

# Comparative Scaling of Humeral Cross-Sections of Felids and Canids Using Radiographic Images

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Published online: 9 March 2010  
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**Abstract** The cortical thickness of long bones can be an effective indicator of locomotor modes and other stresses encountered by bone. Felids and canids are two carnivoran families that have similar levels of phylogenetic diversity and overlap in body size, but differ in their locomotor habits. Many canids and felids are cursorial, but felids also climb more frequently than canids. Felids also display a secondary use for their forelimbs not observed in any canids: they use their forelimbs to grasp and subdue prey. Large felids use their forelimbs much more extensively to subdue prey than do large canids and, therefore, should have proportionately greater forces applied to their forelimbs. This study uses a non-invasive radiographic approach to examine the differences in cortical thickness in the humerus between the Felidae and Canidae, as well as between size groups within these two families. Results show few significant differences between the two families, with a slight trend toward more positive allometry in the felids. Overall, radiographic measurements were found to be better predictors of body mass than either prey killing behavior or locomotor mode in these two carnivoran families. One canid that demonstrated exceptionally high cortical area was the bush dog, *Speothos venaticus*. The rarely observed bush dog has been postulated to swim and dig regularly, and it may be that the thickened cortical bone reflects these behaviors.

**Keywords** Humerus · x-rays · Cortical thickness · Carnivore · Body mass · Allometry

## Introduction

Cortical thickness and limb bone cross-sectional area have been used to assess how the distribution of bone reflects loading in vivo. These can also be effective measures of weight-bearing properties of bones and used in body mass estimation (e.g., Ruff et al. 1989, 1991; Ruff 1990, 2003; Anyonge 1993; Demes and Jungers 1993; Biknevicius 1999; Anyonge and Roman 2006). Cortical bone thickness can also reflect locomotor modes, such as fossoriality (Biknevicius 1993, 1999; Polk et al. 2000) and arboreality, which includes brachiation (Ruff 1990; Demes and Jungers 1993; Runestad 1997; Polk et al. 2000). “Wolff’s law” or more aptly termed “bone functional adaptation” sensu Ruff et al. (2006) states that bone will remodel under the strain of mechanical loading. Bones are commonly loaded in both bending and compression, with the majority of the stresses attributed to bending (Rubin and Lanyon 1982; Bertram and Biewener 1988; Lieberman et al. 2004; Demes and Carlson 2009). Additionally, the speed and gait of locomotion can affect the deposition and strength of cortical bone (Szivek et al. 1992). Lately, this issue has been debated throughout the bone loading literature, and the validity of Wolff’s law has come into question (Bertram and Swartz 1991; Lieberman et al. 2004).

In a recent study, Lieberman et al. (2004) advocated that axial compression in conjunction with bending shifts the neutral axis away from the cross-sectional central axis. In that study, the authors caution that cross-sections of limb midshafts do not always indicate repeated loading patterns in all animals in the same way, and suggest against making any assumptions about bone loading except from in vivo data.

While recent in vivo studies have found that cross-sectional geometry of long bones does not correlate well with strain patterns (Demes et al. 1998, 2001; Lieberman et al. 2004), examining the cross-sectional geometry of

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cortical bone without in vivo data is not necessarily an exercise in futility. There is still evidence that strain does play a role in bone remodeling, although not as simple as was once thought (Rubin et al. 1995; Martin et al. 1998; Robling et al. 2002). Variations in bone structure are still the most effective indicators of locomotor mode among closely related species when in vivo data are absent (Ruff et al. 2006). Additionally, comparisons of bone cross-sectional properties (i.e., second moments of area) remain good estimators of mechanical ability, provided that the examination is in closely related groups that share similar body plans (Ruff et al. 2006).

Members of the families Felidae and Canidae in the mammalian order Carnivora have similar body plans, comparable levels of phylogenetic diversity (Bardeleben et al. 2005; Johnson et al. 2006), and analogous body size ranges with the exception of the largest felids, the lion (*Panthera leo*) and the tiger (*Panthera tigris*) (Smith et al. 2003; Nowak 2005). However these two families differ in their prey-killing behaviors. Felids, especially large species, rely on their forelimbs to kill prey, whereas canids do not (Ewer 1973). Some canids may use their paws while pouncing on small prey, but this behavior is functionally different from the grasping that occurs when felids catch prey (Leyhausen 1979). This ecological difference may be manifested in their cortical bone thickness.

Carbone et al. (1999) demonstrated that there is a physiological threshold that occurs around 21 kg in carnivorans. Above this threshold, carnivorans will no longer hunt small prey because of increased metabolic demands. Along with this physiological change is a concomitant morphological change in the skulls of both canids and felids. Both families show a shift to wider muzzles and more robust canine teeth to cope with the stresses of killing larger prey (Van Valkenburgh and Koepfli 1993; Meachen-Samuels and Van Valkenburgh 2009a). Additionally, felids show a morphological shift in the forelimbs, with larger sites for muscle attachment, larger muscle in-levers, and greater overall robustness for grappling with larger prey. Canids do not show a similar increase in these forelimb attributes, reflecting the fact that they do not use their forelimbs for prey capture as felids do (Meachen-Samuels and Van Valkenburgh 2009b).

Felids and canids also show differences in their locomotor modes and this might be indicated in cortical thickness. Although many canids and felids show cursorial behaviors (Sunquist and Sunquist 2002; Nowak 2005; Wang and Tedford 2008), there are many felid species that are scansorial, as well as a few arboreal species. These arboreal cats include the marbled cat (*Pardofelis marmorata*), the margay (*Leopardus wiedii*), and the clouded leopard (*Neofelis nebulosa*), all of which have been known to hunt prey in the trees (Sunquist and Sunquist 2002; Matsuda et al. 2008). Cheetahs (*Acinonyx jubatus*), on the other hand, are

almost entirely cursorial and may show cortical modifications of their long bones for this purpose (Caro 1994).

As a general rule, canids do not engage in scansorial behavior (Nowak 2005). One exception is the gray fox (*Urocyon cinereoargenteus*), which has been found to climb trees on occasion (Trapp and Hallberg 1975). Additionally, most dogs and some cats will occasionally scratch-dig, but no living cats or dogs are known to have a fossorial lifestyle (Sunquist and Sunquist 2002; Wang and Tedford 2008). One unusual canid that is difficult to place in a locomotor category is the 5–7 kg bush dog (*Speothos venaticus*). *S. venaticus* hunts in packs and uses its forelimbs to hold down prey that may be almost as large as themselves, such as pacas (Kleiman 1972; Deutch 1983). Unlike most canids, the bush dog is not a cursorial pursuit predator (Kleiman 1972), has partially webbed feet for walking through muddy riverbanks (MacDonald 1996; Bieseigel and Zuercher 2005), and has been observed swimming and digging burrows, both in the wild and in captivity (Goldman 1920; Bates 1944).

Different locomotor modes in these species may introduce stresses that differentially load the limb bones during movement and alter their cortical thickness and distribution. For instance, during climbing more rotational and torsional forces are applied to the forelimbs (Cartmill 1985), possibly resulting in a greater cortical area or a different distribution of cortical bone in arboreal species. Fossorial habits also increase stresses and can contribute to thickening or redistribution of cortical bone (Biknevicius 1993).

This study examined different dimensions of cortical shape and thickness in canids and felids and evaluated differences between the two families. Cortical measurements may be indicative of functional differences between the two families. If these two families do not show variation in cortical bone, then it can be suggested that other properties, such as body mass may be more important.

In addition to extant canids and felids, the extinct dire wolf, *Canis dirus*, was also examined. *C. dirus* was slightly larger than any living canid, thus allowing a comparison of canids to larger felids without extrapolating far beyond the range of body sizes seen in extant canids. The dire wolf was a large, Pleistocene, North American wolf-like canid that had similar morphology to extant gray wolves. It most likely lived in packs and hunted large prey by chasing them, analogous to living gray wolves (Merriam 1912; Wang and Tedford 2008).

## Materials and methods

Felids and canids were grouped first by family, and then by size (Table 1). Size category was labeled as “small” if the species average was under 20 kg or “large” if the species

**Table 1** Felid and canid species used in the analysis, sample size, species body size group, locomotor category, and average species masses

Sp. No.	Species	Common name	<i>n</i>	Family	Body size	Locomotion	Average mass in kg
1	<i>Acinonyx jubatus</i>	Cheetah	2	Felidae	Large	Terrestrial	50
2	<i>Caracal aurata</i>	African golden cat	2	Felidae	Small	Terrestrial	13
3	<i>Caracal caracal</i>	Caracal	3	Felidae	Small	Scansorial	16
4	<i>Caracal serval</i>	Serval	2	Felidae	Small	Terrestrial	12
5	<i>Felis chaus</i>	Jungle cat	2	Felidae	Small	Terrestrial	8
6	<i>Felis nigripes</i>	Black-footed cat	2	Felidae	Small	Terrestrial	1.5
7	<i>Felis silvestris lybica</i>	African Wildcat	3	Felidae	Small	Scansorial	5
8	<i>Leopardus colocolo</i>	Pampas cat	2	Felidae	Small	Scansorial	5
9	<i>Leopardus geoffroyi</i>	Geoffroy's cat	2	Felidae	Small	Terrestrial	5
10	<i>Leopardus pardalis</i>	Ocelot	2	Felidae	Small	Scansorial	11
11	<i>Leopardus tigrinus</i>	Tigrina or Oncilla	1	Felidae	Small	Scansorial	2.5
12	<i>Leopardus wiedii</i>	Margay	2	Felidae	Small	Arboreal	3
13	<i>Lynx canadensis</i>	Canadian lynx	2	Felidae	Small	Terrestrial	12
14	<i>Lynx lynx</i>	Eurasian lynx	2	Felidae	Large	Scansorial	22
15	<i>Lynx pardinus</i>	Iberian lynx	1	Felidae	Small	Terrestrial	10
16	<i>Lynx rufus</i>	Bobcat	2	Felidae	Small	Scansorial	12
17	<i>Neofelis nebulosa</i>	Clouded leopard	2	Felidae	Large	Arboreal	20
18	<i>Panthera leo</i>	Lion	2	Felidae	Large	Terrestrial	150
19	<i>Panthera onca</i>	Jaguar	2	Felidae	Large	Scansorial	68
20	<i>Panthera pardus</i>	Leopard	4	Felidae	Large	Scansorial	60
21	<i>Panthera tigris</i>	Tiger	2	Felidae	Large	Terrestrial	180
22	<i>Panthera uncia</i>	Snow leopard	2	Felidae	Large	Scansorial	40
23	<i>Pardofelis marmorata</i>	Marbled cat	1	Felidae	Small	Arboreal	4
24	<i>Pardofelis temminckii</i>	Asian golden cat	2	Felidae	Small	Scansorial	12
25	<i>Prionailurus bengalensis</i>	Leopard cat	2	Felidae	Small	Scansorial	5
26	<i>Prionailurus planiceps</i>	Flat-headed cat	2	Felidae	Small	Terrestrial	2
27	<i>Puma concolor</i>	Puma or Mountain lion	2	Felidae	Large	Scansorial	55
28	<i>Puma yaguarondi</i>	Jaguarundi	2	Felidae	Small	Scansorial	7
29	<i>Alopex lagopus</i>	Arctic fox	1	Canidae	Small	Terrestrial	5.5
30	<i>Canis adustus</i>	Side-striped jackal	1	Canidae	Small	Terrestrial	10.25
31	<i>Canis dirus</i> <sup>a</sup>	Dire wolf	4	Canidae	Large	Terrestrial	63
32	<i>Canis latrans</i>	Coyote	2	Canidae	Small	Terrestrial	13
33	<i>Canis lupus</i>	Grey wolf	2	Canidae	Large	Terrestrial	34
34	<i>Canis mesomelas</i>	Black-backed jackal	2	Canidae	Small	Terrestrial	9.75
35	<i>Cerdocyon thous</i>	Crab-eating fox	1	Canidae	Small	Terrestrial	6.5
36	<i>Chrysocyon brachyurus</i>	Maned wolf	2	Canidae	Large	Terrestrial	23
37	<i>Pseudalopex</i> sp. <sup>b</sup>	South American foxes	1	Canidae	Small	Terrestrial	3.5
38	<i>Lycaon pictus</i>	African hunting dog	2	Canidae	Large	Terrestrial	26.5
39	<i>Nyctereutes procyonoides</i>	Raccoon dog	2	Canidae	Small	Terrestrial	7
40	<i>Otocyon megalotis</i>	Bat-eared fox	2	Canidae	Small	Terrestrial	4
41	<i>Speothos venaticus</i>	Bush dog	2	Canidae	Small	Terrestrial	6
42	<i>Urocyon cinereoargenteus</i>	Grey fox	3	Canidae	Small	Scansorial	5
43	<i>Urocyon littoralis</i>	Channel Island fox	2	Canidae	Small	Terrestrial	1.2
44	<i>Vulpes chama</i>	Cape fox	2	Canidae	Small	Terrestrial	4
45	<i>Vulpes macrotis</i>	Kit fox	2	Canidae	Small	Terrestrial	2.75
46	<i>Vulpes velox</i>	Swift fox	2	Canidae	Small	Terrestrial	2.4
47	<i>Vulpes vulpes</i>	Red fox	2	Canidae	Small	Terrestrial	4.75

