

VARIATION, SEXUAL DIMORPHISM, AND ALLOMETRY IN MOLAR SIZE OF THE BLACK BEAR

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We investigated molar-crown-size variation, sexual dimorphism, and allometry in the black bear (*Ursus americanus*), using hunter-shot specimens ($n = 429$) from the island of Newfoundland, and museum specimens from elsewhere in Canada and the continental United States ($n = 502$). We predicted higher variation in and weaker correlations among molar size in this omnivorous species than in other species of Carnivora with dentition more specialized for carnivory, because of relatively weak normalizing selection on food-processing mechanisms in *U. americanus*. Molar-size variation in Newfoundland bears (mean coefficient of variation $\sim 5.6\%$) was intermediate between species of Carnivora with simpler (e.g., pinnipeds) and more complex (e.g., canids) postcanine dentition. There was negligible size variation within the molar teeth, unlike some mammals. Bilateral symmetry was strong, especially in mandibular length ($r \sim 1.0$ between left and right sides; $r \sim 0.95$ for other mandibular and maxillary variables and molar size); symmetry in molar size was higher than in phocid seals. Size was positively correlated across molars, especially between adjacent (but not occluding) molars; patterns were similar between sexes and geographic regions, and correlation levels did not differ from other species of Carnivora. We also predicted (and found) smaller sexual differences ($= 100[(\text{male}/\text{female}) - 1]$) in molar size than in body size, because definitive molar size is attained early in life: differences in molar size averaged $\sim 5.5\%$ in Newfoundland (higher in continental subsamples), which is less than differences in cranial size (7–9%) or body mass^{1/3} (21%). Sexes did not differ in relative molar size. Molar size was mainly isometric or positively allometric to adult body size (using mandibular and maxillary size as proxies).

Key words: allometry, American black bear, bilateral symmetry, dentition, geographic variation, growth, morphometrics, Newfoundland and Labrador, sexual dimorphism

High morphological complexity and close functional integration of teeth occur in many mammals, including most terrestrial species of Carnivora (Crompton and Hiiemae 1970; Hiiemae 2000; Meiri et al. 2005; Popowics 2003). Structural properties, complexity, and integration of teeth reflect selection for effective food-processing mechanisms that are associated with different diets; for example, carnassial size is more highly correlated within the dentition in species of Carnivora that mainly eat meat than in those that eat invertebrates or fruit (Evans et al. 2007; Friscia et al. 2007; Meiri et al. 2005; Popowics 2003). Most studies of carnivore dentition have been on taxa with complex crowns such as canids, with relatively little attention paid to groups with simpler crowns, such as

pinnipeds or bears (Adam and Berta 2002; Meiri et al. 2005; Miller et al. 2007; Szuma 2000; Werth 2000). Recent studies have investigated the dentition of Ursidae within the Carnivora as a whole, and within the family itself (Christiansen 2007; Christiansen and Adolphsen 2005; Christiansen and Wroe 2007; Mazza et al. 1995; Sacco and Van Valkenburgh 2004; Sorkin 2005). Diets of extant ursids are varied, and include the insectivorous sloth bear (*Melursus ursinus*), hypercarnivorous polar bear (*Ursus maritimus*), and herbivorous giant panda (*Ailuropoda melanoleuca*)—Christiansen and Wroe 2007; Mazza et al. 1995; Sacco and Van Valkenburgh 2004; Van Valkenburgh 2007). However, most species of bear are generalized omnivores, as reflected in the simplified crowns of the postcanine teeth, particularly carnassials (in Carnivora these are the 4th upper premolar [P4] and 1st lower molar [m1]: upper- and lowercase letters distinguish upper from lower teeth, hereafter). Ursids have lost the ancestral carnassial shearing mechanism: molars are the most important postcanine teeth for processing food, and premolars are small and variably present

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(anterior premolars have been lost altogether in the cave bear [*Ursus spelaeus*]—Butler 1946; Erdbrink 1953; Mazza et al. 1995; Sacco and Van Valkenburgh 2004; Van Valkenburgh 2007).

Highly specialized traits such as crown structure and tooth size in specialized dentitions (e.g., for hypercarnivory) must be under strong stabilizing selection, which is in keeping with low intraspecific variation and high intercorrelations in tooth size within the dentition (especially between occluding or adjacent teeth—Gingerich and Schoeninger 1979; Gingerich and Winkler 1979; Kurtén 1967; Meiri et al. 2005; Miller et al. 2007; Pengilly 1984). Conversely, higher variability in tooth size and weaker intercorrelations in tooth size within the dentition occur in dietarily less-specialized species (Dayan et al. 2002; Kurtén 1953, 1963, 1964; Lanyon and Sanson 2006; Rui and Drehmer 2004). In 2 species of phocid seal with simple-crowned, nonoccluding postcanine teeth, tooth size is more variable, size of teeth on left and right sides is more weakly correlated, and intercorrelations among tooth size overall are lower than in species of Carnivora with more complex crowns and occlusion (Miller et al. 2007).

In this paper we report on variation and correlation patterns of molar-crown size in the black bear (*Ursus americanus*), based on samples of the endemic insular form *U. a. hamiltoni* Cameron, 1956, from the island of Newfoundland, Canada, and from throughout the continental United States and Canada. *U. a. hamiltoni* differs from mainland forms by “greater height of the cranium in the frontal region and the relatively shorter rostrum” (Cameron 1956:539), traits that have been interpreted as adaptations to herbivory in the cave bear (Kurtén 1958). However, diet of the Newfoundland black bear appears to be typical of the species throughout its range (Larivière 2001), being varied but mainly vegetarian, and including berries, forbs, and grasses; calves of moose (*Alces americanus*) and caribou (*Rangifer tarandus*; and some adult caribou); spawning fish (especially freshwater Atlantic salmon [*Salmo salar*] and marine caplin [*Mallotus villosus*]); and carrion (Day 1997; Mahoney et al. 2001). The diet (like that of the Haida Gwaii black bear [*U. a. carlottae*]—Reimchen 2000, 2004) differs from that of most black bear populations because of the inclusion of more fish and the absence of hard mast (e.g., nuts), which is rich in proteins, fats, and carbohydrates, and is important in the diet of many continental populations (Larivière 2001). The diet of *U. a. hamiltoni* has changed because of anthropogenic effects on availability of significant dietary items (e.g., Atlantic salmon populations now are very low). Ecogeographic and temporal variation in molar morphology and size (presumably in relation to diet) occurs in bears (Baryshnikov 2006; Baryshnikov et al. 2003; Kennedy et al. 2002a; Meijaard 2004; Virgl et al. 2003), and may occur in the black bear. For example, in areas of allopatry with brown bears (*Ursus arctos*), as in insular Newfoundland, black bears are more carnivorous than where the 2 species are sympatric (Hilderbrand et al. 1999; Jacoby et al. 1999).

