for male vs. female polar bears (*Ursus maritimus*). Differences in polar bear growth rates between two adjacent populations (Chukchi and South Beaufort Seas) during the same temporal period (2008–2011) were likely due to differences in the relative availability of seasonal sea ice habitat and access to nutritional resources [e.g. seals (*Phocidae* spp.)] associated with increased body size and reproduction (Rode *et al.*, 2013). Thus, growth rates and adult body size may vary between sexes due to differential investment in reproduction and offspring rearing, and between populations because of differences in the availability and quality of nutritional resources.

We assessed body size and lean mass in brown bears from four Alaskan ecosystems (Fig. 1). Based on previous results from black, brown, and polar bears (Bartareau *et al.*, 2011, 2012; Rode *et al.*, 2013), we hypothesized that 1) both males and females would achieve a maximum structural body size within each population that broadly reflected the quality and abundance of available food resources, and that 2) males would continue to invest in lean mass beyond the period of structural growth when nutritional resources were not limiting, but females would either shift nutrient allocations to support reproductive costs or invest in additional body size to support their ability to compete for resources or defend offspring.

Materials and methods

We conducted brown bear studies in Gates of the Arctic National Park and Preserve (hereafter Gates; 2014–2016), Katmai National Park and Preserve (Katmai; 2015–2016), Kodiak National Wildlife Refuge (Kodiak; 2014), and Lake Clark National Park and Preserve (Lake Clark; 2014–2016) (Fig. 1). Gates is an interior arctic ecosystem characterized by the mountainous terrain of the Brooks Range, spruce forests (*Picea* spp.), and lowland riparian areas (Wilson, Gustine & Joly, 2014). Primary food resources include moose (*Alces alces*), caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), small mammals, berries and green vegetation with some limited, seasonal salmon (*Oncorhynchus* spp.). Lake Clark includes the western slopes of the Chigmit Mountains, lowland spruce forests, riparian areas, and sub-arctic tundra (Stanek *et al.*, 2017). Moose, caribou, Dall's sheep, small mammals, berries, and salmon are all important resources for Lake Clark brown bears. Kodiak Island is part of the Kodiak Archipelago and home to Sitka black-tailed deer

(*Odocoileus hemionus*), mountain goats (*Oreamnos americanus*), Roosevelt elk (*Cervus canadensis roosevelti*), lush vegetation, numerous berry species, and abundant salmon (Deacy *et al.*, 2016). The coastal portion of Katmai is bounded by the Aleutian Range to the west and the Gulf of Alaska to the east and brown bears utilize marine mammals, marine invertebrates, salmon, flounder (*Platichthys stellatus*), sedge meadows (*Carex* spp., *Plantago maritima*), and berries as primary foods. Based on normalized difference vegetation index (NDVI), Gates generally has a later onset of greenness and shorter duration of greenness than the other three study areas (Markon, Fleming & Binnian, 1995). Site-specific salmon escapement numbers are not available for our full study areas as these counts usually focus on commercial fisheries in salt water and specific fresh water streams important for sport or subsistence fishing. Noting this caveat, Gates has runs of chum salmon (*Oncorhynchus keta*) and Chinook salmon (*Oncorhynchus tshawytscha*) from mid-July to early September (O'Brien & Berggiler, 2005). The salmon systems that feed the other study areas have longer duration runs (May to October with peaks in June through September) of greater abundance (an order of magnitude or more, <https://www.adfg.alaska.gov/sf/FishCounts/>). Furthermore, more salmon species are present and more broadly distributed in Lake Clark [chum salmon, Chinook salmon, sockeye salmon (*Oncorhynchus nerka*), and coho salmon (*Oncorhynchus kisutch*)], Kodiak [chum salmon, Chinook salmon, sockeye salmon, coho salmon, and pink salmon (*Oncorhynchus gorbuscha*)], and Katmai (chum salmon, sockeye salmon, coho salmon, and pink salmon) than Gates (Alaska Department of Fish and Game Anadromous Waters Catalog <https://www.adfg.alaska.gov/sf/SARR/AWC/Catalog>).

No explicit bear density or population estimates nor long-term demographic data were available for any of our four study areas. We inferred the relative habitat quality based on the abundance and availability of nutritional resources, especially salmon, and qualitative assessments of our encounter rates when conducting captures; however, estimates of carrying capacity have not been explicitly developed. Each of the study areas is part of a largely intact ecosystem and we infer that the population is relatively close to carrying capacity as hunting is either prohibited (Katmai), very limited (Gates and Lake Clark), and/or highly regulated (Kodiak).

