

## Body mass in large extant and extinct carnivores

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(With 4 figures in the text)

Body mass in six species of Plio-Pleistocene carnivores was estimated based on the relationship between mass and cross-sectional geometric properties, distal articular surface area, lengths and circumferences of proximal limb bones (femur and humerus) in 28 species of extant carnivores. All measures, except lengths, were found to give congruent body mass estimates. Two of the extinct carnivores (*Smilodon fatalis* and *Panthera atrox*) are estimated to be as much as one and a half times heavier than previously thought. Based on these results inferences are made concerning possible prey species.

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### Introduction

Understanding the relationship between body mass and various skeletal measures in living mammals enables paleontologists to make reasonable predictions of body mass and associated ecological features in fossil species. The prevalence of teeth in the fossil record has inevitably resulted in the extensive use of dental measures in studies aimed at predicting body mass in extinct mammalian species (Gingerich, 1977; Kay & Simons, 1980; Gingerich, Smith & Rosenberg, 1982; Smith, 1984; Steudel, 1985; Conroy, 1987; Legendre & Roth, 1988; Van Valkenburgh, 1990). The use of postcranial elements in predicting body mass has more recently received greater attention. Most of these studies have tended to concentrate on allometric scaling relationships between body mass and external skeletal measures such as long bone lengths, diameters and circumferences (Alexander *et al.*, 1979; Anderson, Hall-Martin & Russell, 1985; Jungers, 1985; Preuschoft & Demes, 1985; Scott, 1985, 1990; Gingerich, 1990).

Structural characteristics of limb bones other than lengths, diameters and circumferences have been shown to be better predictors of body mass in several vertebrate groups (Biewener, 1982; Shaffler *et al.*, 1985; Ruff, 1987, 1988, 1989; Ruff, Walker & Teaford, 1989). This is not surprising because the forces acting on the limbs of an animal are proportional to the weight the limbs have to support and consequently to the stresses developed in the cross-section of the bones (Alexander, 1989, 1991). The analysis of the relationship between body mass and cross-sectional structural

properties of long bones is important because deviations from expected scaling may help define some of the mechanically relevant complexes of traits that describe the adaptation of bone to different biomechanical environments (Biewener, 1982; Rubin & Lanyon, 1984; Currey & Alexander, 1985; Ruff, 1989). Other aspects of the postcranial skeleton, such as hind limb articular surface areas, are not only good predictors of body mass but are linked also to locomotor and postural adaptations (Jungers, 1988, 1990; Ruff, 1988).

Here these allometric relationships are explored in 28 species of large extant carnivores. In addition to investigating the general scaling relationships between body mass and femoral and humeral measures in several carnivoran families, this paper presents body mass estimates for six extinct Plio-Pleistocene carnivores based on equations relating body mass to long bone length, circumference, articular area and cross-sectional geometric properties in large modern carnivores.

### Materials and methods

A total of 28 species of modern carnivores representing 4 families are included in this study: Felidae ( $n=14$ ), Canidae ( $n=7$ ), Ursidae ( $n=4$ ) and Hyaenidae ( $n=3$ ) (Table I). Measurements made on the femur included maximum proximodistal length between articulating surfaces, anteroposterior and mediolateral diameters at the midshafts (Fig. 1a), and length and width of the distal condyles (articular area was assumed to be approximately rectangular and was calculated as the sum of the areas of the 2 condyles (Fig. 1c)). Humeral measures included maximum proximodistal length between articulating surfaces, circumference and anteroposterior and mediolateral diameters at a point located at 35% of humeral length (measured from the distal end) (Fig. 1b). The locations along the femoral and humeral diaphyses were chosen because they have fairly regular subperiosteal perimeters that allow accurate reconstruction of cross-sectional shapes (Biknevicius & Ruff, 1992; Runestad *et al.*, 1993). Biplanar radiographs were obtained for each of the limb bones. For each species, 3 femora and humeri were X-rayed in the sagittal and frontal planes (Fig. 1a, b). The thickness of cortical bone was measured on the radiographs using needle-point digital callipers to the nearest 0.1 mm. For calculation of cortical area (CA) (units, mm<sup>2</sup>) and second moments of area (units, mm<sup>4</sup>) in the anteroposterior and mediolateral plane,  $I_y$  and  $I_x$ , respectively, the femur and humerus were modelled as hollow elliptical beams with symmetrical cross-sectional areas. This model allows the use of the following formulae (Roark, 1965; Alexander, 1968).