We predicted that molar-size variation and integration (as reflected in correlations and bilateral symmetry) in the black bear would be intermediate between species of Carnivora with

more-complex (e.g., canids and felids) and less-complex (e.g., pinnipeds) crowns and occlusion patterns in cheek teeth. We also investigated sex-related differences, for 3 reasons. First, sexual differences may be accentuated in body size and trophic morphology such as teeth through ecological release in simple island ecosystems such as Newfoundland (Davies et al. 2007; Dayan et al. 1992; Isaac 2005; Kieser 1995; Mahoney et al. 2001; Selander 1966, 1972). Therefore we predicted greater sexual size differences in Newfoundland than in mainland samples. Second, females have high food-processing demands in pregnancy and cub-rearing, so we predicted that molars of females would have relatively larger grinding areas than those of males (Kieser and Groeneveld 1992; but see Thom et al. 2004). Our final prediction about sexual differences was based on knowledge of growth patterns: molars erupt early in life, and crown size does not change thereafter, whereas growth in body size continues for years; therefore, adult males and females should differ less in molar size than in body size. For the same reason, we predicted that molar size would be weakly related or unrelated to adult body size, as in phocid seals (Corruccini and Henderson 2005; Gould 1975; Miller et al. 2007; Ungar 1998).

MATERIALS AND METHODS

We used 2 sets of specimens for our analyses: hunter-shot bears on the island of Newfoundland; and museum collections from eastern and western North America, including Mexico (Kennedy et al. 2002a, 2002b). The non-Newfoundland data sets covered a large geographic area (in the east, from Quebec, Canada, to Florida; in the west, from Alaska to Mexico), and we combined them for analysis because regional subsamples represented areas of different size, and they were based on variable (sometimes small) numbers of specimens. Those data included some island samples, but for simplicity we use the term “continental” hereafter, to distinguish them from Newfoundland data.

Skinned heads of bears shot by hunters on the island of Newfoundland from 1985 to 1991 were frozen ($n = 429$). Later the specimens were thawed, simmered in boiling water for several hours, cleaned by hand, and dried at room temperature. They were measured in 2003–2004. Before boiling, P1 was extracted and age was determined for 265 specimens by counting cementum annuli (Willey 1974). Age classes are referred to by year of life (0 = 1st year, etc.). Age structure of the Newfoundland sample was: females, 0–19 years (median = 2.0 years, $\bar{X} = 3.21$ years ± 3.56 SD, $n = 39$); males, 0–21 years (median = 3.5 years, $\bar{X} = 4.65 \pm 3.91$ years, $n = 106$); and unknown sex, 1–15 years (median = 3.0 years, $\bar{X} = 3.50 \pm 2.89$ years, $n = 120$). All specimens were deposited in The Rooms Provincial Museum, St. John’s, Newfoundland and Labrador, Canada. Age structure of the continental samples was: females, 3–13 years (median = 7.0 years, $\bar{X} = 7.05 \pm 2.10$ years, $n = 209$); and males, 4–13 years (median = 7.5 years, $\bar{X} = 7.65 \pm 2.45$ years, $n = 206$).

To increase the sample size of Newfoundland specimens with known sex, we used anteroposterior length of the alveolus of the lower canine as a proxy for sex (Gordon and Morejohn

1975). We 1st measured alveoli of all females and males aged >6 years old, and determined that there was no overlap between the sexes in canine size. This allowed us to assign sex to specimens >6 years of age, and to assign large specimens of unknown age as males.

Kennedy et al. (2002a, 2002b) made all measurements to ± 0.01 mm with digital calipers. They did not measure right and left sides, so we could not evaluate bilateral symmetry from continental data. For comparability with Newfoundland data, we conducted some analyses on regional subsamples of the overall continental sample, as explained below.

Measurement protocols for Newfoundland and continental samples were developed independently, so we used some approximate correspondences between variables from the 2 studies (see below). Using digital calipers, we measured the following variables on left and right sides of Newfoundland specimens.

Mandibular variables.—Mandibular length (from anteriormost point on dentary to midpoint on posterior surface of mandibular condyle), to ± 1 mm; and breadth of mandibular condyle, to ± 0.1 mm. We analyzed 1 variable of Kennedy et al. (2002a, 2002b) that approximated mandibular length: distance between the anterior margin of the lower canine alveolus, to the anteriormost point on the posterior margin of the coronoid process (their variable 30, “coronoid process–canine length”).

Toothrow variables.—Lengths of maxillary and mandibular tooththrows (from anterior margin of P4 or p4 alveolus to posterior margin of M2 or m3 alveolus, respectively), to ± 1 mm. As approximations to these variables, we analyzed 2 variables of Kennedy et al. (2002a, 2002b): distance between the anterior margin of the left upper canine, to the posterior margin of the M2 alveolus (their variable 6, “maxillary canine–M2 length”); and distance between the anteriormost point on the lower incisors, to the posterior margin of m3 (their variable 25, “mandibular m3–incisors distance”).

Molar variables.—Breadths of M1, M2, m1, m2, and m3 crowns; and coronal lengths of M2 and m3 crowns. These variables were selected because these teeth were always present (Rausch [1961] noted only 1 missing m3 in a sample of 219 Alaskan black bears), and repeatability of measurements was high (this was why coronal length was measured only for molars at the end of the tooththrow). All dental measurements were made to ± 0.1 mm. All these variables also were measured directly or indirectly by Kennedy et al. (2002a, 2002b). Breadths of M1 and M2 were variables 12 and 11 (respectively) of Kennedy et al. (2002a, 2002b). Coronal lengths of lower molars, and breadth of m3, were variables 28, 27, 26, and 29 (respectively) of Kennedy et al. (2002a, 2002b). Kennedy et al. (2002a, 2002b) also measured coronal lengths of M1 and M1 + M2 (their variables 13 and 14, respectively), so we estimated M2 coronal length as the difference between these variables.

On Newfoundland specimens, all variables were measured twice for both left and right sides by the same person, blind, and at 1-day to 1-week intervals. Pearson's product-moment correlation coefficient (r) between the 2 sets of measurements for each variable was used as a quantitative measure of repeatability (Nespolo et al. 2003). Repeatability was extremely high, with r ranging from a minimum of 0.971 ($n = 280$) for

breadth of left M1, to >0.999 for both left ($n = 260$) and right ($n = 259$) mandibular lengths. Therefore, we did not correct for measurement error. For statistical analyses on Newfoundland data, we used left- and right-side means of the repeated measurements, or grand means of those means, as appropriate. Our measurement procedures had low measurement error, and the use of means led to conservative estimates of variation; nevertheless, absolute levels of variation are comparable within our analyses, and relative levels that we measured can be compared with relative levels in other published studies.

We 1st analyzed relationships of molar size to age within each sex, separately for Newfoundland and continental samples, using general linear models. No relationships were significant, so ages were combined within sexes for non-allometric analyses of molar size. We computed descriptive statistics, and explored relationships among molar variables with correlation analyses and principal component analyses.

To explore general relationships of molar size to body size (using mandibular and maxillary size as proxies), we examined bivariate relationships, and also carried out separate principal component analyses for Newfoundland and continental samples for molar variables and mandibular and maxillary variables. The 1st principal component (PC1) is conventionally interpreted in terms of size, so we plotted PC1 scores from molar variables against those from mandibular and maxillary variables to depict overall size relationships.

We used general linear models to investigate effects of age, sex, and mandibular and maxillary size on molar size. If interaction terms (age \times mandibular–maxillary variables; sex \times mandibular–maxillary variables) were not significant ($P > 0.05$), they were removed, and then the models were rerun (Grafen and Hails 2002). If mandibular or maxillary variables had significant effects on molar size, then we performed further analyses using log-transformed variables and reduced major axis regression (Lüpold et al. 2004; Tatsuta et al. 2001). These analyses revealed several variables with significant relationships to molar size with few age or interaction effects: maxillary tooththrow length in the Newfoundland sample; and mandibular m3–incisors distance, coronoid process–canine length, and maxillary canine–M2 length in the continental sample (separate regressions were run for males and females for the latter variable, because of significant sex effects). Therefore, these variables were used for allometric analyses.

