Forelimb Indicators of Prey–Size Preference in the Felidae

Article *in* Journal of Morphology · June 2009

DOI: 10.1002/jmor.10712 · Source: PubMed

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Forelimb Indicators of Prey-Size Preference in the Felidae

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ABSTRACT   The forelimbs, along with the crania, are an essential part of the prey-killing apparatus in cats. Linear morphometrics of the forelimbs were used to determine the morphological differences between felids that specialize on large prey, small prey, or mixed prey. We also compared the scaling of felid forelimbs to those of canids to test whether prey capture strategies affect forelimb scaling. Results suggest that large prey specialists have relatively robust forelimbs when compared with smaller prey specialists. This includes relatively more robust humeri and radii, relatively larger distal ends of the humerus, and relatively larger articular areas of the humerus and radius. Large prey specialists also had relatively longer olecranon processes of the ulna and wider proximal paws. These characters are all important for subduing large prey while the cat positions itself for the killing bite. Small prey specialists have relatively longer distal limb elements for swift prey capture, and mixed prey specialists had intermediate values with relatively more robust metacarpals. Arboreal felids also had more robust limbs. They had relatively longer proximal phalanges for better grip while climbing, and a relatively short brachial index (radius to humerus ratio). Additionally, we found that felids and canids differ in forelimb scaling, which emphasizes the dual use of forelimbs for locomotion and prey capture in felids. This morphometric technique worked well to separate prey-size preference in felids, but did not work as well to separate locomotor groups, as scansorial and terrestrial felids were not clearly distinguished. J. Morphol. 270:729–744, 2009.   © 2009 Wiley-Liss, Inc.

KEY WORDS: Felidae; Canidae; morphometrics; forelimbs; prey size; allometric scaling

INTRODUCTION

Members of the family Felidae differ little in their diets. They are all hypercarnivores that specialize on vertebrates, but may differ in their choice of prey and prey-size preference. Optimal foraging theory suggests that while small felids can subsist on abundant small vertebrate prey, large felids require larger prey because the relative cost of foraging for small prey is too great to sustain the physiological demands of their increased body mass (Emlen, 1966; MacArthur and Pianka, 1966). Studies by Carbone et al. (1999, 2007) suggest that there is a size threshold in extant carnivorans, between 15 and 25 kg, where they shift from killing prey much smaller than themselves to prey 45% of their own size or larger. Because felids kill their prey using two distinct modules (sensu Gatesy and Dial, 1996), a cranial module and a forelimb module, both skull and forelimb morphology are likely to reflect prey size. The cranial module, which includes the skull, the mandibles, and dentition, was explored previously (Meachen-Samuels and Van Valkenburgh, in press); and here, we examine the forelimb module, which includes the brachium, antebrachium, and manus.

Using morphology to infer forelimb use has been well documented in carnivores (Gonyea and Ashworth, 1975; Gonyea, 1978; Van Valkenburgh, 1987; Bertram and Biewener, 1990; Iwaniuk et al., 1999; Andersson and Werdelin, 2003; Andersson, 2004). Forelimb use is a critical part of prey killing behavior in felids (Ewer, 1973; Leyhausen, 1979). They use a turning (palms rotate in and out) movement of the forepaws and insert their claws to subdue prey (Gonyea, 1978). This pronating and supinating motion is facilitated by flexibility of the humeral-radial articulation of the elbow joint (Andersson, 2004), and the scapholunar bone of the wrist joint allows palmar flexion and mobility in the wrist (Yalden, 1970; Gonyea, 1976a, 1978). This flexibility must be accompanied by sufficient strength to stabilize joints when under load.

In felids, large prey specialists employ their forelimbs to grapple and subdue prey while they position themselves for the killing bite, usually a suffocating hold on the trachea or snout. Small prey specialists will generally use a quick swipe of the paws to bring prey up to their mouths before dispatching it with a spinal cord severing bite to the dorsal neck (Ewer, 1973; Leyhausen, 1979).

These differences in prey killing strategies between large and small prey specialists should have functional consequences for the morphology of the fore-limbs. Large prey specialist felids should show increased forelimb robustness to deal with the increased stress of subduing prey and should have shorter distal limbs to increase mechanical advantage. They should have wider distal breadths of the humerus and radius for increased muscle attachment and larger articular surfaces to distribute heavier loads. They should also display elongated olecranon processes of the ulna for increased triceps insertion area and greater mechanical advantage while attacking with the forelimbs. Large prey specialists should also have wider paws to distribute forces while grasping and a wider articular surface of the scapholunar that confers increased mobility of the wrist. Small prey specialists may have elongated distal elements (radii and ulnae) for a velocity advantage for swift prey capture.

In contrast to felids, canids generally pursue large prey in packs and bring them down by swift shallow bites to the rear, muzzle, sides, or the flank of the animal, usually ending in disembowelment that ultimately kills the animal. Small prey is caught in the jaws and bitten or may be shaken to break the prey's neck (Ewer, 1973). Despite differences in prey killing techniques between canids and felids, both show similar adaptations in cranial morphology for taking large prey (Van Valkenburgh and Koepfli, 1993; Van Valkenburgh et al., 2004; Meachen-Samuels and Van Valkenburgh, in press). However, dogs do not use their forelimbs to grasp prey and therefore are unlikely to parallel felids in forelimb scaling and proportions. Because of the demands of large body size, both larger canids and felids are expected to have stouter limb bones than smaller species (Bertram and Biewener, 1990; Day and Jayne, 2007); but in felids, this may be accentuated because of the added requirement of using the limbs to grapple with prey.

Locomotor differences are also important to consider when examining forelimb morphology. Gonyea (1978) found differences in the tuberosity of the olecranon process and its associated muscle attachments between arboreal and terrestrial felids. Arboreal species tend to have a larger lateral tuberosity on the olecranon process and larger triceps muscles than terrestrial felids. Van Valkenburgh (1987) found a long phalanx to metacarpal ratio and more recurved claws in arboreal carnivores, both of which facilitate a better grip on branches while climbing. Arboreal carnivores also have a cranially directed olecranon process of the ulna, whereas terrestrial carnivores have a more caudally bent olecranon process. Each of these orientations has distinct functional advantages: a cranially directed olecranon process allows better leverage of the triceps muscle while the elbow is bent; whereas a caudally directed olecranon process

allows for better leverage of the triceps with an extended limb posture (Van Valkenburgh, 1987). Like other groups of arboreal mammals, arboreal felids may also have more robust forelimbs for increased muscle mass to sustain their own body weight while climbing and wider articular surfaces of the long bones for increased mobility of the joints (Wood, 1953; Thorington, 1972; Cartmill, 1985).

In this study, along with a previous study on the cranial module in the Felidae (Meachen-Samuels and Van Valkenburgh, in press), we examine the morphological differences in the forelimbs between cats that choose predominantly small prey, predominantly large prey, or a mixture of both. We will also assess the scaling differences between forelimbs in canids and felids, and we will take into account locomotor or habitat differences that may influence the morphology of felid forelimbs or confound the interpretations between felid prey-size groups.

MATERIALS AND METHODS

A total of 249 adult individuals were measured from 31 species in the family Felidae (Table 1; Appendix). Wild-caught specimens were preferentially measured; however, for some species, wild-caught specimens were rare in museum collections, and thus for these species captive (zoo) animals were included. Captive specimens were included in the subsequent statistical analyses only if their measurements were not significantly different from wild individuals (ANOVA, $\alpha = 0.05$). The data set includes specimens that were measured at the following museums: Natural History Museum of Los Angeles County (LACM), George C. Page Museum (LACMHC), Donald R. Dickey Collection, University of California, Los Angeles, (UCLA), Museum of Vertebrate Zoology at the University of California, Berkeley (MVZ), Field Museum of Natural History (FMNH), and U.S. National Museum of Natural History (USNM).

A set of 39 forelimb measurements were taken following von den Dreisch (1976), Merriam and Stock (1932) and Van Valkenburgh (1987) using digital calipers to the nearest 0.01 mm (Table 2; Fig. 1). These measurements were chosen because they reflect functional properties of the forelimbs while capturing prey. These raw measurements were used to compute a set of 13 functional indices (ratios). Some of these ratios were used from previous studies (Hildebrand, 1985b; Van Valkenburgh, 1987; Iwaniuk et al., 1999; Elissamburu and Vizcaíno, 2004; Samuels and Van Valkenburgh, 2008) and some of these ratios were created for this study. These ratios were used to estimate the shape and proportion of the forelimbs and their uses in prey-killing (Table 3). In addition to functional indices, Mosimann shape variables were calculated for the raw measurements through geometric mean transformation of data prior to statistical analyses. The geometric mean (GM) is an overall size variable derived from the nth root of the product of n measurements, and the ratio of any particular measurement to the overall geometric mean is a Mosimann shape variable (Mosimann and James, 1979). GM transformed data and ratios were analyzed separately, and the results were found to be similar. For ease of discussion, only the ratio data will be presented here.

Ratios were used in this study because they reflect functionally relevant features and are easy to interpret. However, one problem posed by ratios is the violation of assumptions of statistical tests, such as homoscedasticity and normality in parametric tests (Sokal and Rohlf, 1995). Despite these issues, many studies have found ratios to be statistically robust (Van Valkenburgh, 1987; Van Valkenburgh and Koepfli, 1993; Elissamburu and Vizcaíno, 2004).