Bears were anesthetized via darting from a helicopter using tiletamine hydrochloride and zolazepam hydrochloride (Telazol[®], Fort Dodge Laboratories, Fort Dodge, IA, USA) according to Taylor, Reynolds & Ballard (1989). Bears were weighed using an electronic load cell (± 0.5 kg; MSI-7200; Measurement Systems International, Seattle, WA, USA) and body composition (lean and fat mass) was determined by bioelectric impedance analyses (RJL Systems, Clinton Township, MI, USA; Farley & Robbins, 1994; Hilderbrand, Farley & Robbins, 1998). Skull length was measured as the straight-line distance from the upper incisors to the occipital condyle and skull width was the straight line distance at the zygomatic arches. Skull size was the sum of the skull length and width. Body length was the distance from the tip of the nose and the base of the tail following body contours (Farley & Robbins, 1994). We selected skull size and body length as measures that reflected fixed structural growth, though

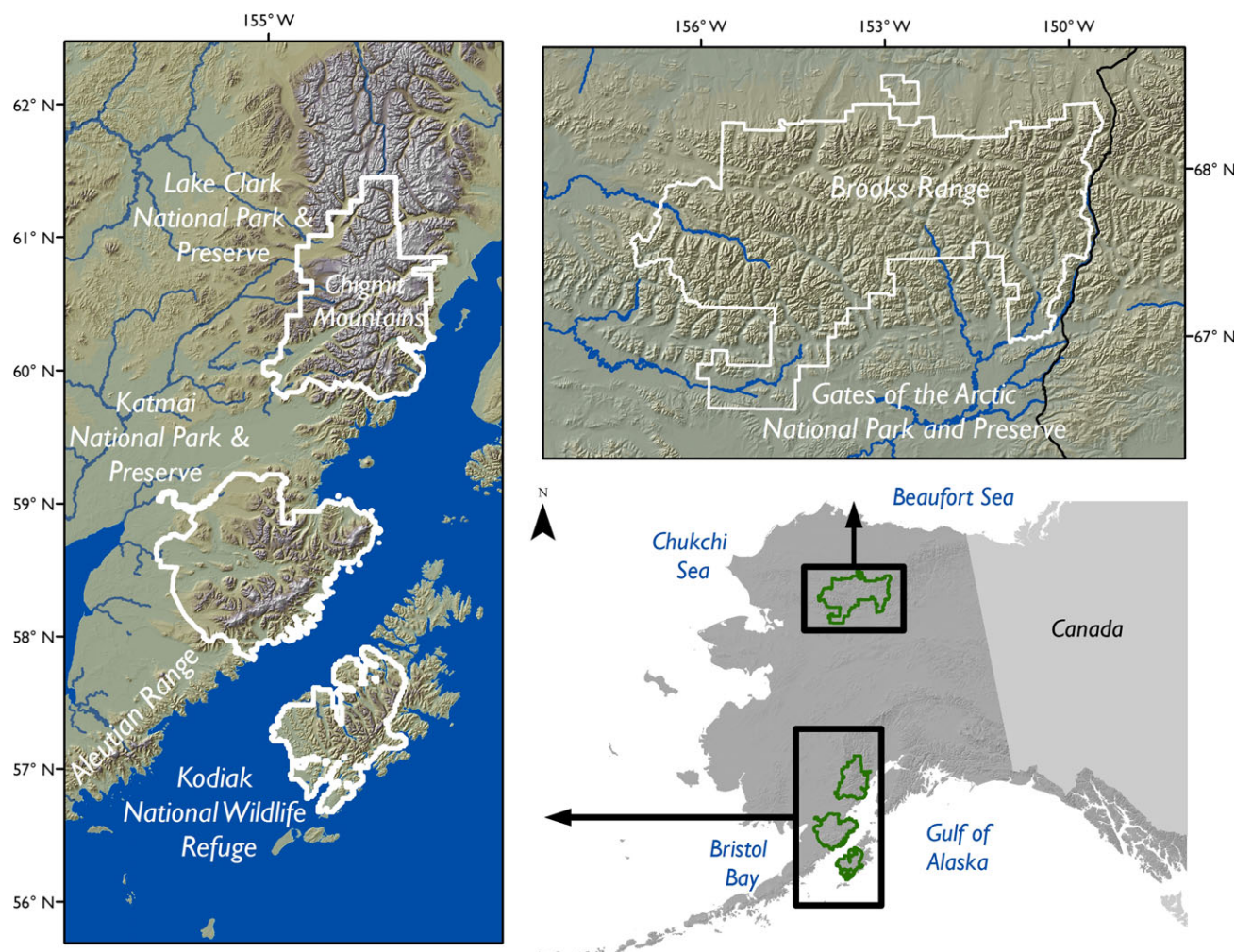


Figure 1 Four Alaskan brown bear study areas, 2014–2016.