Our data represented mixed cross-sectional data (Cock 1966), so to confirm that our analyses revealed trends in static allometry, uncomplicated by growth (age), we carried out further allometric regressions restricted to older (>6 years old) bears: Newfoundland males ($n = 33$), continental males ($n = 93$), and continental females ($n = 82$). Allometric slopes are invariably steeper in interspecific analyses (Green et al. 2001; Reilly et al. 1997). Therefore, to determine whether the greater expression of positive allometry in the continental sample resulted from its multipopulation composition, we also computed allometric regressions for continental subsamples (and sexes within those subsamples) with $n \geq 20$: Alaska ($n = 27$ females, 27 males); Arkansas ($n = 20$ males); British Columbia, Canada ($n = 26$ females, 23 males); California

TABLE 1.—Descriptive statistics for molar size in the black bear (*Ursus americanus*), shot on the island of Newfoundland (1985–1991), and from museum specimens from selected regions of the United States. Statistics are mean \pm SD (CV; *n*) in mm (except mm² for m3 area and M2 area). Statistics for Newfoundland are based on means of left and right sides except for CV, which is given for left-side measurements for comparability with published figures. SSD is sexual size dimorphism (= 100[(male/female) – 1]).

Variable	Geographic sample or subsample			
	Newfoundland	Alaska	New York: Adirondacks	California
m1 breadth				
Male	8.4 \pm 0.48 (5.8; 207)	8.9 \pm 0.62 (7.0; 27)	9.0 \pm 0.55 (6.0; 27)	9.1 \pm 0.47 (5.2; 23)
Female	7.9 \pm 0.50 (6.8; 50)	8.4 \pm 0.52 (6.2; 26)	8.0 \pm 0.49 (6.2; 24)	8.4 \pm 0.42 (4.9; 25)
SSD	6.4	5.8	13.0	7.6
m2 breadth				
Male	11.2 \pm 0.57 (5.1; 198)	11.8 \pm 0.77 (6.5; 26)	11.9 \pm 0.59 (5.0; 27)	11.8 \pm 0.60 (5.1; 23)
Female	10.5 \pm 0.52 (5.2; 48)	11.0 \pm 0.44 (4.0; 25)	10.9 \pm 0.51 (4.7; 24)	11.0 \pm 0.46 (4.2; 25)
SSD	6.6	6.8	9.6	7.7
m3 breadth				
Male	11.2 \pm 0.53 (5.0; 191)	11.7 \pm 1.12 (9.5; 24)	11.5 \pm 0.56 (4.8; 24)	12.1 \pm 0.57 (4.7; 23)
Female	10.7 \pm 0.43 (4.5; 49)	10.8 \pm 0.64 (5.9; 25)	10.5 \pm 0.53 (5.0; 23)	11.2 \pm 0.53 (4.7; 25)
SSD	4.7	8.6	10.0	8.9
m3 length				
Male	14.2 \pm 0.86 (6.1; 175)	15.2 \pm 1.19 (7.8; 24)	14.9 \pm 0.86 (5.8; 22)	15.7 \pm 0.61 (3.9; 21)
Female	13.4 \pm 0.79 (6.1; 49)	14.2 \pm 1.13 (7.9; 24)	13.3 \pm 0.76 (5.7; 20)	14.1 \pm 1.24 (8.8; 23)
SSD	6.1	7.0	11.4	11.5
m3 area				
Male	158 \pm 14.2 (—; 175)	179 \pm 31.8 (—; 23)	171 \pm 15.2 (—; 22)	192 \pm 14.2 (—; 21)
Female	144 \pm 13.6 (—; 49)	153 \pm 19.1 (—; 23)	140 \pm 13.2 (—; 20)	158 \pm 19.5 (—; 23)
SSD ^a	4.7	8.2	10.3	10.1
M1 breadth				
Male	12.3 \pm 0.67 (5.5; 161)	13.2 \pm 0.79 (6.0; 27)	13.0 \pm 0.49 (3.8; 24)	13.1 \pm 0.57 (4.3; 23)
Female	11.8 \pm 0.58 (4.8; 28)	12.6 \pm 0.69 (5.5; 26)	11.9 \pm 0.67 (5.6; 25)	12.4 \pm 0.59 (4.8; 25)
SSD	5.6	5.0	8.9	6.0
M2 breadth				
Male	14.0 \pm 0.74 (5.4; 163)	14.7 \pm 1.05 (7.1; 26)	15.1 \pm 0.94 (6.2; 24)	15.3 \pm 0.75 (4.9; 24)
Female	13.2 \pm 0.63 (4.8; 28)	13.6 \pm 0.64 (4.7; 27)	14.0 \pm 0.53 (3.8; 25)	14.3 \pm 0.57 (4.0; 25)
SSD	6.1	8.0	7.7	6.5
M2 length				
Male	24.6 \pm 1.54 (6.1; 162)	26.6 \pm 2.20 (8.3; 25)	26.6 \pm 1.51 (5.7; 24)	27.7 \pm 1.17 (4.2; 17)
Female	23.6 \pm 1.35 (5.8; 28)	24.1 \pm 1.28 (5.3; 26)	24.5 \pm 1.19 (4.9; 25)	25.2 \pm 1.48 (5.9; 19)
SSD	4.4	10.5	8.9	10.0
M2 area				
Male	344 \pm 37.0 (—; 162)	394 \pm 60.0 (—; 25)	403 \pm 44.5 (—; 24)	428 \pm 30.5 (—; 17)
Female	311 \pm 31.0 (—; 28)	329 \pm 29.0 (—; 26)	343 \pm 26.9 (—; 25)	361 \pm 32.0 (—; 19)
SSD ^a	5.2	10.0	8.4	8.8
SSD \bar{x} ^b	5.7	7.4	9.9	8.3

^a For molar areas, SSD was computed as male^{0.5}/female^{0.5}.

^b Excluding measures of area, because they are derived variables. By 1-way ANOVA, $P < 0.001$ ($F = 8.34$, $df = 3, 24$).

($n = 25$ females, 24 males); Florida ($n = 38$ females, 36 males); Louisiana ($n = 23$ males); Michigan ($n = 20$ females, 23 males); Minnesota ($n = 22$ males); New York, Adirondack Mountains ($n = 25$ females, 27 males); New York, Catskill Mountains ($n = 24$ females, 25 males); and Virginia ($n = 25$ females).

Finally, relative size differences in molar-surface area between the sexes were investigated through general linear models, with surface areas of m3 and M2 as dependent variables, and sex plus maxillary or mandibular variables as covariates (we also used PC1 scores from analyses with maxillary and mandibular variables as size covariates).

RESULTS

Molar-size variation: coefficient of variation.—Variation (coefficient of variation [CV], based on left-side measurements only, for comparability with published values) averaged 5.6% in males and 5.4% in females from Newfoundland, and 5.8% and 5.4% (respectively) across continental subsamples (Table 1). For the Newfoundland sample only, CVs were concordant between sexes: $r = 0.78$ ($P = 0.04$; based on means of left and right measurements) and $r = 0.74$ ($P = 0.06$; left-side measurements).