TABLE 1. Felid species used in this study

Sp. no.	Species	Common name	n	Prey size	Cat lineage	Locomotor category	Felid mass range in kg
1	*Acinonyx jubatus*	Cheetah	12	Large	Puma	Terrestrial	40–65
2	*Caracal aurata*	African golden cat	3	Mixed	Caracal	Terrestrial	5–16
3	*Caracal caracal*	Caracal	9	Mixed	Caracal	Scansorial	7–20
4	*Caracal serval*	Serval	11	Small	Caracal	Terrestrial	8–18
5	*Felis chaus*	Jungle cat	3	Small	Domestic	Terrestrial	2–13
6	*Felis margarita*	Sand cat	7	Small	Domestic	Terrestrial	1–4
7	*Felis nigripes*	Black-footed cat	3	Small	Domestic	Terrestrial	1–3
8	*Felis silvestris lybica*	African Wildcat	8	Small	Domestic	Scansorial	3–6
9	*Leopardus colocolo*	Pampas cat	4	Small	Ocelot	Scansorial	2–4
10	*Leopardus geoffroyi*	Geoffroy's cat	6	Small	Ocelot	Terrestrial	2–8
11	*Leopardus pardalis*	Ocelot	10	Mixed	Ocelot	Scansorial	6–16
12	*Leopardus tigrinus*	Tigrina or Oncilla	7	Small	Ocelot	Scansorial	2–4
13	*Leopardus wiedii*	Margay	9	Small	Ocelot	Arboreal	2–4
14	*Lynx canadensis*	Canadian lynx	9	Mixed	Lynx	Terrestrial	5–17
15	*Lynx lynx*	Eurasian lynx	2	Large	Lynx	Scansorial	11–30
16	*Lynx pardinus*[a]	Iberian lynx	1	Small	Lynx	Terrestrial	7–16
17	*Lynx rufus*	Bobcat	19	Mixed	Lynx	Scansorial	4–16
18	*Neofelis nebulosa*	Clouded leopard	10	Mixed	Panthera	Arboreal	11–25
19	*Otocolobus manul*	Manul or Pallas's cat	10	Small	Leopard Cat	Terrestrial	2–5
20	*Panthera leo*	Lion	12	Large	Panthera	Terrestrial	110–250
21	*Panthera onca*	Jaguar	5	Large	Panthera	Scansorial	36–120
22	*Panthera pardus*	Leopard	11	Large	Panthera	Scansorial	28–65
23	*Panthera tigris*	Tiger	11	Large	Panthera	Terrestrial	75–325[b]
24	*Panthera uncia*	Snow leopard	10	Large	Panthera	Scansorial	22–52
25	*Pardofelis marmorata*	Marbled cat	7	Small	Bay Cat	Arboreal	2–4
26	*Pardofelis temminckii*	Asian golden cat	8	Mixed	Bay Cat	Scansorial	8–16
27	*Prionailurus bengalensis*	Leopard cat	11	Small	Leopard Cat	Scansorial	2–9
28	*Prionailurus planiceps*	Flat-headed cat	11	Small	Leopard Cat	Terrestrial	1–3
29	*Prionailurus viverrinus*	Fishing cat	4	Small	Leopard Cat	Terrestrial	5–16
30	*Puma concolor*	Puma or Mountain lion	19	Large	Puma	Scansorial	23–80
31	*Puma yaguarondi*	Jaguarundi	6	Small	Puma	Scansorial	3–7

Lineages follow Johnson et al., 2006.
[a]Indicates this species was not included in some statistical tests because of its low sample size.
[b]Study includes primarily southern Asian tigers; size range given includes all tiger subspecies. Mass ranges from Sunquist and Sunquist, 2002 and Nowak, 1999.

To assess interspecific allometry within the Felidae, $\log_{10}$ raw measurements were regressed against the log GM of individual elements (i.e. humerus epicondyles were regressed against log humerus GM; olecranon length was regressed against log ulna GM, etc.) (as a proxy for body size), using reduced major axis regression (RMA). Regressions were performed using individual elements instead of the forelimb as a whole because some specimens did not include all elements, and our method ensured that all individuals were included in the analysis. Reduced major axis regression was chosen because of its appropriateness for examining allometric relationships (Warton et al., 2006). RMA analyses were run using the program SMATR (Falster et al., 2006) with equations in the form of:

$$\log y = a + b \log x$$

where x = body size (GM), y = raw measurement, a = y-intercept, and b = slope. Negative allometry was indicated by slopes significantly <1, positive allometry by slopes significantly >1, and isometry by slopes not significantly different from one (Schmidt-Nielsen, 1993; Read and Tolley, 1997).

Body mass ranges for each species were taken from the literature (Sunquist and Sunquist, 2002; Nowak, 2005). Because sexual dimorphism is pronounced in many felids (Gittleman and Van Valkenburgh, 1997), this was taken into consideration when performing each analysis by including equal numbers of males and females when possible and using species averages; juvenile individuals with unfused epiphyses were excluded from this study.

Typical prey sizes and locomotor categories for each cat species were compiled from several sources: Young and Goldman (1946), Schaller (1972), Ewer (1973), Leyhausen (1979), Kitchener (1991), Sunquist and Sunquist (2002), and Hunter (2005). Prey size preference rather than cat size was assessed in this study because the two are correlated, but do not wholly overlap. All cats more than 25 kg will kill large prey, and all cats less than 15 kg will kill small prey; however, within a size range of 15 to 25 kg, cats may choose to kill prey of many different sizes, and cat mass alone does not determine this choice. Three prey size categories for the analysis based on Carbone et al. (2007) and the author's compiled database of preferred prey types were defined as follows: cats that predominantly kill prey smaller than themselves (small prey), cats that predominantly kill prey as large or larger than themselves (large prey), and cats that readily kill both sizes of prey depending on what prey is preferred or easily available (mixed prey) (Table 1).

When examining postcrania, factors other than prey size must also be considered. In this study, we examined locomotor mode as a second factor. Although all cats are capable of climbing as a means of escape, different species of cats climb to different degrees, ranging from those that rarely, if ever, climb to those that live and hunt in trees. Three locomotor categories were assigned and examined; 1) Terrestrial—cats that rarely, if ever, climb; 2) Scansorial—cats that often climb for refuge, but rarely hunt in the trees; and 3) Arboreal—cats that spend most of their time in trees and often hunt there (Table 1).

Data were analyzed using multivariate analysis of variance (MANOVA) using Scheffe's F and Tamhane's $T2$ procedures for post hoc comparisons, principal component analysis (PCA), and

TABLE 2. *List of measurements used in this study*

Measurement	Abbreviation
Greatest length of the humerus	HL
Smallest transverse diameter of the diaphysis of the humerus	HD
Anteroposterior depth of the proximal humerus	HPAP
Humerus epicondylar mediolateral breadth	HEB
Humerus distal articular anteroposterior depth	HDAP
Humeral distal articulation breadth from the trochlea to the capitulum	HDAB
Greatest length of the ulna	UL
Length of the olecranon process of the ulna	ULO
Anteroposterior depth of the olecranon process	UOD
Anteroposterior depth across the processus anconeus of the ulna	UPA
Mediolateral breadth across the coronoid process and radial notch	UCP
Greatest length of the radius	RL
Smallest transverse diameter of the diaphysis of the radius	RD
Mediolateral breadth of the proximal radius	RPML
Anteroposterior depth of the proximal radius	RPAP
Mediolateral breadth of the distal radius	RDML
Anteroposterior depth of the distal radius	RDAP
Mediolateral breadth of the distal articulation of the radius	RMLA
Anteroposterior depth of the distal articulation of the radius	RAPA
Greatest length of metacarpals 2–5	M2L–M5L
Smallest transverse diameter of the diaphysis of metacarpals 2–5	M2D–M5D
Mediolateral breadth of the proximal end of metacarpals 2–5	M2PML–M5PML
Anteroposterior depth of the proximal end of metacarpals 2–5	M2PAP–M5PAP
Mediolateral breadth of the distal end of metacarpals 2–5	M2DML–M5DML
Anteroposterior depth of the distal end of metacarpals 2–5	M2DAP–M5DAP
Greatest length of proximal phalanx 3	PPL
Smallest transverse diameter of diaphysis of proximal phalanx 3	PPD
Mediolateral breadth of the proximal end of proximal phalanx 3	PPPML
Anteroposterior depth of the proximal end of proximal phalanx 3	PPPAP
Mediolateral breadth of the distal end of proximal phalanx 3	PPDML
Anteroposterior depth of the distal end of proximal phalanx 3	PPDAP
Greatest length of medial phalanx 3	PML
Smallest transverse diameter of diaphysis of medial phalanx 3	PMD
Mediolateral breadth of the proximal end of medial phalanx 3	PMPML
Anteroposterior depth of the proximal end of medial phalanx 3	PMPAP
Mediolateral breadth of the distal end of medial phalanx 3	PMDML
Anteroposterior depth of the distal end of medial phalanx 3	PMDAP
Proximal articular proximodistal length of scapholunar	SPAL
Proximal articular mediolateral width of scapholunar	SPAW