$$\begin{aligned} CA &= \pi (AB - ab)/4 \\ I_x &= (AB^3 - ab^3)/64 \\ I_y &= \pi(A^3B - a^3b)/64 \end{aligned}$$

where  $A$ =external (subperiosteal) anteroposterior diameter,  $B$ =external (subperiosteal) mediolateral diameter,  $a$ =anteroposterior diameter of the medullary cavity, and  $b$ =mediolateral diameter of the medullary cavity, of each bone at the location of the cross-section (mid-shaft for the femur and 35% of the humeral shaft from the distal end) (Fig. 2). Cortical cross-sectional area is proportional to axial compressive and tensile rigidity, whereas the second moment of area is proportional to bending rigidity perpendicular to the axis about which it is measured. Both these parameters are estimated because the bones of an animal experience both axial and transverse forces that result from having to support the animal's weight, especially during locomotion (Ruff, 1989; Alexander, 1991).

The relationships between body mass and femoral and humeral length and circumference, CA,  $I$  and femoral condylar area were evaluated for the total sample and for 3 families (Felidae, Canidae, Ursidae) using least-squares regressions of  $\log_{10}$  transformed data. Regressions were not performed for the Hyaenidae because of the small sample size ( $n=3$ ). With body mass as the dependent variable ( $y$ ), the relationship between the independent ( $x$ ) and dependent variable is expressed by the power function  $y = bx^k$  which can be rewritten as  $\log_{10}(y) = k\log_{10}(x) + \log_{10}(b)$ . Least-squares and Model II reduced major axis regression models

TABLE I  
Body weights of the extant carnivores

Species	Body weight (kg)	Source
<b>Felidae</b>		
<i>Neofelis nebulosa</i>	18	1
<i>Puma concolor</i>	60	4
<i>Felis caracal</i>	20	1
<i>F. pardalis</i>	14	1, 4
<i>Acinonyx jubatus</i>	52	1, 2
<i>Panthera onca</i>	85	2, 3
<i>P. pardus</i>	50	2, 4
<i>P. leo</i>	181	1
<i>P. tigris</i>	160	1, 2
<i>Felis serval</i>	16	1
<i>Lynx rufus</i>	19	1
<i>Felis lybica</i>	5	1
<i>Uncia uncia</i>	70	1
<i>Felis yagouaroundi</i>	8	1
<b>Canidae</b>		
<i>Lycaon pictus</i>	24	1
<i>Canis lupus</i>	46	1, 4
<i>C. latrans</i>	13	1, 4
<i>C. mesomelas</i>	11	1, 4
<i>Speothos venaticus</i>	6	1, 4
<i>Canis adustus</i>	11	1
<i>Chrysocyon brachyurus</i>	23	1
<b>Ursidae</b>		
<i>Ursus americanus</i>	150	4
<i>U. arctos</i>	250	1, 4
<i>U. maritimus</i>	500	1
<i>Melursus ursinus</i>	102	1, 2
<b>Hyaenidae</b>		
<i>Crocuta crocuta</i>	65	1
<i>Hyaena hyaena</i>	35	1
<i>H. brunnea</i>	40	1

Weight references: (1) Macdonald (1984); (2) Walker *et al.* (1964); (3) Eisenberg *et al.* (1979); (4) Van Valkenburgh (1987).

give similar results when the correlation coefficient between a pair of variables is high (Jungers, 1984), as is the case here (Tables II and III). The least-squares model was used because it remains the appropriate methodology when the goal of the allometric analysis is to develop 'predictive' equations (Sokal & Rohlf, 1981). A geometrically similar or isometric slope for the regression of body mass on linear dimensions, such as length and circumference, is 3; for body mass on cortical and distal articular areas, 1.5 and for body mass on second moments of area, 0.75.