Mass averages from Smith et al. (2003). Locomotor mode for cats compiled from Young and Goldman (1946), Schaller (1972), Ewer (1973), Leyhausen (1979), Kitchener (1991), Sunquist and Sunquist (2002), and Hunter (2005). For canids, locomotor categories were taken from Nowak (2005) and Goldman (1920) (bush dog)

<sup>a</sup>Denotes an estimated body mass from Anyonge and Roman (2006)

<sup>b</sup>Denotes the mean mass for all *Pseudalopex* spp.

average was at or above 20 kg. Species masses (average values, Smith et al. 2003) and behavioral locomotor categories were compiled from the literature (Young and Goldman 1946; Schaller 1972; Ewer 1973; Leyhausen 1979; Kitchener 1991; Sunquist and Sunquist 2002; Hunter 2005; Nowak 2005; Wang and Tedford 2008). The locomotor groups used include: 1) Terrestrial—cursorial species that do not climb unless they have no other choice as a means of escape; 2) Scansorial—species that often climb for escape, eating or leisure, but do not hunt in the trees; 3) Arboreal—species that do at least some hunting in trees as well as many other activities, like escape, eating, or resting (Table 1). The bush dog was difficult to categorize, because there are accounts that it has been known to swim and burrow (Goldman 1920; Bates 1944). Because this species could not be definitively shown to be semi-fossorial or semi-aquatic, it was placed in the terrestrial category.

Radiographic images are an effective way to examine the cortical thickness of limb bones in museum collections without destructive sampling. Previous studies have demonstrated that mandibular cortical thickness can be modeled as a hollow asymmetrical beam and estimated using radiographic techniques (Biknevicius and Ruff 1992a, 1992b). This technique has been successfully applied to limb bone studies by modeling the bone shaft as a hollow symmetrical beam (e.g., Anyonge 1993; Runestad et al. 1993; Runestad and Ruff 1995; Runestad 1997).

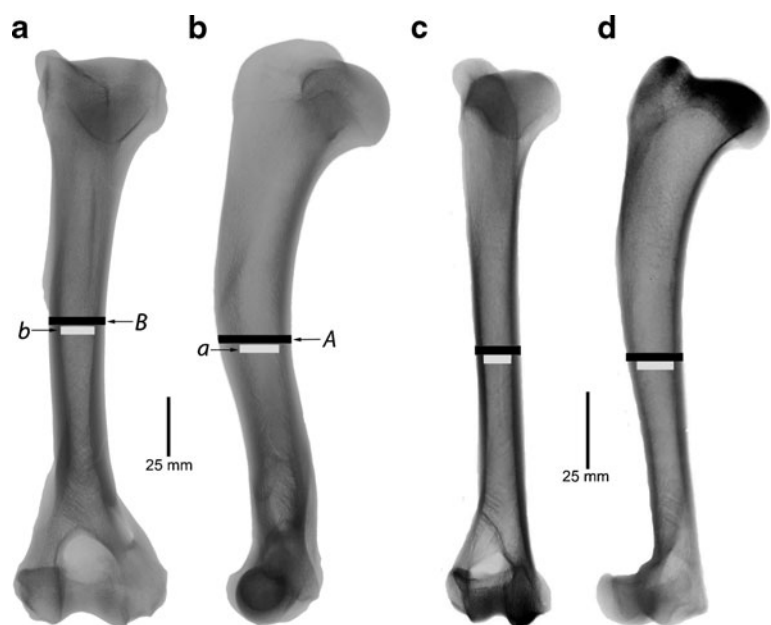
Radiographs were taken of the mediolateral and anteroposterior views of the humerus, as in Anyonge (1993) and Runestad (1997) (Fig. 1). Specimens were radiographed from the following collections: U.S. National Museum of Natural History (USNM), Natural History Museum of Los Angeles County (LACM), George C. Page Museum

(LACMHC), and UCLA Donald R. Dickey collection (UCLA). For a complete list of species, see Table 1; a full list of specimens is available in Appendix I. Twenty-five of 28 extant felid species in the analyses were x-rayed on a digital x-ray machine housed at the National Museum of Natural History at the Smithsonian Institution (USNM). The remaining three felids (*Puma concolor*, *Lynx rufus*, and *Lynx canadensis*), 17 extant canids, and *Canis dirus*, were x-rayed by placing the humerus directly on a Dupont Quanta Rapid x-ray cassette containing 3M green light sensitive UVL film using a portable x-ray machine.

Approximately two individuals were radiographed for each extant species, including one of each sex whenever possible to account for sexual dimorphism (Gittleman and Van Valkenburgh 1997). For the dire wolf, four humeri of various sizes were chosen to increase the chances that at least one of each sex was sampled. Juvenile individuals with unfused epiphyses were excluded for all species and wild caught specimens were preferentially chosen.

Mediolateral and anteroposterior cortical thicknesses and lengths were measured on digital x-rays in ImageJ (Rasband 2007). For film radiographs, both exterior and interior humerus diameters and lengths were measured from the x-ray film using a light box and digital calipers to the nearest 0.1 mm. In order to assure that parallax was kept constant among all specimens (Heinrich and Biknevicius 1998), the x-ray machine was placed at a constant height above the film in all radiographs taken. To be sure that parallax was not unduly biasing measurements, external measurements were also taken directly from the bone for comparison. A negligible difference (less than 1 mm) was found between the radiograph and the actual bone for *Canis dirus*, the largest species radiographed using this method.

**Fig. 1** Digital radiographic images of **a** Jaguar, *Panthera onca*, humerus USNM 49393 in mediolateral and **b** anteroposterior view; film radiographs of African hunting dog, *Lycaon pictus*, humerus LACM 30588 in **c** mediolateral and **d** anteroposterior view. *Black bars* indicate the measurement taken for external diameter and *white bars* indicate measurements taken for internal diameter. *Arrows and italicized letters* indicate measurements that went into equations for cortical variables.



Measurements were taken at the midshaft, directly distal to the deltopectoral crest. Illustrations of the planes in which the bones were radiographed as well as examples of the internal and external measurements taken from the radiographs can be found in Fig. 1. Variables calculated include cortical area (CA, mm<sup>2</sup>), second moments of area, which estimate the ability to resist cross-sectional bending in the anteroposterior (Ix) and mediolateral (Iy) planes, and polar moment of area or inertia (J) (Ruff and Hayes 1983).

Cortical area estimates the total axial tensile and compressive rigidity, and was estimated using the formula:

$$CA = \pi(AB - ab)/4$$

A = external anteroposterior diameter, B = external mediolateral diameter, a = anteroposterior diameter of the medullary cavity, and b = mediolateral diameter of the medullary cavity (Fig. 1). Since CA should not be used as an estimator of non-axial rigidity, it was used to represent the amount of cortical bone in the cross-section and as a means to estimate body mass (Ruff et al. 2006).

Second moments of area were measured to estimate anteroposterior (Ix) and mediolateral (Iy) bending rigidity of the humerus (Heinrich and Biknevicius 1998). Second moments of area were calculated using the following formulas (Roark 1965; Alexander 1968; Anyonge 1993; Runestad 1997):

$$Ix = \pi(A^3B - a^3b)/64$$

$$Iy = \pi(AB^3 - ab^3)/64$$

The ability of an object to resist torsional stress was estimated as the polar moment of inertia using the formula:

$$J = Ix + Iy$$

Together these calculations estimate the resistance to loads during activities (Runestad 1997). The polar moment of inertia, J, was divided by two as it estimates the average bending rigidity of the humerus (Polk et al. 2000).

Species averages were calculated and were used in regression analyses. Using species averages gives each species equal weight in the comparisons of families, otherwise taxa with larger sample sizes would likely have greater influence on the regression lines. To assess the differences in scaling between canids and felids, dimensionality of the measurements were adjusted by taking the square root of CA, and the fourth root of Ix, Iy, and J/2 and then by applying log<sub>10</sub> transformation. All measurements were modified before being used for analysis, unless otherwise stated. These four adjusted measurements were regressed against log<sub>10</sub> humerus length using ordinary least squares regression (OLS) (Smith 2009).