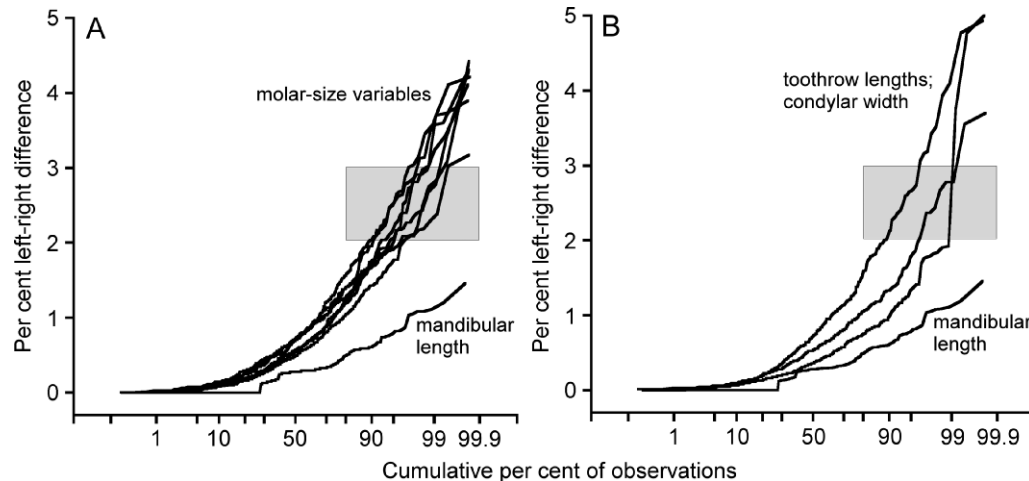


FIG. 1.—Bilateral asymmetry was highest in mandibular length, and was slightly lower but similar for all other (molar, maxillary, and other mandibular) variables for black bears (*Ursus americanus*) from Newfoundland (values given in text). Absolute values of left- and right-side differences are shown as normal probability plots. The gray rectangles enable visual comparison between the 2 plots; they cover the vertical range of 2–3%, over the probability interval 80–99.9%. Molar-size variables (A) and tooththrow lengths plus condylar width (B) are plotted separately, for clarity; mandibular length is shown in both plots, to emphasize its high left–right symmetry. Note the small left–right differences in mandibular length, compared with all other variables. Six large differences were excluded: width of lower 1st molar (6.5%), length of 3rd lower molar (5.9%), width of 2nd upper molar (6.6%), length of mandibular tooththrow (7.0%), and condylar width (7.6% and 8.1%).

The range of CVs across variables was small, averaging 5.0% (m2 breadth) to 6.5% (m3 length), for data summarized in Table 1. In the Newfoundland sample, breadth of m3 varied least in both sexes (based on means of left and right measurements: males, 5.0%; females, 4.5%).

Molar-size variation: bilateral symmetry.—Molar size was highly correlated between left (L) and right (R) sides in Newfoundland bears (all $r_{LR} > 0.9$, for sexes analyzed separately, or combined), and size was statistically indistinguishable between left and right sides (1-way analysis of variance [ANOVA], $P > 0.9$ for all molar-size variables). Correlations averaged $r_{LR} = 0.94$, ranging from 0.92 for m3 breadth ($n = 85$; m3 length was 2nd lowest: $r_{LR} = 0.93$, $n = 232$) to 0.96 for M2 length ($n = 82$). Differences between left and right molar measurements in individual specimens averaged 0.5–0.9% ($= 100(L - R)/(L + R)$). Bilateral tooththrow and mandibular measurements also were strongly correlated, averaging $r_{LR} = 0.96$: length of maxillary tooththrow, $r_{LR} = 0.96$ ($n = 268$); length of mandibular tooththrow, $r_{LR} = 0.95$ ($n = 300$); mandibular length, $r_{LR} > 0.99$ ($n = 226$); and condylar breadth, $r_{LR} = 0.96$ ($n = 238$).

Bilateral symmetry was high in all molar and cranial variables, especially in mandibular length (Fig. 1). The median of left–right differences for mandibular length was 0.28% (range, 0–1.5%), averaged 0.49–0.72% (range, 0–4.4%) across molar variables, and averaged 0.36–0.71% (range, 0–5.1%) for maxillary and other mandibular variables (Fig. 1). Asymmetry was not correlated across variables, based on correlation analyses of left–right differences.

Molar-size integration: correlation structure.—All measures of molar size were positively intercorrelated, and patterns were similar between males and females. The 21 pairwise r -estimates between the 7 variables were significantly correlated

between sexes for both Newfoundland and continental samples (Fig. 2). Male Newfoundland bears showed lowest levels of intercorrelation, which accounts for the sexual differences for Newfoundland (Fig. 2A), and for differences between Newfoundland and continental samples for males (compare Figs. 2A and 2B). Correlation patterns were slightly lower between Newfoundland and continental samples (males, $r = 0.51$, $P = 0.02$; females, $r = 0.35$, $P = 0.06$; sexes combined, $r = 0.53$, $P = 0.02$). All pairwise r -estimates were significant, with low estimates mainly involving size of m3 (Table 2). The low correlations involving m3 size were reflected in principal component analysis results (Table 3), in which breadth and length of m3 differed from other variables by loading strongly on PC2 in both Newfoundland and continental analyses (and also in analyses for sexes within regions; data not presented). The low values are partly explicable by proximity of teeth: correlations were higher between adjacent (i.e., m1–m2 and m2–m3) than nonadjacent (i.e., m1–m3) mandibular teeth. No differences were apparent for correlations between occluding (i.e., M1–m1/m2; M3–m2/m3) and nonoccluding teeth. Within-tooth size correlations (i.e., r between m3 breadth and m3 length, and between M2 breadth and M2 length) were similar in strength to size correlations between different teeth (Table 2).

Sexual differences in molar size.—Descriptive statistics for molar size in bears from Newfoundland, and from the 3 continental regions with the largest subsamples, are summarized in Table 1. Males from Newfoundland averaged ~6% larger than females in molar size. Sexual size dimorphism was greater in the continental subsamples; for example, for the Adirondack Mountains, New York, dimorphism across molar variables averaged 10%. General linear models of tooth-surface area were uniform across all variables and both samples (all size

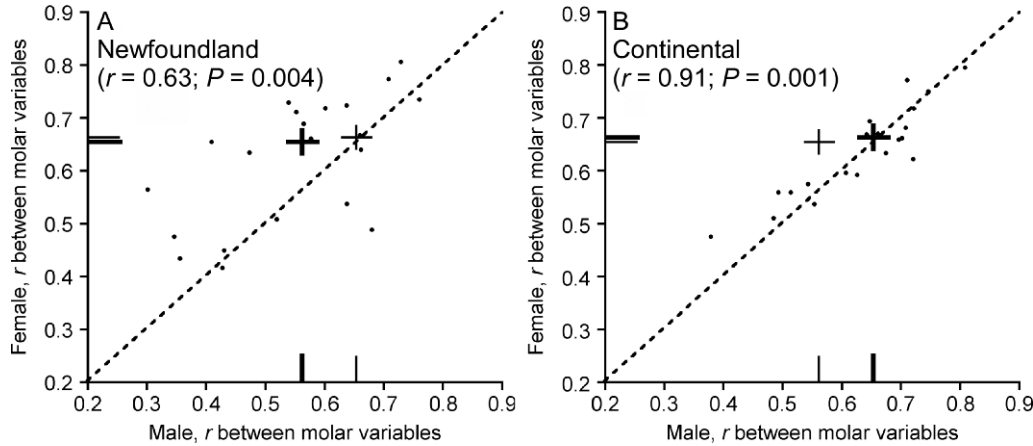


FIG. 2.—The pattern of correlations between molar-size variables in black bear (*Ursus americanus*) is similar between the sexes in both A) insular Newfoundland and B) continental North America; it is also similar between those 2 sample areas (see text). Bivariate plots of correlations (Pearson’s *r*) between 7 molar-size variables are shown for each sample. Bars along the axes represent medians of males and females, and plus (+) symbols represent joint medians (thin symbols are for joint medians from the other panel, for comparison). Low correlations for male Newfoundland bears account for the sexual difference apparent in panel A.

effects but no interaction terms were significant). Therefore, relative molar surface area did not differ between sexes.