Measurements follow von den Dreisch, 1976; Merriam and Stock, 1932; and Van Valkenburgh, 1987.
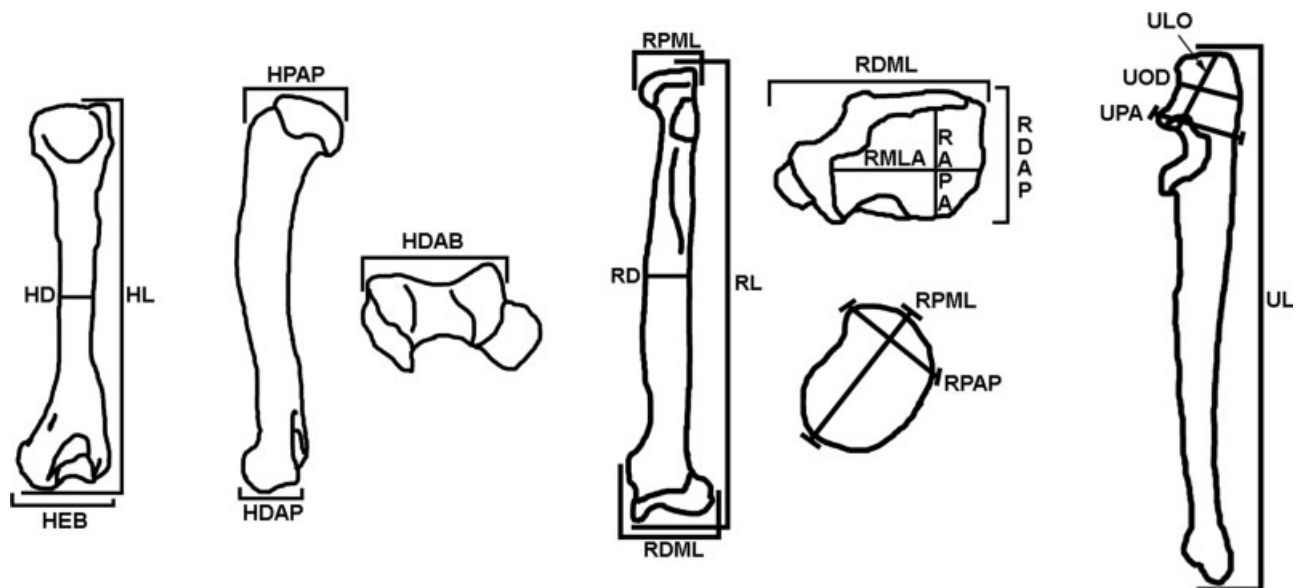

Fig. 1. Line drawings of lion limb elements of measurements taken on humerus, radius, and ulna.

TABLE 3. Functional indices used in this study

Ratio explanation	Abbreviation	Calculation
Proximal paw width	PAW	(M2PML + M3PML + M4PML + M5PML)/M3L
Brachial index	BI	RL/HL
Humeral robustness index	HRI	HD/HL
Humeral epicondylar index	HEI	HEB/HL
Olecranon index	OI	ULO/(UL−ULO)
Radial robustness index	RRI	RD/RL
Manus proportions	MCP	PPL/M3L
Radial articular index	RAI	RMLA/RL
Humeral condylar index	HCI	HDAB/HL
Metacarpal 3 robustness index	MC3RI	M3D/M3L
Humeral distal articular area	HAA	$^{1/2}$(HDAB*HDAP)/HL
Radial distal articular area	RAA	$^{1/2}$(RMLA*RAPA)/RL
Metacarpal 3 distal articular area	MC3AA	$^{1/2}$(M3DML*M3DAP)/M3L

Indices follow Hildebrand, 1985; Van Valkenburgh, 1987; Iwaniuk et al., 2000; Elissamburu and Vizcaino, 2004; and Samuels and Van Valkenburgh, 2008.

discriminant function analysis (DFA). These statistical techniques were chosen because they are often used to examine eco-morphological differences among taxa (Van Valkenburgh, 1987; Van Valkenburgh and Koepfli, 1993; Mora et al., 2003). The MANOVA tested for significant differences in morphology among both the prey size and locomotor categories, respectively. PCA was used to explore and visualize shape variations within the data set. Stepwise discriminant function analysis (DFA) was performed to identify variables that discriminate between prey sizes and also locomotor modes. All statistical analyses were performed using SPSS v13.0.

To assess expected allometric differences between canids and felids, forelimb (humerus, ulna, radius, third metacarpal) measurements that were taken for felids were measured for 17 species of extant canids and the extinct dire wolf, *Canis dirus* (Table 4; Appendix). The dire wolf was included in the study because it is larger than any extant canid and thus closer in size to larger pantherines and pumas. All extant canid species were measured from the Natural History Museum of Los Angeles County (LACM) and the Donald R. Dickey UCLA collection (UCLA); dire wolves were measured from the George C. Page Museum (LACMHC). When possible, care was taken to measure equal numbers of males and females, and individuals with unfused epiphyses were excluded. Species averages were computed for these measurements, raw data were $\log_{10}$ transformed and then linearly regressed against the log geometric mean of the corresponding skeletal element. The homogeneity of the least squares regressions slopes for these two families was compared using an analysis of covariance (ANCOVA), where a *P*-value of 0.05 or less indicated a significant difference between the two families. In addition to a least squares regression, RMA regression was also used to compare the slopes of canid forelimbs to felid forelimbs and as previously described to test for significant differences from isometry.

Because all of the cats in this study are phylogenetically related, they are not entirely independent samples. To assess the influence of phylogeny, independent contrasts were applied to the results (Felsenstein, 1985) based on the recent molecular phylogeny of the Felidae (Johnson et al., 2006). Independent contrasts of log GM transformed measurements and log mean prey size were calculated using the PDAP module in Mesquite v. 2.5 (Maddison and Maddison, 2006). Log GM transformed

TABLE 4. Canid species used in interfamilial allometry comparison

Sp. no.	Species	Common name	n	Canid mass range in kg
32	*Alopex lagopus*	Arctic fox	1	1.4–9
33	*Canis adustus*	Side-striped jackal	1	6.5–14
34	*Canis dirus*[a]	Dire wolf	10[b]	58–68[c]
35	*Canis latrans*	Coyote	11	7–20
36	*Canis lupus*	Grey wolf	2	18–50
37	*Canis mesomelas*	Black backed jackal	1	6–13.5
38	*Cerdocyon thous*	Crab-eating fox	1	5–8
39	*Chrysocyon brachyurus*	Maned wolf	5	20–26
40	*Lycaon pictus*	African hunting dog	2	17–36
41	*Nyctereutes procyonoides*	Raccoon dog	2	4–10
42	*Otocyon megalotis*	Bat-eared fox	4	3–5.3
43	*Speothos venaticus*	Bush dog	4	5–7
44	*Urocyon cinereoargenteus*	Grey fox	5	3–7
45	*Urocyon littoralis*	Channel Islands fox	5	1–2
46	*Vulpes chama*	Cape fox	3	4
47	*Vulpes macrotis*	Kit fox	5	1.5–3
48	*Vulpes velox*	Swift fox	5	1.8–3
49	*Vulpes vulpes*	Red fox	5	4–5.5

Body mass estimates from Nowak, 1999.
[a]Denotes extinct species.
[b]Denotes 10 individuals measured for each forelimb element.
[c]Denotes an estimated body mass from Anyonge and Roman, 2006.

TABLE 5. Mean values and standard deviations (SD) of functional indices for each prey size category

Ratio	Small prey mean (n = 15, 105)	Small prey SD	Mixed prey mean (n = 8, 69)	Mixed prey SD	Large prey mean (n = 7, 80)	Large prey SD
PAW	0.6004[L]	0.06120	0.6112[L]	0.08921	0.7151[S,M]	0.10565
BI	0.9018	0.05001	0.9005	0.05690	0.8805	0.05251
HRI	0.0662[M,L]	0.00528	0.0709[S,L]	0.00629	0.0803[S,M]	0.00787
HEI	0.1881[M,L]	0.01554	0.2016[S,L]	0.02554	0.2314[S,M]	0.03307
OI	0.1396[M,L]	0.01851	0.1526[S,L]	0.02325	0.1961[S,M]	0.02384
RRI	0.0629[M,L]	0.00768	0.0705[S,L]	0.01371	0.0913[S,M]	0.01257
MCP	0.4957	0.07747	0.5021	0.07268	0.4783	0.06004
RAI	0.1049[L]	0.01295	0.1111[L]	0.01801	0.1387[S,M]	0.01774
HCI	0.1283[M,L]	0.01132	0.1379[S,L]	0.01786	0.1582[S,M]	0.02057
RAA	0.0881[L]	0.00962	0.0917[L]	0.01393	0.1108[S,M]	0.01482
HAA	0.1401[M,L]	0.01072	0.1510[S,L]	0.01693	0.1850[S,M]	0.02470
MC3AA	0.1518[L]	0.01697	0.1581[L]	0.02326	0.1809[S,M]	0.01768
MC3RI	0.0891[M,L]	0.00974	0.0976[S,L]	0.01440	0.1159[S,M]	0.01641

N is number of species, individuals used in the analysis of each prey size category.
Superscripts indicate significant differences from the other groups in a multivariate analysis of variance, (S) small, (M) mixed, and (L) large prey.

contrasts were regressed against log mean prey size through the origin using linear regression to determine if phylogeny had a significant effect on any of the functional ratios used. During independent contrasts analyses, data were standardized to avoid spurious conclusions.