Because individual masses were not available for the specimens that were radiographed, another proxy for size,

geometric mean (GM), was used here. The geometric mean can be defined as the  $n^{\text{th}}$  root of the product of  $n$  measurements (Mosimann and James 1979; Madar et al. 2002). In this study the GM was calculated using the following measurements: humerus length, anteroposterior and mediolateral external humeral diameters and the mediolateral width of the distal humeral articular surface (trochlea and capitulum). Some of these measurements, such as the humeral diameters and articular widths, have been shown to be good predictors of body size in primates, ungulates, and carnivorans (Ruff 1990; Scott 1990; Anyonge 1993; Andersson 2004). Therefore, this geometric mean should give a rough overall estimate of body size for each individual, which may be more accurate than species body mass averages taken from the literature. All cortical variables were also regressed against the GM.

For cortical variables versus both humerus length and GM, differences in slope between families were tested using a likelihood ratio test in the program SMATR (Falster et al. 2006).

In addition to comparing the slopes between the two families, slopes were tested for isometric scaling (cortical variables versus bone length or GM) using reduced major axis regression (RMA). RMA was used here because it has been shown to be an effective tool when describing how size variables are related, especially when dealing with linear relationships on a logarithmic scale; it is also useful when testing the value of a slope against a known isometric constant (Warton et al. 2006).

Because of the dimensional adjustment applied to all of the data, each regression coefficient can be treated as a linear measurement. Negative allometry was indicated by slopes significantly less than one, positive allometry by slopes significantly greater than one, and isometry by slopes not significantly different from one (Schmidt-Nielsen 1993; Read and Tolley 1997). All RMA slope comparisons were calculated with SMATR using the H<sub>0</sub> slope comparison option (Falster et al. 2006).

If these cortical measurements scale isometrically to humerus length, then cortical thickness would increase proportionally to bone length. In other words, as the bone gets longer, then the strength of the bone would lag behind the mass it is required to support. If scaling is positively allometric, then cortical bone is proportionally thickened as the animal increases in mass, helping to accommodate the larger mass. Thus, the prediction for the outcome of these slope comparisons would be positive allometric scaling in both carnivoran families, with a significantly greater positive allometry in felids to accommodate the additional use of their forelimbs for prey-killing.

To test for significant differences in cortical variables between canids and felids and between different subdivided body size groups within families, the square root of CA and the fourth root of Ix, Iy, and J/2 were taken.

Since size differences between the largest and smallest cats are of a great magnitude, an analysis of covariance (ANCOVA) was performed with GM as a covariate using SPSS v. 17.0 to test for significant differences between means and intercepts between families. To test for significant differences between the means of sub-divided size groups within and between families, an ANOVA was run using Scheffé's F (for equal variances) and Tamhane's T2 (for unequal variances) procedures for *post hoc* comparisons ( $p < 0.05$ ). ANCOVA and ANOVA procedures were performed using individual specimens, to increase the sample size of each group and to reduce the variance between groups.

To test the accuracy of using cortical area as a tool for body mass estimation,  $\log_{10}$  mean species masses of extant canids and felids (Smith et al. 2003) were plotted against dimensionally adjusted mean species CA for each family individually. More often than not, individual body masses are not available from museum collections. When this is the case, mean species body mass is often used as a substitute (e.g., Roth 1990; Ruff 1990; Van Valkenburgh 1990; Anyonge 1993; Mendoza et al. 2006; De Esteban-Trivigno et al. 2008; Sorkin 2008; Clauset et al. 2009). Additionally, geometric mean was also regressed against CA as another, more individual measurement, for body size. Since  $r^2$  can be a poor gauge of the predictive power of the independent variable (Smith 1981; Van Valkenburgh 1990), two other measures of predictive variation were considered. Percent prediction error (%PE) and the standard error of the estimate (%SEE) were both calculated as in Van Valkenburgh (1990). These values were calculated for all species collectively, and each family separately.

Although interfamilial variation, not interspecific variation, is the focus of this study, to insure that results were not being distorted or masked by phylogeny, phylogenetically independent contrasts (Felsenstein 1985) were applied to the data set. Log transformed cortical variable contrasts were regressed against log humerus length or log GM through the origin using linear regression in the PDAP module in

Mesquite v. 2.6 (Maddison and Maddison 2006) to determine if phylogeny had a significant effect on scaling of any of the cortical measurements used. Phylogenies used included Johnson et al. (2006) for the Felidae and Lindblad-Toh et al. (2005) and Bardeleben et al. (2005) for the Canidae. Branch lengths were assigned from molecular data using the appropriate phylogenies.

## Results

### Ordinary least squares regression

The results for OLS regressions of adjusted measurements versus humerus length and GM for extant species are summarized in Tables 2 and 3, respectively. Comparisons of the slopes of OLS regressions of humerus length for felids and canids (Fig. 2a, b) show significant differences between the two families for J/2 ( $p=0.53$ ), and values that approach significance for Ix ( $p=0.56$ ). For cortical variables versus humerus length there was only one canid outlier for CA. The bush dog (#41) fell above the 95% confidence interval (CI) calculated using individual species means. Felids had lower variances than canids for all regressions (Table 2); however, there was also only one felid that fell outside of the 95% confidence interval. *Caracal serval* (#4) fell below the CI for all measurements, with relatively gracile humeri.

The OLS regression of adjusted measurements, versus GM found no significant differences between canids and felids, and most species fell within the 95% confidence interval when body size (GM) is taken into account (Table 3; Fig. 3a, b). Outliers include *Leopardus pardalis* (#10) that fell consistently below the 95% confidence interval for CA, Ix, and J/2 with gracile humeri. Additionally, the maned wolf (#34) also fell below the CI for Iy. Falling above the CI were the Canadian lynx (#13) for J/2 and the bush dog (#41) for CA.

**Table 2** OLS regression of  $\log_{10}$  variables against  $\log_{10}$  humerus length for the Felidae and the Canidae and RMA isometry assessment

Variable	Family	Slope (SE)	Intercept (SE)	$r^2$	$p^a$	F <sup>a</sup>	$p$ (isometry RMA)
CA <sup>1/2</sup>	Felidae <sup>b</sup>	1.274 (.046)	-1.855 (.100)	0.967	0.087	2.951	0.000
	Canidae	1.079 (.099)	-1.440 (.208)	0.874			0.108
Ix <sup>1/4</sup>	Felidae <sup>b</sup>	1.324 (.043)	-2.125 (.099)	0.969	0.056	3.702	0.000
	Canidae	1.106 (.091)	-1.666 (.192)	0.896			0.055
Iy <sup>1/4</sup>	Felidae <sup>b</sup>	1.258 (.041)	-2.025 (.089)	0.973	0.066	3.173	0.000
	Canidae	1.068 (.082)	-1.614 (.174)	0.907			0.135
J/2 <sup>1/4</sup>	Felidae <sup>b</sup>	1.297 (.043)	-2.087 (.093)	0.972	0.053	3.801	0.000
	Canidae	1.090 (.087)	-1.644 (.182)	0.902			0.056

<sup>a</sup> F and  $p$  values refer to homogeneity of slopes between families using a likelihood test

<sup>b</sup> Indicates a deviation from isometry using RMA

**Table 3** OLS regression of  $\log_{10}$  variables against log GM for the Canidae and the Felidae and RMA isometry assessment

Variable	Family	Slope (SE)	Intercept (SE)	r <sup>2</sup>	p <sup>a</sup>	F <sup>a</sup>	p (isometry RMA)
CA <sup>1/2</sup>	Felidae <sup>b</sup>	1.074 (.022)	-0.594 (.031)	0.989	0.510	0.420	0.000
	Canidae	1.048 (.045)	-0.551 (.059)	0.969			0.156
Ix <sup>1/4</sup>	Felidae <sup>b</sup>	1.116 (.018)	-0.815 (.026)	0.993	0.240	1.437	0.000
	Canidae <sup>b</sup>	1.071 (.029)	-0.750 (.039)	0.987			0.007
Iy <sup>1/4</sup>	Felidae <sup>b</sup>	1.060 (.014)	-0.779 (.020)	0.995	0.476	0.500	0.001
	Canidae	1.029 (.027)	-0.722 (.036)	0.988			0.217
J/2 <sup>1/4</sup>	Felidae <sup>b</sup>	1.094 (.015)	-0.803 (.022)	0.995	0.194	1.686	0.000
	Canidae <sup>b</sup>	1.053 (.026)	-0.739 (.034)	0.990			0.009

<sup>a</sup> F and p values refer to homogeneity of slopes between families using a likelihood test

<sup>b</sup> Indicates a deviation from isometry using RMA

Additionally, another set of regressions were performed where the variables were simply log transformed (no roots were taken first) and relative results between families and p-values of tests involving both rooted and non-rooted variables were not significantly different. For ease of presentation only the initially rooted variables will be discussed.

Reduced major axis regression

Reduced major axis regression was performed for each variable versus both humerus length and GM to check for the presence of allometric scaling in both families. For humerus length, felids were positively allometric for all measurements, and canids were not significantly different from isometry for any measurements (Table 2). The result was similar for all measurements versus GM, with felids showing consistent positive allometry and canids displaying positive allometry only for Ix and J/2 (Table 3). Although canids were not significantly different from isometry for humerus length, they did display a positively allometric trend for both Ix and J/2.

In order to assure that the differences in allometry between canids and felids were not being driven by the inclusion of lions and tigers, separate regressions of all variables were performed that excluded these cats. When these two largest felid species were excluded, the slope values decreased for all variables, but all felid slopes were still significantly positively allometric.

Analysis of covariance and analysis of variance

Analyses of covariance (ANCOVA) were performed using GM as a covariate in order to assess the effects of size between canids and felids. The ANCOVA performed between families showed no significant differences with regard to mean values for any measurement (Table 4). There were significant differences found between the intercepts of the two families for all measurements (p<0.001 for all measurements).

When ANOVA *post hoc* tests were performed on body size categories (Table 5), small canids and small felids were not significantly different for any measurement. Large felids were significantly different from all other groups for

Ix. For all other measurements, large species (canids and felids) were not significantly different from one another, but they were significantly different from small species (canids and felids). In a second analysis that excluded lions and tigers, large felids were no longer distinct from large canids for any measurement. Both Scheffe's F and Tamhane's T2 gave similar results. Additionally, *post hoc* tests in ANOVA were performed on locomotor types. No locomotor groups were significantly different from any other group.