body length may be slightly influenced by metabolically active tissues such as lean and fat mass as we followed the contour of the body. We used lean mass rather than body mass due to the annual and multiannual dynamics of the fat component (Hilderbrand *et al.*, 2000). Experienced observers (GVH and/or TC) estimated age of bears based on tooth wear. A vestigial premolar was extracted from a subset [maximum number of bears authorized by the reviewing Animal Care and Use Committees (ACUC)] of handled bears in this and a prior study and aged by cementum annuli (Matson's Laboratory, Manhattan, MT, USA). Capture and handling procedures were approved by the ACUCs of the National Park Service (AKR_KATM_Hilderbrand_BrownBear_2014, AKR_LACL_Mangipane_BrownBear_2014, AKR_GAAR_Gustine_GrizzlyBear_2014), the US Geological Survey, Alaska Science Center (2014-01, 2015-04, 2015-06), and the US Fish and Wildlife Service (ADFG ACUC 07-08, USFWS IACUC Permit 2012008, USFWS IACUC Permit 2012008 Renewal, USFWS IACUC Permit #2015-001).

Accuracy of age estimates were determined by linear regression comparing estimated age to age determined from

cementum annuli and precision of age estimates was determined by comparing age estimates from repeated captures to the age estimated at the initial capture and age estimate from initial captures were not reviewed prior to subsequent captures. We assessed the effect of animal age on the accuracy of our estimates using linear regression and calculated standard deviations for each of three age classes (<10 years, 10–14 years, ≥15 years).

Asymptotic values for each body metric (skull size, body length, spring lean mass) were assessed by gender and study area using two parameter single exponential growth curves:

$$y = a(1 - e^{-bx}).$$

Where y = morphological size at age x , a = value of the asymptote, and b = is a growth rate constant. Full maturity was defined as the age at which bears reached 97% of their maximum size (Derocher & Wiig, 2002; Rode, Amstrup & Regehr, 2010; Bartareau *et al.*, 2011; Rode *et al.*, 2013).

For comparisons across and within populations, we defined adult bears as ≥8 years of age because both sexes across the

Table 1 Non-linear regression analyses (single exponential growth curves) for skull size, body length, and lean mass from Gates of the Arctic National Park and Preserve (Gates), Lake Clark National Park and Preserve (Lake Clark), Kodiak National Wildlife Refuge (Kodiak), and Katmai National Park and Preserve (Katmai)

Gender	Measurement	Study area	<i>n</i>	<i>L</i> or <i>W</i> ($\pm$ SD)	97%	<i>P</i>	<i>r</i> ²	S.E.E.
Female	Skull size	Gates	33	51.36 $\pm$ 0.69	8.06	<0.0001	0.26	3.00
		Lake Clark	30	56.89 $\pm$ 0.68	8.83	<0.0001	0.29	3.01
		Kodiak	16	60.64 $\pm$ 1.39	10.03	<0.0001	0.13	3.73
		Katmai	18	61.42 $\pm$ 1.61	13.07	<0.0001	0.58	4.60
	Body length	Gates	32	166.10 $\pm$ 2.13	8.38	<0.0001	0.38	8.95
		Lake Clark	14	182.10 $\pm$ 6.08	13.34	<0.0001	0.20	12.40
		Kodiak	16	194.08 $\pm$ 3.72	11.03	<0.0001	0.34	9.38
		Katmai	18	189.48 $\pm$ 3.22	10.01	<0.0001	0.58	10.53
	Lean mass	Gates	31	85.62 $\pm$ 4.59	14.72	<0.0001	0.26	13.78
		Lake Clark	12	150.31 $\pm$ 17.66	37.11	<0.0001	0.62	13.44
		Kodiak	11	168.25 $\pm$ 23.20	19.80	<0.0001	0.28	20.07
		Katmai	18	170.45 $\pm$ 13.26	25.40	<0.0001	0.71	18.14
Male	Skull size	Gates	19	61.28 $\pm$ 2.10	12.86	<0.0001	0.42	4.73
		Lake Clark	17	63.73 $\pm$ 1.84	10.79	<0.0001	0.14	5.59
	Body length	Gates	15	190.72 $\pm$ 4.72	12.17	<0.0001	0.57	9.21
		Lake Clark	15	206.36 $\pm$ 5.28	14.11	<0.0001	0.50	13.53
	Lean mass	Gates	13	147.38 $\pm$ 36.66	27.78	0.0020	0.32	28.54
		Lake Clark	14	258.49 $\pm$ 73.4	53.45	0.0042	0.56	32.17

n, sample size; *L*, asymptotic length (cm); *W*, asymptotic mass (kg); 97%, age at which 97% of asymptote was reached (years), *P*, *P*-value; *r*², coefficient of determination; S.E.E., standard error of the estimate (cm or kg).