In addition to the correlation coefficient ( $r$ ), the percentage prediction error (%PE) and the percentage standard error of the estimate (%SEE) were used as indicators of the predictive power of the independent variable (Smith, 1981, 1984; Van Valkenburgh, 1990). Smith (1984) described the %PE as an indicator of the percentage difference between the actual weight and that predicted by the regression. The mean of the absolute values of the %PEs for each regression was computed and compared among regressions. The %SEE

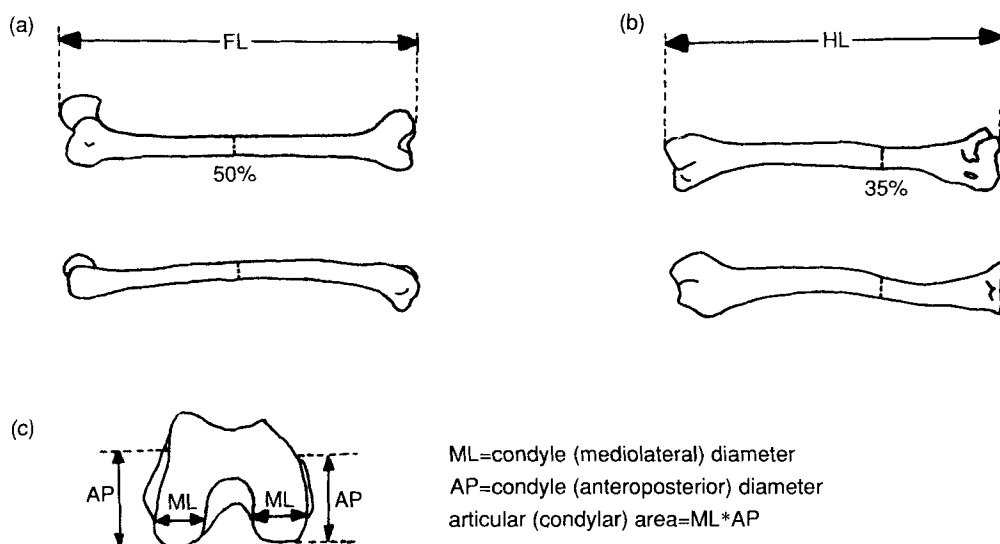


FIG. 1. (a) Cross-section locations and X-ray planes in the femur: frontal, top; sagittal, bottom; FL, femur proximodistal length; (b) Cross-section locations and X-ray planes in the humerus: frontal, top; sagittal, bottom; HL, humerus proximodistal length. (c) Articular surfaces of distal femur and calculation of condylar area.

reflects the overall ability of the independent variable to predict the dependent variable (Van Valkenburgh, 1990). The computations are:

$$\begin{aligned}\%PE &= 100 \times [\text{observed} - \text{predicted}] / \text{predicted} \\ \%SEE &= \text{antilog} [2 + \log_{10} SEE] - 100\end{aligned}$$

Assuming a normal distribution, 1%SEE indicates the range within which 68% of the actual values would be expected to fall. The slopes, y-intercepts and standard error of the mean (SE) are also given for each regression. Statistical differences between familial regression slopes were tested using the ANCOVA program