Relative molar size: allometric analyses.—Separate principal component analyses for Newfoundland and continental samples disclosed a strong positive relationship of molar size to body size (i.e., using the proxy of combined mandibular and maxillary variables; Fig. 3). Strength of bivariate relationships was variable for the Newfoundland sample and uniformly moderate for the continental sample (mean *r* between molar and mandibular–maxillary variables: 0.16–0.80 and 0.57–0.65, respectively).

Allometric analyses for mandibular–maxillary variables unaffected by age are summarized in Table 4 (selected regressions are shown in Fig. 4). Of the 24 regressions summarized in Table 4, 5 were isometric, 16 exhibited positive allometry, and 3 showed negative allometry (the latter confined to a single mandibular measure). Allometric slope was greatest for distance from upper canine to M2 (continental sample), with slopes averaging greater than 1.50. Levels of *r*² varied substantially, averaging lowest for distance from upper canine to M2

(continental sample; range, 0.09–0.17) and highest for maxillary tooththrow length (Newfoundland sample; range, 0.30–0.71; Table 4). The trend toward positive allometry also held for analyses on older (>6 years old) continental specimens, but disappeared in comparable analyses on Newfoundland data: most slopes displayed isometry, and a few were negatively allometric (Table 4, footnotes 1 and 2).

To determine whether Newfoundland–continental differences resulted from single- versus multiple-population differences, we analyzed some continental subsamples (see “Materials and Methods”). For the variable mandibular m3–incisors distance, regression slopes averaged lower than for the sample as a whole in all cases, and only 1 of 7 slopes (for m3 length) was notably greater than isometry (Table 4, footnote 4). For the variable coronoid process–canine length (sexes analyzed separately), 5 of 18 regressions were significant for m3 width (2 positive allometry, 3 isometry), 3 of 19 for m3 length (1 positive allometry, 2 isometry), 5 of 18 for M1 width (2 positive allometry, 3 isometry), and 5 of 18 for M2 width (0 positive allometry, 5 isometry). To summarize, allometric analyses at the level of continental subsamples resulted in weakening of the trend toward positive allometry for the continental sample as a whole, as predicted.

TABLE 2.—Correlation (Pearson’s *r*) matrix for molar variables of black bears (*Ursus americanus*) from Newfoundland (below diagonal) and continental (above diagonal) samples. Values for adjacent teeth are in bold font, and those for the nonadjacent lower 1st (m1) and 3rd (m3) molars are underlined.

Variable	Variable						
	A	B	C	D	E	F	G
A. m1 breadth	—	0.843	<u>0.739</u>	<u>0.610</u>	0.772	0.729	0.699
B. m2 breadth	0.784	—	0.820	0.630	0.752	0.774	0.742
C. m3 breadth	<u>0.413</u>	0.601	—	0.720	0.673	0.751	0.768
D. m3 length	<u>0.469</u>	0.553	0.573	—	0.557	0.641	0.700
E. M1 breadth	0.734	0.698	0.423	0.469	—	0.767	0.670
F. M2 breadth	0.694	0.676	0.386	0.507	0.627	—	0.771
G. M2 length	0.616	0.642	0.480	0.590	0.613	0.718	—

DISCUSSION

Molar-size variation.—Some measures of molar-size variation in black bears were intermediate between species of Carnivora with simpler and more-complex crowns. Mean *CV* ± *SD* for Newfoundland black bears was 5.6 ± 0.65 (*n* = 14, using values for males and females from Table 1); corresponding values for postcanines of the harp seal (*Pagophilus groenlandicus*), which have simple crowns and do not occlude, are 7.5 ± 0.69 (*n* = 10; for the central postcanine tooth of ringed seals [*Pusa hispida*], mean *CV* = 9.7% [Miller et al. 2007]; by 1-way ANOVA, black bears versus harp seals, *F* = 54.6, *df.* = 1, 22, *P* < 0.0001). Molar-size variation in other

TABLE 3.—Principal component analyses on molar variables of black bears (*Ursus americanus*) for Newfoundland and continental samples revealed similar patterns, with all variables loading evenly on the 1st principal component (PC1), and m3 loading heavily on the 2nd principal component (PC2). Sexes were combined for analyses summarized here; separate analyses for the sexes gave similar results.

Variables	Variable loadings for samples			
	Newfoundland		Continental	
	PC1	PC2	PC1	PC2
m1 breadth	0.383	-0.326	0.399	-0.345
m2 breadth	0.396	-0.204	0.417	-0.041
m3 breadth	0.389	0.204	0.314	0.677
m3 length	0.342	0.717	0.341	0.507
M1 breadth	0.368	-0.472	0.385	-0.294
M2 breadth	0.386	-0.103	0.389	-0.279
M2 length	0.379	0.251	0.391	-0.024
Eigenvalue	5.33	0.53	4.54	0.82
Cumulative percent	76.2	83.8	64.8	76.5

bear species is similar to our estimates (Baryshnikov 2006; Baryshnikov et al. 2003; Kurtén 1964, 1966). The exception is the polar bear: CV for M1 length is only 3.3% (Manning 1971), lower than our estimates for black bear, and much lower than for M2 in polar bears—a tooth that has become reduced in size in association with this species’ specialized carnivory (CV = 7.2–9.6% [Kurtén 1964]; 6.5% for males and 8.2% for females [Manning 1971]).

Tooth-size variation is higher in Newfoundland black bears than most published values for species that display greater complexity in crown morphology and occlusion-shearing mechanisms. For several species of Canidae, CVs for P4 and m1 averaged 4.8% and 4.5%, respectively (Pengilly 1984; Prevosti and Lamas 2006; Szuma 2000, 2003). Variation appears to be even lower in Mustelidae: m1, CVs = 2.3–4.2% in 11 populations (with $n \geq 10$) of European pine marten

(*Martes martes*—Reig 1992); P4 and m1, CVs = 4.5–4.6% and 2.7–4.4% (respectively) in marbled polecat (*Vormela peregusna*—Rozhnov and Abramov 2006); and m1, CVs = 1.9–4.7% in the sea otter (*Enhydra lutris*—Wilson et al. 1991). Similarly, for P4 length in tigers (*Panthera tigris*) from southeastern Asia, CVs averaged only 3.2% (Mazák and Groves 2006). In some mammals, size of m1 and M1 is less variable than that of other cheek teeth (Gingerich and Winkler 1979, 1985; Pengilly 1984; Szuma 2000). This pattern was not detected for black bears; however, m3 tended to vary less than other molars.