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. Bears reach sexual maturity as early as 4 years of age (Hensel, Troyer & Erickson, 1969), thus we are defining adulthood based on structural size rather than age of first reproduction.

Skull size, body length, body mass, and lean mass were compared across populations using a one-way ANOVA with pairwise comparisons between populations following the Holm-Sidak method (Sidak, 1967; Holm, 1979; Zar, 1999). Box and whisker plots were generated for skull size, body length, and lean mass by sex for each study area using R (R Core Team 2013). 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 (2018).

Results

We overestimated age by 0.26 years based on comparisons of age estimates from tooth wear to age determined by cementum analyses ($n = 50$). The error of our estimates were positively related to age ($r^2 = 0.2$, $P = 0.01$) with standard deviations lower in younger age classes (<10 years of age = 2.1, 10–14 years of age = 2.7, ≥ 15 years of age = 3.0). Precision of age estimates from repeatedly handled individuals was 1.89 ± 2.24 years (1 SD, $n = 53$ repeated measures) years.

Adult males and females in all populations reached 97% of their maximum skull size and body length between the ages of 8 and 14 (Table 1, Figs 2 and 3). Females attained 97% of their maximum lean mass by age 15 in Gates (montane, low arctic production) but accumulated lean mass throughout their life in the other three populations (Table 1, Fig. 4). Males in

both Gates and Lake Clark (montane, interior population) increased lean mass throughout their life.

Differences existed across adult females from the four populations in all morphological measurements assessed (body length: $F_{3,80} = 26.338$, $P < 0.001$; skull size: $F_{3,81} = 23.159$, $P < 0.001$; lean mass: $F_{3,60} = 43.672$, $P < 0.001$). In pairwise comparisons, adult female skull size and body length did not differ between Lake Clark, Katmai (coastal population), and Kodiak (island population), but all three populations had larger skulls and longer bodies than adults from Gates (Table 2). Adult females from Kodiak and Katmai did not differ in lean mass but all other pairwise comparisons between populations were significantly different. Adult males from Gates were smaller than adults from Lake Clark across all morphological measures (body length: $F_{1,27} = 12.798$, $P = 0.001$; skull size: $F_{1,28} = 6.370$, $P < 0.018$; lean mass: $F_{1,22} = 10.125$, $P = 0.004$).

Within populations, morphological metrics ranged widely (Figs 5 and 6), particularly lean mass with females showing a 2-fold range in this metric (Fig. 5) and males showing a 3–4 fold range (Fig. 6), though the pattern of the box and whisker plots varied across metrics and populations.

Discussion

The results support our hypotheses that adult body size for both sexes of brown bears reflects our qualitative assessment of habitat quality. As we hypothesized, males reach full structural frame size and then continue to invest in overall body size by increasing lean body mass while females showed different results across populations. Females from Gates reached asymptotes for skull size, body length, and lean body mass suggesting that the costs of reproduction generally equaled the