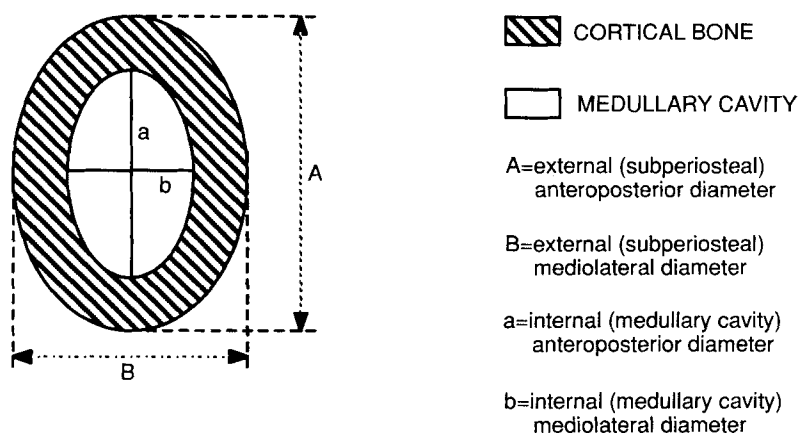


FIG. 2. Hollow elliptical model used for calculation of femoral and humeral cross-sectional geometric properties. The model assumes a symmetrical distribution of cortical bone to the outside of the medullary cavity.

TABLE II  
Regression of  $\log_{10}$  (body mass) on  $\log_{10}$  (femoral measures)

Measure	Group	Slope	Int.	r	SE	%SEE	%PE
FL	Total	2.92	-5.27	0.95	0.201	46	25
	Felidae	3.20	-5.90	0.96	0.282	39	26
	Canidae	1.67	-2.54	0.88	0.398	41	20
	Ursidae	3.85	-7.62	0.95	0.932	33	29
FC	Total	2.88	-3.40	0.98	0.131	30	22
	Felidae	2.92	-3.46	0.96	0.251	38	27
	Canidae	2.37	-2.60	0.96	0.318	23	18
	Ursidae	3.96	-5.55	0.99	0.391	13	41
FCA	Total	1.25	-1.04	0.98	0.053	29	23
	Felidae	1.31	-1.18	0.97	0.099	33	28
	Canidae	1.05	-0.67	0.95	0.159	26	25
	Ursidae	1.66	-2.15	0.96	0.349	29	37
FIX	Total	0.69	-0.77	0.98	0.030	29	24
	Felidae	0.69	-0.79	0.96	0.056	36	30
	Canidae	0.55	-0.37	0.95	0.078	25	19
	Ursidae	0.95	-1.91	0.99	0.095	13	42
FIY	Total	0.67	-0.76	0.98	0.029	29	33
	Felidae	0.71	-0.91	0.96	0.056	35	27
	Canidae	0.56	-0.42	0.96	0.074	23	20
	Ursidae	0.90	-1.83	0.98	0.123	18	41
FDA	Total	1.31	-2.12	0.99	0.047	24	22
	Felidae	1.32	-2.16	0.98	0.072	24	22
	Canidae	1.06	-1.52	0.96	0.139	23	19
	Ursidae	1.55	-2.94	0.93	0.446	41	32

Note: Sample sizes are as follows: Felidae, 14; Canidae, 7; Ursidae, 4; Total, total sample of 28 species including the Hyaenidae ( $n=3$ ).

Abbreviations: FL, femur length; FC, femur circumference; FCA, femur cortical cross-sectional area; FIX, femur second moment of area (mediolateral axis); FIY, femur second moment of area (anteroposterior axis); FDA, femur distal articular (condylar) area; Int., y-intercept; r, correlation coefficient; SE, standard error of the mean; %SEE, percentage standard error of the estimate; %PE, mean absolute value of percentage prediction error.

of the statistical package SYSTAT (Wilkinson, 1986) and the Student's *t*-test (2-tailed) as described by Zar (1984).

Six equations based on femoral measures and 5 equations based on humeral measures were obtained for the regressions performed on the felid and total sample. The equations were then used to predict the body mass of 6 extinct species of Plio-Pleistocene carnivores including 5 felids (*Smilodon fatalis*, *Homotherium serum*, *Machairodus coloradensis*, *Nimravides galiani*, *Panthera atrox*) and 1 nimravid (*Barbourofelis morrisi*). A correction factor was applied to each regression equation to counteract the systematic bias that results from the direct transformation of logarithmic values back to arithmetic units (Baskerville, 1972; Sprugel, 1982).