Body mass estimation

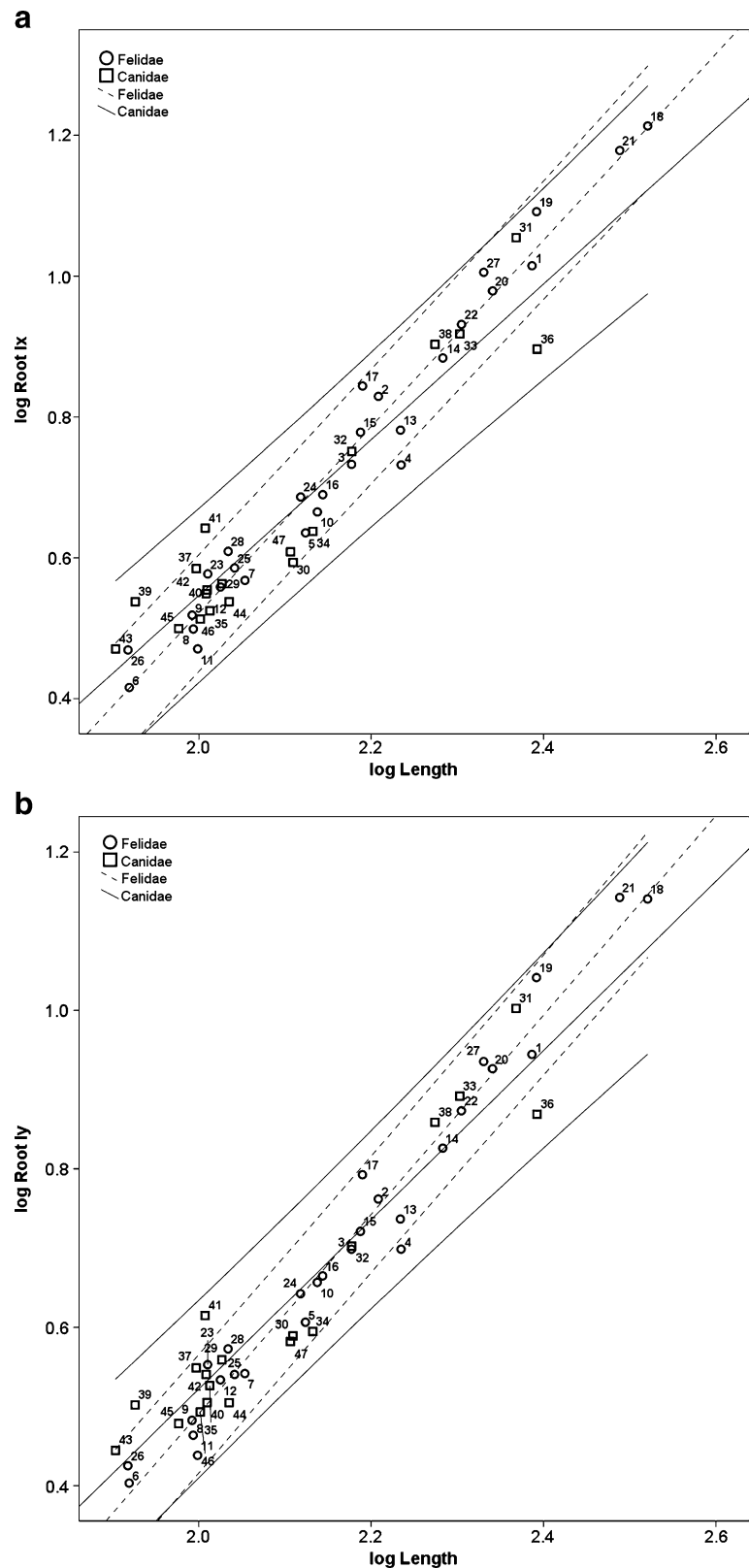
Results of the body mass estimation regression show that log  $\sqrt{\text{cortical area}}$  and log mean species mass are strongly correlated in both cats (r<sup>2</sup>=0.928, Fig. 4a) and dogs (r<sup>2</sup>=0.915, Fig. 4b). Percent prediction error and %SEE indicate that cortical area is a good predictor of average mass in both canids and felids and that cortical area is slightly better at estimating canid body mass based on the equation for that family, than for felids (36% SEE in canids versus 41% SEE in felids) (Table 6). There was one species that fell outside the 95% confidence interval for individual species for the log mean body mass regression, *Prionailurus planiceps* (#26).

In the regression of log root CA versus log GM (Fig. 4c, d), no species are outside of the 95% confidence interval except *S. venaticus*, whose size is overestimated based on geometric mean (Fig. 4d). These regressions of log GM show that geometric mean is a good predictor of cortical area for both families (Table 6). However, contrary to mean species body mass estimates, the GM is slightly better at predicting the cortical area of cats (4.7% SEE) than dogs (6.6% SEE). This lower error compared to mean species mass is most likely because GM is a more realistic predictor of individual size than mean species masses from literature.

Independent contrasts

Results of independent contrasts were similar to results from the original linear regressions, with a few differences (Table 7). Once phylogeny was accounted for, the regressions of log humerus length versus the cortical variables

**Fig. 2** OLS regression plot of **a** log root Ix and **b** log root Iy versus log humerus length for the Felidae and Canidae. Points represent species averages. Refer to Table 1 for species numbers. Refer to Table 3 for slope, intercept and  $r^2$ . *Dashed lines* represent Felidae, *solid lines* Canidae.

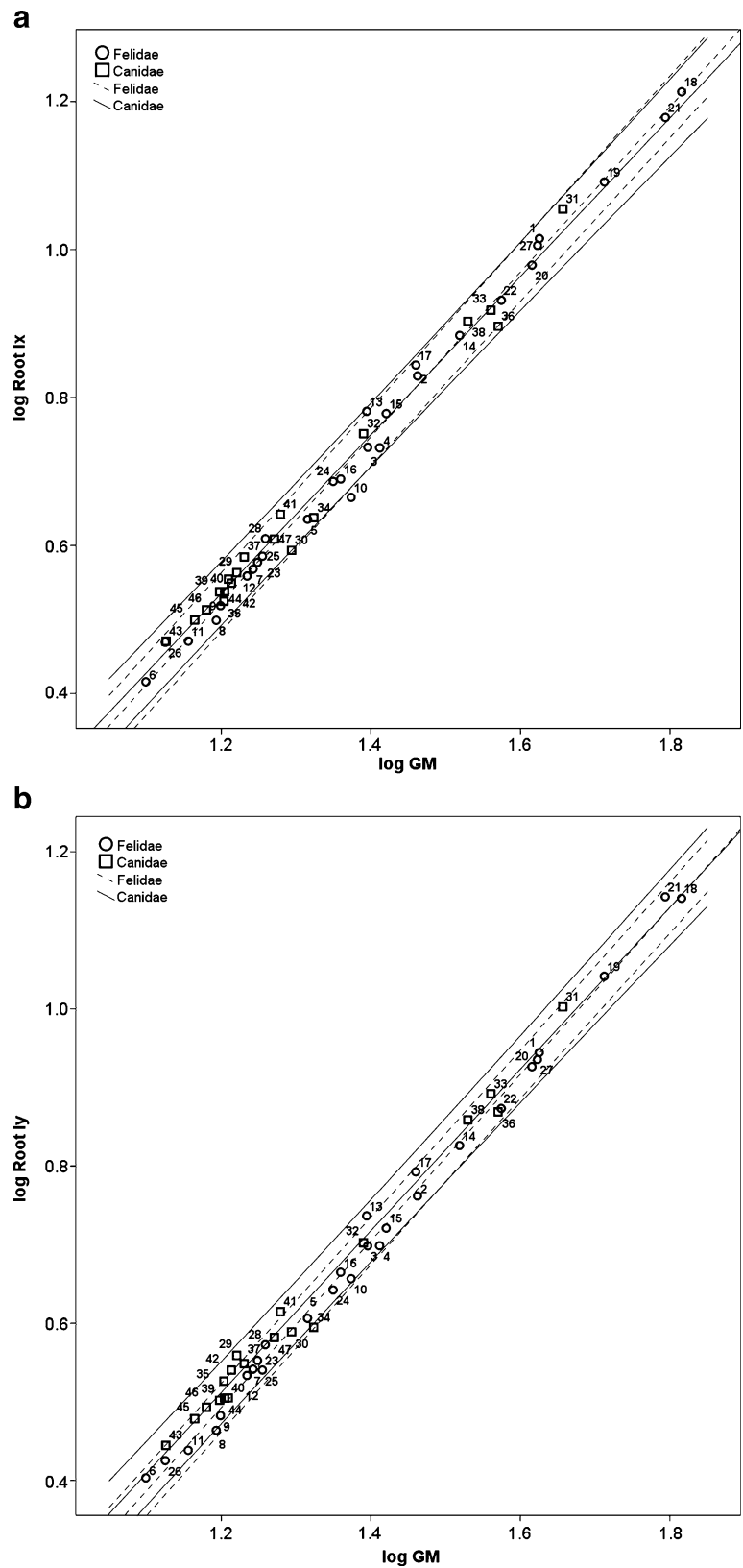


were not significantly different between the two families for any measurement (only  $J/2$  was significant before), and the regressions of log GM versus the cortical variables were still non-significant.

## Discussion

Canids and felids showed few overall differences in cortical bone thickness. Results of the OLS regressions only showed

**Fig. 3** OLS regression plot of **a** log root Ix and **b** log root Iy versus log GM for the Felidae and Canidae. Points represent species averages. Refer to Table 1 for species numbers. Refer to Table 4 for slope, intercept and  $r^2$ . *Dashed lines* represent Felidae, *solid lines* Canidae.



**Table 4** ANCOVA results, including mean values (and standard deviations) of rooted values CA, Ix, Iy, and J/2 (see text) using GM as a covariate for the Canidae and Felidae

Variable	Felidae (all species) n=56	Canidae n=37
CA <sup>a</sup>	9.574 (5.332)	7.755 (4.019)
Ix <sup>a</sup>	6.582 (3.670)	5.271 (2.726)
Iy <sup>a</sup>	5.881 (3.142)	4.595 (1.862)
J/2 <sup>a</sup>	6.265 (3.434)	4.999 (2.387)

Numbers of individuals included are listed below each category. No significant differences between canids and felids were found at the  $p \leq 0.05$  level. A significant difference found in the intercepts between canids and felids are indicated with <sup>a</sup>

significant differences when J/2 was regressed against log humerus length. Results of the ANCOVA suggest no differences between families. When further broken down into size groups, large felids were significantly different from other groups with regards to bending in the anteroposterior plane (Ix). However, once lions and tigers were removed from the analysis, this difference disappeared. The intercepts between the two families were distinct both including and excluding lions and tigers, the two largest felids. This may suggest that the ancestral proportions between canids and felids were different, but the overall scaling differences are very subtle. In other words, canids and felids came from different evolutionary starting points (the intercept), but are functionally on the same trajectory with regards to humerus cortical dimensions (the slope).