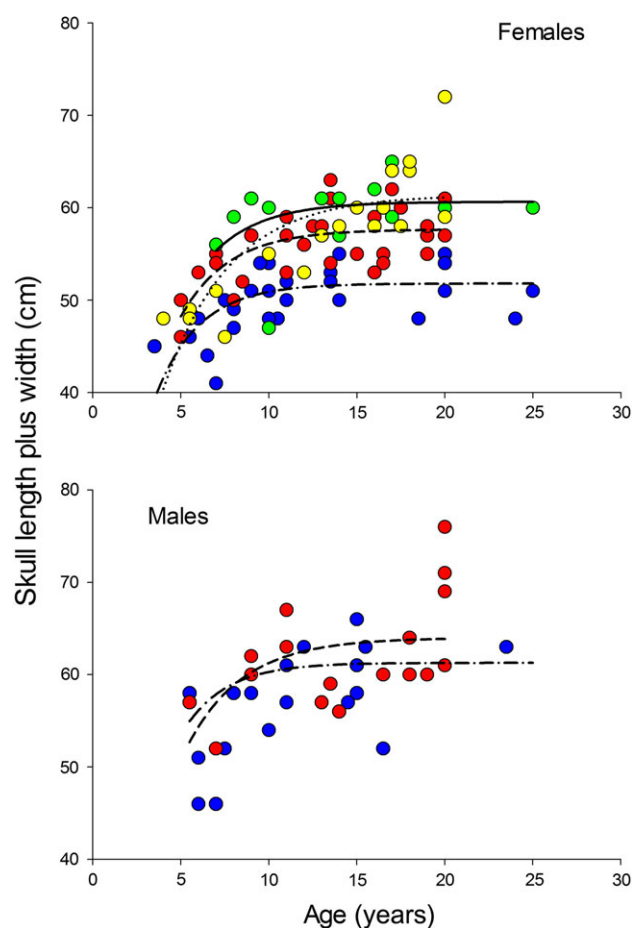


Figure 2 Relationships between estimated age of brown bears and skull size in four Alaskan brown bear study areas, 2014–2016 (Gates: blue circles and dotted and dashed line; Lake Clark: red circles and dashed line; Kodiak: green circles and solid line; Katmai: yellow circles and dotted line).

resources available and utilized. Females in other areas continued to invest in overall body size (i.e. lean mass) after achieving full structural frame size indicating that resource availability and the longer growing season combined provided nutrients that exceeded the costs of reproduction. Bear density varies significantly across populations in Alaska with bears feeding on salmon having densities an order of magnitude greater than non-salmon trophic systems (Hilderbrand *et al.*, 1999b) and bears tend to rely heavily on salmon when it is available (Mowat & Heard, 2006). In Lake Clark, Katmai, and Kodiak, relative bear density is greater than Gates and the highest quality food resources (e.g. salmon) tend to be spatially congregated. Both increased density (and thus potential for aggressive interactions) and competition for concentrated food resources may select for larger bears when resources support investment in body growth in excess of reproductive costs.

Of particular note was the degree of variation in the adult size of both sexes within each population. Fluctuations in

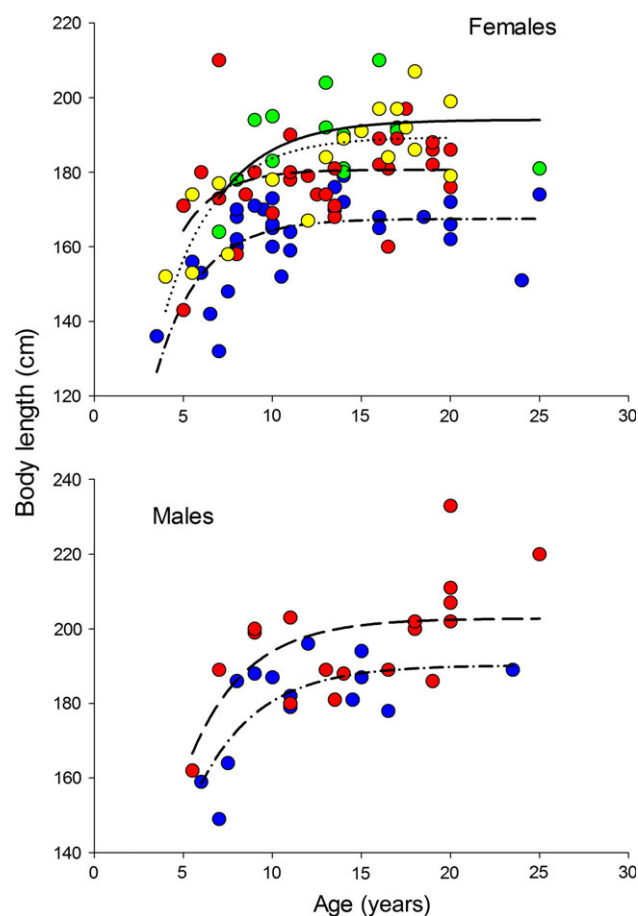


Figure 3 Relationships between estimated age of brown bears and body length in four Alaskan brown bear study areas, 2014–2016 (Gates: blue circles and dotted and dashed line; Lake Clark: red circles and dashed line; Kodiak: green circles and solid line; Katmai: yellow circles and dotted line).