Bilateral asymmetry is another manifestation of morphometric variation. Molar size of Newfoundland black bears was highly symmetric between left and right sides, and symmetry was higher than for postcanine teeth of 2 species of phocid seal: corresponding teeth on left and right sides differed in size by <1% in black bears, but by ~2–4% in seals (Miller et al. 2007). In the European pine marten, r between size of cheek teeth on left and right sides averaged 0.88 (maximum, 0.92—Wolsan et al. 1985), similar to our estimate for black bears. The greater symmetry in bears than in seals agrees with our predictions; we expected mustelids such as marten to be more symmetric in size of cheek teeth. Surprisingly, bilateral symmetry in molar size was similar to that in most mandibular and maxillary measures, except for mandibular length; left and right mandibular lengths differed very little. The same pattern occurs in harp and ringed seals, suggesting that symmetry in mandibular length must be of general importance in Carnivora (at least those that lack symphyseal fusion, such as bears and seals), regardless of dietary differences (Miller et al. 2007).

The molar-size correlation patterns of the black bears that we measured are not intermediate between species of Carnivora with more and less morphologically complex crowns. Nevertheless, our estimates appear to be sound, because r -matrices were similar between Newfoundland and continental samples. Some of our estimates are even higher than for some fox

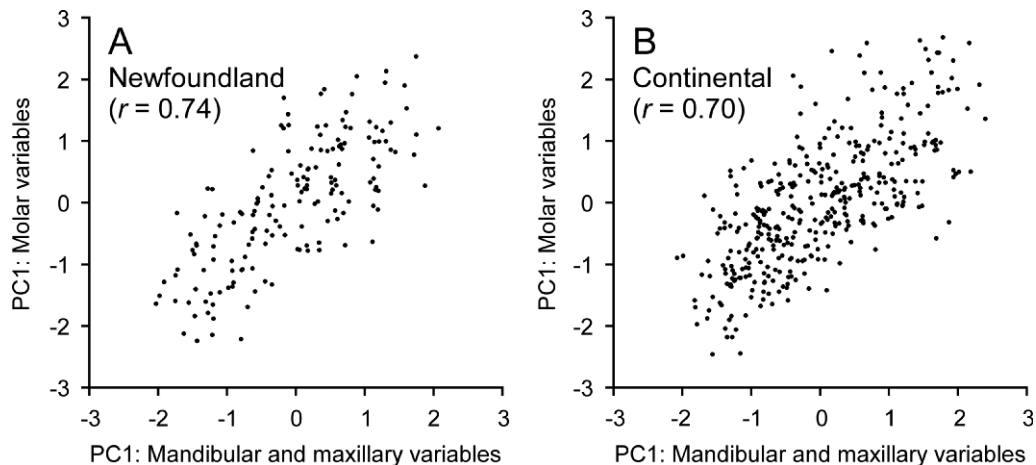


FIG. 3.—Molar size is positively related to body size (using mandibular and maxillary size as proxies) in the black bear (*Ursus americanus*), in both Newfoundland (A) and other (“Continental”) North American (B) samples. This is shown in bivariate plots of scores on the first principal components (PCs), for molar variables versus mandibular and maxillary variables (data for both sexes and all age classes are illustrated; see text and Table 3).

TABLE 4.—Summary of allometric (log–log) regressions, expressed as reduced major axis regressions. Body-size variables (maxillary tooththrow length, etc.) were selected for allometric analysis if they had significant relationships to molar size and few age or interaction effects (as determined by general linear model analyses; see “Materials and Methods”). Each cell entry shows reduced major axis regressions slope \pm SE, with statistical details in parentheses. Positive allometry is in bold font, and negative allometry is indicated by underlining; other regressions are indistinguishable from isometry (all $P < 0.01$). Selected examples (*) are shown in Fig. 4.

Molar variables	Newfoundland sample ^a		Continental sample ^b		
	Maxillary tooththrow length (sexes combined)	Incisors to m3 (sexes combined)	Canine to coronoid process (sexes combined)	Canine to M2	
				Males	Females
m1 breadth	1.12 \pm 0.05 ($r^2 = 0.58$, $F = 288$, $df. = 1, 213$)	— ^c	— ^c	— ^c	— ^c
m2 breadth	1.07 \pm 0.05 ($r^2 = 0.58$, $F = 270$, $df. = 1, 198$)	— ^c	— ^c	— ^c	— ^c
m3 breadth	0.98 \pm 0.06 ($r^2 = 0.34$, $F = 102$, $df. = 1, 197$)	1.29 \pm 0.04^d ($r^2 = 0.45$, $F = 396$, $df. = 1, 474$)	— ^c	1.56 \pm 0.09 ($r^2 = 0.14$, $F = 44.8$, $df. = 1, 285$)	1.67 \pm 0.09 ($r^2 = 0.17$, $F = 59.0$, $df. = 1, 296$)
m3 length	1.25 \pm 0.08 ($r^2 = 0.34$, $F = 93.4$, $df. = 1, 179$)	1.33 \pm 0.05^d ($r^2 = 0.43$, $F = 349$, $df. = 1, 460$)	1.06 \pm 0.04 ($r^2 = 0.30$, $F = 230$, $df. = 1, 530$)	1.51 \pm 0.09 (*) ($r^2 = 0.11$, $F = 35.1$, $df. = 1, 270$)	1.92 \pm 0.10 (*) ($r^2 = 0.15$, $F = 51.7$, $df. = 1, 285$)
M1 breadth	1.02 \pm 0.04 ($r^2 = 0.54$; $F_{1,281} = 332$)	1.12 \pm 0.04^d (*) ($r^2 = 0.34$, $F = 245$, $df. = 1, 473$)	<u>0.84 \pm 0.03 (*)</u> ($r^2 = 0.28$, $F = 231$, $df. = 1, 588$)	1.31 \pm 0.07 ($r^2 = 0.15$, $F = 55.6$, $df. = 1, 311$)	1.48 \pm 0.08 ($r^2 = 0.09$, $F = 33.2$, $df. = 1, 318$)
M2 breadth	1.06 \pm 0.04 ($r^2 = 0.60$, $F = 421$, $df. = 1, 282$)	1.16 \pm 0.04^d ($r^2 = 0.39$, $F = 303$, $df. = 1, 475$)	<u>0.88 \pm 0.03</u> ($r^2 = 0.31$, $F = 264$, $df. = 1, 590$)	1.42 \pm 0.07 ($r^2 = 0.14$, $F = 49.9$, $df. = 1, 314$)	1.45 \pm 0.08 ($r^2 = 0.13$, $F = 47.4$, $df. = 1, 322$)
M2 length	1.20 \pm 0.04 (*) ($r^2 = 0.72$, $F = 738$, $df. = 1, 281$)	1.21 \pm 0.04^d ($r^2 = 0.50$; $F_{1,453} = 452$)	<u>0.94 \pm 0.03</u> ($r^2 = 0.38$, $F = 350$, $df. = 1, 560$)	— ^c	— ^c
Mean slope and r^2	1.10, 0.53	1.22, 0.42	0.93, 0.32	1.45, 0.14	1.63, 0.14