RESULTS
Prey Size Categories

Multivariate analysis of variance. The multivariate analysis of variance (MANOVA) found all prey size groups to be significantly different ($P < 0.001$) (Table 5). Differences for individual indices were assessed by univariate ANOVAs with Scheffe's F and Tamhane's $T2$ procedures for post hoc comparisons. Results show that all three prey groups were distinct with respect to relative robusticity of the humerus, radius, and metacarpals (HRI, RRI, MC3RI) as well as size of the humeral epicondyles, distal articular surface area (HEI, HCI, HAA), and olecranon length (OI). For all of these ratios, the mean was largest in large prey

TABLE 6. PCA loadings, eigenvalues, and % variance explained for functional indices principle components 1 and 2

Ratio	PC1	PC2
PAW	0.898	−0.208
BI	−0.656	0.409
HRI	0.886	0.217
HEI	0.943	0.106
OI	0.898	0.218
RRI	0.899	0.095
MCP	0.271	−0.886
RAI	0.946	0.058
HCI	0.933	0.097
RAA	0.947	0.033
HAA	0.943	0.232
MC3AA	0.895	−0.238
MC3RI	−0.828	0.072
Eigen values	9.642	1.240
% Variance	75.16	9.53

specialists, and intermediate in mixed prey feeders. In addition, large prey specialists differed significantly from both of the other groups in having relatively broader paws (PAW), and larger distal radial and metacarpal articular surface areas (RAI, RAA, and MC3RAA).

Principal component analysis. The principal component analysis (PCA) performed on forelimb ratios yielded two significant principal components (eigenvalues >1), which accounted for 84.7% of the total variance in the data set (Table 6). Principal component 1 (PC1) accounted for 75.1% of the variance, and separated cats that kill large prey from the other two groups, with the exception of the cheetah and the Eurasian lynx (see Fig. 2). Large prey specialists (positive PC1 scores) had relatively wider paws, (PAW), greater humeral and radial robustness (HRI, RRI), larger humeral epicondyles (HEI), longer olecranon processes (OI), and larger humeral, radial and metacarpal articular areas (HAA, RAA, MC3AA, HCI and RAI). Small and mixed prey specialists (negative PC1 scores) had more robust metacarpals (MC3RI) and a longer radius relative to humerus length (BI).

Principal component two (PC2) accounted for 9.5% of the variance. Large-prey specialists had positive scores associated with a smaller proximal phalanx to metacarpal ratio (MCP). Mixed prey and small prey feeders show a great deal of scatter, but had generally more negative scores on PC2, indicating longer proximal phalanges relative to metacarpals (MCP).

Discriminant function analysis. Stepwise discriminant function analysis (DFA) was performed on all forelimb ratio data using the three a priori groups for prey size. Separation of the groups was highly significant (Wilks' $\lambda = 0.177$, $P < 0.001$). The analysis yielded two discriminant functions, which accounted for 100% of the total variance in the data (Table 7; Fig. 3). Prey size
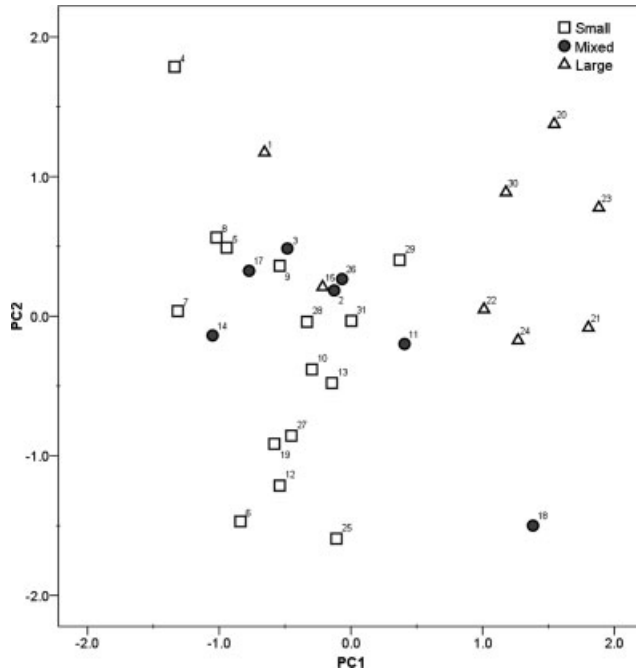
Fig. 2. Plot of first and second principal components for felid functional indices. Individual specimens for each species were collapsed to a single point. Refer to Table 1 for species key.

TABLE 7. *Discriminant analysis structure matrix for prey size preference, eigenvalues, and proportion of variance explained by each function and Wilks' lamda*

Ratio	DF1	DF2
OI	0.565	0.026
HAA	0.560	−0.002
RRI	0.506	−0.197
MC3RI	−0.468	0.371
HEI	0.395	−0.122
PAW	0.333	0.220
BI	−0.086	0.030
Eigen value	4.001	0.131
% Variance	96.8	3.2
Wilks λ	0.177	0.884

Locomotor Categories

Multivariate analysis of variance. The multivariate analysis of variance (MANOVA) found all locomotor groups to be significantly different ($P <$ 0.001) (Table 8). As in the previous analysis, differences for individual indices were assessed by univariate ANOVAs with Scheffe's F and Tamhane's $T2$ procedures for post hoc comparisons. The results show that all locomotor groups were distinct with respect to relative robusticity of the metacarpals (MC3AA), relatively wider paws (PAW) and longer proximal phalanges relative to metacarpals (MCP). For all of these ratios, the mean was largest in arboreal felids and smallest in terrestrial felids. However, arboreal felids had

groups were correctly classified in 81.3% of all cases (79.9% were correctly classified in a cross-validation, a method used to further validate classifications by jack-knifing). In the discriminant function analysis, most misclassifications were between mixed prey and small prey specialists. However, one large prey specialist, the Eurasian lynx, grouped with the mixed prey feeders.

The first discriminant function (DF1) accounted for 96.8% of the total variance. Large-prey specialists had positive DF1 scores, which were associated with longer olecranon processes (OI), greater distal humeral articular area (HAA), wider humeral epicondyles (HEI), greater radial robustness (RRI), and relatively wider paws (PAW). Mixed and small prey specialists had negative DF1 scores associated with more robust metacarpals (MC3RI). The misclassified Eurasian lynx had DF1 scores of ~0. Although the clouded leopard was not misclassified, it did show slightly positive scores, closer to large prey specialists.

The second discriminant function (DF2) accounted for 3.2% of the total variance. Large prey specialists had negative DF2 scores and relatively less robust metacarpals (MC3RI). Mixed prey feeders had mostly positive DF2 scores associated with an increase in metacarpal robustness (MC3RI) and small prey cats were scattered throughout. Again, the Eurasian lynx was an outlier with positive DF2 scores, grouping with the mixed prey specialists.
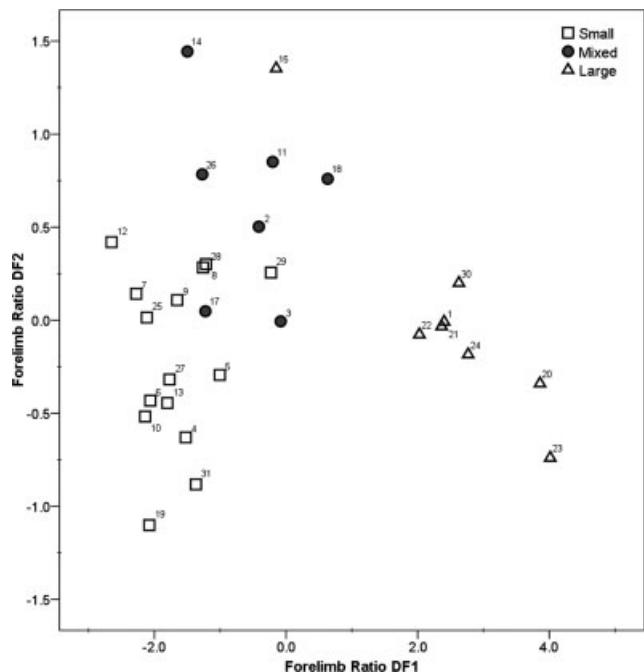

Fig. 3. Plot of first and second discriminant function scores for functional indices relating to prey size preference. Individual specimens for each species were collapsed to a single point. Refer to Table 1 for species key.

TABLE 8. Mean values and standard deviations (SD) of forelimb ratios for each locomotor category

Variable	Terrestrial mean ($n = 13, 100$)	Terrestrial SD	Scansorial mean ($n = 14, 128$)	Scansorial SD	Arboreal mean ($n = 3, 26$)	Arboreal SD
PAW	0.6161[A]	0.11094	0.6428[A]	0.08613	0.6986[T,S]	0.07052
BI	0.9241[S,A]	0.04530	0.8813[T,A]	0.04538	0.8450[T,S]	0.05713
HRI	0.0699	0.00946	0.0733	0.00811	0.0733	0.00832
HEI	0.2001[A]	0.03521	0.2078	0.02768	0.2156[T]	0.02561
OI	0.1581	0.03804	0.1643	0.02954	0.1581	0.02331
RRI	0.0700[A]	0.01512	0.0759	0.01710	0.0804[T]	0.01619
MCP	0.4776[A]	0.07376	0.4847[A]	0.05736	0.5814[T,S]	0.05905
RAI	0.1128[A]	0.02443	0.1191	0.01974	0.1266[T]	0.01662
HCI	0.1382[A]	0.02429	0.1402	0.01808	0.1499[T]	0.01670
RAA	0.0929[A]	0.01796	0.0978	0.01466	0.1024[T]	0.01271
HAA	0.1555	0.03096	0.1588	0.02346	0.1577	0.01992
MC3AA	0.1569[A]	0.02387	0.1632[A]	0.02006	0.1795[T,S]	0.02216
MC3RI	0.0952[A]	0.01688	0.1021	0.01458	0.0996[T]	0.01641

N is number of species, individuals used in the analysis of each locomotor category.
Superscripts indicate significant differences from the other groups in a multivariate analysis of variance, (T) terrestrial, (S) scansorial, and (A) arboreal locomotor modes.

the lowest means for brachial index (BI). Additionally, arboreal felids differed significantly from both of the other groups in having relatively more robust radii and metacarpals (RRI, MC3RI), larger distal humerus and radius articulations (HCI, RAI, RAA), and wider humeral epicondyles (HEI).