The body weights of the extant carnivores (Table I) were obtained from the literature (Walker *et al.*, 1964; Eisenberg, O'Connell & August, 1979; Macdonald, 1984; Van Valkenburgh, 1987). Mean body weights for



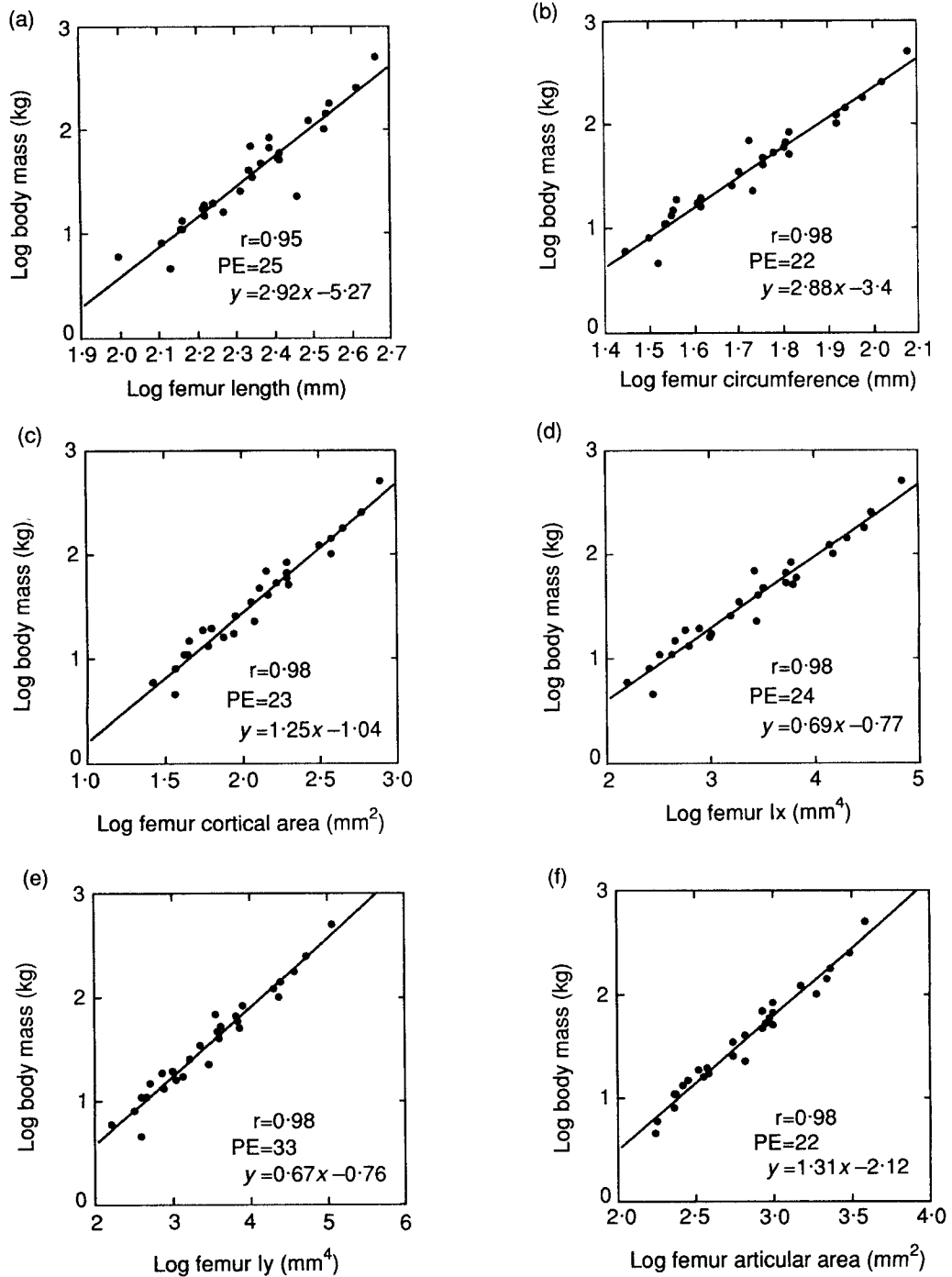


FIG. 3. Plot of  $\log_{10}$  body mass against  $\log_{10}$  femoral measures for the total sample of 28 species of extant carnivores. Abbreviations and regression statistics as in Table III.