female lean mass do result from the annual and multi-annual costs of reproduction. The difference in spring lean mass between lone females and females with cubs of the year was ~17% on the Kenai (Hilderbrand *et al.*, 2000). Thus, reproductive status does not explain the roughly 2-fold range in lean mass seen in adult females within each population (Fig. 5). Skull size and body length reach maximums with age and similarly varied widely within each population in both sexes (Figs 5 and 6). Other than costs of competition, males are largely free of reproductive costs and there was a roughly 3-fold range observed in lean mass of adult males within both Gates and Lake Clark (Fig. 6). While lean mass does continue to increase with age, the level of variation seen in both sexes within each population cannot be entirely explained by age. Males in Gates reach 63.5% of their maximum lean mass by age 8 but display a 2.7-fold difference in lean mass while males in Lake Clark reached 40.8% of their maximum lean mass by age 8 but showed a 3.6-fold difference (Fig. 6). With the exception of Lake Clark (53.04%, 1.88), the same pattern

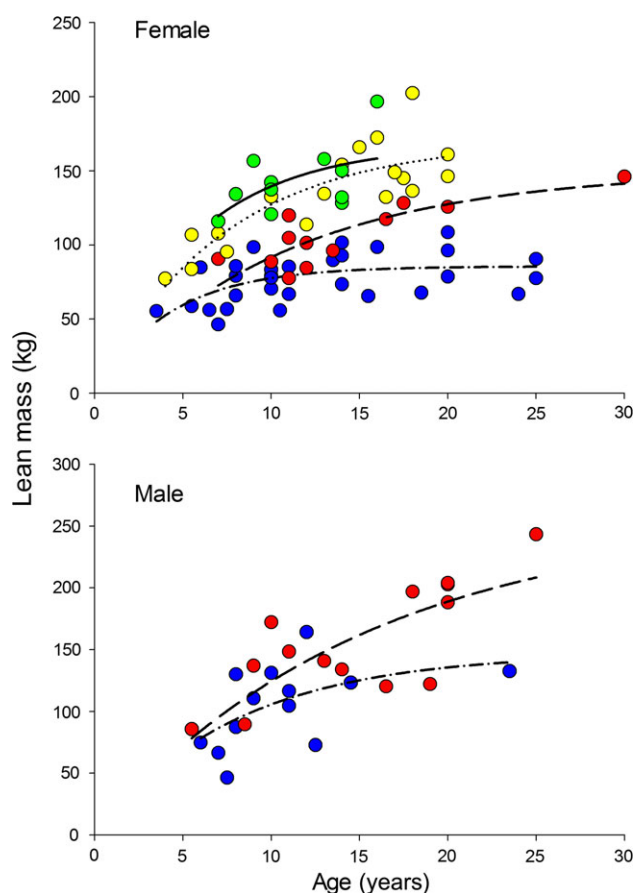


Figure 4 Relationships between estimated age of female brown bears and lean body mass in four Alaskan brown bear study areas, 2014–2016 (Gates: blue circles and dotted and dashed line; Lake Clark: red circles and dashed line; Kodiak: green circles and solid line; Katmai: yellow circles and dotted line).

of variation in lean mass exceeding remaining growth holds true for females: Gates (85.2%, 2.37), Kodiak (75.8%, 1.70) and Katmai (66.7%, 2.04; Fig. 5).

Within ecosystems, partitioning of nutritional resource has been documented between sympatric black and brown bears, between brown bear males and females, and amongst females. This partitioning can lead to differences in body size though not necessarily proportional body composition (i.e. percent body fat) (Ben-David, Titus & Beier, 2004; Belant *et al.*, 2006, 2010; Lafferty *et al.*, 2015; Mangipane *et al.*, 2017). Our study areas all showed broad variation in body size despite different levels of available nutritional resources, relative densities, and management regimes. It appears that within each population, a range of life-history strategies are being employed including, but not limited to, energy or risk minimizers (i.e. smaller bears) and bears that look to gain a physical advantage in direct competition (i.e. larger bears). Due to the short duration of our studies, we cannot assess if, within a population, greater investment in structural body size or lean body mass leads to larger litter sizes or improves cub survival.

Table 2 Results of pairwise multiple comparisons of morphological measurements of adult females across Alaskan brown bear populations

	Difference of means	<i>t</i>	<i>P</i>
Skull size (cm)			
Kodiak vs. Gates	8.669	6.878	<0.001
Katmai vs. Gates	8.283	6.422	<0.001
Lake Clark vs. Gates	5.902	5.397	<0.001
Kodiak vs. Lake Clark	2.767	2.121	0.107
Katmai vs. Lake Clark	2.381	1.786	0.150
Kodiak vs. Katmai	0.386	0.262	0.794
Body Length (cm)			
Kodiak vs. Gates	25.593	7.854	<0.001
Katmai vs. Gates	21.679	6.504	<0.001
Lake Clark vs. Gates	14.226	5.022	<0.001
Kodiak vs. Lake Clark	11.367	3.391	0.003
Katmai vs. Lake Clark	7.452	2.176	0.064
Kodiak vs. Katmai	3.914	1.034	0.304
Lean mass (kg)			
Kodiak vs. Gates	64.716	8.669	<0.001
Katmai vs. Gates	63.466	9.791	<0.001
Lake Clark vs. Gates	26.373	3.545	0.002
Kodiak vs. Lake Clark	38.343	4.289	<0.001
Katmai vs. Lake Clark	37.093	4.545	<0.001
Kodiak vs. Katmai	1.250	0.153	0.879

