

Geographic variation in size, growth, and sexual dimorphism of Alaska brown bears, *Ursus arctos*

Author(s): Thomas J. McDonough and Aaron M. Christ

Source: Journal of Mammalogy, 93(3):686-697.

Published By: American Society of Mammalogists

DOI: <http://dx.doi.org/10.1644/11-MAMM-A-010.1>

URL: <http://www.bioone.org/doi/full/10.1644/11-MAMM-A-010.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Geographic variation in size, growth, and sexual dimorphism of Alaska brown bears, *Ursus arctos*

THOMAS J. McDONOUGH* AND AARON M. CHRIST

Alaska Department of Fish and Game, Division of Wildlife Conservation, 3298 Douglas Place, Homer, AK 99603, USA (TJM)

Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518, USA (AMC)

* Correspondent: thomas.mcdonough@alaska.gov

We modeled the growth in skull size of brown bears (*Ursus arctos*) using 11,651 individuals across 6 regions in Alaska with the von Bertalanffy function. The study areas varied greatly in habitat types and included coastal areas in south-central Alaska, interior regions, and the most northern reaches of the species' North American range. The top-ranking model supported region- and sex-specific growth curves. The large differences in parameter estimates of asymptotic size and the growth coefficient across regions were likely influenced by variation in habitat quality, especially the availability of salmon (*Oncorhynchus* spp.), and these differences relate to other known life-history traits. Contrary to other studies of North American bears, we found a strong hyperallometric relationship in sexual size dimorphism (SSD) where SSD increased with asymptotic size. This relationship supports sexual selection as the driving mechanism of SSD in brown bears. However, the variable intensity of sexual selection across these regions, as demonstrated through hyperallometry in SSD, is likely influenced by proximate factors such as variable food resources and population densities that vary by more than 2 orders of magnitude. The ecological implications of the variation in growth, size, and SSD of brown bears across their Alaskan range are substantial and need to be recognized and incorporated into area-specific management and conservation strategies.

Key words: bear, growth, hyperallometry, Rensch's rule, sexual dimorphism, *Ursus arctos*, von Bertalanffy

© 2012 American Society of Mammalogists

DOI: 10.1644/11-MAMM-A-010.1

Geographic differences in growth and body size within a species can be influenced by various physiological, ecological, and evolutionary constraints (Clutton-Brock and Harvey 1983; Marquet and Taper 1998; Peters 1983). The omnivorous diet of brown bears (*Ursus arctos*) allows them to live in diverse and disparate ecological conditions and makes them apt subjects for the investigation of geographic variation. Energy availability for brown bears in Alaska varies from southern coastal areas with abundant salmon (*Oncorhynchus* spp.) and high primary productivity, to interior and northern regions with harsher climates and lower quality food resources (Ferguson and McLoughlin 2000; Miller et al. 1997). Nutritional plane affects body size in bears as well as several other life-history and demographic traits including population density, growth, age at 1st reproduction, and reproductive rate (Blanchard 1987; Bunnell and Tait 1981; Derocher and Stirling 1996, 1998; Hilderbrand et al. 1999b; Mowat and Heard 2006). Theory predicts that larger and faster growing females reproduce earlier, have higher natality rates, and

produce offspring of better quality than do smaller females (Sterns 1992), and this holds true empirically for brown bears (Hilderbrand et al. 1999b; Mowat and Heard 2006; Zedrosser et al. 2006). Therefore, quantifying growth patterns in the body size of bears can allow for meaningful comparisons of life-history patterns between populations or for tracking changes in a single population over time.

Previous research on brown bears has shown that skull size and body size varied greatly across Alaska (Hall 1984; Hilderbrand et al. 1999b; Rausch 1963). This variation has influenced the use of different common names according to where the bears reside. Southern coastal populations of Alaska have large bears that are generally termed "brown" bears whereas interior and northern populations are commonly categorized as the smaller sized "grizzly" bears (Schwartz



et al. 2003). However, “brown” and “grizzly” bears are considered the same species throughout their range. Rausch (1963) 1st suggested the availability of salmon in the diet as the main putative cause of body-size variation in brown bears. This hypothesis has since gained empirical support with a greater amount of salmon in the diet contributing to both larger body size and higher fitness in brown bears (Hilderbrand et al. 1999b; Mowat and Heard 2006; Robbins et al. 2007). Variation in size and growth of brown bears could potentially have a genetic component. However, large coastal “brown” bear populations do not have absolute barriers to gene flow with physically smaller “grizzly” bears of inland areas and differences in body size have been attributed to variation in the availability of salmon, not genetic differences (Hilderbrand et al. 1999a; Paetkau et al. 1998a; Robbins et al. 2004). Kodiak Island is an exception in that bears have been isolated from the mainland population for about 10,000 years and show low genetic diversity (Paetkau et al. 1998a, 1998b; Talbot and Shields 1996). Paetkau et al. (1998a) noted that the genetic uniqueness of Kodiak Island bears might account for their unusually wide skulls compared to bears in similar coastal habitats. Salmon are not an available food source in northern Alaska, and although bears have access to abundant caribou (*Rangifer tarandus*) populations in some parts of the region (Mowat and Heard 2006; Reynolds and Garner 1987), access to these migratory caribou varies over space and time, resulting in bears having a primarily vegetarian diet (Hechtel 1985). In addition, bears at high latitudes have longer denning periods due to more severe climatic conditions (Ferguson and McLoughlin 2000; Kojola and Laitala 2001; Rausch 1969). A low-quality diet and a reduced period of active foraging would reduce the ultimate size bears can attain (Rode et al. 2001; Welch et al. 1997) and also influence productivity and population density.

The availability of high-quality resources also may influence the rate of somatic growth. Higher growth rates in polar bears (*Ursus maritimus*) were suggested to be associated with greater access to prey (Derocher and Stirling 1998; Kingsley 1979). Zedrosser et al. (2006) suggested differences in growth rate in brown bears were related to resource availability. Size and growth of brown bears in northern Alaska and Canada varied little (Kingsley et al. 1988) suggesting populations with similar ecological constraints share similar rates of growth and ultimate body size. Growth in body size has been shown to be substantially complete near the age at 1st reproduction for female brown bears (Glenn 1980; Kingsley et al. 1983, 1988) and female polar bears (Derocher and Stirling 1998; Derocher and Wiig 2002). Fast growth and, therefore, early maturation would potentially increase fitness levels (He and Stewart 2001; Sterns 1992; Stearns and Koella 1986).

Sexual size dimorphism (SSD) is universal in North American bears (Derocher et al. 2005; Kingsley et al. 1988; Mahoney et al. 2001). Variation in SSD within a species can have important implications for its ecology, behavior, population dynamics, and the evolution of life-history traits

(Issac 2005). Three main mechanisms are thought to potentially influence SSD; sexual selection, different sex roles in reproduction, and intersexual food competition (see review in Fairbairn et al. 2007). However, there is not likely a single selective force directing SSD (Isaac 2005). Sexual selection through mate competition is often cited as the principal mechanism driving SSD for species with a male-bias in size (Andersson 1994; Darwin 1871; Ralls 1977; Trivers 1972). In brown bears, delayed estrus due to prolonged offspring care limits the number of receptive females available for breeding, ostensibly creating a competitive advantage for larger body size in males (Clutton-Brock et al. 1977; Emlen and Oring 1977; Fairbairn et al. 2007). Indeed, male brown bears that attained a large size showed a higher reproductive success than smaller males (Zedrosser et al. 2007). Furthermore, as mate competition between males increases with population density, the intensity of sexual selection also increases (Capellini 2007; Leutenegger 1978; Weckerly 1998) potentially influencing the mating strategy employed (Emlen and Oring 1977). Brown bears do not employ the same mating strategy across their range. The mating strategy may be promiscuous (Schwartz et al. 2003), polyandrous (Hornocker 1962), or polygynous (Dahle and Swenson 2003). Therefore, determining the degree and patterns of SSD across populations may provide insights as to the type of mating strategy employed across populations.

Along with sexual selection as a mechanism for causing SSD, brown bears also have different sex roles in reproduction, where females invest energy producing and caring for young and therefore, have fewer resources to invest in growth and body size. However, direct intersexual competition for food is not a likely mechanism influencing SSD in brown bears because of their diverse and omnivorous diet. Rather, females with cubs have been found to segregate from males and forage on lower quality foods purportedly to avoid infanticidal males (Ben-David et al. 2004). Rode et al. (2006) argued that SSD was responsible for sexual segregation because female brown bears are smaller than males and can use poorer quality habitats to avoid infanticide. As in some mustelid species (Erlinge 1979; Holmes and Powell 1994; Moors 1980), intersexual resource partitioning in brown bears is likely the result of SSD, not a mechanism causing SSD.