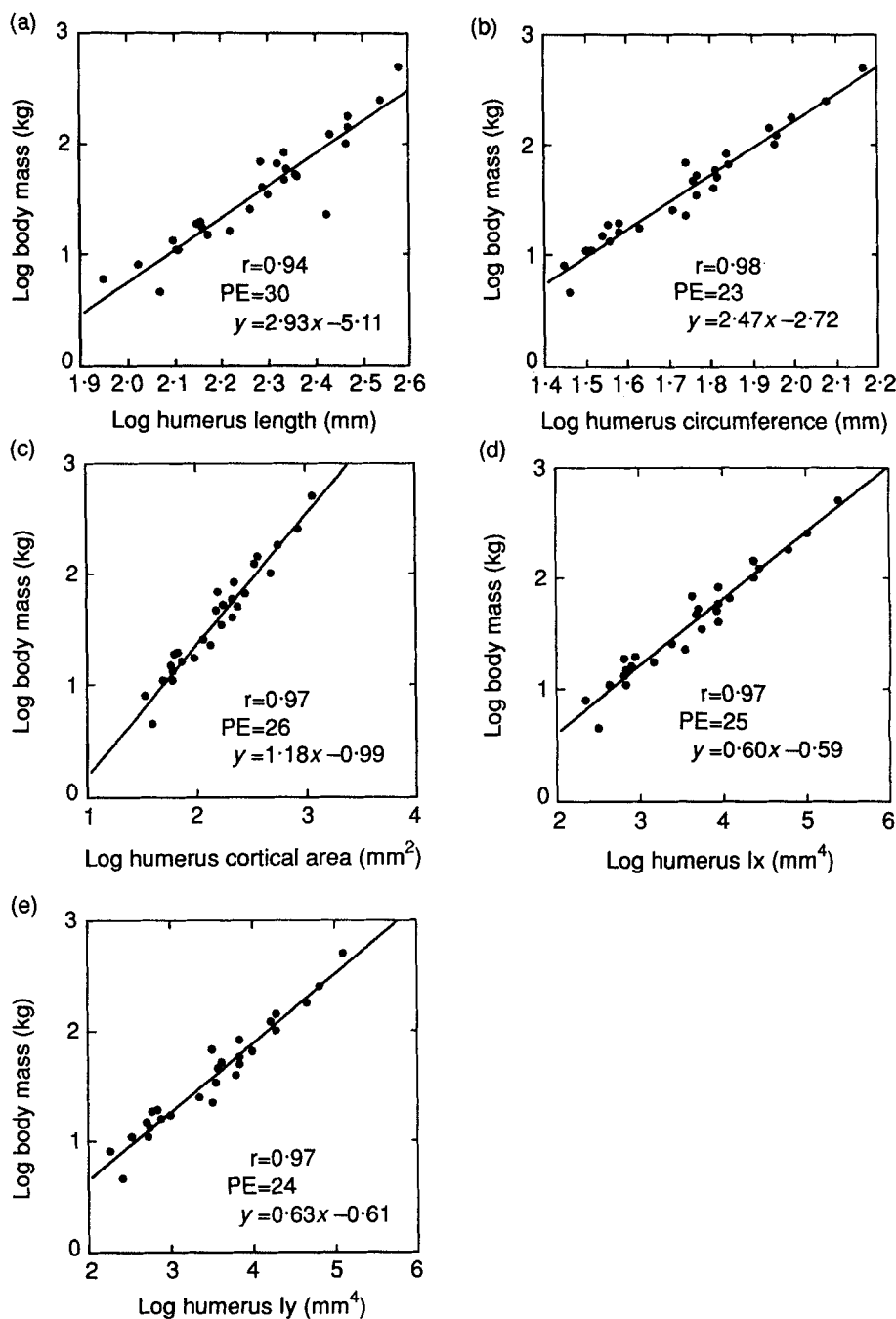


FIG. 4. Plot of  $\log_{10}$  body mass against  $\log_{10}$  humeral measures for the total sample of 28 species of extant carnivores. Abbreviations and regression statistics as in Table III.



and humeral measures, are listed in Table IV. Predicted body weights derived from the felid regression are also listed for comparison with those obtained from the total sample regression.

The slopes produced by the regression of body mass against femoral length and circumference and humeral length for the total sample do not significantly depart from isometry. All other slopes for the total samples show evidence of non-isometry. Based on *r*-values, %PEs and %SEEs, the best predictor of body mass among all femoral measures for the total is distal articular area, closely followed by cortical cross-sectional area, circumference, second moment of area and length. Among felids, the best predictor is distal articular area followed by cortical cross-sectional area, second moments of area, circumference and length. For ursids, femoral second moments of area is the best predictor, followed by circumference, cortical cross-sectional area, length and distal articular area. For canids, the best predictor is femoral circumference, followed by second moment of area (IX), distal articular area, cortical cross-sectional area and length.

The best predictor of body mass among all humeral measures for the total sample is humeral circumference followed by second moments of area, cortical area and length. For felids the best predictor is circumference followed by cortical area, second moments of area and length. For canids, humeral circumference is the best predictor, followed by second moment of area (HIX), cortical area (HCA) and length. Finally, among ursids the best predictor is humeral circumference followed by second moments of area, cortical area and length.