^a For old (> 6 years) males in the Newfoundland sample, 3 regressions were significant but indistinguishable from isometry: M1 breadth versus mandibular tooththrow length, 1.21 ± 0.27 ($r^2 = 0.31$, $F = 6.20$, $df. = 1, 14$, $P = 0.03$); M2 length versus mandibular tooththrow length, 1.33 ± 0.25 ($r^2 = 0.50$, $F = 14.3$, $df. = 1, 14$, $P < 0.01$); and M2 length versus maxillary tooththrow length, 1.40 ± 0.30 ($r^2 = 0.36$, $F = 8.02$, $df. = 1, 14$, $P = 0.01$). Four other regressions exhibited negative allometry: m2 breadth versus mandibular length, 0.61 ± 0.07 ($r^2 = 0.30$, $F = 4.77$, $df. = 1, 14$, $P < 0.05$); m2 breadth versus condylar breadth, 0.33 ± 0.07 ($r^2 = 0.30$, $F = 6.83$, $df. = 1, 16$, $P < 0.02$); m2 breadth versus maxillary tooththrow length, 0.75 ± 0.15 ($r^2 = 0.51$, $F = 12.7$, $df. = 1, 12$, $P < 0.01$); and M1 breadth versus condylar breadth, 0.51 ± 0.12 ($r^2 = 0.25$, $F = 4.79$, $df. = 1, 14$, $P < 0.05$).

^b For old (> 6 years) males and females in the continental sample, all regressions except 1 (those involving M1 breadth for females) were significant. Of these regressions, all exhibited positive allometry except 1 for females that was indistinguishable from isometry: M2 breadth versus mandibular tooththrow length, 1.15 ± 0.13 ($r^2 = 0.07$, $F = 5.51$, $df. = 1, 72$, $P = 0.02$).

^c Not analyzed because of significant or near-significant age effects (see Table 4).

^d Mean slopes \pm SE for 11 localities with sample sizes ≥ 20 ($n = 22$ –74; all slopes significant): 1.13 ± 0.06 , **1.29 \pm 0.06**, **2.23 \pm 0.10**, 1.02 ± 0.04 , 1.03 ± 0.04 , **1.17 \pm 0.06**, and 2.05 ± 0.07 (top to bottom), respectively.

species (Kurtén 1953, 1967; Miller et al. 2007; Pengilly 1984; Prevosti and Lamas 2006; Szuma 2000). Comparatively weak integration of black bear dentition may be reflected in the lack of position effects (except possibly m3); in many mammals, m1 and M1 vary less in size than do other cheek teeth (Gingerich and Winkler 1979, 1985; Pengilly 1984). Our measures of molar size were crude, and finer-scale analyses are needed to interpret adaptive and phylogenetic significance of correlation patterns within and across species: size and morphology of cheek teeth in some species of Carnivora exhibit much geographic and temporal variation (Baryshnikov et al. 2002, 2003; Daitch and Guralnick 2007; Grandal-d’Anglade 1993; Grandal-d’Anglade and López-González 2005; Szuma 2003), tooth morphology can evolve quickly, and fine-scale dental

adaptations to species’ diets are well documented (Evans and Sanson 2006; Evans et al. 2007; Friscia et al. 2007; Jernvall 2000; Jernvall et al. 2000; Salazar-Ciudad and Jernvall 2002).

In summary, the predicted intermediate level of variation in molar size of black bears was supported by CVs, and (partly) by bilateral asymmetry and the absence of marked positional differences in variability, but not by tooth-size correlation patterns. Therefore, some of our findings are consistent with our predictions about molar-crown-size variability, in relationship to omnivory and generalized food-processing requirements. The use of CVs to infer ecologically meaningful variation must be considered carefully, however. First, it assumes that populations or species under consideration are

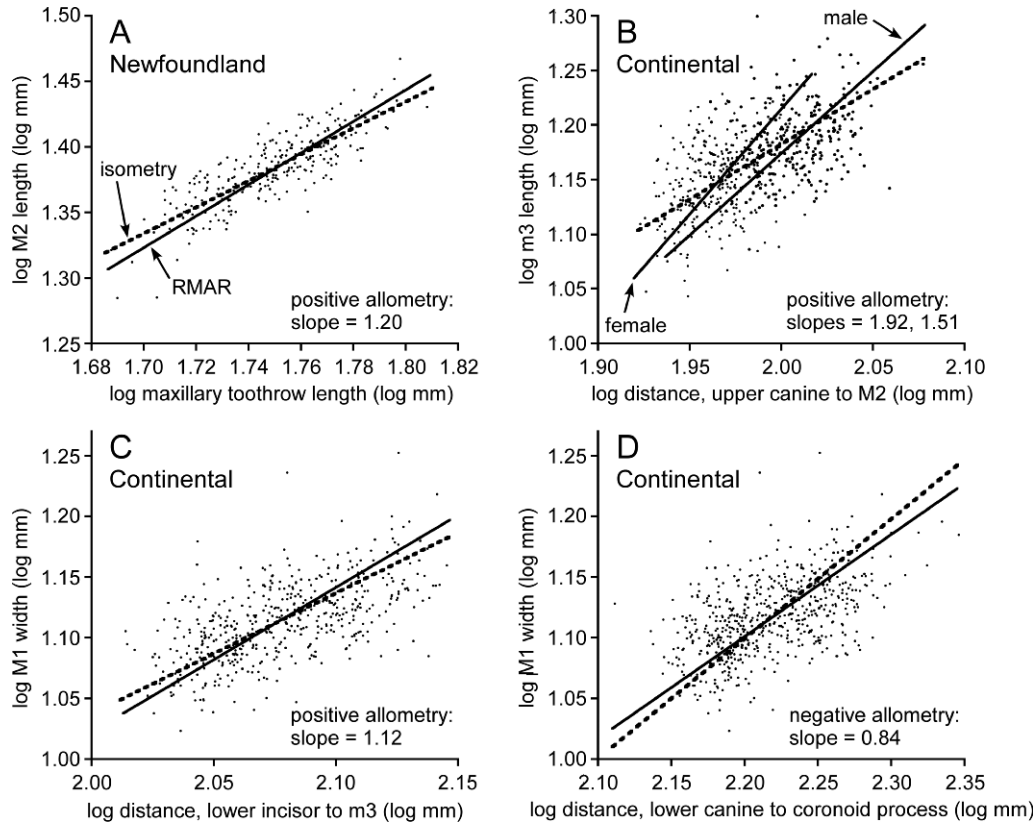


FIG. 4.—Examples of allometric regressions of molar size on mandibular and maxillary size of black bears (*Ursus americanus*), for relationships in which age had no significant effect (see text and Table 4). Slopes of isometry and reduced major axis regression (RMAR) are shown. Allometric relationships did not differ (A, C, and D) or differed (B) between the sexes, for different combinations of variables. Allometric relationships also depended on which molar and mandibular–maxillary variables were analyzed: M1 width is an example (C and D).

comparably specialized or generalized. For example, CVs of similar magnitude could characterize a population of variably sized individuals, each with precisely occluding teeth, or a population of similarly sized individuals with more imprecise

occlusion patterns. Second, CV estimates are affected by allometric relationships, which are rarely considered in studies on variation; species differences in trait variability can arise from differences in allometric slope, or different amounts of