Gates of the Arctic National Park and Preserve = Gates; Kodiak National Wildlife Refuge = Kodiak; Katmai National Park and Preserve = Katmai; Lake Clark National Park and Preserve = Lake Clark.

There is a growing body of literature across a range of taxa identifying the importance of variation in behavior and personality to individual and population health, suggesting that populations of generalist species are often a collection of specialized individuals (Bolnick *et al.*, 2003, 2007; Wolf *et al.*, 2007; Biro & Stamps, 2008; Smith & Blumstein, 2008; Dall *et al.*, 2012). Differences in realized foraging niches within populations have been seen in brown bears (Leclerc *et al.*, 2016) as well as other species (e.g. wolves – Semmens *et al.*, 2009; sea lions – Villegas-Amtmann *et al.*, 2008; sea otter – Tinker *et al.*, 2012) and individual specialization may increase at higher population densities (Tinker *et al.*, 2012) as potential niche diversity increases with ecosystem complexity (i.e. foraging options). Lafferty *et al.* (2015) assessed the niche variation hypothesis in brown bear in Denali National Park and Preserve and noted among-individual variation in proportional contribution of salmon to bear diets. Proportional fall body fat did not vary with diet suggesting that utilization of varied dietary niches resulted in similar physiological condition (Lafferty *et al.*, 2015).

Larger males have been shown to have higher annual reproductive success but population density and relatedness are also important factors (Zedrosser *et al.*, 2007). Larger females from more productive populations tend to produce larger litters within populations, although the effect of body size is not well understood. Age of primiparity was related to overlap with the mother's home range and not body size or mass in Scandinavian brown bears (Stoen *et al.*, 2006), and litter size was

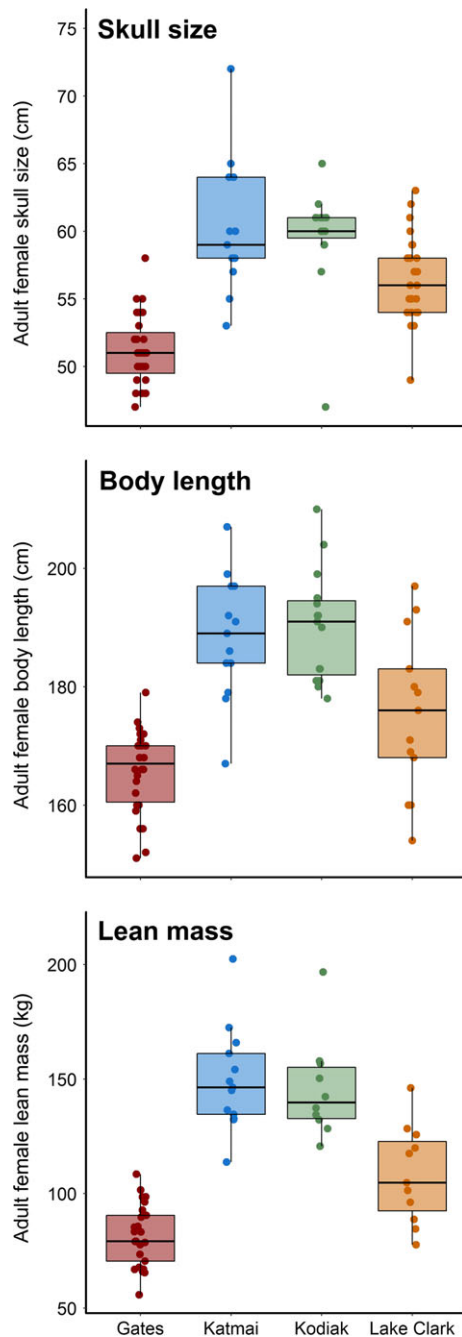


Figure 5 Box and whisker plots of skull size, body length, and lean body mass of adult female brown bears from four Alaskan brown bear study areas, 2014–2016. Each dot represents an individual bear. Boxes indicate the first and third quartiles, the bar indicates the median, and the whiskers delineate $1.5 \times$ interquartile range.