TABLE IV

*Prediction of body mass in six Plio-Pleistocene carnivores based on the total sample and felid regressions for log<sub>10</sub> body mass against log<sub>10</sub> femoral and humeral measures*

Species	Weight (kg) based on						MEAN
	FL HL	FC HC	FCA HCA	FIX HIX	FIY HIY	FDA	
<i>Smilodon</i> <i>fatalis</i>	218 (240) 238 (287)	339 (369) 345 (440)	358 (389) 359 (462)	401 (391) 339 (437)	356 (405) 375 (428)	285 (292)	347 (369) 355 (442)
<i>Homotherium</i> <i>serum</i>	159 (171) 134 (156)	237 (258) 153 (185)	236 (252) 140 (171)	228 (222) 142 (175)	207 (229) 148 (165)	193 (192)	220 (231) 146 (174)
<i>Machairodus</i> <i>coloradensis</i>	189 (206) 126 (146)	213 (231) 140 (166)	151 (158) 141 (172)	200 (194) 128 (156)	194 (212) 152 (169)	195 (195)	191 (198) 140 (166)
<i>Barbourofelis</i> <i>morrisi</i>	91 (92) 57 (61)	138 (148) 108 (127)	137 (142) 102 (122)	124 (121) 101 (129)	144 (154) 101 (112)	91 (90)	127 (131) 99 (116)
<i>Panthera</i> <i>atrox</i>	278 (314) 264 (320)	350 (382) 341 (434)	345 (374) 471 (616)	344 (335) 358 (461)	336 (380) 509 (580)	345 (355)	344 (365) 420 (523)
<i>Nimravides</i> <i>galiani</i>	259 (289) 253 (306)	233 (252) 246 (307)	209 (222) 139 (170)	216 (210) 146 (180)	215 (237) 146 (163)	201 (213)	215 (227) 169 (205)

Note: Abbreviations as in Tables II and III. Values in parentheses represent the body weight estimates based on the felid regressions. Values not in parentheses represent the body weight estimates based on the total sample regressions. The mean values represent the mean species body weights calculated from the total sample and felid regressions (after excluding length measures).