The only clear difference between canids and felids seemed to be in the relative allometry of cortical variables. When tested against an isometric slope value of one, canids were not significantly different from isometry for CA or Iy when regressed against GM, although felids were for all variables, even when lions and tigers were excluded from the analysis. Although there was no statistically significant difference in slopes between families, felids always had a higher slope value than canids, suggesting that there is a subtle trend toward thicker cortical bone in felids. Bertram

and Biewener (1990) and Meachen-Samuels and Van Valkenburgh (2009b) found similar results when they examined the external osteology of canids and felids. Felids always displayed greater positive allometry in the humerus than did canids; however, Bertram and Biewener (1990) found that canids demonstrated positive allometry more frequently than felids with regard to the femur. It is possible that a larger sample size of individual species may reduce the risk of Type II error and elucidate significant differences between humeral cortical bone in these two families that were not found in this study (Jacquemont et al. 2009).

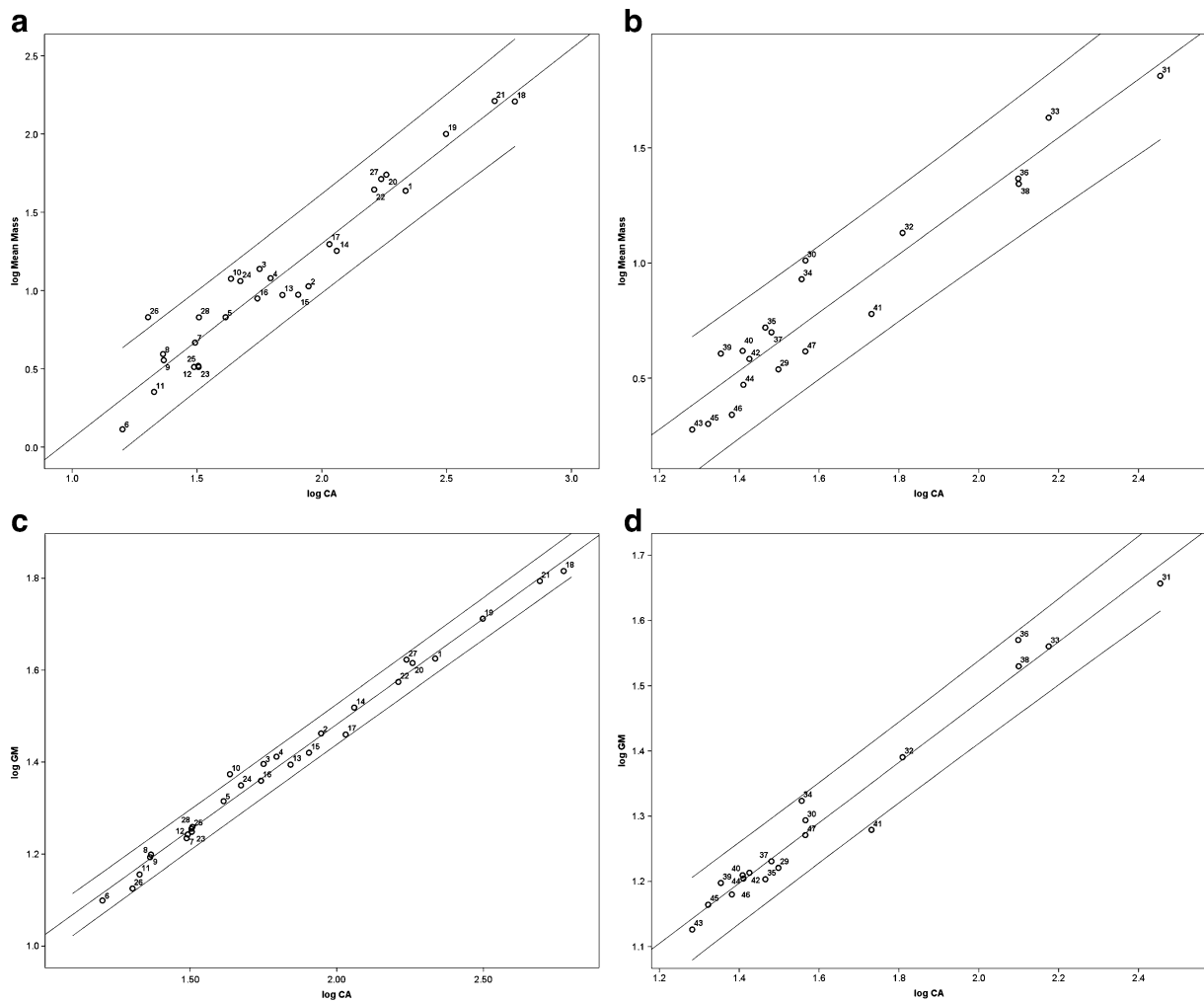
In this study, no differences were found in the humeral cortical thicknesses of arboreal, scansorial, and terrestrial canid and felid species. Polk et al. (2000) had similar results in their comparative study of rodents, primates, and carnivorans. They found no consistent differences in compressive strength of the femora of arboreal and terrestrial rodents, and no significant differences in compressive strength of the humeri or femora between arboreal and terrestrial primates. They did, however, find a significant difference between the cortical thicknesses of terrestrial and arboreal carnivorans, with arboreal carnivorans having relatively greater cortical cross-sectional properties. But their study only included one felid species (*Felis* sp.) and six canid species, all of which were classified as terrestrial. The results of the present study may have been confounded by the low number of truly arboreal felids ( $n=3$ ) and the complete lack of arboreal canids. The locomotor categories used in this study were also very general and broad; still, arboreal cats did show significant differences from other cats in external osteological characters (Meachen-Samuels and Van Valkenburgh 2009b).

Cortical thickness of long bones has been shown to be a good predictor of body mass in many species (e.g., Ruff et al. 1989, 1991; Ruff 1990, 2003; Anyonge 1993; Demes and Jungers 1993; Biknevicius 1999; Anyonge and Roman 2006). This seems to be the case in felids and canids, as body mass prediction regressions show comparatively low error relative to non-cortical measurements (Van Valkenburgh 1990). Although the prediction error was relatively low, it

**Table 5** ANOVA results, including mean values (and standard deviations) of rooted values CA, Ix, Iy, and J/2 (see text) for the Canidae and Felidae separated by size

Variable	Small felids n=37	Large felids n=19	Large felids (without lions and tigers) n=15	Small canids n=27	Large canids n=10
CA	6.491 (1.818)	15.579 (4.760)	13.553 (2.548)	5.564 (1.074)	13.670 (2.832)
Ix	4.433 (1.352)	10.768 (3.085)	9.529 (1.840)	3.763 (0.703)	9.341 (1.757)
Iy	4.051 (1.136)	9.444 (2.702)	8.335 (1.571)	3.527 (0.599)	7.481 (0.402)
J/2	4.257 (1.254)	10.176 (2.908)	8.996 (1.714)	3.653 (0.652)	8.634 (1.206)

Numbers of individuals included are listed below each category. Small canids and felids were never significantly different ( $p \leq 0.05$ ). Large canids and felids were significantly different only for Ix. After lions and tigers were removed, there were no significant differences between large canids and felids



**Fig. 4** Linear regression plot of log mean species mass versus log cortical area (CA) for **a** Felidae and **b** Canidae, shown with a 95% confidence interval for individual species. Points represent species averages; Linear regression plot of log GM versus log cortical area

(CA) for **c** Felidae and **d** Canidae, shown with 95% confidence interval for individual species. Refer to Table 1 for species numbers, and to Table 6 for line equations. *Dashed lines* represent extant Felidae, *solid lines* extant Canidae.

could be improved if individual body masses were used; however, this is generally not possible given the dearth of actual body masses available from museum collections.

The flat-headed cat, *Prionailurus planiceps*, had unusually low values for CA when compared to literature body mass estimates, but not for GM. This seems to indicate an individual (or individuals) that are heavier than the average species mass are biasing the results. However, this may also indicate the flat-headed cat has unusually thin cortical bone,

although it is unclear what the functional significance of this result might be.

Interestingly, the bush dog, *Speothos venaticus*, was also an exception to the general trend seen in felids and canids. Relative to the rest of the Canidae, it had significantly thicker cortical bone than would be predicted by its mean species mass or humerus length. When compared to humerus length, only CA was very large in the bush dog, and this value remained high when regressed against geometric mean. Yet,

**Table 6** Regression of log  $\sqrt{CA}$  versus log average species mass and log GM

Variable	Family	Slope	Intercept	r <sup>2</sup>	SE	%SEE	%PE
Mass	All	2.515	-1.216	0.928	0.142	38.69	16.742
	Felidae	2.492	-1.187	0.928	0.151	41.84	16.419
	Canidae	2.533	-1.242	0.915	0.133	36.09	16.958
GM	All	0.926	0.554	0.984	0.023	5.438	1.255
	Felidae	0.919	0.563	0.989	0.020	4.712	1.132
	Canidae	0.925	0.550	0.969	0.028	6.659	1.369

**Table 7** Independent contrasts results of variable contrasts versus log humerus length (HL) or log GM regressed through the origin

Variable contrasts	Family	Slope	r <sup>2</sup>	F <sup>a</sup>	p <sup>a</sup>
Log root CA vs Log HL	Felidae	1.164	0.938	1.009	0.297
	Canidae	1.027	0.810		
Log root Ix vs Log HL	Felidae	1.198	0.953	1.779	0.157
	Canidae	1.046	0.869		
Log root Iy vs Log HL	Felidae	1.137	0.956	0.775	0.340
	Canidae	1.042	0.875		
Log root J/2 vs Log HL	Felidae	1.213	0.951	1.909	0.171
	Canidae	1.056	0.877		
Log root CA vs Log GM	Felidae	1.036	0.971	0.270	0.591
	Canidae	1.070	0.959		
Log root Ix vs Log GM	Felidae	1.063	0.978	0.006	0.950
	Canidae	1.066	0.984		
Log root Iy vs Log GM	Felidae	1.010	0.983	1.544	0.199
	Canidae	1.060	0.987		
Log root J/2 vs Log GM	Felidae	1.079	0.981	0.010	0.928
	Canidae	1.074	0.988		

<sup>a</sup>F and p values refer to homogeneity of slopes between families

this still shows that the bush dog is relatively more robust than other canids with similar bone lengths. Since CA is a poor estimator of non-axial strength, it is perplexing as to what these high CA values mean, functionally. Although the values of Ix and Iy in the bush dog did not fall outside of the confidence interval, they were relatively high, and these values would reflect functional adaptations to activities. As mentioned previously, bush dogs may frequently swim or burrow (Goldman 1920; Bates 1944), and they also restrain prey with their forelimbs (Kleiman 1972).

As a parallel to the bush dog, Biknevicius (1993) found that cortical bone is thicker in species that consistently use their limbs in strenuous activities, such as digging. A fossorial rodent, the tuco-tuco (*Ctenomys*), has a much higher mean moment of area (J/2) in the humerus than would be predicted for a rodent of its body mass, and considerably thicker cortical bone than similarly sized members of its family (Biknevicius 1993).