Along with the traditional mechanisms that may drive SSD outlined above, proximate environmental factors may shape the magnitude of SSD within populations (Cox et al. 2008). For example, Ralls and Harvey (1985) suggested regional differences in the abundance of prey affected adult size much more in male weasels (*Mustela erminea* and *M. frenata*) than in females, thus contributing to geographic variation in SSD. A decrease in population density caused greater SSD in bighorn sheep (*Ovis canadensis*) purportedly due to reduced resource competition (LeBlanc et al. 2001). In these studies, environmental variables are potential proximate causes of SSD, whereas the ultimate mechanism is governed by sexual selection. Accurate explanations of the ultimate causes of SSD

may be dependent on understanding the underlying proximate mechanisms (Watkins 1996). If sexual selection is the ultimate mechanism driving SSD, dimorphism should increase with body size across regions (hyperallometry or Rensch's rule—Abouheif and Fairbairn 1997; Fairbairn 1997; Fairbairn and Preziosi 1994; Lindenfors et al. 2007; Rensch 1960), while proximate factors would likely shape the magnitude of the hyperallometry. North American bears are fitting subjects to show hyperallometry in SSD due to the role sexual selection likely plays in dictating sex-specific growth and size, and the variability of proximate factors, such as food resources and population densities, across their distribution. However, hyperallometry in SSD has not been found in polar bears (Derocher et al. 2005) or black bears (*Ursus americanus*—Mahoney et al. 2001). Stirling and Derocher (1990) addressed this question for brown bears, but their regression analysis violated the assumption of mathematical independence of the variables. Therefore, to our knowledge, hyperallometry in SSD has not been adequately tested in brown bears. We believe that brown bears that live in extremely disparate habitats with variation in population densities exceeding 2 orders of magnitude may show hyperallometry in SSD, whereas polar bears and black bears that live in relatively more homogeneous habitats with lower variation in population densities would not.

Rausch (1963) and Hall (1984) qualitatively identified geographic variation in skull size of brown bears, and subsequent studies have modeled growth (Kingsley et al. 1988; Mowat and Heard 2006; Ohdachi et al. 1992; Zedrosser et al. 2006). However, no study has modeled growth in brown bears across different areas in Alaska. We compared growth of brown bears in 6 regions of Alaska that include a diversity of habitats. Our objective was to evaluate geographic variation in size and growth of brown bears using the information-theoretic approach, specifically identifying patterns in the variation of growth curves, asymptotic skull size (a measure of the average maximum size attained by the population), and the growth rate coefficient. Because environmental variation can affect body size (Hilderbrand et al. 1999b; Mowat and Heard 2006) and growth rate (Zedrosser et al. 2006), we hypothesized, 1st, that bears in areas with high primary productivity and access to salmon would show greater asymptotic size and faster growth than bears living in harsher environments. Through the principal of parsimony, we further refined this hypothesis and predicted that the variation in growth rate and asymptotic size would be best described by combining regions as aggregate groups of coastal populations versus noncoastal or interior populations (i.e., “grizzly” versus “brown” bears). Given the likelihood that sexual selection and proximate factors such as environmental variation and population density influence male and females bears differently, we also hypothesized, 2nd, that an interaction between sex and region would improve models describing size and growth in brown bears. Regarding SSD, we hypothesized, 3rd, that an increase in adult size across regions would result in an increase in SSD (i.e., hyperallometry in SSD).

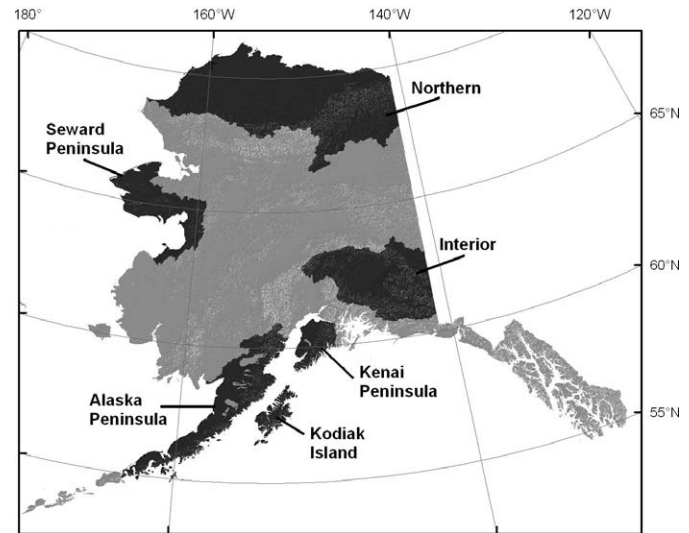


FIG. 1.—Six regions in Alaska used to compare growth of brown bears.

MATERIALS AND METHODS

Study areas.—Our study focused on 6 regions in Alaska (Fig. 1) with large differences in habitat types and therefore large differences in bear densities and life-history patterns (Table 1). Three areas are coastal habitats in south-central Alaska (Alaska Peninsula, Kodiak Island, and Kenai Peninsula), where bears are large (Hilderbrand et al. 1999b) and have access to salmon. These are all considered large-bodied and high-density “brown” bear populations. In 3 contrasting areas, including the Seward Peninsula, interior Alaska, and northern Alaska, bears have greatly reduced or no access to salmon and overall habitat quality is lower than in the 3 southern coastal regions (Miller et al. 1997). Bears in these areas are considered “grizzly” bears with smaller body size and lower population densities.

The Alaska Peninsula (87,000 km²) is 800 km long, with the Bering Sea and Bristol Bay to the north and the Gulf of Alaska to the south. It includes Katmai National Park and the McNeil River area, which hold some of the highest concentrations of brown bears in the world (Aumiller and Matt 1994). Kodiak Island (10,000 km², including Afognak Island) is in the Gulf of Alaska and lies about 40 km southeast of the Alaska Peninsula. The Kenai Peninsula (24,000 km²) is bounded by Prince William Sound, the Gulf of Alaska, and Cook Inlet. These 3 southern coastal areas have abundant runs of all 5 species of Pacific salmon, which are heavily used by brown bears (Barnes 1990; Gende et al. 2001; Hilderbrand et al. 1999a, 1999b; Rode et al. 2006). The Seward Peninsula region (65,000 km²) includes drainages around Norton Sound and part of Kotzebue Sound on the west-central coast of Alaska where salmon runs are highly variable between years and are not as abundant or available to bears as in the southern coastal areas (Miller et al. 1997). The interior Alaska region (120,000 km²) is south of the Alaska Range, east of the Wrangell Mountain range, and includes parts of the Chugach and Talkeetna mountains to the south. Bears in this region

TABLE 1.—Population densities (bears/1,000 km²) and selected life-history traits from past studies of brown bears (*Ursus arctos*) within 6 regions in Alaska.

Region	Density	Mean litter size	Mean age at 1st litter (years)	Birth interval (years)
Kodiak Island	292–343 ^a	2.4 ^b	6.4 ^b	4.0 ^b
Alaska Peninsula	191–551 ^c	2.3 ^d	6.3–7.2 ^d	3.6 ^e
Kenai Peninsula	—	2.2 ^f	—	3.2 ^f
Seward Peninsula	29 ^g	—	—	—
Interior Alaska	11 ^c –41 ^h	2.1 ^d	5.6 ^d	4.1 ⁱ
Northern Alaska	4 ^j –24 ^k	1.6–2.0 ^k	7.3–9.7 ^l	4.1 ^k

^a Barnes and Smith 1998.

^b Van Daele 2007.

^c Miller et al. 1997.

^d Miller et al. 2003.

^e Glenn et al. 1976.

^f Farley 2005.

^g Miller and Nelson 1993.

^h Miller 1997.

ⁱ Miller 1993.

^j Crook 1971.

^k Reynolds and Hechtel 1984.

^l Reynolds and Garner 1987.

have either no or limited access to salmon (Hilderbrand et al. 1999b). The northern Alaska region (265,000 km²) encompasses the northernmost distribution of North American brown bears and includes parts of the eastern Brooks Range as well as treeless tundra north of the range. Bears in this region have no access to salmon (Hilderbrand et al. 1999b; Mowat and Heard 2006), the nondenning period at these high latitudes is short, and available food is of relatively low quality (Hechtel 1985).