### *Predicted body weights for fossil carnivores*

Femoral and humeral length produced the lowest body mass estimates for all species except *Nimravides galiani*. The other measures produced body mass estimates that are reasonably congruent (the lowest body mass estimate is at least 65% of the highest). The equations derived from the felid and total sample regressions resulted in fairly congruent body mass estimates, especially for the femoral measures. Femoral measures generally give higher estimates than humeral measures. Only in *Panthera atrox* did the humerus give a significantly higher mean body mass estimate than the femur.

### Discussion

The femoral and humeral cross-sectional geometric and articular properties used to predict body mass in this study were chosen based on two assumptions: (1) that they reflect some aspect of the mechanical loading the limbs are subjected to as a result of the body weight of the animal; and (2) that significant deviations from expected scaling patterns may be indicative of specialization in locomotor behaviour. Unlike limb length, limb circumference is closely associated with cross-sectional properties and therefore its relationship to body mass would be expected to follow that of the cross-sectional properties. The regression coefficients for all the regressions are relatively high and range between 0.88 and 0.99.

The body mass estimates of the Pliocene species (*Barbourofelis morrisoni*, *Machairodus coloradensis* and *Nimravides galiani*) (Table IV) are in agreement with body size ranges suggested by various authors (Barbour & Cook, 1915; Burt, 1931; Schultz, Schultz & Martin, 1970). However, the predicted body weights for the Pleistocene carnivores bring to light some interesting implications of body size in some of these extinct predators. The late Pleistocene species, *Smilodon fatalis*, has been described as having attained a size equal to or greater than that of a modern lion (Kurtén, 1968; Kurtén & Anderson, 1980; Akersten, 1985). The mean body weight estimate for *Smilodon fatalis* based on both the total sample and felid regressions is between 347 and 442 kg (femoral and humeral measures considered together) (Table IV). If this is taken as an approximation for the body size range in this species, then *Smilodon fatalis* can be thought of as having been about twice the body mass of the modern African lion (*Panthera leo*) which on average weighs 180 kg.

The gigantic size of the North American lion (*Panthera atrox*) has received attention by many authors (Merriam & Stock, 1932; Kurtén & Anderson, 1980), however, the phenomenal size of this animal may not have been fully appreciated. *Panthera atrox* is here estimated to have weighed 344–523 kg (Table IV), a range in body size comparable to that of the large living ursids. A cat of such enormous size was probably capable of preying on sub-adult and adult individuals of some of the largest herbivores, including proboscideans, that roamed the vast Pleistocene grasslands. Both *Smilodon fatalis* and *Panthera atrox* are well known from the Rancho La Brea deposits in California and other Pleistocene sites in North America (Merriam & Stock, 1932; Kurtén & Anderson, 1980). In addition to having preserved a large number of carnivores, the Rancho La Brea deposits have yielded bones of large herbivores that may have been potential prey for the big cats, such as giant bison (*Bison latifrons*), horse (*Equus occidentalis*), mylodont sloth (*Glossotherium harlani*), camel (*Camelops hesternus*), mastodon (*Mammuth americanus*), mammoth (*Mammuthus columbi*) and tapir (*Tapirus* sp.) (Marcus & Berger, 1984).

*Homotherium serum* is estimated to have weighed between 146–231 kg, a body size range that

closely matches that of modern African lions or Asian tigers. This species probably preyed on juvenile mastodons and mammoths as has been suggested by fossil remains from Friesenhahn Cave, Texas (Meade, 1961). These three species are known to have been sympatric with other felid species during the Pleistocene and the question of resource partitioning or prey selection has been one of great speculation (Gonyea, 1976; Kurtén & Anderson, 1980; Akersten, 1985). To understand the dietary and locomotor adaptations of these extinct predators further, it will be necessary to investigate, in greater detail, the structural properties of both their cranial and postcranial anatomy. Studies on canine microwear features and the biomechanics of locomotion in some of these species are currently in progress (Anyonge, In prep.).

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