The dire wolf was not significantly different from other canids and felids. However, its presence in this study was significant. The dire wolf allowed a comparison of middle range pantherines, such as the jaguar, to canids. Without *C. dirus*, a false positive result may have occurred between canids and felids even when lions and tigers were removed from the data set. Even though this animal is extinct, it was not a stretch to include it in this analysis, because its ecological strategy was well known (Merriam 1912; Wang and Tedford 2008) and it was sufficiently similar to extant *Canis* to be placed within that genus.

Although both cats and dogs show similar scaling of cortical thickness relative to GM, cats are significantly different from isometry, whereas dogs are not for CA and Iy. Felids possibly experience more bending forces in the mediolateral plane (Iy), which may be a consequence of forces encountered when holding onto struggling large

prey. This may also be due to the mediolateral distal diaphyseal accumulation of cortical bone seen in some cats as in Fig. 1. This portion of the humerus may need to be reinforced to avoid breakage during prey struggle, because of the anteroposteriorly flatter shape of the distal end of the diaphysis. This thickening may also be due, in part, to the increased use of the wrist flexor and extensor muscles that originate on the distal end of the humerus and facilitate the expansion of the humeral epicondyles observed in the felids (Meachen-Samuels and Van Valkenburgh 2009b). These flexors and extensors allow grasping of prey with the paws during the initial attack. For both families, cortical variables seem to scale with body mass; however, cats trend towards positive allometry, possibly as a result of prey-capturing techniques.

Recently, Doube et al. (2009), using CT scan data, found that larger felids showed greater cortical thicknesses in the forelimbs than the hind limbs and this difference became more apparent with increasing cat size. This suggests that mass may not be the only factor determining cortical thickness and larger cats may indeed have reinforced forelimb cortical bone to cope with the increased stresses of large prey capture. These results agree with the findings of this study that although cats and dogs are not significantly different from each other, cats show a positive significant deviation from isometry that may be functionally related to prey-killing habits. However, Doube et al. (2009) did not examine any dog humeri, so they could not compare canid and felid scaling.

While results suggest no major significant differences between the humeral midshaft cortical thicknesses of canids and felids, there are external morphological differences in the humerus associated with different prey-capture strategies in felids. Specializations for different prey sizes are accomplished through changes in mechanical advantage (i.e., muscle size and in the size of their origins and insertions),

as shown in Meachen-Samuels and Van Valkenburgh (2009b). Further differences may come to light between canids and felids if both the forelimbs (humerus) and the hind limbs (femur) are compared. Additionally, an examination of the forelimbs of these two families using CT scans may provide better resolution of the differences between them.

In conclusion, it seems as though humeral cortical thickness and distribution is a conserved character between canids and felids and that these variables are more profoundly affected by body mass constraints than by prey-killing behavior or locomotor mode. These ecological roles are instead more evident in external osteological morphology (Meachen-Samuels and Van Valkenburgh 2009b). Few significant differences were found between the humeral cortical thicknesses of felids and canids, but there was a trend towards greater positive allometry in felids that may be attributable to the additional use of their forelimbs in prey killing. A noticeable exception to this rule among living canids is the bush dog, which showed increased cortical thickness that may reflect digging and/or swimming habits, or possibly even prey-killing strategies similar to felids (i.e., using the forelimbs to hold down pacas or other larger prey) (Goldman 1920; Bates 1944; Kleiman 1972).

Future directions for this project include comparing cortical thickness of the humerus and the femur in canids and felids to see if the same patterns hold true for the hind limbs. Another current project includes examining the cortical thickness of the extinct saber-toothed felid *Smilodon fatalis*, to see if this species shows cortical patterns similar to living cats or if their humeri have been secondarily thickened because of differing prey-killing strategies. Preliminary results suggest that they have disproportionately thick humeral cortical bone relative to conical toothed cats.

**Acknowledgments** The following curators and collection managers kindly allowed access to specimens (and digital radiographic equipment) in their care: J. Dines (Museum of Natural History of Los Angeles County), C. Shaw and S. Cox (George C. Page Museum), K. Molina (Donald R. Dickey Collection of the University of California, Los Angeles), and L. Gordon and J. Jacobs (U.S. National Museum of Natural History). Discussion with and comments by B. Van Valkenburgh, J. Samuels, W. Binder, X. Wang, D. Jacobs, R. Wayne, P. J. Brantingham, K. Koepfli, V.L. Roth, T. Roberts, P. Durst, and two anonymous reviewers greatly improved this paper. This project was partially funded by a U.S. Dept. of Education Graduate Assistance in Areas of National Need (GAANN) fellowship from UCLA and partially funded by NESCent NSF Grant # EF-0423641.

## Appendix I

### Individual humeri measured for this study

Family	Genus	Species	Sex	Museum	Catalog number	CA (mm <sup>2</sup> )	Ix (mm <sup>4</sup> )	Iy (mm <sup>4</sup> )	J (mm <sup>4</sup> )	Length (mm)
Felidae	<i>Acinonyx</i>	<i>jubatus</i>	M	USNM	161922	237.71	12,649.79	6,536.29	19,186.08	248.33
Felidae	<i>Acinonyx</i>	<i>jubatus</i>	F	USNM	162929	195.66	10,313.15	5,453.52	15,766.67	238.83
Felidae	<i>Caracal</i>	<i>aurata</i>	M	USNM	278523	89.86	2,131.50	1,116.76	3,248.26	155.49
Felidae	<i>Caracal</i>	<i>aurata</i>	M	USNM	282637	87.03	2,019.90	1,114.64	3,134.55	167.95
Felidae	<i>Caracal</i>	<i>caracal</i>	M	LACM	42383	52.88	1,130.73	757.17	1,887.90	156.50
Felidae	<i>Caracal</i>	<i>caracal</i>	F	USNM	384162	58.38	670.36	531.55	1,201.91	147.83
Felidae	<i>Caracal</i>	<i>caracal</i>	M	USNM	396160	57.69	760.69	577.15	1,337.84	147.09
Felidae	<i>Caracal</i>	<i>serval</i>	F	USNM	163092	50.32	626.83	525.57	1,152.40	159.20
Felidae	<i>Caracal</i>	<i>serval</i>	M	USNM	258240	74.36	1,069.30	719.46	1,788.76	185.06
Felidae	<i>Felis</i>	<i>chaus</i>	F	USNM	173375	38.93	339.39	268.14	607.54	129.45
Felidae	<i>Felis</i>	<i>chaus</i>	F	USNM	398570	43.34	357.08	264.28	621.35	136.55
Felidae	<i>Felis</i>	<i>nigripes</i>	M	USNM	395135	17.78	57.56	51.13	108.69	87.06
Felidae	<i>Felis</i>	<i>nigripes</i>	F	USNM	395519	14.01	34.65	30.96	65.61	79.20
Felidae	<i>Felis</i>	<i>silvestris</i>	F	USNM	327090	29.84	204.32	134.42	338.73	112.06
Felidae	<i>Felis</i>	<i>silvestris lybica</i>	M	LACM	56696	32.22	194.38	153.97	348.35	119.70
Felidae	<i>Felis</i>	<i>silvestris lybica</i>	M	USNM	450971	31.12	163.18	151.84	315.02	107.89
Felidae	<i>Leopardus</i>	<i>colocolo</i>	U	USNM	172785	19.20	86.13	55.83	141.96	87.41
Felidae	<i>Leopardus</i>	<i>colocolo</i>	M	USNM	540876	27.00	111.73	87.42	199.16	111.06
Felidae	<i>Leopardus</i>	<i>geoffroyi</i>	F	USNM	297847	25.87	157.09	106.37	263.46	101.25
Felidae	<i>Leopardus</i>	<i>geoffroyi</i>	F	USNM	574136	20.66	80.37	63.84	144.21	95.28
Felidae	<i>Leopardus</i>	<i>pardalis</i>	M	USNM	256918	48.76	614.65	352.53	967.18	137.76