Data.—More than 11,650 skulls were measured from 1969 to 2009 from brown bears killed by hunters or by other human causes (Fig. 2; Table 2). Skull size has been used extensively as an index for body size in bears (Derocher et al. 2005; Meiri et al. 2004; Mowat and Heard 2006; Zedrosser et al. 2006) and has been reported as a better measure for quantifying size and growth compared to other body morphometry because of lower measurement error (Eason et al. 1996; Glenn 1980). Brown bears can gain 70% of their spring body mass by the fall (Kingsley et al. 1983) and muscle strength also can vary significantly seasonally (Lohuis et al. 2007). This level of seasonal variation renders measures of mass or bulk much more problematic in assessing size-at-age than linear measurements. We used linear skull measurements as indexes of body length (Derocher and Stirling 1998; Rode et al. 2010) and assumed this to be an assessment of overall body size. Determining what traits male bears assess in each other when competing for mates is important when addressing questions about causes and consequences of SSD. Inferences made about measurements should ideally have a theoretical context (representational measurement theory—Houle et al. 2011). However, given that outcomes of male : male competition for mates (a likely mechanism causing SSD) are determined by a complex and uncertain mix of size, behavior, condition, age, density of available females, density of competing males, experience, prior contact, and other unknown variables, pragmatic measures are needed to address questions about complex interactions (Houle et al. 2011). Given the uncertain

complexity of how male brown bears assess each other during mate competition, we believe, as exemplified in other studies (Derocher et al. 2005; Rode et al. 2010), that a valid index of body size can be used to further our understanding of complex morphological relationships such as SSD.

State regulations in place since the late 1960s have required that an employee of the Alaska Department of Fish and Game inspect the skull and hide of every brown bear taken by humans within 30 days of the kill. Data collected include specific location of the kill, sex determined by inspecting evidence retained on the hide, and skull measurements of length and width. Skull length is defined as the distance between the anterior surface of the premaxillary bone to the most posterior dorsal process of the sagittal crest. Skull width is defined as the widest breadth across the zygomatic arches.

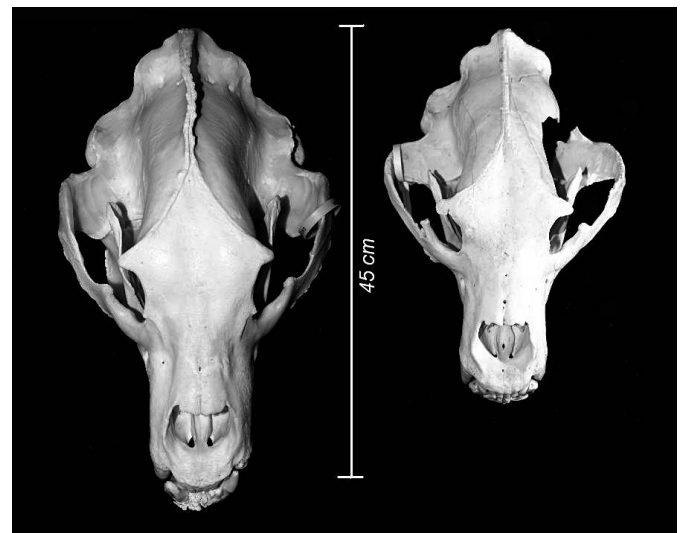


FIG. 2.—Dorsal view of 2 skulls of male *Ursus arctos* showing the large size difference between a 19-year-old coastal “brown” bear from the Kenai Peninsula (left) and a 22-year-old “grizzly” bear from interior Alaska (right). Photograph by M. Renner.

TABLE 2.—Sample sizes of skulls of brown bears (*Ursus arctos*) measured from 1969 to 2009 used to model growth from 6 regions in Alaska.

Region	Males	Females
Alaska Peninsula	3,175	1,442
Interior Alaska	1,286	829
Kenai Peninsula	152	121
Kodiak Island	1,992	868
Northern Alaska	537	255
Seward Peninsula	638	356
Total	7,780	3,871

Measurements were taken to the nearest 1/16 inch (1.6 mm). The age of each bear was estimated in whole years by counting annual cementum layers in the root of a premolar tooth (Willey 1974). Our analysis only included teeth aged with the highest precision rating and were assumed to be aged accurately (Matson et al. 1993). Fractional age was calculated to the day using the reported date of death and assuming day of birth was 1 January. Skull measurements collected over 40 years likely hold significant temporal variation due to variability in food availability, food quality, population densities, and other sources that would affect the growth and body size in cohorts of brown bears. Accurate measures of environmental variability over long time periods used to analyze changes in size and growth in bears are rare (Rode et al. 2010). Without area-specific data on temporal environmental variation (e.g., food availability) across our large study areas, which are largely unknown and likely vary greatly within regions, we were unable to incorporate this likely source of variation into our analysis. We acknowledge that bears taken by hunters that ostensibly select the largest animal available may be a biased sample. However, we assume that any potential bias would be consistent for all populations allowing for valid comparisons of the data across study areas. This study conformed to guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

Statistical analysis.—Skull measurements were analyzed with nonlinear regression (PROC NL MIXED—SAS Institute Inc. 2003) fitting the von Bertalanffy growth function (von Bertalanffy 1938, 1960):

$$L_a = L_\infty - (L_\infty - L_0)e^{-ka},$$

where L_a is the skull size at age a , L_∞ is the asymptotic or average maximum skull size, L_0 is the skull size at birth, k is the growth coefficient, and e is the base of the natural logarithm. This version of the von Bertalanffy function also has been called the monomolecular function when used to model growth in weight (Garel et al. 2006, 2009). To minimize bias when fitting models with a lack of data during the early growth period (Garel et al. 2006, 2009; Shrader et al. 2006; Solberg et al. 2008), skull size at birth was fixed by taking the average skull size from 6 neonate brown bears < 1 week old measured from collections at the Alaska Department of Fish and Game, the American Museum of Natural History, the Museum of Southwestern Biology, and the Royal Ontario Museum. The

mean neonate skull length was 5.62 cm (coefficient of variation [CV] = 4.5%); the mean neonate skull width was 3.44 cm (CV = 16.2%). The relatively low variation in neonate skull measurements is likely due to the short 6- to 8-week gestation period in brown bears, which limits fetal development (Pasitschniak-Arts 1993). Therefore, we believe our sample adequately describes size at birth.

Variation in growth and asymptotic size by region, sex, and their interaction were explored and competing models were assessed by Akaike's information criterion, with a correction for sample bias (AIC_c—Akaike 1973; Burnham and Anderson 2002), and model probabilities (Burnham et al. 2010). We did not include models where asymptotic size was constant across sexes or regions because of a posteriori knowledge of SSD and regional differences (Hilderbrand et al. 1999b). Also, we did not include models where growth rate was equal across sexes because of a posteriori knowledge of intersexual variation in growth rate where male bears grew slower to achieve their greater size (Kingsley et al. 1988; Mowat and Heard 2006). Additionally, to assess the hypothesis that bears could be described as coastal versus noncoastal or interior (i.e., “grizzly” versus “brown” bears), models using these 2 aggregated regions were explored along with models with 6 distinct regions. Interactions between region and sex for both asymptotic skull size and growth coefficient parameters were modeled as a linear offset in male size by region so the full model was:

$$L_\infty(\text{region}, \text{sex}) = \alpha_{\text{region}} + I_{\text{sex}=\text{male}}(\beta + \gamma_{\text{region}})$$

$$k(\text{region}, \text{sex}) = \delta_{\text{region}} + I_{\text{sex}=\text{male}}(\varepsilon + \eta_{\text{region}}),$$

where α , β , γ , δ , ε , and η are all regression parameters to be estimated and $I_{\text{sex}=\text{male}}$ is an indicator function, which equals 1 for males and 0 for females. The growth coefficient (k) has units of reciprocal age and, although comparisons across populations are valid, is difficult to interpret biologically. To assess k in a biological context, we used age when 97% of asymptotic skull size was attained to compare growth patterns of bears across regions (Derocher and Stirling 1998; Rode et al. 2010).

We assessed SSD by modeling a linear relationship between male and female asymptotic skull size from each region for both skull length and width with the model:

$$L_\infty(\text{region}, \text{sex}) = \alpha_{\text{region}} + I_{\text{sex}=\text{male}}(\beta + \gamma * \alpha_{\text{region}})$$

$$k(\text{region}, \text{sex}) = \delta_{\text{region}} + I_{\text{sex}=\text{male}}(\varepsilon + \eta_{\text{region}}).$$

A hyperallometric relationship would be supported if the slope of this relationship is significantly >1 (Blackenhorn et al. 2006; Lindenfors et al. 2007). The β parameter allows for a common male increase in asymptotic size and is essentially the intercept for the relationship between male and female asymptotic size. Directly modeling the linear relationship in this way incorporates the variability in the estimated parameters in contrast to simply regressing the point estimates of the asymptotic size parameters, which could lead to increased type I errors.