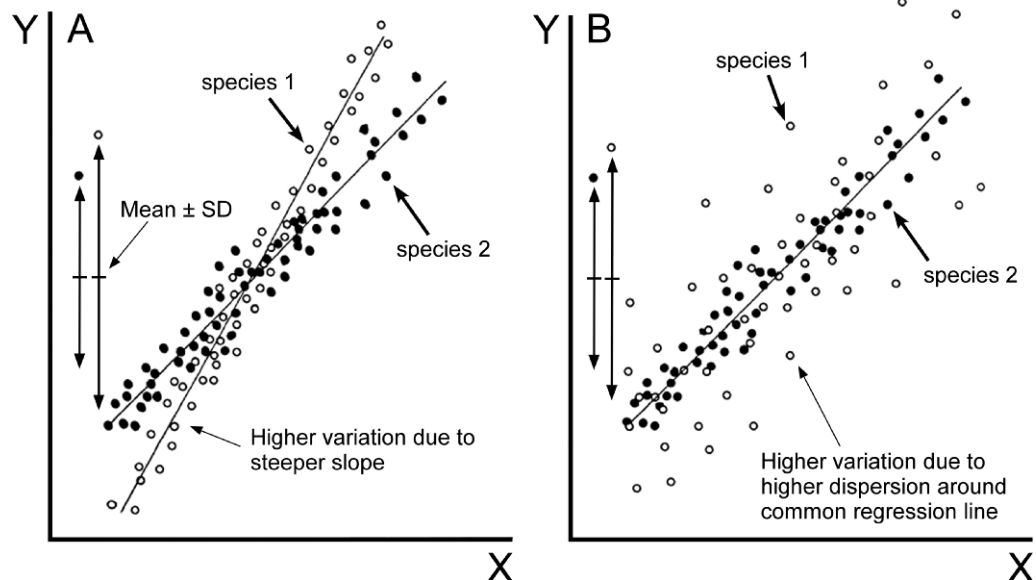


FIG. 5.—Quantitative estimates of variation (e.g., coefficient of variation [CV]) are influenced by both allometric slope and variation around the line of allometric regression. For example, CV of a trait y could be larger in species 1 A) because of differences in allometric slope with respect to a body-size measure x, or B) because of greater dispersion of points around a common line of regression. After Eberhard et al. (1998: figure 1).

variation around a common line of regression, or both (Eberhard et al. 1998; Fig. 5). This matter merits separate analysis, but it likely would not have affected our comparisons between bears and seals; significant isometry and positive allometry were found in black bears, whereas postcanine size is unrelated to body size in harp and ringed seals (Miller et al. 2007)—a difference that should contribute to higher variation in bears, not lower variation as we observed. A preliminary interpretation would be that the dispersion of points around the regression line in bears must be relatively small. In any event, the matter needs to be investigated properly in a comparative context, to enable better assessment of variation across traits and species.

Sexual size dimorphism in molars.—Sexual size dimorphism is weaker in molars than in body-size measures, as predicted. In Newfoundland bears, males averaged <6% larger than females in molar size, less than sexual differences in cranial size (7–9%—Virgl et al. 2003), and much less than in canine size (21%; anteroposterior extent of alveolus) or body mass^{1/3} (21%—Mahoney et al. 2001). Continental subsamples displayed similar trends: for Alaska, New York (Adirondacks), and California, sexual size dimorphism for molar-size traits averaged 7.4%, 9.9%, and 8.3%, respectively (Table 1), compared with 10.4%, 13.2%, and 12.1% for the 3 cranial variables used in this study. For Michigan and New York bears, Marks and Erickson (1966) reported sexual size dimorphism of ~16% for several measures of canine size. A similar pattern is apparent for polar bears. Crown lengths of M1 and M2, respectively, average 13% and 7% larger in males throughout life (Manning 1971: table 2), whereas sexual dimorphism in body mass^{1/3}, body length, head length, and head width increase from 9%, 7%, 7%, and 8%, respectively, in yearlings, to 28%, 18%, 16%, and 31% in adults (Derocher et al. 2005: tables 2 and 3).

The explanation for this trend seems straightforward: molar-crown size is established early in life, whereas body growth and canine growth and emergence continue for years, especially in males (Mahoney et al. 2001; Marks and Erickson 1966; Rausch 1961). The permanent postcanine dentition in black bears starts to erupt at around 3 months of age, whereas canines erupt in the 2nd spring, at about 15 months of age (Dalquest 1986; Rausch 1961, 1967). Endocrine factors during and after puberty do not affect molar-crown size, but influence both body size and canine size (Gingerich 1972, 1974); presumably for the same reason, molar size is invariably less variable than canine size (allometric differences may affect these levels of variation, as discussed above [Abramov and Puzachenko 2005; Meiri et al. 2005; Prevosti and Lamas 2006; Szuma 2000]).

Relationship of molar size to mandibular and maxillary size.—Molar size was positively correlated with body size (using mandibular and maxillary size as proxies) in multivariate and most bivariate analyses, for both Newfoundland and continental samples. Molars erupt early in life and do not grow thereafter; therefore, adult body size can be predicted to some extent early in life as well. Size of bear cubs is variable within and across litters, and is affected by litter size, and by age, body size, and condition of the female (Alt 1989; Bridges et al. 2002; Derocher and Stirling 1998). These factors must be particularly

important because they influence fetal and early cub growth. Positive correlations between size of lower cheek teeth and cranial or mandibular size have been reported for various species of Carnivora. Kurtén (1953, 1967) reported values for red foxes (*Vulpes vulpes*; $r = 0.56\text{--}0.67$), cave bears ($r = 0.63$; but not brown bear), and spotted hyenas (*Crocuta crocuta*; $r = 0.47$). Size of upper and lower carnassials is positively correlated with condylobasal length in lions (*Panthera leo*; $r = 0.54$ and 0.57 , respectively), leopards (*P. pardus*; $r = 0.71$ and 0.70), and jaguars (*P. onca*; $r = 0.79$ and 0.71 —Turner and O'Regan 2002). Significant positive relationships also have been found between size of cheek teeth and various measures of body size in rodents and primates (Dayan et al. 2002; Gould and Garwood 1969; Moyer et al. 1985; Olson and Miller 1958; Wood 1979). A clear trend emerges from the preceding examples, but it is not universal: in harp and ringed seals, size of postcanine teeth is unrelated to or only very weakly correlated with mandibular size (Miller et al. 2007).

The difference between bears (and other taxa), and harp plus ringed seals, is explicable by differences in growth patterns. In newborn harp and ringed seals, crowns of permanent postcanine teeth have an enamel layer and are of adult size (Stewart et al. 1998; Stewart and Stewart 1987). In contrast, permanent cheek teeth in the black bear start to erupt only after considerable body growth: by 3 months of age (when cheek teeth start to erupt), body mass has increased ~10-fold relative to natal mass (Alt 1989; Dalquest 1986; Oftedal et al. 1993; Rausch 1961). Therefore, postnatal factors, such as nutrition, have little or no influence on postcanine size in harp or ringed seals, but have considerable importance for bears, felids, and many other taxa.

In paleobiology, body size is often estimated from tooth size (Creighton 1980; Gingerich et al. 1982; Pan and Oxnard 2003; Van Valkenburgh 1990). The validity of how body size is estimated depends on factors such as those discussed and on the strength of correlation (Turner and O'Regan 2002); in most intraspecific analyses (including ours), correlations are of only moderate strength, so size estimates can be only approximate.

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