Family	Genus	Species	Sex	Museum	Catalog number	CA (mm <sup>2</sup> )	Ix (mm <sup>4</sup> )	Iy (mm <sup>4</sup> )	J (mm <sup>4</sup> )	Length (mm)
Felidae	<i>Leopardus</i>	<i>pardalis</i>	F	USNM	287774	60.56	737.75	494.25	1,232.00	136.70
Felidae	<i>Leopardus</i>	<i>tigrina</i>	M	USNM	395089	21.27	76.37	56.73	133.09	99.68
Felidae	<i>Leopardus</i>	<i>wiedii</i>	M	USNM	240860	31.52	193.78	151.44	345.22	107.45
Felidae	<i>Leopardus</i>	<i>wiedii</i>	F	USNM	339683	30.06	149.95	121.06	271.01	104.47
Felidae	<i>Lynx</i>	<i>canadensis</i>	F	UCLA	13089	61.92	1,081.35	728.58	1,809.93	166.90
Felidae	<i>Lynx</i>	<i>canadensis</i>	M	UCLA	13098	77.28	1,588.71	1,038.21	2,626.92	175.90
Felidae	<i>Lynx</i>	<i>lynx</i>	U	USNM	1034	130.80	4,980.96	2,804.62	7,785.59	209.93
Felidae	<i>Lynx</i>	<i>lynx</i>	F	USNM	84090	98.75	1,889.46	1,228.43	3,117.90	175.48
Felidae	<i>Lynx</i>	<i>pardinus</i>	M	USNM	152619	80.41	1,298.92	766.09	2,065.01	154.05
Felidae	<i>Lynx</i>	<i>rufus</i>	M	UCLA	13933	56.77	593.60	461.53	1,055.13	144.05
Felidae	<i>Lynx</i>	<i>rufus</i>	F	UCLA	13943	53.64	555.89	452.20	1,008.08	134.58
Felidae	<i>Neofelis</i>	<i>nebulosa</i>	M	USNM	49974	149.63	3,914.82	2,383.52	6,298.34	175.04
Felidae	<i>Neofelis</i>	<i>nebulosa</i>	F	USNM	198705	64.97	840.15	574.39	1,414.54	137.05
Felidae	<i>Panthera</i>	<i>leo</i>	F	USNM	161914	503.63	44,969.95	27,492.87	72,462.82	307.30
Felidae	<i>Panthera</i>	<i>leo</i>	M	USNM	162919	684.38	97,698.04	45,452.05	143,150.09	358.11
Felidae	<i>Panthera</i>	<i>onca</i>	U	USNM	12296	262.81	17,127.07	9,554.62	26,681.69	236.59
Felidae	<i>Panthera</i>	<i>onca</i>	U	USNM	49393	366.83	29,371.88	19,728.63	49,100.51	256.87
Felidae	<i>Panthera</i>	<i>pardus</i>	M	LACM	31068	130.80	6,545.83	3,890.34	10,436.17	218.90
Felidae	<i>Panthera</i>	<i>pardus</i>	F	USNM	161911	180.66	5,348.05	4,136.13	9,484.18	196.91
Felidae	<i>Panthera</i>	<i>pardus</i>	M	USNM	164763	229.55	11,917.02	7,713.57	19,630.59	254.73
Felidae	<i>Panthera</i>	<i>pardus</i>	U	LACM	648/559	184.35	9,195.44	4,555.55	13,750.99	210.10
Felidae	<i>Panthera</i>	<i>tigris</i>	U	USNM	49728	602.67	77,283.13	56,839.44	134,122.57	325.81
Felidae	<i>Panthera</i>	<i>tigris</i>	F	USNM	174981	382.99	26,331.50	17,424.83	43,756.33	290.87
Felidae	<i>Panthera</i>	<i>uncia</i>	F	USNM	84091	151.57	4,573.54	2,343.69	6,917.23	193.41
Felidae	<i>Panthera</i>	<i>uncia</i>	F	USNM	321948	172.90	6,075.12	3,877.55	9,952.67	210.44
Felidae	<i>Pardofelis</i>	<i>marmorata</i>	M	USNM	239326	32.06	203.74	162.73	366.47	102.39
Felidae	<i>Pardofelis</i>	<i>temmincki</i>	U	USNM	258552	33.25	291.85	180.39	472.24	121.93
Felidae	<i>Pardofelis</i>	<i>temmincki</i>	F	USNM	362188	61.07	823.50	561.37	1,384.87	141.24
Felidae	<i>Prionailurus</i>	<i>bengalensis</i>	F	USNM	201069	24.10	122.17	92.36	214.52	100.75
Felidae	<i>Prionailurus</i>	<i>bengalensis</i>	M	USNM	240006	39.88	317.88	198.00	515.87	120.16
Felidae	<i>Prionailurus</i>	<i>planiceps</i>	F	USNM	145593	22.82	96.11	62.43	158.54	83.21
Felidae	<i>Prionailurus</i>	<i>planiceps</i>	M	USNM	A49973	17.43	54.48	38.07	92.56	82.29
Felidae	<i>Puma</i>	<i>concolor</i>	U	LACM	54511	232.38	18,722.02	8,742.17	27,464.19	236.60
Felidae	<i>Puma</i>	<i>concolor</i>	U	LACM	70296	135.31	5,811.35	4,052.89	9,864.24	208.50
Felidae	<i>Puma</i>	<i>concolor</i>	F	LACM	85438	151.07	7,064.90	3,761.44	10,826.34	198.90
Felidae	<i>Puma</i>	<i>yagouondi</i>	M	USNM	49716	34.99	333.86	221.08	554.94	111.58
Felidae	<i>Puma</i>	<i>yagouondi</i>	F	USNM	153531	29.38	213.06	169.61	382.67	104.80
Canidae	<i>Alopex</i>	<i>lagopus</i>	U	LACM	52188	31.48	179.24	172.35	351.59	106.36
Canidae	<i>Canis</i>	<i>adustus</i>	U	LACM	52230	36.81	236.80	227.20	463.99	128.63
Canidae	<i>Canis</i>	<i>dirus</i>	U	UCLA	2589–1	260.00	13,897.02	8,222.14	22,119.16	216.12
Canidae	<i>Canis</i>	<i>dirus</i>	U	UCLA	2589–2	323.59	21,782.26	13,946.55	35,728.81	242.57
Canidae	<i>Canis</i>	<i>dirus</i>	U	UCLA	2589–3	302.14	17,031.93	10,471.60	27,503.53	235.94
Canidae	<i>Canis</i>	<i>dirus</i>	U	UCLA	2589–4	253.12	13,555.48	8,286.37	21,841.85	239.78
Canidae	<i>Canis</i>	<i>latrans</i>	F	LACM	31164	71.50	1,148.78	814.05	1,962.83	148.00
Canidae	<i>Canis</i>	<i>latrans</i>	M	LACM	22588	57.38	872.61	476.87	1,349.48	153.00
Canidae	<i>Canis</i>	<i>lupus</i>	M	UCLA	16403	156.94	5,332.05	4,315.35	9,647.40	206.66
Canidae	<i>Canis</i>	<i>lupus</i>	F	UCLA	16404	142.37	4,074.53	3,070.28	7,144.81	195.22
Canidae	<i>Canis</i>	<i>cf. mesomelas</i>	F	LACM	67508	38.43	326.66	212.94	539.60	131.45
Canidae	<i>Canis</i>	<i>mesomelas</i>	M	LACM	42382	33.58	383.35	265.73	649.08	139.88
Canidae	<i>Cerdocyon</i>	<i>thous</i>	F	LACM	56720	29.20	125.69	127.47	253.16	102.96
Canidae	<i>Chrysocyon</i>	<i>brachyurus</i>	F	LACM	90772	128.78	3,250.95	2,982.96	6,233.90	258.93
Canidae	<i>Chrysocyon</i>	<i>brachyurus</i>	M	LACM	52548	122.34	4,450.02	2,995.92	7,445.94	235.40
Canidae	<i>Lycalopex</i>	<i>sp.</i>	F	UCLA	16498	30.24	217.97	156.69	374.65	99.31

Family	Genus	Species	Sex	Museum	Catalog number	CA (mm <sup>2</sup> )	Ix (mm <sup>4</sup> )	Iy (mm <sup>4</sup> )	J (mm <sup>4</sup> )	Length (mm)
Canidae	<i>Lycaon</i>	<i>pictus</i>	M	LACM	30588	119.08	3,240.38	2,236.02	5,476.39	173.14
Canidae	<i>Lycaon</i>	<i>pictus</i>	U	LACM	60621	132.73	4,963.47	3,207.01	8,170.48	204.10
Canidae	<i>Nyctereutes</i>	<i>procyonoides</i>	F	LACM	74122	22.67	163.54	110.01	273.55	83.24
Canidae	<i>Nyctereutes</i>	<i>procyonoides</i>	M	LACM	90831	22.52	119.40	93.50	212.90	85.51
Canidae	<i>Otocyon</i>	<i>megalotis</i>	M	LACM	41793	28.44	183.72	118.87	302.58	102.12
Canidae	<i>Otocyon</i>	<i>megalotis</i>	F	LACM	41790	22.81	147.07	90.27	237.34	102.29
Canidae	<i>Speothos</i>	<i>venaticus</i>	F	LACM	90833	59.13	456.25	334.20	790.45	98.80
Canidae	<i>Speothos</i>	<i>venaticus</i>	M	LACM	54008	48.59	284.50	241.37	525.88	104.67
Canidae	<i>Urocyon</i>	<i>cinereoargenteus</i>	F	UCLA	15408	21.58	98.00	83.87	181.88	95.59
Canidae	<i>Urocyon</i>	<i>cinereoargenteus</i>	M	UCLA	15958	23.17	113.23	113.80	227.03	107.26
Canidae	<i>Urocyon</i>	<i>cinereoargenteus</i>	M	UCLA	15808	35.15	261.12	237.50	498.62	103.46
Canidae	<i>Urocyon</i>	<i>littoralis</i>	F	UCLA	13394	18.87	65.07	59.46	124.52	81.45
Canidae	<i>Urocyon</i>	<i>littoralis</i>	M	UCLA	13452	19.43	87.57	60.74	148.31	78.70
Canidae	<i>Vulpes</i>	<i>chama</i>	F	LACM	58093	26.43	161.97	114.03	276.00	110.07
Canidae	<i>Vulpes</i>	<i>chama</i>	M	LACM	41795	25.04	121.43	94.79	216.22	106.81
Canidae	<i>Vulpes</i>	<i>macrotis</i>	F	LACM	28228	20.58	103.18	69.11	172.29	94.54
Canidae	<i>Vulpes</i>	<i>macrotis</i>	M	LACM	30420	21.41	95.62	94.83	190.45	94.95
Canidae	<i>Vulpes</i>	<i>velox</i>	M	LACM	86859	23.81	111.71	84.09	195.80	101.50
Canidae	<i>Vulpes</i>	<i>velox</i>	F	LACM	86860	24.34	113.58	103.28	216.86	99.28
Canidae	<i>Vulpes</i>	<i>vulpes</i>	F	LACM	54171	32.53	219.83	172.07	391.90	126.97
Canidae	<i>Vulpes</i>	<i>vulpes</i>	M	LACM	87624	41.03	323.81	253.52	577.32	128.49

Museum abbreviations include: Natural History Museum of Los Angeles County (LACM), UCLA Donald R. Dickey collection (UCLA), U.S. Museum of National History (USNM). Sex abbreviations include: M (male), F (female), U (unknown sex).

## References

- Alexander RM (1968) *Animal Mechanics*. Sidgwick and Jackson, London
- Andersson K (2004) Predicting body mass from a weight bearing joint. *J Zool Lond* 262:161–172
- Anyonge W (1993) Body mass in large extant and extinct carnivores. *J Zool Lond* 231:339–350
- Anyonge W, Roman C (2006) New body mass estimates for *Canis dirus*, the extinct Pleistocene dire wolf. *J Vertebr Paleontol* 26:209–212
- Bardeleben C, Moore RL, Wayne RK (2005) A molecular phylogeny of the Canidae based on six nuclear loci. *Mol Phylogenet Evol* 37:815–831
- Bates M (1944) Notes on a captive *Icticyon*. *J Mammal* 25:152–154
- Bertram JEA, Biewener AA (1988) Bone curvature: sacrificing strength for load predictability? *J Theor Biol* 131:75–92
- Bertram JEA, Biewener AA (1990) Differential scaling of the long bones in the terrestrial Carnivora and other mammals. *J Morphol* 204:157–169
- Bertram JEA, Swartz SM (1991) The ‘law of bone transformation’: a case of crying wolf? *Biol Rev* 66:245–273
- Bieseigel BD, Zuercher GL (2005) *Speothos venaticus*. *Mammalian Species* 783:1–6
- Biknevicius AR (1993) Biomechanical scaling of limb bones and differential limb use in caviomorph rodents. *J Mammal* 74:95–107
- Biknevicius AR (1999) Body mass estimation in armoured mammals: cautions and encouragements for the use of parameters from the appendicular skeleton. *J Zool Lond* 248:179–187
- Biknevicius AR, Ruff CB (1992a) Use of biplanar radiographs for estimating cross-sectional geometric properties of mandibles. *Anat Rec* 232:157–163
- Biknevicius AR, Ruff CB (1992b) The structure of the mandibular corpus and its relationship to feeding behaviors in extant carnivorans. *J Zool Lond* 228:479–507
- Carbone C, Mace GM, Roberts SC, Macdonald DW (1999) Energetic constraints on the diet of terrestrial carnivores. *Nature* 402:286–288
- Caro TM (1994) *Cheetahs of the Serengeti Plains*. University of Chicago Press, Chicago
- Cartmill M (1985) Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB (eds) *Functional Vertebrate Morphology*. Harvard University Press, Cambridge, pp 73–88
- Clauset A, Schwab DJ, Redner S (2009) How many species have mass M? *Am Nat* 173:256–263
- De Esteban-Trivigno S, Mendoza M, De Renzi M (2008) Body mass estimation in Xenarthra: A predictive equation suitable for all quadrupedal terrestrial placentals? *J Morphol* 269:1276–1293
- Demes B, Carlson K (2009) Locomotor variation and bending regimes of capuchin limb bones. *Am J Phys Anthropol* 139:558–571
- Demes B, Jungers WL (1993) Long bone cross-sectional dimensions, locomotor adaptations in body size in prosimian primates. *J Hum Evol* 25:57–74
- Demes B, Qin Y-X, Stern JT Jr, Larson SG, Rubin CT (2001) Patterns of strain in the macaque tibia during functional activity. *Am J Phys Anthropol* 116:257–265
- Demes B, Stern JT Jr, Hausman MR, Larson SG, McLeod KJ, Rubin CT (1998) Patterns of strain in the macaque ulna during functional activity. *Am J Phys Anthropol* 106:87–100