Principal component analysis. On the basis of the same PCA analysis described above, univariate analysis of variance (ANOVA) tests were used to examine whether prey size and locomotor categories showed significantly different PC scores. Despite the fact that some individual ratios differed significantly among the three locomotor groups, their PC scores when all variables were considered did not differ significantly. Instead, it appears that the PCA results and variance in postcranial morphology are better explained by prey size preferences than locomotor habits.

Discriminant function analysis. Stepwise discriminant function analysis (DFA) was performed on all forelimb ratio data using the three a priori groups for locomotor mode. Separation of the arboreal group was significant (Wilks' $\lambda = 0.536$, $P < 0.001$). This analysis also yielded two discriminant functions, which accounted for 100% of the total variance in the data (Table 9; Fig. 4). Loco-

motor groups were correctly classified only 66.1% of the time and 65.0% when cross-validated. This classification was not as robust as the classification for prey-size groups (81.3%) and suggests that the ratios used in this study classify felids more effectively into prey size groups than locomotor groups. All misclassifications occurred between scansorial and terrestrial cats, which were not well separated.

TABLE 9. Discriminant analysis structure matrix for locomotor categories, eigenvalues, and proportion of variance explained by each function and Wilks' lamda

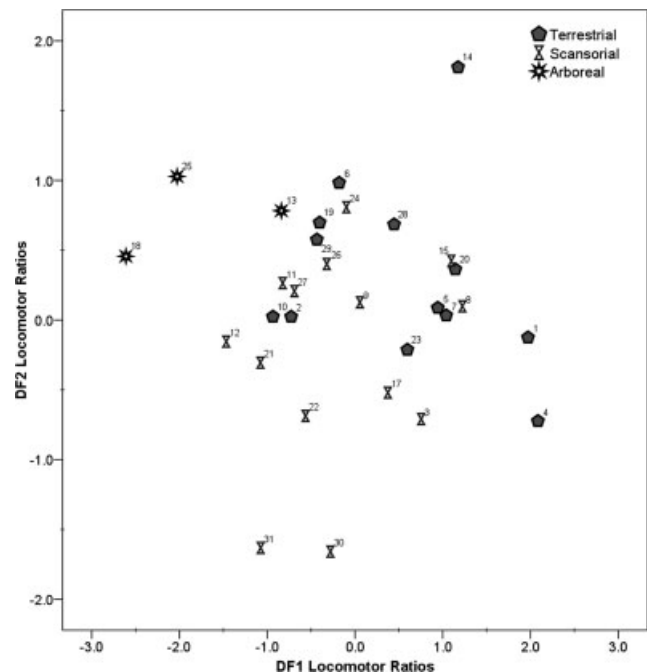| Ratio	DF1	DF2
BI	0.719	0.343
MCP	−0.584	0.586
HCI	−0.188	0.111
HRI	−0.207	−0.349
HAA	−0.050	−0.099
Eigenvalue	0.591	0.172
% Variance	77.4	22.6
Wilks λ	0.536	0.853

Fig. 4. Plot of first and second discriminant function scores for functional indices relating to locomotor category. Individual specimens for each species were collapsed to a single point. Refer to Table 1 for species key.

The first discriminant function (DF1) accounted for 77.4% of the total variance and separated arboreal felids from all other cats. Arboreal cats had negative DF1 scores, which were associated with a smaller brachial index (BI), longer proximal phalanges relative to metacarpals (MCP), and greater humeral robusticity (HRI).

The second discriminant function (DF2) accounted for 22.6% of the total variance. Arboreal cats had positive DF2 scores, which were correlated with longer proximal phalanges relative to metacarpals (MCP), smaller humeral robustness (HRI), and slightly larger brachial index (BI). The contradictory scores for brachial index in arboreal cats for DF1 and DF2 could be caused by autocorrelation. In other words, significant loadings with opposite signs and seemingly opposite interpretations on two different discriminant functions may be caused by the correlation of BI with another, more important variable on discriminant function two. This autocorrelation may violate one of the assumptions of discriminant function analysis, which is independence of variables. (Sokal and Rohlf, 1995) and may confound the importance of BI and HRI on discriminant function two.

The second discriminant function may also be largely driven by the Canadian lynx, an outlier species with unusually elongate phalanges, which are most likely used for greater surface area for snow travel, rather than climbing (Murray and Boutin, 1991). This species also has a longer radius as well, which may skew the results of this test for brachial index results. The contradiction in the humeral robustness index is likely influenced by humerus length. A relatively longer humeral length would create a smaller brachial index and would also make the humerus appear less robust. However, these contradictions along DF1 and DF2 are of minor importance because the eigenvalues and Wilk's lambda values for DF2 show poor separation, and therefore DF1 should be considered of primary importance.

Independent Contrasts

Phylogeny and ancestry constrain morphology, and thus phylogenetically independent contrasts were applied to our data to examine the effects of phylogeny on morphological ratios (Felsenstein, 1985). As prey size preference had a more pronounced influence on forelimb morphology than locomotor habits in our analysis, independent contrasts were used to examine the degree to which phylogeny affects prey size preference. Prey size preference was transformed into a continuous variable by entering log mean prey size in kilograms for each species; and using the phylogeny by Johnson et al. (2006), branch lengths were assigned using the supplementary material from Johnson et al. (2006). Log GM of each measured variable

TABLE 10. *Results of phylogenetically independent contrasts of log GM variables versus log mean prey size preference*

Variable	P-value	F	Slope	r^2
HL	$1.011e^{-5}$	28.82	-0.020	0.498
HD	0.150	2.183	0.003	0.070
HPAP	0.251	1.370	-0.002	0.045
HEB	0.016	6.505	0.005	0.183
HDAP	$1.18e^{-4}$	19.967	0.012	0.407
HDAB	0.329	0.985	0.002	0.032
RL	$1.59e^{-6}$	36.61	-0.023	0.557
RD	0.020	6.060	0.013	0.172
RPML	0.070	3.548	-0.003	0.109
RPAP	0.813	0.056	-6.110	0.001
RDML	0.004	9.672	0.008	0.250
RDAP	0.268	1.274	0.003	0.042
RMLA	0.271	1.257	0.004	0.041
RAPA	0.509	0.446	-0.001	0.015
UL	$1.35e^{-4}$	19.53	-0.016	0.402
ULO	0.999	$8.49e^{-9}$	$-3.31e^{-7}$	$2.92e^{-10}$
M2PML	0.584	0.445	0.001	0.015
M3L	$3.39e^{-5}$	24.26	-0.014	0.455
M3D	$2.69e^{-4}$	17.345	0.008	0.374
M3PML	0.029	5.25	0.007	0.153
M3PAP	0.901	0.015	$6.16e^{-4}$	$5.33e^{-4}$
M3DML	0.475	0.523	0.001	0.017
M3DAP	0.142	2.271	-0.002	0.072
M4PML	0.278	1.22	0.003	0.040
M5PML	0.185	1.843	-0.005	0.059
PPL	$3.65e^{-5}$	24.32	-0.018	0.464
PPPML	0.003	10.371	0.004	0.270
PPPAP	0.018	6.258	-0.006	0.182
PPDML	0.052	4.102	0.004	0.127
PPDAP	0.084	3.21	0.004	0.102
PPD	0.004	9.408	0.009	0.251

Variables in bold were found to be significant at the $\alpha = 0.05$ level.

was regressed against mean prey size through the origin using linear regression to examine correlations between the contrasts and mean prey size.

The results of the regressions indicate that mean prey size is significantly correlated with the following features: UL, RL, RD, RDML, HL, HEB, HDAP, M3L, M3D, PPL, PPPML, PPPAP, PPDML, and PPD (Table 10). This indicates that large prey specialists have more robust radii (RRI), larger humerus epicondyles (HEI), and larger humeral articular areas (HAA), and mixed prey feeders have relatively more robust metacarpals (MC3RI) regardless of phylogenetic relationships ($\alpha = 0.05$).

Independent contrast analysis was not necessary for locomotor categories because scansorial and terrestrial felids were not sufficiently different from each other for the variables tested. Arboreal felids were significantly different from the two other locomotor groups; however, the three arboreal species included, *Neofelis nebulosa*, *Pardofelis marmorata*, and *Leopardus wiedii*, are all from different lineages within the Felidae and therefore phylogeny appears to have a negligible effect on these results.