TABLE 3.—Model selection results using the von Bertalanffy function for skull growth in brown bears. Model structure of asymptotic skull size (L_{∞}) and the growth coefficient (k) were allowed to vary by 6 regions (Reg), sex (Sex), and their interaction. Region also was allowed to vary by 2 aggregate categories of coastal versus interior ($\text{Reg}_{(c \vee i)}$). Shown are the number of parameters for L_{∞} , k , and the variance (V) for each model; Akaike information criterion corrected for small sample sizes (AIC_c); difference of AIC_c from the lowest model value in the suite (ΔAIC_c); and model weights (ω_i s).

Model structure		No. parameters				Skull width			Skull length		
L_{∞}	k	L_{∞}	k	V^a	Total	AIC_c	ΔAIC_c	ω_i	AIC_c	ΔAIC_c	ω_i
Reg \times Sex	Reg \times Sex	12	12	12	36	41,489	0	1.0	49,782	0	1.0
Reg \times Sex	Sex	12	2	12	26	41,846	357	0	49,984	202	0
Reg \times Sex	Reg	12	6	12	30	42,764	1,275	0	50,792	1,010	0
Reg \times Sex	Constant	12	1	12	25	43,213	1,724	0	51,059	1,277	0
$\text{Reg}_{(c \vee i)} \times \text{Sex}$	$\text{Reg}_{(c \vee i)} \times \text{Sex}$	4	4	4	12	43,709	2,220	0	50,863	1,081	0
$\text{Reg}_{(c \vee i)} \times \text{Sex}$	Sex	4	2	4	10	44,019	2,530	0	51,110	1,328	0
$\text{Reg}_{(c \vee i)} \times \text{Sex}$	$\text{Reg}_{(c \vee i)}$	4	2	4	10	44,769	3,280	0	51,792	2,010	0
$\text{Reg}_{(c \vee i)} \times \text{Sex}$	Constant	4	1	4	9	45,155	3,666	0	52,089	2,307	0
Sex	Reg \times Sex	2	12	12	26	44,509	3,020	0	53,020	3,238	0
Sex	Reg	2	6	12	20	45,657	4,168	0	54,074	4,292	0
Sex	$\text{Reg}_{(c \vee i)} \times \text{Sex}$	2	4	4	10	46,030	4,541	0	53,927	4,145	0
Sex	Sex	2	2	2	6	47,868	6,379	0	56,408	6,626	0
Sex	Constant	2	1	2	5	48,813	7,324	0	57,146	7,364	0

^a Parameterization allowed both region- and sex-specific variances when region was included in the model.

RESULTS

We used the von Bertalanffy equation to model growth of brown bears from 6 regions of Alaska (Fig. 1). The top-ranking model with the lowest AIC_c value supported an interaction between region and sex for both parameters (asymptotic size and growth coefficient) and, therefore, region- and sex-specific curves (Table 3). The hypothesis that size and growth would be best described through aggregate groups of coastal versus noncoastal or interior bears (i.e., “grizzly” versus “brown” bears) was not supported (Table 3). The top model not only minimized the information lost compared to the other models but had all the evidence (model probability = 1.0), precluding the need to calculate evidence ratios or multimodel inference (Table 3). Differences in growth curves across the 6 regions were due to variation in either the growth coefficient or asymptotic size, or both parameters (Figs. 3 and 4).

Geographic variation in asymptotic size.—The percent difference across regional estimates of asymptotic skull length in our study was 15% for female brown bears and 18% for males (Fig. 3A). The percent difference across regional estimates of asymptotic skull width was 18% for females and 25% for males (Fig. 3B). Bears from the 3 southern coastal populations (Kodiak Island, Alaska Peninsula, and Kenai Peninsula) attained much larger asymptotic skull size than the regions of lower habitat quality (Seward Peninsula, interior Alaska, and northern Alaska; Fig. 3). However, differences were not discrete; the model with 2 aggregate regions of coastal (Kodiak Island, Alaska Peninsula, and Kenai Peninsula) and noncoastal or interior areas (northern Alaska, interior Alaska, and Seward Peninsula) received no evidentiary support (Table 3). Alaska Peninsula bears showed the greatest asymptotic skull length but Kodiak Island bears showed the greatest asymptotic skull width (Fig. 3). Northern Alaska bears had the smallest asymptotic skull size for both

sexes (Fig. 3). Of the 30 regional comparisons made for both skull length and width of male bears, the only pairwise comparisons that showed no significant differences for asymptotic size were for the skull width between Kenai Peninsula and Alaska Peninsula bears ($t_{11,651} = 0.4$, $P = 0.70$), and skull length between Kodiak Island and Kenai Peninsula bears ($t_{11,651} = 1.9$, $P > 0.05$). Of the 30 comparisons made across regions for both length and width for female bears, the only pairwise comparison across regions that showed no significant differences for asymptotic size were for the skull width between Seward Peninsula and interior Alaska females ($t_{11,651} = 0.5$, $P = 0.63$). All other pairwise comparisons across regions for both sexes and both skull measurements were significantly different (all tests $P \leq 0.02$).

Geographic variation in growth coefficients.—The age when 97% of the asymptotic size was achieved allows the growth coefficient to be interpreted biologically. The percent difference across regions for the age to achieve 97% of asymptotic length was 24% for females and 21% for males; asymptotic width was 38% for females and 32% for males (Fig. 4). Males had lower growth coefficients than females, resulting in a greater age to achieve 97% of asymptotic size (Fig. 4). Across all regions, males took 1.4–2.3 years longer to reach 97% of asymptotic skull length, and 2.0–4.1 years longer to attain 97% of asymptotic skull width than did females (Fig. 4).

In contrast to differences in the estimates of asymptotic size, there were many similarities in the age to achieve 97% of asymptotic size across regions (Fig. 4). However, there were some notable differences. Growth in the 3 southern coastal populations was not similar. Kenai Peninsula females reached 97% of asymptotic skull length significantly faster than Alaska Peninsula ($t_{11,651} = 5.2$, $P < 0.0001$) and Kodiak Island females ($t_{11,651} = 4.0$, $P < 0.001$) as did Kenai

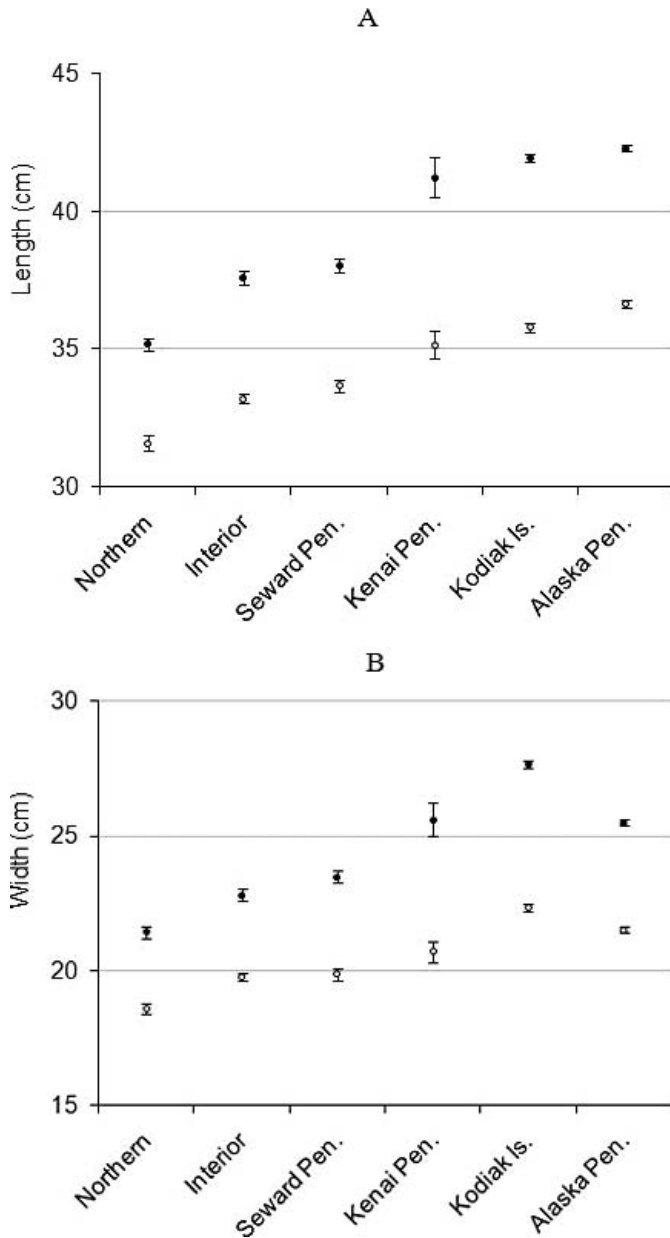


FIG. 3.—Estimates of asymptotic skull A) length and B) width for female (open circles) and male (filled circles) brown bears ($\pm 95\%$ CI) derived from region- and sex-specific von Bertalanffy growth functions from 6 regions of Alaska.