- Deutch LA (1983) An encounter between bush dog (*Speothos venaticus*) and paca (*Agouti paca*). *J Mammal* 64:532–533
- Doube M, Wiktorowicz-Conroy A, Christiansen P, Hutchinson JR, Shefelbine S (2009) Three-dimensional geometric analysis of felid limb bone allometry. *PLoS ONE* 4:e4742. doi:10.1371/journal.pone.0004742
- Ewer RF (1973) *The Carnivores*. Cornell University Press, New York
- Falster DS, Warton DI, Wright IJ (2006) SMATR: Standardised Major Axis Tests & Routines. Macquarie University, Australia. <http://www.bio.mq.edu.au/ecology/SMATR/>
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15
- Gittleman JL, Van Valkenburgh B (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioral ecology. *J Zool Lond* 242:97–117
- Goldman EA (1920) Mammals of Panama. *Smithson Misc Coll* 69:1–309
- Heinrich R, Biknevicius A (1998) Skeletal allometry and interlimb scaling patterns in mustelid carnivores. *J Morphol* 235:121–134
- Hunter L (2005) *Cats of Africa: Behavior, Ecology and Conservation*. The Johns Hopkins University Press, Baltimore
- Jacquemont S, Jacquenet F, Sebban M (2009) A lower bound on the sample size needed to perform a significant frequent pattern mining task. *Pattern Recogn Lett* 30:960–967
- Johnson WE, Eizirik E, Pecon-Slattery J, Murphy WJ, Agostinho A, Teeling E, O'Brien SJ (2006) The late Miocene radiation of modern Felidae: a genetic assessment. *Science* 31:73–77
- Kitchener A (1991) *The Natural History of the Wild Cats*. A&C Black, London
- Kleiman D (1972) Social behavior of the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. *J Mammal* 53:791–806
- Leyhausen P (1979) *Cat Behavior: The Predatory and Social Behavior of Domestic and Wild Cats*. Garland STMP Press, New York
- Lieberman DE, Polk JD, Demes B (2004) Predicting long bone loading from cross-sectional geometry. *Am J Phys Anthropol* 123:156–171
- Lindblad-Toh K, Wade CM, Mikkelsen TS, Karlsson EK, Jaffe DB, Kamal M, Clamp M, Chang JL, Kulbokas EJ, Zody MC, Mauceli E, Xie XH, Breen M, Wayne RK, Ostrander EA, Ponting CP, Gilbert F, Smith DR, deJong PJ, Kirkness E, Alvarez P, Biagi T, Brockman W, Butler J, Chin CW, Cook A, Cuff J, Daly MJ, DeCaprio D, Gnerre S, Grabherr M, Kellis M, Kleber M, Bardeleben C, Goodstadt L, Heger A, Hitte C, Kim L, Koepfli KP, Parker HG, Pollinger JP, Searle SMJ, Sutter NB, Thomas R, Webber C, Lander ES (2005) Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438:803–819
- MacDonald DW (1996) Social behaviour of captive bush dogs (*Speothos venaticus*). *J Zool Lond* 239:525–543
- Madar SI, Rose MD, Kelly J, MacLatchy L, Pilbeam D (2002) New *Sivapithecus* postcranial specimens from the Sivaliks of Pakistan. *J Hum Evol* 42:705–752
- Maddison WP, Maddison DR (2006) *Mesquite: A Modular System for Evolutionary Analysis*. Version 2.6. Available at <http://mesquiteproject.org>
- Martin RB, Burr DB, Sharkey NA (1998) *Skeletal Tissue Mechanics*. Springer, New York
- Matsuda I, Tuuga A, Higashi S (2008) Clouded leopard (*Neofelis diardi*) predation on proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. *Primates* 49:227–231
- Meachen-Samuels J, Van Valkenburgh B (2009a) Craniodental indicators of prey-size preference in the Felidae. *Biol J Linn Soc* 96:784–799
- Meachen-Samuels J, Van Valkenburgh B (2009b) Forelimb indicators of prey-size preference in the Felidae. *J Morphol* 270:729–744
- Mendoza M, Janis CM, Palmqvist P (2006) Estimating the body mass of extinct ungulates: a study on the use of multiple regression. *J Zool Lond* 270:90–101
- Merriam JC (1912) The fauna of Rancho La Brea. Part II Canidae. *Mem Univ Calif* 1:217–273
- Mosimann JE, James FC (1979) New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* 33:444–459
- Nowak RM (2005) *Walker's Carnivores of the World*, 7th edn. The Johns Hopkins University Press, Baltimore
- Polk JD, Demes B, Jungers WL, Biknevicius AR, Heinrich RE, Runestad JA (2000) A comparison of primate, carnivore and rodent limb bone cross-sectional properties: are primates really unique? *J Hum Evol* 39:297–325
- Rasband WS (2007) *ImageJ*. U. S. National Institutes of Health, Bethesda. <http://rsb.info.nih.gov/ij/>, 1997–2007
- Read AJ, Tolley KA (1997) Postnatal growth and allometry of harbor porpoises from the Bay of Fundy. *Can J Zool* 75:122–130
- Roark RJ (1965) *Formulas for Stress and Strain*. McGraw-Hill, New York
- Robling AG, Hinant FM, Burr DB, Turner CH (2002) Improved bone structure and strength after long-term mechanical loading is greatest if loading is separated into short bouts. *J Bone Miner Res* 17:1545–1554
- Roth VL (1990) Insular dwarf elephants: a case study in body mass estimation and ecological inference. In: Damuth J, MacFadden B (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, pp 151–180
- Rubin CT, Gross TS, McLeod KJ, Bain SD (1995) Morphologic stages in lamellar bone formation stimulated by a potent mechanical stimulus. *J Bone Miner Res* 10:488–495
- Rubin CT, Lanyon LE (1982) Limb mechanics as a function of speed and gait: a study of functional strains in the radius and tibia of horse and dog. *J Exp Biol* 101:187–211
- Ruff CB (1990) Body mass and hindlimb bone cross-sectional and articular dimensions in anthropoid primates. In: Damuth J, MacFadden B (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, pp 119–150
- Ruff CB (2003) Long bone articular and diaphyseal structure in old world monkeys and apes. II: estimation of body mass. *Am J Phys Anthropol* 129:16–37
- Ruff CB, Hayes WC (1983) Cross-sectional geometry of Pecos Pueblo femora and tibiae - a biomechanical investigation: 1. method and general patterns of variation. *Am J Phys Anthropol* 60:359–381
- Ruff CB, Holt BH, Trinkaus E (2006) Who's afraid of the big bad Wolff? Wolff's law and bone functional adaptation. *Am J Phys Anthropol* 129:484–498
- Ruff CB, Scott WW, Liu AY-C (1991) Articular and diaphyseal remodeling of the proximal femur with changes in body mass in adults. *Am J Phys Anthropol* 86:397–413
- Ruff CB, Walker A, Teaford MF (1989) Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Islands, Kenya. *J Hum Evol* 18:515–536
- Runestad JA (1997) Postcranial adaptations for climbing in the Lorisiidae (Primates). *J Zool Lond* 242:261–290
- Runestad JA, Ruff CB (1995) Structural adaptations for gliding mammals with implications for locomotor behavior in paromomyids. *Am J Phys Anthropol* 98:101–119
- Runestad JA, Ruff CB, Nieh JC, Thorington RW Jr, Teaford MF (1993) Radiographic estimation of long bone cross-sectional geometric properties. *Am J Phys Anthropol* 90:207–213
- Schaller GB (1972) *The Serengeti Lion: A Study of Predator Prey Relationships*. University of Chicago Press, Chicago
- Schmidt-Nielsen K (1993) *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge
- Scott KM (1990) Postcranial dimensions of ungulates as predictors of body mass. In: Damuth J, MacFadden BJ (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, pp 301–336

- Smith RJ (1981) Interpretation of correlations in intraspecific and interspecific allometry. *Growth* 45:291–297
- Smith RJ (2009) Use and misuse of the reduced major axis for line-fitting. *Am J Phys Anthropol* 140:476–486
- Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP (2003) Body mass of late Quaternary mammals. *Ecology* 84:3403
- Sorkin B (2008) A biomechanical constraint on body mass in terrestrial mammalian predators. *Lethaia* 41:333–347
- Sunquist M, Sunquist F (2002) *Wildcats of the World*. University of Chicago Press, Chicago
- Szivek JA, Johnson EM, Magee FP (1992) In vivo strain analysis of the greyhound femoral diaphysis. *J Invest Surg* 5:91–108
- Trapp GR, Hallberg DL (1975) Ecology of the gray fox (*Urocyon cinereoargenteus*): a review. In: Fox MW (ed) *The Wild Canids, Their Systematics, Behavioral Ecology and Evolution*. Van Nostrand Reinhold, New York, pp 164–178
- Van Valkenburgh B (1990) Skeletal and dental predictors of body mass in carnivores. In: Damuth J, MacFadden B (eds) *Body Size in Mammalian Paleobiology: Estimation and Biological Implications*. Cambridge University Press, Cambridge, pp 181–206
- Van Valkenburgh B, Koepfli KP (1993) Cranial and dental adaptations to predation in canids. *Sym Zool S* 65:15–37
- Wang X, Tedford RH (2008) *Dogs: Their Fossil Relatives and Evolutionary History*. Columbia University Press, New York
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Young SP, Goldman EA (1946) *The Puma: Mysterious American Cat*. Dover Publications, Inc, New York