The results of the independent contrasts show that phylogeny has a significant effect on morphology. Even so, this does not mean that these indices

TABLE 11. Least squares regression slope comparison between canids and felids

Variable	a		b		r^2		SE_b	ANCOVA F	ANCOVA P
	Canidae	Felidae	Canidae	Felidae	Canidae	Felidae			
HL	0.993	0.982	0.846	0.816	0.905	0.976	0.034	0.513	0.478
HD[a]	−0.419	−0.424	0.975	0.995	0.960	0.997	0.030	12.68	0.001
HPAP[a]	0.088	0.019	0.985	1.027	0.973	0.995	0.030	4.268	0.044
HEB[a]	0.021	0.002	0.972	1.015	0.955	0.992	0.033	27.79	0.000
HDAP[a]	−0.250	−0.404	1.076	1.132	0.976	0.997	0.048	165.82	0.000
HDAB[a]	−0.181	−0.166	0.985	1.016	0.964	0.993	0.035	73.19	0.000
ULO	−0.125	−0.183	1.025	1.058	0.968	0.986	0.021	1.961	0.168
RL	0.947	1.146	0.981	0.795	0.890	0.933	0.040	1.616	0.210
RD[a]	−0.339	−0.377	1.102	1.106	0.976	0.985	0.025	16.25	0.000
RPML[a]	−0.030	−0.098	0.974	1.007	0.985	0.993	0.018	31.78	0.000
RPAP	−0.276	−0.269	1.031	1.024	0.982	0.995	0.014	0.750	0.786
RDML[a]	0.044	0.039	1.018	1.041	0.994	0.995	0.013	24.31	0.000
RDAP[a]	−0.166	−0.174	0.993	1.032	0.979	0.993	0.021	38.98	0.000
RMLA	−0.039	−0.096	1.001	1.040	0.989	0.993	0.014	3.956	0.064
RAPA[a]	−0.144	−0.159	0.904	0.956	0.958	0.992	0.025	39.27	0.000
M3L[a]	0.798	0.815	0.974	0.868	0.895	0.958	0.046	40.004	0.000
M3D[a]	−0.315	−0.417	1.023	1.087	0.968	0.997	0.022	43.18	0.000
M3PML[a]	−0.124	−0.051	0.963	0.995	0.970	0.975	0.046	131.46	0.000
M3PAP	−0.136	−0.077	1.093	1.017	0.990	0.976	0.022	2.495	0.121
M3DML[a]	−0.078	−0.107	0.932	1.010	0.975	0.992	0.023	48.42	0.000
M3DAP	−0.143	−0.149	1.017	1.017	0.997	0.997	0.009	2.774	0.103

[a]Denotes a significant difference between the slopes of canids and felids.
Regression equations were calculated in the form log y = log a + b log x, where x = log GM score, y = log raw measurement, a = y intercept, b = slope, r^2 = correlation coefficient, SE_b = standard error of the slope. SE is for the pooled variance. All other values are for individual regressions for each family.

do not have functional relevance. Phylogenetically correlated traits may have arisen first in one ancestral member of each lineage and were then subsequently retained in future species; however, retained functional traits may have allowed these individuals to excel at catching and killing large prey. For that reason, each ratio found to be significant in discriminating different prey types by the MANOVA, PCA, and DFA will be discussed in a functional context. Although these indices are linked to certain functional traits, they are also influenced by phylogeny, and the importance of both should be recognized.

Allometry

When a least squares regression was performed, the slopes of felid and canid forelimbs differed significantly (Table 11). The slopes for canids were significantly greater than those of felids for metacarpal length (M3L). Felid slopes were significantly greater for measures of limb robustness (see Fig. 5), size of muscle attachments, and articular areas, indicating greater limb robustness, larger relative muscle attachments, and larger articular areas. Thus, relative to canids, felids show the expected augmentation of positive allometry in their forelimbs that reflects their dual function in both body support and prey grappling.

In contrast, the results of the RMA regression (Table 12) show that canids and felids do not have significantly different slopes, with the exception of radius length (RL) and the anteroposterior depth

of the third metacarpal (M3PAP). Still, the pattern remains the same with felids having shorter lengths and wider diameters, showing an overall trend of robusticity. However, when slopes were
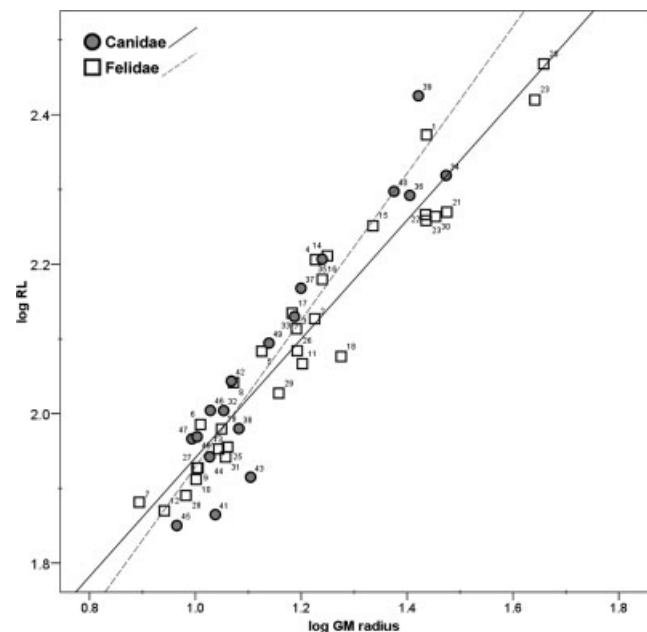

Fig. 5. Linear regression of log radius length versus log GM of the radius for Felidae and Canidae to demonstrate the differences in slope between the two families. Refer to Table 10 for correlation coefficients and slopes. Refer to Tables 1 and 4 for species keys.

TABLE 12. Reduced major axis regression (RMA) comparing slopes and interspecific allometry of canids and felids

Variable	Family	a	b	r^2	$F_{\text{allometry}}$	$P_{\text{allometry}}$	Isometry $b = 1$	F_{slope}	p_{slope}
HL	Canidae	0.869	0.892	0.906	2.219	0.156	$b = 1$	0.822	0.338
	Felidae	0.966	0.826	0.975	42.83	0	$b < 1$		
HD	Canidae	−0.451	0.997	0.959	0.002	0.963	$b = 1$	0.009	0.930
	Felidae	−0.421	0.992	0.997	0.465	0.501	$b = 1$		
HPAP[a]	Canidae	0.083	0.987	0.975	0.095	0.762	$b = 1$	0.840	0.370
	Felidae	0.017	1.027	0.995	4.214	0.049	$b > 1$		
HEB	Canidae	−0.009	0.992	0.951	0.018	0.894	$b = 1$	0.239	0.626
	Felidae	−0.008	1.021	0.991	1.515	0.228	$b = 1$		
HDAP	Canidae	−0.266	1.088	0.976	4.636	0.047	$b > 1$	0.910	0.346
	Felidae	−0.405	1.131	0.997	151.920	0	$b > 1$		
HDAB	Canidae	−0.202	1.000	0.964	0	0.997	$b = 1$	0.065	0.797
	Felidae	−0.161	1.013	0.993	0.707	0.407	$b = 1$		
ULO	Canidae	−0.146	1.040	0.966	0.717	0.410	$b = 1$	0.174	0.680
	Felidae	−0.189	1.063	0.986	7.541	0.010	$b > 1$		
RL	Canidae	0.870	1.047	0.891	0.317	0.581	$b = 1$	5.628	0.026
	Felidae	1.113	0.822	0.935	17.168	0	$b < 1$		
RD	Canidae	−0.356	1.118	0.974	7.796	0.013	$b > 1$	0.002	0.971
	Felidae	−0.394	1.121	0.985	25.070	0	$b > 1$		
RPML	Canidae	−0.041	0.984	0.984	0.250	0.624	$b = 1$	0.354	0.553
	Felidae	−0.097	1.005	0.992	0.123	0.728	$b = 1$		
RPAP[a]	Canidae	−0.291	1.044	0.983	0.081	0.779	$b = 1$	0.201	0.648
	Felidae	−0.271	1.027	0.994	4.618	0.040	$b > 1$		
RDML	Canidae	0.041	1.021	0.994	1.22	0.286	$b = 1$	1.292	0.256
	Felidae	0.030	1.048	0.996	14.290	0.001	$b > 1$		
RDAP[a]	Canidae	−0.186	1.011	0.977	0.081	0.779	$b = 1$	0.329	0.552
	Felidae	−0.178	1.036	0.992	4.618	0.040	$b > 1$		
RMLA	Canidae	−0.048	1.008	0.987	0.073	0.791	$b = 1$	1.131	0.279
	Felidae	−0.098	1.044	0.993	7.623	0.010	$b > 1$		
RAPA	Canidae	−0.164	0.921	0.955	2.376	0.143	$b = 1$	0.467	0.508
	Felidae	−0.161	0.958	0.991	5.799	0.023	$b < 1$		
M3L	Canidae	0.741	1.034	0.895	0.176	0.681	$b = 1$	2.684	0.101
	Felidae	0.794	0.887	0.958	9.819	0.004	$b < 1$		
M3D	Canidae	−0.330	1.039	0.966	0.690	0.419	$b = 1$	1.017	0.296
	Felidae	−0.419	1.091	0.997	73.146	0	$b > 1$		
M3PML	Canidae	−0.139	0.978	0.970	0.248	0.625	$b = 1$	0.304	0.605
	Felidae	−0.062	1.007	0.975	0.069	0.795	$b = 1$		
M3PAP	Canidae	−0.145	1.103	0.989	14.562	0.002	$b > 1$	3.445	0.052
	Felidae	−0.085	1.025	0.976	0.747	0.394	$b = 1$		
M3DML	Canidae	−0.087	0.942	0.975	2.266	0.152	$b = 1$	2.415	0.115
	Felidae	−0.107	1.009	0.993	0.375	0.545	$b = 1$		
M3DAP	Canidae	−0.141	1.017	0.997	1.442	0.247	$b = 1$	0.077	0.780
	Felidae	−0.153	1.022	0.996	3.375	0.076	$b = 1$		