Peninsula males over Alaska Peninsula ($t_{11,651} = 5.2$, $P < 0.0001$) and Kodiak Island males ($t_{11,651} = 5.7$, $P < 0.0001$). For skull width, Kenai Peninsula males reached 97% of asymptotic size significantly faster than Alaska Peninsula ($t_{11,651} = 5.8$, $P < 0.0001$) and Kodiak Island males ($t_{11,651} = 8.5$, $P < 0.0001$). Kenai Peninsula females reached 97% of asymptotic skull width significantly faster than bears from all other regions (all tests $P < 0.0001$).

Sexual dimorphism.—Males attained a much larger skull size than females (Fig. 3). However, there were varying degrees of sexual dimorphism in skull size across the 6 regions, with the males showing 11–17% greater asymptotic skull length and 15–24% greater asymptotic skull width than

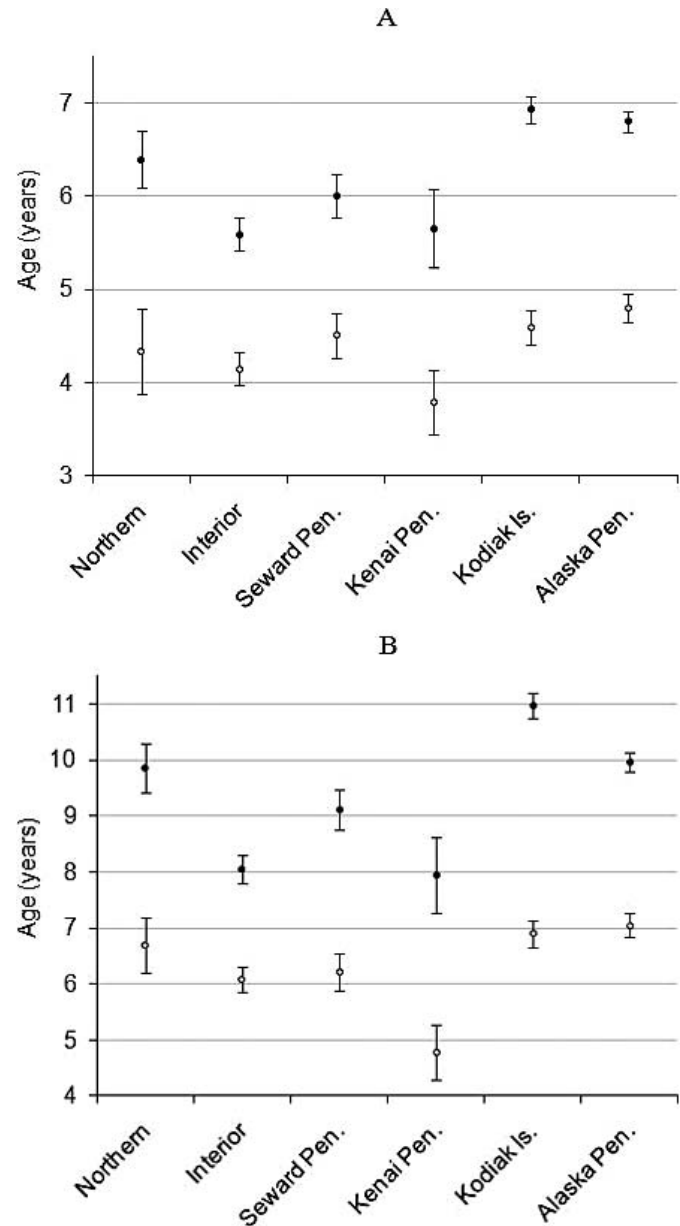


FIG. 4.—Age when 97% of asymptotic size is attained for skull A) length and B) width for female (open circles) and male (filled circles) brown bears ($\pm 95\%$ CI) derived from region- and sex-specific von Bertalanffy growth functions from 6 regions of Alaska.

females (Fig. 5). The test for a hyperallometric relationship was supported with the slope of the relationship between male and female asymptotic size significantly >1 for both skull length ($\gamma = 1.49$, 95% confidence interval [95% CI]: 1.41–1.58) and skull width ($\gamma = 1.69$, 95% CI: 1.58–1.81).

DISCUSSION

Geographic variation.—Our results confirmed previous research (Hall 1984; Rausch 1963) showing significant regional variation in skull size of brown bears. However, our study quantified this variation using known-aged bears and growth curves and is also the 1st study to show a

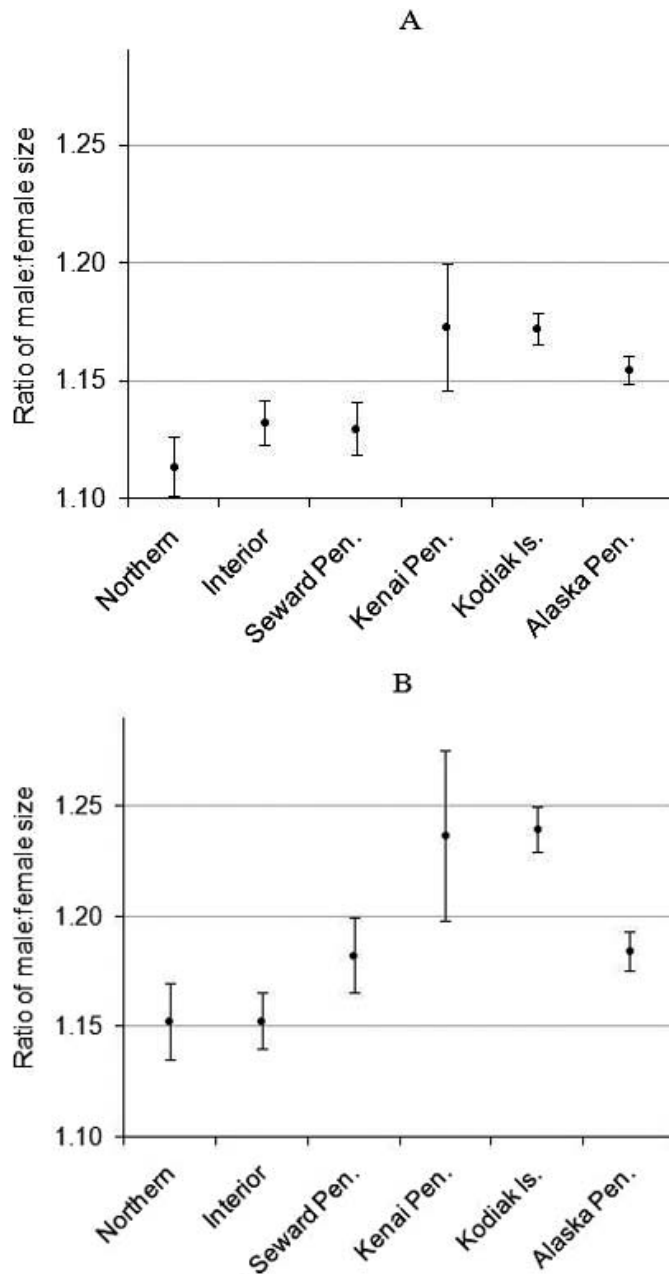


FIG. 5.—Ratio of male : female asymptotic skull A) length and B) width (\pm 95% CI) derived from region- and sex-specific von Bertalanffy growth functions from 6 regions of Alaska.

hyperallometric relationship in SSD of brown bears in Alaska. Aside from a purported genetic influence on the large skull width of Kodiak Island bears (Fig. 3B; Paetkau et al. 1998a), the phenotypic plasticity in skull size we report reflects different nutritional planes across the 6 regions (Hilderbrand et al. 1999b; Mowat and Heard 2006). The correspondence of nutritional condition in bears to life-history traits such as body size, age at 1st reproduction, litter size, and the interval between litters has been well established (Blanchard 1987; Bunnell and Tait 1981; Ferguson and McLoughlin 2000; Hilderbrand et al. 1999b; Mowat and Heard 2006; Schwartz et al. 2003). Although bears with the largest estimates of asymptotic size (Fig. 3) came from locations with higher

densities and life-history patterns reflecting greater population productivity (Table 1), variation in growth rates was unpredicted.