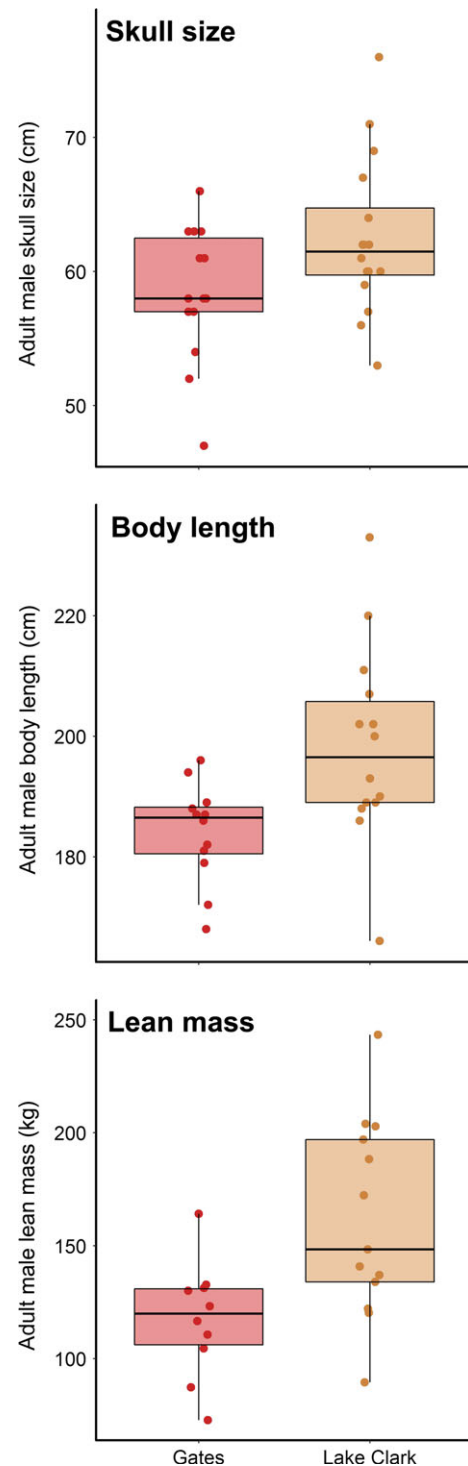


Figure 6 Box and whisker plots of skull size, body length, and lean body mass of adult male brown bears from two Alaskan brown bear study areas, 2014–2016. Each dot represents an individual bear. Boxes indicate the first and third quartiles, the bar indicates the median, and the whiskers delineate $1.5 \times$ interquartile range.

negatively correlated with yearling mass indicating that trade-offs likely occur between litter size and offspring growth (Gonzalez *et al.*, 2012). Relative to the interval between litters, females were more likely to retain low body weight yearlings and this additional maternal investment had a positive effect on yearling weight gain (Dahle & Swenson, 2003).

Relative to structural size, female brown bears ceased growth before males in both Gates and Lake Clark. Bartareau *et al.* (2011) reported the same pattern in brown bears from northern Canada and concluded this divergence was due to females dedicating resources to reproductive costs whereas males continued to invest in body growth. Gates was likely the most nutritionally limited of our four study areas, as females reached 97% of their maximum lean mass at 14.7 years of age. Males from Gates and Lake Clark and females from all other populations reached 97% of their maximum lean mass at 20 years of age or greater, which approaches or exceeds the typical lifespan of a bear (28 years, Bartareau *et al.*, 2011). Rode *et al.* (2010, 2013) reported declines in body metrics, growth rates, and productivity of polar bears with reduced access to sea ice, which is closely associated with availability of their primary prey (i.e. seals). Thus, reduced availability of nutritional resources can result in smaller, less productive bears, such as females in Gates.

The observed phenotypic plasticity within populations in both sexes is likely due to a combination of dietary specialization, individual behaviors related to risk tolerance or aversion, learned behavior, reproductive strategies, diversity and abundance of available resources, and population density (e.g. Lafferty *et al.*, 2015; Mangipane *et al.*, 2017). Generally, a population comprised of a diversity of specialized individuals may be more stable and thus resilient to perturbations that may occur at higher densities by minimizing intra-specific competition (Bolnick *et al.*, 2003). While changes in resource availability may affect individual body size, productivity, and population density, the phenotypic plasticity seen in the four populations assessed in this study suggests resilience to future changes in climate, habitat, growing season, or availability of specific food resources.

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Authors' contribution

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