Where x = log GM score, y = log raw measurement, a = y intercept, b = slope, r^2 = correlation coefficient, F_{slope} = F-value for the comparison of canid and felid slopes, p_{slope} = P-value for canid and felid slope comparison, a value of 0.05 or less indicates slopes are significantly different between families. $F_{\text{allometry}}$ = F-value for interspecific allometry for each family separately, $p_{\text{allometry}}$ = P-value for interspecific allometry, a value of 0.05 or less indicates the slope is significantly different from isometry ($b = 1$). Variables in bold are significantly different from isometry in felids.
[a]Indicates that this value was no longer significantly different from isometry in felids when lions and tigers were excluded.

tested for isometry ($b = 1$), felids differed significantly from isometry for 13 out of 21 variables examined. Humerus, radius and third metacarpal lengths (HL, RL, M3L), and anteroposterior depth of the distal radius articulation (RAPA) were all negatively allometric ($b < 1$). Humerus proximal and distal anteroposterior depths (HPAP, HDAP), olecranon length of the ulna (ULO), radius and third metacarpal diameters (RD, M3D), anteroposterior breadth of the proximal end of the radius (RPAP), anteroposterior and mediolateral widths of the distal end of the radius (RDAP, RDML), and the mediolateral breadth of the distal articular surface of the radius (RMLA) were all positively allometric ($b > 1$). Because lions and tigers are sig-

nificantly larger than any canid species used in this analysis, a second analysis was performed with those two species removed. The results of this secondary analysis found the variables HPAP, RPAP, and RDAP to be nonsignificant from isometry. The remaining 10 previously discussed variables remained significantly different from isometry in the Felidae.

Canid slopes were only significantly different from isometry for two out of 21 variables examined. They were positively allometric for radius diameter (RD) and anteroposterior proximal depth of the third metacarpal (M3PAP). Although the RMA results show that canid and felid slopes may not be significantly different from one another, canids

show significantly more isometric scaling in their forelimbs than felids do.

DISCUSSION

On the basis of the measurements we used, prey-size preference influences felid forelimb morphology more than locomotor mode does. This analysis also shows important differences in scaling between canids and felids that most likely relate to prey-killing behaviors. Cats that kill large prey will generally stalk their prey and run a short distance to attack, employing the use of their forelimbs and claws to initially subdue prey (Ewer, 1973). Their forelimbs must be able to withstand the forces of struggling prey while they position the killing bite. The MANOVA, PCA, and DFA all confirm that large prey specialists have more robust limbs that are suited to withstand these extra forces placed upon them during prey-killing of large animals. Because the goal of this study was to examine differences between prey size groups and classify them according to this criterion, the discussion will focus on results of the MANOVA and the DFA as they highlight the differences between the groups.

Prey Size Categories

The results of this study suggest that large prey specialists have relatively robust forelimbs when compared with smaller prey specialists. Both the humerus (HRI) and radius (RRI) diaphyses were found to be consistently robust. This increased robusticity functions to protect against bending and torsion when under increased stress (Ruff and Hayes, 1983; Lanyon and Rubin, 1985), such as that encountered when grappling with large prey. The increased robustness in the humeri and radii of large prey specialists may also translate into a proportionally thicker cortical area of the humerus diaphysis, a possibility that will be explored in a future study.

The humeral epicondylar index (HEI) was larger in large prey specialists. The humeral epicondyles serve as the origin for many muscles that stabilize the wrist during prey capture, such as: *m. pronator teres*, *m. extensor carpi radialis*, *m. extensor carpi ulnaris*, *m. flexor carpi radialis*, and *m. flexor carpi ulnaris* (Hebel and Stromberg, 1976; Schaller, 1992). The humeral epicondyles are also the point of origin of many of the digital flexor and extensor muscles that facilitate grasping of large prey during capture, such as: *m. extensor digitorum communis*, *m. extensor digitorum lateralis*, *m. flexor digitorum superficialis*, *m. palmaris longus*, and *m. flexor digitorum profundus*, in part (Hebel and Stromberg, 1976; Schaller, 1992). These larger epicondyles allow for larger originations and thereby larger muscles. The distal articulation of the humerus (HCI) is also relatively larger in large prey specialists. Andersson (2004) also found increased distal articular area of the humerus in forelimb grappling carnivorans. This portion of the humerus articulates with the ulna and is responsible for unilateral extension of the forearm and also pronation and supination of the antebrachium. A larger articular area would provide more stability for antebrachial extension and non-parasagittal movements (Gonyea and Ashworth, 1975; Gonyea, 1978; Andersson, 2004), a wider range of motion for forearm positioning and prey grappling and also an increased ability to better distribute large loads (Ruff, 1988).

As found by Iwaniuk et al. (1999), the olecranon process of the ulna was relatively larger (OI) in large prey specialists. The triceps muscles insert on the olecranon process and are used primarily in arm extension. Increased size of these muscles would proffer a greater ability to push prey to the ground and hold them down while they position themselves for a killing bite. In addition, large prey specialists have proportionally large proximal paw widths (PAW). The width of the proximal paws facilitates a stronger, more stable grip on large prey animals during the initial attack, as it would in gripping substrate (Watkins, 2003) or while climbing (Cartmill, 1985), and allows the force to be distributed more evenly across the entire paw. As well as increasing the surface area, the proximal metacarpals are the insertion for wrist extensor, *m. extensor carpi ulnaris* and wrist flexor, *m. flexor carpi radialis*, and also the insertion for the *m. adductor digiti primi* which adducts the first digit and facilitates grasping with the dewclaw (Hebel and Stromberg, 1976; Schaller, 1992).

Small prey specialists do not meet with as much resistance while catching prey. However, their prey is fast and requires speed to catch (Ewer, 1973). The cats that kill small prey have relatively gracile limbs that have a high brachial index (BI), that is, they are relatively distally elongated. Small prey specialists also have elongated phalanges relative to metacarpals (MCP), which again shows distal elongation. Distal elongation likely provides a velocity advantage for catching small, elusive prey. Mixed prey feeders were found to have relatively robust metacarpals that were not found in large prey specialists. These robust metacarpals may be an adaptation for smaller sized cats to grapple with and hold on to the larger prey that they catch, without sacrificing the velocity advantage needed to catch smaller prey.

Locomotor Categories

Although few variables separated scansorial and terrestrial felids, arboreal cats differed significantly from both of the other groups in having

more robust and shorter radii, and a greater proximal phalanx to metacarpal ratio. With regards to brachial index (BI), Iwaniuk et al. (1999) and Gonyea (1976a) also found similar results. Arboreal felids have shorter radii relative to humeri, and therefore a smaller brachial index (BI) because shortened distal limbs increase the mechanical advantage of forelimb flexors and extensors, allowing arboreal species to climb more effectively. Shorter limbs also lower the center of gravity for arboreal cats favoring the ability to balance on high, narrow tree branches (Cartmill, 1985). A large proximal phalanx to metacarpal ratio (MCP) in arboreal carnivores is consistent with the findings of Van Valkenburgh (1987). Long phalanges offer increased surface area for grasping and climbing in the trees (Hildebrand, 1974; Van Valkenburgh, 1987).

Proximal paw width (PAW) and the distal articular area of the third metacarpal (MC3RAA) differed significantly among prey size and locomotor groups. Both of these variables would confer an advantage while climbing. As in large prey specialists, a wider paw would increase the surface area of the manus while climbing and increase frictional resistance (Cartmill, 1985). Greater distal articular area of the metacarpals would increase the range of motion in the digits to assure a better grip while climbing on thinner branches (Ruff, 1988).

As most cats are proficient climbers, many of the beneficial adaptations for climbing are also beneficial for large prey grappling, such as increased humeral robusticity, and wider distal articulations and epicondyles. Only one living felid, the cursorial cheetah (*Acinonyx jubatus*), has largely lost the ability to grapple prey with its forelimbs and instead has evolved a secondary mode of prey capture that involves a specialized dew claw that trips prey to bring it down before suffocation (Londei, 2000; Russell and Bryant, 2001). This likely explains why the cheetah does not group with the other large prey specialists in the PCA; however, it does fall out as a large prey specialist in the DFA, which suggests that it still retains some characters that are important in prey grappling despite its cursorial adaptations.

Allometry

Felid limb bone lengths displayed significant negative allometry, but the diameters and the ends of the limb bones showed a trend toward positive allometry (Table 12), and this same trend was found in the prey-killing apparatus of felid skulls (canine and muzzle robustness) (Meachen-Samuels and Van Valkenburgh, in press). This suggests that as felids become larger, their forelimb lengths become relatively shorter; and as a consequence, forelimb robustness becomes greater. This func-

tional shortening of the long bones proffers increased mechanical advantage in the forelimbs of large prey specialists (Hildebrand, 1985a).