Asymptotic skull size was greatest in coastal bears, but growth rates were not higher in coastal areas (Fig. 3 versus Fig. 4). Although it is more costly to grow to a larger size, we hypothesized that habitats filled with lipid-rich resources would allow individuals to grow to a larger size at a faster rate than bears in environments with few lipid-rich resources, longer denning times, and reduced primary productivity. This was not the case (Fig. 4). Also, the lack of support for aggregate groups of coastal versus noncoastal or interior bears (i.e., “grizzly” versus “brown” bears) was exemplified by the variation in growth found within the 3 southern coastal areas where bears attain a large size. Specifically, both male and female bears from the Kenai Peninsula grew to 97% of maximum skull size significantly faster than the other southern coastal populations (Fig. 4). Although the exact cause of this relatively fast growth is unknown, it may be tied to food availability to a greater degree than we predicted. Bears on the Kenai Peninsula were shown to have similar or greater amounts of salmon in their diets compared to populations on Kodiak Island and the Alaska Peninsula (Hilderbrand et al. 1999b) but greater levels of terrestrial meat in their diet than bears from those populations (Mowat and Heard 2006). The difference of terrestrial meat in the diet of Kenai Peninsula bears may contribute to their growth rate exceeding that of bears without terrestrial meat but still with abundant salmon. Although terrestrial meat was not found to significantly affect body size, there may be more seasonality in the consumption of terrestrial meat compared to that of salmon (Mowat and Heard 2006). If the use of terrestrial meat comes early in the spring before salmon is available and other food sources are scarce, access to terrestrial meat at this time may contribute to fast growth. Future studies that determine the seasonal use of terrestrial meat on the Kenai Peninsula may help reveal contributions this food source has on somatic growth. Clearly, the Kenai Peninsula, as judged from our analysis showing fast growth and large size, and judged from other studies comparing the utilization of high-quality foods (Hilderbrand et al. 1999b; Mowat and Heard 2006), is an especially rich environment for bears.

It was unexpected to find such a fast growth rate in interior Alaska bears compared to other regions (Fig. 4). There has been heavy hunting pressure on interior Alaska bears for decades (Miller 1993, 1997; Miller et al. 2003). The high growth rate of bears from this region may relate to a positive density-dependent response to heavy hunting pressure (Fowler 1988). Previous work suggesting density-dependent effects on brown bear populations showed lower growth rates in the area with lower densities (Zedrosser et al. 2006). However, the populations in their study have had a long history of exploitation and are more limited in potential population densities than bears in interior Alaska (Zedrosser et al. 2011).

Sexual dimorphism.—The hyperallometric relationship (Rensch’s rule—Abouheif and Fairbairn 1997; Rensch 1960)

we found in our study, where SSD increases with body size, is widely accepted to be caused by sexual selection (Fairbairn 1997). However, hyperallometry in SSD was not found in polar bears (Derocher et al. 2005) or black bears (Mahoney et al. 2001) despite a high degree of SSD in these species. The magnitude of the hyperallometry in SSD of brown bears may be influenced by proximate environmental factors such as variable environmental conditions (Ferguson and McLoughlin 2000). Specifically, coastal areas with high-quality food resources (Hilderbrand et al. 1999b; Mowat and Heard 2006) produce large bears (Fig. 3) and these populations appear to respond to these proximate cues by showing greater SSD than interior or northern populations (Fig. 5). Another likely proximate factor influencing hyperallometry in SSD is the substantial variation in population densities, which exceeds 2 orders of magnitude in Alaska (Table 1). These densities are more variable than those found across studied polar bear or black bear populations (Derocher et al. 2005; Mahoney et al. 2001) and would logically influence the intensity of sexual selection and, therefore, the magnitude of the SSD across regions. The highest dimorphism ratios (Fig. 5) and the largest asymptotic sizes (Fig. 3) come from bears living in areas with the highest population densities (Table 1). However, even in areas with high densities, such as the southern coastal regions in our study (Table 1) where bears were large (Fig. 3), differences in SSD were variable (Fig. 5) and likely influenced by factors such as the quality of available food resources and the intensity of polygyny (Capellini 2007; Leutenegger 1978; Weckerly 1998). Without explicit testing of how these proximate environmental factors influence SSD, our explanations remain hypothetical. However, this shortcoming could be overcome. Each of the bears used in our analysis were measured by staff at the Alaska Department of Fish and Game. During the process of measuring skulls and determining sex and location of the kill, hair and tissue samples could be collected for isotope analysis to determine components of diet on a large scale. With >1,000 hunter-killed brown bears tallied each year in Alaska, comprehensive insights on the diet composition of bears across these study sites could allow for a much more expansive analysis of how diet influences size and SSD than addressed previously (Hilderbrand et al. 1999b; Mowat and Heard 2006). Furthermore, samples collected and archived over time would provide means for future studies investigating potential changes in diet over time as a result of environmental change.

Patterns we found in SSD also may have important implications for understanding variation in sexual segregation. Rode et al. (2006) argued that SSD was responsible for sexual segregation because female brown bears are smaller than males and can use poorer quality habitats to avoid infanticide. The variation in SSD found in our study may correlate with variable degrees of sexual segregation. There have been few studies quantifying sexual segregation in brown bears (Ben-David et al. 2004; Rode et al. 2006), and no study has compared the degree of sexual segregation in Alaska where variation in density, SSD, and other factors likely influence or allow for the segregation. Potential patterns of sexual

segregation across populations of brown bears in Alaska warrant future study.

The hyperallometric relationship in SSD we found, and the variable intensity of polygyny it may indicate, would likely help predict the type of mating system employed across the regions. Areas with the highest relative levels of SSD (Kodiak Island, Alaska Peninsula, and Kenai Peninsula) likely show variable intensity of polygyny, whereas a region such as northern Alaska with low population densities (Table 1) and low SSD (Fig. 5) may display a more promiscuous strategy. Genetic studies determining patterns of paternity (Kovach and Powell 2003) in areas with disparate levels of SSD might clarify questions of both mating strategy and the degree of mate competition in highly polygynous systems.

Implications for conservation.—The variation in growth, size, and SSD of brown bears found in our study illustrates their highly variable life-history patterns across Alaska. Brown bear populations in Alaska are clearly more complex than simplistic categories of “brown” versus “grizzly” bears. This variability reflects complex interactions between growth and body size and a diversity of factors including the availability of high-quality food resources (Hilderbrand et al. 1999b; Mowat and Heard 2006), climate (Ferguson and McLoughlin 2000; Kojola and Laitala 2001; Rausch 1969), population density (Zedrosser et al. 2006), and the intensity of polygyny (Capellini 2007; Leutenegger 1978; Weckerly 1998). Despite this variation, management actions such as sustainable exploitation rates (Miller 1990) are often accepted as fixed across diverse brown bear populations. Considering recent criticism of brown bear management in Alaska (Miller et al. 2011), sustainable management of diverse brown bear populations in Alaska will require identifying variation in life-history patterns, such as body size and growth rate, and incorporating this area-specific variation into management and conservation strategies.

ACKNOWLEDGMENTS

We thank V. Barnes, G. Hilderbrand, T. Lohuis, J. McDonough, R. Powell, K. Rode, J. Selinger, and 2 anonymous reviewers for comments on drafts of this manuscript. We thank D. Young (Alaska Department of Fish and Game), D. Lunde (American Museum of Natural History), C. Ramotnik (Museum of Southwestern Biology), and J. Eger (Royal Ontario Museum) for measuring skulls of neonate brown bears in their collections. We also thank L. D. Aumiller for insights on bear behavior, and S. Meyer and K. Goldman for their insights on data analysis.

LITERATURE CITED

- ABOUHEIF, E., AND D. J. FAIRBAIRN. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *American Naturalist* 149:540–562.
- AKAIKE, H. 1973. Information theory and an extension of the maximum likelihood principle. Pp. 267–281 in *International symposium on information theory* (B. N. Tetran and F. Csaki, eds.). 2nd ed. Akademiai Kiado, Budapest, Hungary.
- ANDERSSON, M. B. 1994. *Sexual selection*. Princeton University Press, Princeton, New Jersey.

- AUMILLER, L. D., AND C. A. MATT. 1994. Management of McNeil River State Game Sanctuary for viewing of Alaskan brown bears. *Ursus* 9:51–61.
- BARNES, V. G., JR. 1990. The influence of salmon availability on movements and range of brown bears on southwest Kodiak Island. *Ursus* 8:305–313.
- BARNES, V. G., JR., AND R. B. SMITH. 1998. Estimates of brown bear abundance on Kodiak Island, Alaska. *Ursus* 10:1–9.
- BEN-DAVID, M., K. TITUS, AND L. R. BEIER. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? *Oecologia* 138:465–474.
- BLANCHARD, B. M. 1987. Size and growth patterns of the Yellowstone grizzly bear. *Ursus* 7:99–107.
- BLANCKENHORN, W. U., R. C. STILLWELL, K. A. YOUNG, C. W. FOX, AND K. G. ASHTON. 2006. When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* 60:2004–2011.
- BUNNELL, F. L., AND D. E. N. TAIT. 1981. Population dynamics of bears—implications. Pp. 75–98 in *Dynamics of large mammal populations* (C. W. Fowler and T. D. Smith, eds.). John Wiley & Sons, Inc., New York.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.
- BURNHAM, K. P., D. R. ANDERSON, AND K. P. HUYVAERT. 2010. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology* 65:23–35.
- CAPELLINI, I. 2007. Sexual size dimorphism in mammals. Pp. 124–132 in *Sex, size and gender roles: evolutionary studies of sexual size dimorphism* (D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds.). Oxford University Press Inc., New York.
- CLUTTON-BROCK, T. H., AND P. H. HARVEY. 1983. The functional significance of variation in body size among mammals. Pp. 632–663 in *Advances in the study of mammalian behavior* (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication 7, The American Society of Mammalogists.
- CLUTTON-BROCK, T. H., P. H. HARVEY, AND B. RUDDER. 1977. Sexual dimorphism, socioeconomic sex ratio and body weight in primates. *Nature* 269:797–800.
- COX, R. M., M. M. BARRETT, AND H. B. JOHN-ALDER. 2008. Effects of food restriction on growth, energy allocation, and sexual size dimorphism in Yarrow's spiny lizard, *Sceloporus jarrovi*. *Canadian Journal of Zoology* 86:268–276.
- CROOK, J. L. 1971. Determination of abundance and distribution of brown bear (*Ursus arctos*) north of the Brooks Range, Alaska. M.S. thesis, University of Alaska, Fairbanks.
- DAHLE, B., AND J. E. SWENSON. 2003. Seasonal range size in relation to reproductive strategies in brown bears, *Ursus arctos*. *Journal of Animal Ecology* 74:660–667.
- DARWIN, C. 1871. The descent of man and selection in relation to sex. John Murray, London, United Kingdom.
- DEROCHER, A. E., M. ANDERSEN, AND Ø. WIIG. 2005. Sexual dimorphism of polar bears. *Journal of Mammalogy* 86:895–901.
- DEROCHER, A. E., AND I. STIRLING. 1996. Aspects of survival in juvenile polar bears. *Canadian Journal of Zoology* 74:1246–1252.
- DEROCHER, A. E., AND I. STIRLING. 1998. Geographic variation in growth of polar bears (*Ursus maritimus*). *Journal of Zoology (London)* 245:65–72.
- DEROCHER, A. E., AND Ø. WIIG. 2002. Postnatal growth in body length and mass of polar bears (*Ursus maritimus*) at Svalbard. *Journal of Zoology (London)* 256:343–349.
- EASON, T. H., B. H. SMITH, AND M. R. PELTON. 1996. Researcher variation in collection of morphometrics on black bears. *Wildlife Society Bulletin* 24:485–489.
- EMLEN, S. T., AND L. W. ORING. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197:215–223.
- ERLINGE, S. 1979. Adaptive significance of sexual dimorphism in weasels. *Oikos* 33:233–245.
- FAIRBAIRN, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 28:659–687.
- FAIRBAIRN, D. J., W. U. BLANCKENHORN, AND T. SZÉKELY. 2007. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press Inc., New York.
- FAIRBAIRN, D. J., AND R. F. PREZIOSI. 1994. Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. *American Naturalist* 144:101–118.
- FARLEY, S. D. 2005. Ecological studies of the Kenai Peninsula brown bear. Alaska Department of Fish and Game, Federal Aid Final Report, Study 4.29:1–11.
- FERGUSON, S. H., AND P. D. MCLOUGHLIN. 2000. Effects of energy availability, seasonality, and geographic range on brown bear life history. *Ecography* 23:193–200.
- FOWLER, C. W. 1988. A review of density dependence in populations of large mammals. *Current Mammalogy* 1:401–441.
- GAREL, M., A. LOISON, J.-M. JULLIEN, D. DUBRAY, D. MAILLARD, AND J.-M. GAILLARD. 2009. Sex-specific growth in alpine chamois. *Journal of Mammalogy* 90:954–960.
- GAREL, M., E. J. SOLBERG, B.-E. SÆTHER, I. HERFINDAL, AND K.-A. HØGDA. 2006. The length of growing season and adult sex ratio affect sexual size dimorphism in moose. *Ecology* 87:745–758.
- GENDE, S. M., T. P. QUINN, AND M. F. WILLSON. 2001. Consumption choice by bears feeding on salmon. *Oecologia* 127:372–382.
- GLENN, L. P. 1980. Morphometric characteristics of brown bears on the central Alaska Peninsula. *Ursus* 4:313–319.
- GLENN, L. P., J. W. LENTFER, J. B. FARO, AND L. H. MILLER. 1976. Reproductive biology of female brown bears (*Ursus arctos*), McNeil River, Alaska. *Ursus* 3:381–390.
- HALL, E. R. 1984. Geographic variation among brown and grizzly bears (*Ursus arctos*) in North America. University of Kansas Publications, Museum of Natural History 13:1–16.
- HE, J. X., AND D. J. STEWART. 2001. Age and size at first reproduction of fishes: predictive models based only on growth trajectories. *Ecology* 82:784–791.
- HECHTEL, J. L. 1985. Activity and food habits of barren ground grizzly bears in Arctic Alaska. M.S. thesis, University of Montana, Missoula.
- HILDERBRAND, G. V., S. G. JENKINS, C. C. SCHWARTZ, T. A. HANLEY, AND C. T. ROBBINS. 1999a. Effect of seasonal differences in dietary meat intake on changes in body mass and composition in wild and captive brown bears. *Canadian Journal of Zoology* 77:1623–1630.
- HILDERBRAND, G. V., ET AL. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- HOLMES, T., AND R. A. POWELL. 1994. Morphology, ecology, and the evolution of sexual dimorphism in North American *Martes*. Pp. 72–84 in *Martens, sables, and fishers: biology and conservation* (S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell, eds.). Cornell University Press, Ithaca, New York.
- HORNOCKER, M. G. 1962. Population characteristics and social and reproductive behavior of the grizzly bear in Yellowstone National Park. M.S. thesis, Montana State University, Bozeman.