This allometric trend also facilitates forelimb grappling and arboreal adaptations in larger felids, such as the clouded leopard (*N. nebulosa*) and possibly scansorial cats such as the jaguar (*Panthera onca*) and the leopard (*P. pardus*). The decreased length and increased thickening of the long bones gives increased mechanical advantage to felid forelimbs when climbing as well as prey grappling (Runestad, 1997), whereas the relatively longer and thinner forelimbs in the smaller felids confer a higher speed of the forelimbs to catch small, fast-moving prey.

Where felids displayed a trend toward shorter, more robust limbs; canids tend to have longer, more gracile limbs. Canids also show much more uniformity in the slopes of all of the forelimb measurements than do felids, with most slopes not significantly different from isometry ($b = 1$). An isometric trend in canid forelimbs was also found in Wayne's (1986) study in which the lengths of the radius, ulna, humerus, and metacarpals were not different from isometry, and neither were the widths of the humerus or metacarpals. In canids, the robusticity of the forelimbs increase to support body weight, but no more than is necessary for that purpose. Felids demonstrated positively allometric slopes ($b > 1$) for diaphyseal and epiphyseal widths, indicating relatively higher limb robustness, larger articular surfaces and larger areas for muscle attachment. This difference between canids and felids, two families that have similar levels of specific diversity (Bardeleben et al., 2005; Johnson et al., 2006) most likely reflects the duality of felid limbs for both locomotion and prey capture and the need to reinforce the forelimbs for the latter purpose.

Although canids and felids also have similar size distributions, with the exception of the much larger lion and tiger in the Felidae (Nowak, 1999; Sunquist and Sunquist, 2002), canid limbs do not scale allometrically. The marked negative allometry in felid limb-bone lengths and positive allometry in epiphyseal and diaphyseal widths, even with the exclusion of lions and tigers, suggests that this is not simply an ontogenetic process, but that it also has significant functional implications and is most likely a response to the added pressure of prey-killing stresses in large-prey cats. In skulls, positive allometry affects the ability of a group to take progressively larger prey (Emerson and Bramble, 1993). This may also be true of the forelimbs when they are used as prey-killing tools. Even if the same scaling processes that act on the skull do not act on the forelimbs, negative allometry in limb bone lengths and positive allometry in muscle attachment sites and articular areas helps to reinforce the forelimbs against the stresses encountered by large, struggling prey.

The next step is to apply this approach to extinct felids. Extinct conical-toothed cats should show similar patterns to extant cats in terms of both large prey specialization and arboreality, which could elucidate paleoecological predator-prey interactions. Our measurements may also be able to shed light on forelimb use in enigmatic saber-toothed cats. Previous studies (Gonyea, 1976b; Van Valkenburgh, 1987) have shown that saber-toothed cats have more robust forelimbs than conical-toothed cats, which may be an adaptation to fully immobilize prey with the forelimbs before administering a precisely directed killing bite, thus minimizing the risk of canine tooth fracture.

ACKNOWLEDGMENTS

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APPENDIX LIST OF FELID AND CANID MEASUREMENTS USED FOR THIS STUDY

TABLE A1. List of felid and canid specimens measured for this study

Species	Museum	Catalog number
Acinonyx jubatus	FMNH	29633, 127834, 34589, 34589
	LACM	52226, 72506
	MVZ	184066
	USNM	162928, 162929, 161922, 251793, 521037
Caracal aurata	FMNH	121528
	USNM	278523, 282637
Caracal caracal	FMNH	135042, 57220, 95922
	LACM	42383
	USNM	270130, 151671, 396160, 384162, 520686
Caracal serval	FMNH	127844, 18956, 95921, 18862, 127843, 95997
	LACM	90836
	USNM	521039, 163092, 548666, 258240,
Felis chaus	USNM	176049, 173375, 398570
Felis margarita	FMNH	159994, 159995, 127295, 186437, 127296, 60613, 180664
Felis nigripes	USNM	395838, 395519, 395135
Felis silvestris lybica	FMNH	127835
	LACM	41786, 56696
	USNM	261109, 327090, 450971, 241562, 296136
Leopardus colocolo	FMNH	104925, 52488
	USNM	172785, 540867
Leopardus geoffroyi	FMNH	134485, 121290, 129394
	USNM	396638, 574136, 297847
Leopardus pardalis	FMNH	68995, 93174, 125115
	LACM	90775
	MVZ	112248
	USNM	287774, 256918, 244859, 287773, 12182
Leopardus tigrinus	FMNH	70569, 70570, 94319, 70572, 70571
	USNM	395090, 395089
Leopardus wiedii	FMNH	94321, 121293, 52437, 126093, 70568
	LACM	53676
	MVZ	128841, 124326
	UCLA	10817

Species	Museum	Catalog number
Lynx canadensis	LACM	90776, 90777
	MVZ	9519, 184071
	UCLA	13097, 15351, 13093, 13089, 13098
Lynx lynx	USNM	84090, A01034
Lynx pardinus	USNM	152619
Lynx rufus	LACM	52220, 45023, 45024, 87628, 31665, 87422, 52218, 45026, 45022, 45027, 712, 52214, 52209, 52210, 52307
	MVZ	74569, 47138, 78414, 96800
Neofelis nebulosa	FMNH	104730, 183653, 54304, 186436
	USNM	399291, 198705, 399290, 396639, 545387, A49974
Otocolobus manul	FMNH	57629, 125386, 129496, 60691, 60733, 135737, 60734, 60612, 60611
	LACM	90728
Panthera leo	LACM	171
	LACMHC	1144
	MVZ	184076
	UCLA	2470
	USNM	161914, A12319, 163329, A22705, 172677, 163330, 162919, 162913
Panthera onca	UCLA	183
	USNM	155603, 141897/A49762, A12296/10390, A49393
Panthera pardus	LACM	648, 31068
	MVZ	184078
	USNM	161911, 172662, 013357/A16609, 155613, 156284, 254536, 258660, 164763
Panthera tigris	LACM	72165, 54239, 51573
	LACMHC	MJO8
	MVZ	184080
	USNM	174981, 251789, 269320, A49773, A49728, 258210
Panthera uncia	FMNH	127297, 153724, 101860, 187454, 153725, 160000, 122235, 60413
	MVZ	124189
	USNM	176048
Pardofelis marmorata	FMNH	60020, 68728, 104901, 129395, 60358
	USNM	325000, 239326
Pardofelis temminckii	FMNH	72804, 60584
	USNM	258552, 395758, 339645, 362188, 395843, 258694
Prionailurus bengalensis	FMNH	62885, 62886, 68726, 62888, 99363, 114386, 101977
	USNM	196601, 317283, 201070, 240006
Prionailurus planiceps	FMNH	129397, 58951, 129398, 127432, 127433, 147997, 60476
	USNM	395254, 360975, 145593, A49973
Prionailurus viverrinus	FMNH	129499, 123070, 60672, 168869
Puma concolor	LACM	52600, 85438, 85440, 70296, 87430, 31128, 54511
	MVZ	175990, 33560, 98310, 198447, 175989, 33559, 47199, 81547
	USNM	244857, 282623, A01385, 264166
Puma yagouroundi	MVZ	98311, 113296
	USNM	153531, 281396, A03838, 124336, 258328
Alopex lagopus	LACM	52188
Canis adustus	LACM	52230
Canis latrans	LACM	83, 22588, 30358, 31244, 31164, 52175, 52253, 52277, 52276, 52176, 51300
Canis lupus	UCLA	16404, 16403
Canis mesomelas	LACM	42382
Cerdocyon thous	LACM	56720
Chrysocyon brachyurus	LACM	52548, 52199, 31261, 90773, 90772
Lycaon pictus	LACM	30588, 60621
Nyctereutes procyonoides	LACM	74122, 90831
Otocyon megalotis	LACM	41793, 41791, 41790, 52239
Speothos venaticus	LACM	52187, 45007, 45008, 45006
Urocyon cinereoargenteus	UCLA	11256, 15808, 16312, 15958, 15408
Urocyon littoralis	LACM	74997, 74999
	UCLA	13394, 13452, 13841
Vulpes chama	LACM	58093, 41794, 41795
Vulpes macrotis	LACM	86865, 86868, 88320, 86866, 88321
Vulpes velox	LACM	86861, 86860, 86863, 86859, 86862
Vulpes vulpes	LACM	87624, 54274, 54170, 54171, 96263
Canis dirus	LACMHC	5762, 5800, 5785, 5749, 5769, 5742, 5782, 5741, 5766, 5790, 11222, 6881, 6897, 6885, 6894, 6898, 6867, 6875, 6924, 6938, 5655, 5644, 5673, 5728, 5671, 5663, 5668, 5651, 5666, 5670, 7194, 7198, 3669, 7065, 6996, 7228, 7044, 7056, 7437, 7429, 17311, 9710, 9719, 9734, 9735, 9695, 9725, 17288, 17310, 9688, 8656, 8732, 8646, 8700, 8738, 8649, 8722, 8691, 8710, 8718, 4255, 4279, 4298, 4301, 4300, 4244, 4277, 4280, 4307, 4252, 1448, 1511, 1518, 1453, 1517, 1507, 1510, 1461, 1525, 1458, 8194, 8219, 8181, 8222, 8244, 8267, 8184, 8195, 8251, 8189

Museum abbreviations include: FMNH, field museum of natural history; LACM, natural history museum of Los Angeles County; LACMHC, George C. page museum; MVZ, museum of vertebrate zoology, University of California, Berkeley; UCLA, UCLA Donald R. Dickey Collection; USNM, U.S. national museum of natural history.