- HOULE, D., C. PELABON, G. P. WAGNER, AND T. F. HANSEN. 2011. Measurement and meaning in biology. *Quarterly Review of Biology* 86:3–34.
- ISAAC, J. L. 2005. Potential causes and life-history consequences of sexual dimorphism in mammals. *Mammal Review* 35:101–115.
- KINGSLEY, M. C. S. 1979. Fitting the von Bertalanffy growth equation to polar bear age–weight data. *Canadian Journal of Zoology* 57:1020–1025.
- KINGSLEY, M. C. S., J. A. NAGY, AND H. V. REYNOLDS. 1988. Growth in length and weight of northern brown bears: differences between sexes and populations. *Canadian Journal of Zoology* 66:981–986.
- KINGSLEY, M. C. S., J. A. NAGY, AND R. H. RUSSELL. 1983. Patterns of weight gain and loss for grizzly bears in northern Canada. *Ursus* 5:174–178.
- KOJOLA, I., AND H.-M. LAITALA. 2001. Body size variation of brown bear in Finland. *Annales Zoologici Fennici* 38:173–178.
- KOVACH, A. I., AND R. A. POWELL. 2003. Effects of body size on male mating tactics and paternity in male black bears, *Ursus americanus*. *Canadian Journal of Zoology* 81:1257–1268.
- LEBLANC, M., M. FESTA-BIANCHET, AND J. T. JORGENSEN. 2001. Sexual size dimorphism in bighorn sheep (*Ovis canadensis*): effects of population density. *Canadian Journal of Zoology* 79:1661–1670.
- LEUTENEGGER, W. 1978. Scaling of sexual dimorphism in body size and breeding system in primates. *Nature* 272:610–611.
- LINDENFORS, P., J. L. GITTLEMAN, AND K. E. JONES. 2007. Sexual size dimorphism in mammals. Pp. 16–26 in Sex, size and gender roles: evolutionary studies of sexual size dimorphism (D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, eds.). Oxford University Press Inc., New York.
- LOHUIS, T. D., H. J. HARLOW, T. D. I. BECK, AND P. A. IAIZZO. 2007. Hibernating bears conserve muscle strength and maintain fatigue resistance. *Physiological and Biochemical Zoology* 80:257–269.
- MAHONEY, S. P., J. A. VIRGL, AND K. MAWHINNEY. 2001. Potential mechanisms of phenotypic divergence in body size between Newfoundland and mainland black bear populations. *Canadian Journal of Zoology* 79:1650–1660.
- MARQUET, P. A., AND M. L. TAPER. 1998. On size and area: patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology* 12:127–139.
- MATSON, G., L. VAN DAELE, E. GOODWIN, L. AUMILLER, H. REYNOLDS, AND H. HRISTENKO. 1993. A laboratory manual for cementum age determination of Alaska brown bear first premolar teeth. Alaska Department of Fish and Game and Matson's Laboratory, Milltown, Montana, Technical Report:1–52.
- MEIRI, S., T. DAYAN, AND D. SIMBERLOFF. 2004. Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnean Society* 81:579–588.
- MILLER, S. D. 1990. Population management of bears in North America. *Ursus* 8:357–373.
- MILLER, S. D. 1993. Impacts of increased hunting pressure on the density, structure, and dynamics of brown bear populations in Alaska's game management unit 13. Alaska Department of Fish and Game, Federal Aid Final Report, Study 4.21:1–182.
- MILLER, S. D. 1997. Impacts of heavy hunting pressure on the density and demographics of brown bear populations in southcentral Alaska. Alaska Department of Fish and Game, Federal Aid Report, Study 4.26:1–54.
- MILLER, S. D., AND R. R. NELSON. 1993. A brown bear density and population estimate for a portion of the Seward Peninsula, Alaska. Alaska Department of Fish and Game, Federal Aid Report, Study 4.0:1–48.
- MILLER, S. D., J. W. SCHOEN, J. FARO, AND D. R. KLEIN. 2011. Trends in intensive management of Alaska's grizzly bears, 1980–2010. *Journal of Wildlife Management* 75:1243–1252.
- MILLER, S. D., R. A. SELLERS, AND J. A. KEAY. 2003. Effects of hunting on brown bear cub survival and litter size in Alaska. *Ursus* 14:130–152.
- MILLER, S. D., ET AL. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicated mark–resight techniques. *Wildlife Monographs* 133:1–55.
- MOORS, P. J. 1980. Sexual dimorphism in the body size of mustelids (Carnivora): the roles of food habits and breeding systems. *Oikos* 34:147–158.
- MOWAT, G., AND D. C. HEARD. 2006. Major components of grizzly bear diet across North America. *Canadian Journal of Zoology* 84:473–489.
- OHDAKI, S., T. AOI, T. MANO, AND T. TSUBOTA. 1992. Growth, sexual dimorphism, and geographic variation of skull dimensions of the brown bear *Ursus arctos* in Hokkaido. *Journal of the Mammalogical Society of Japan* 17:27–47.
- PAETKAU, D., G. F. SHIELDS, AND C. STROBECK. 1998a. Gene flow between insular, coastal and interior populations of brown bears in Alaska. *Molecular Ecology* 7:1283–1292.
- PAETKAU, D., ET AL. 1998b. Variation in the genetic diversity across the range of North American brown bears. *Conservation Biology* 12:418–429.
- PASITSCHNIK-ARTS, M. 1993. *Ursus arctos*. *Mammalian Species* 439:1–10.
- PETERS, R. H. 1983. The ecological implication of body size. Cambridge University Press, New York.
- RALLS, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. *American Naturalist* 111:917–938.
- RALLS, K., AND P. H. HARVEY. 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society* 25:119–167.
- RAUSCH, R. L. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. *Canadian Journal of Zoology* 41:33–45.
- RAUSCH, R. L. 1969. Morphogenesis and age-related structure of permanent canine teeth in the brown bear, *Ursus arctos*, L. in Arctic Alaska. *Zeitschrift für Morphologie der Tiere* 66:167–188.
- RENSCH, B. 1960. Evolution above the species level. Columbia University Press, New York.
- REYNOLDS, H. V., AND G. W. GARNER. 1987. Patterns of grizzly bear predation on caribou in northern Alaska. *Ursus* 7:59–67.
- REYNOLDS, H. V., AND J. L. HECHTEL. 1984. Structure, status, reproductive biology, movement, distribution, and habitat utilization of a grizzly bear population. Alaska Department of Fish and Game, Federal Aid Final Report, Study 4.14R:1–29.
- ROBBINS, C. T., J. K. FORIN, K. D. RODE, S. D. FARLEY, L. A. SHIPLEY, AND L. A. FELICETTI. 2007. Optimizing protein intake as a foraging strategy to maximize mass gain in an omnivore. *Oikos* 116:1675–1682.
- ROBBINS, C. T., C. C. SCHWARTZ, AND L. A. FELICETTI. 2004. Nutritional ecology of ursids: a review of newer methods and management implications. *Ursus* 15:161–171.
- RODE, K. D., S. C. AMSTRUP, AND E. V. REGEHR. 2010. Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* 20:768–782.
- RODE, K. D., S. D. FARLEY, AND C. T. ROBBINS. 2006. Sexual dimorphism, reproductive strategy, and human activities determine resource use by brown bears. *Ecology* 87:2636–2646.

- RODE, K. D., C. T. ROBBINS, AND L. A. SHIPLEY. 2001. Constraints on herbivory by grizzly bears. *Oecologia* 128:62–71.
- SAS INSTITUTE INC. 2003. SAS/STAT user's guide, version 9.1.3. SAS Institute Inc., Cary, North Carolina.
- SCHWARTZ, C. C., S. D. MILLER, AND M. A. HAROLDSON. 2003. Grizzly bear. Pp. 556–586 in *Wild mammals of North America: biology, management, and conservation* (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- SHRADER, A. M., S. M. FERREIRA, M. E. McELVEEN, P. C. LEE, C. J. MOSS, AND R. J. VAN AARDE. 2006. Growth and age determination of African savanna elephants. *Journal of Zoology (London)* 270:40–48.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SOLBERG, E. J., M. GAREL, M. HEIM, V. GRØTAN, AND B.-E. SÆTHER. 2008. Lack of compensatory body growth in a high performance moose *Alces alces* population. *Oecologia* 158:485–498.
- STERN, S. C. 1992. *The evolution of life histories*. Oxford University Press, New York.
- STERN, S. C., AND J. C. KOELLA. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution* 40:893–913.
- STIRLING, I., AND A. E. DEROCHE. 1990. Factors affecting the evolution and behavioral ecology of the modern bears. *Ursus* 8:189–204.
- TALBOT, S. L., AND G. F. SHIELDS. 1996. Phylogeography of brown bears (*Ursus arctos*) of Alaska and paraphyly within the Ursidae. *Molecular Phylogenetics and Evolution* 5:477–494.
- TRIVERS, R. 1972. Parental investment and sexual selection. Pp. 136–179 in *Sexual selection and the descent of man* (B. Campbell, ed.). Aldine, Chicago, Illinois.
- VAN DAELE, L. J. 2007. Population dynamics and management of brown bears on Kodiak Island, Alaska. Ph.D. dissertation, University of Idaho, Moscow.
- VON BERTALANFFY, L. 1938. A quantitative theory of organic growth (inquires on growth laws. II). *Human Biology* 10:181–213.
- VON BERTALANFFY, L. 1960. Principles and theory of growth. Pp. 137–259 in *Fundamental aspects of normal and malignant growth* (W. W. Wovinski, ed.). Elsevier, Amsterdam, Netherlands.
- WATKINS, G. G. 1996. Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology* 77:1473–1482.
- WECKERLY, F. W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *Journal of Mammalogy* 79:33–52.
- WELCH, C. A., J. KEAY, K. C. KENDALL, AND C. T. ROBBINS. 1997. Constraints of frugivory by bears. *Ecology* 78:1105–1119.
- WILLEY, C. H. 1974. Aging black bears from first premolar tooth sections. *Journal of Wildlife Management* 38:97–100.
- ZEDROSSER, A., E. BELLEMAIN, P. TABERLET, AND J. E. SWENSON. 2007. Genetic estimates of annual reproductive success in male brown bears: the effects of body size, age, internal relatedness and population density. *Journal of Animal Ecology* 76:368–375.
- ZEDROSSER, A., B. DAHLE, AND J. E. SWENSON. 2006. Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy* 87:510–518.
- ZEDROSSER, A., S.M.J.G. STEYAERT, H. GOSSOW, AND J. E. SWENSON. 2011. Brown bear conservation and the ghost of persecution past. *Biological Conservation* 144:2163–2170.

Submitted 1 November 2011. Accepted 23 November 2011.

Associate Editor was Roger A. Powell.