Biological Journal of the Linnean Society, 2009, **96**, 784–799. With 4 figures

Craniodental indicators of prey size preference in the Felidae

JULIE MEACHEN-SAMUELS* and BLAIRE VAN VALKENBURGH

Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Charles E. Young Drive South, Los Angeles, CA 90095, USA

Received 21 June 2008; accepted for publication 18 August 2008

In the present study, we used linear morphometrics of the crania, mandible and dentition to explore the association between craniodental shape and prey size among 35 species of living felids. To accomplish this, felids were divided into three prey-size groups: (1) large prey specialists; (2) small prey specialists; and (3) mixed prey feeders. From these linear measurements, large prey specialist felids can be distinguished from small and mixed prey feeders by their relatively robust canines and incisors and relatively wide muzzles. These cranial characters are advantageous when dispatching large prey, due to the stranglehold that cats employ during this activity. Robust canines resist the bending and torsional forces applied by struggling prey and a wider muzzle helps to stabilize grip and distribute bite forces more evenly during the killing bite. Small prey specialists had smaller canines, narrower muzzles and slightly longer jaws for a speed advantage when catching small, quick prey. Mixed prey feeders were intermediate between large and small prey specialists, indicating they are adapted to killing both sizes of prey. Given the success of this ecomorphological analysis of living felids that specialize on different prey sizes, we look forward to applying this same approach to extinct species. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, **96**, 784–799.

ADDITIONAL KEYWORDS: crania – dentition – morphology.

INTRODUCTION

Subsequent to their first appearance in the fossil record approximately 30 Mya, felids have changed little (Turner & Antón, 1997). They have always been hypercarnivores, eating relatively little other than vertebrate prey, as reflected by loss of the crushing molars that would allow them to deviate from hypercarnivory. In addition to their reduced tooth rows, enlarged canine teeth, and short snouts, felids differ from most other carnivorans in having well-developed retractile claws that maintain their sharpness for use with flexible forelimbs to grasp and hold prey (Ewer, 1973; Gonyea & Ashworth, 1975; Bryant *et al.*, 1996). Of course, the most remarkable exceptions to the general similarity of form in felid crania are the saber-tooth morphs, of which there have been many over the past 20 Myr.

Interpretation of the behaviour and ecology of sabertooths as well as other extinct felids relies on understanding the relationship between skeletal morphology and function in living felids. Although there has been some work on the relationship between habitat and limb morphology in felids (Gonyea & Ashworth, 1975; Gonyea, 1978; Van Valkenburgh, 1987; Russell & Bryant, 2001; Andersson & Werdelin, 2003; Andersson, 2004), less attention has been paid to diet and craniodental morphology. This is because the diets of felids are largely invariant, differing only in prey size or type. However, the impact of taking large prey (prey that approaches or exceeds the predator's body mass) should be apparent in aspects of the skulls and teeth in felids. For example, canids and hyaenids that kill prey as large or larger than themselves have evolved relatively short snouts, deep jaws and enlarged anterior teeth (incisors and canines) (Van Valkenburgh & Koepfli, 1993; Van Valkenburgh, Sacco & Wang, 2003). Recent studies

*Corresponding author. E-mail: jmeachen@ucla.edu

by Carbone *et al.* (1999) and Carbone, Teacher & Rowcliffe (2007) suggest that there is a size threshold in extant carnivorans, in the range 15–25 kg, where they shift to taking prey 45% of their own size or larger in response to energetic demands. This behavioural transition is paralleled by changes in craniodental form within canids (Van Valkenburgh & Koepfli, 1993; Van Valkenburgh, Wang & Damuth, 2004) and the same may be true of felids. Felids should show craniodental modifications that reflect the higher stresses sustained when attacking large prey, although specific modifications may differ from those of canids and hyaenids due to differences in killing behaviour. Felids most often hunt alone and usually kill their prey with a single strangulating bite to the throat for large prey or a spinal cord severing bite to the dorsal neck for small prey (Leyhausen, 1979). Large prey specialist cats hold onto their prey with their jaws for an extended period of time in order to kill it (Ewer, 1973) and are therefore expected to show adaptations for producing high bite forces, such as relatively shorter rostra, greater biomechanical advantage of jaw adductor muscles, and deeper and wider dentaries. In the present study, we used morphometrics to explore the association between craniodental shape and prey size among 35 species of living felids.

Based on the fossil record, we consider small prey as the basal condition for felids, and large prey specialization as a derived condition. Despite the fact that small species are less likely to be preserved than large species (Jablonski, Gould & Raup, 1986), the earliest known felid from the Eocene/Oligocene boundary [*Proailurus* (Filhol, 1879)], was approximately the size of a bobcat (Peigné, 1999) and probably specialized on small prey. Nevertheless, two recent studies of extant felid relationships, one morphological (Mattern & McLennan, 2000) and one molecular (Johnson *et al.*, 2006), find the large cat Pantherine lineage to be basal with small cat lineages originating more recently. Because these studies are based entirely on living felids, they do not contradict the fossil record of origination at small size; rather, they indicate only that the modern small cats represent a more recent radiation instead of the retained primitive condition.

MATERIAL AND METHODS

A total of 338 individuals were measured from 35 species in the Family Felidae (average of nine individuals per species; Table 1; see also Supporting information, Appendix S1). A total of 44 cranial, dental and mandibular measurements were taken following the methods of Van Valkenburgh & Koepfli (1993) using digital calipers to the nearest 0.01 mm (Fig. 1; Table 2). These measurements were chosen because they have been previously shown to accurately reflect functional properties of the skull and mandibles in carnivores (Van Valkenburgh & Koepfli, 1993; Friscia, Van Valkenburgh & Biknevicius, 2007). For ease of discussion, the 44 measurements are divided into four categories: skull, anterior dentition, cheek teeth, and dentary (Table 2). An average mass for each species was scored from the literature (Sunquist & Sunquist, 2002; Nowak, 2005). Because sexual dimorphism is pronounced in many felids (Gittleman & Van Valkenburgh, 1997), this was taken into consideration when performing each analysis by using equal numbers of males and females, whenever possible, and using average species masses and prey sizes. Juvenile individuals were excluded from the study. Wild-caught specimens were preferentially measured; however, skulls from a few zoo animals were used for those species where wild-caught specimens were rare in museum collections. Zoo animals were included in the study only after an analysis of variance (ANOVA) was performed comparing zoo to wild animals of the same species, and only individuals whose measurements were not significantly different from wild ($\alpha = 0.05$) were included in further analyses. The data set includes specimens from the following museums: Natural History Museum of Los Angeles County (LACM); University of California, Los Angeles, Donald R. Dickey Collection (UCLA); Museum of Vertebrate Zoology at the University of California, Berkeley (MVZ); Field Museum of Natural History (FMNH); and National Museum of Natural History (USNM) (see Supporting information, Appendix S1).

Size difference tends to be more pronounced than shape between large and small felids and can thus mask shape differences. To reduce effects of size, Mosimann shape variables were calculated through geometric mean transformation of data prior to statistical analyses (Mosimann & James, 1979). The geometric mean (GM) is a size variable derived from the N_{th} root of the product of N measurements, and the ratio of any particular measurement to the overall geometric mean is a Mosimann shape variable. In addition to reducing the effects of size, the GM is an excellent predictor of individual body mass, more so than the average species mass. Because most of the specimens measured did not have associated body mass data, GMs were used in regressions of scaling relationships instead of body mass. Because GM is the N_{th} root of N measurements, it is the equivalent of a linear dimension and therefore when it is regressed against another linear measurement, a slope not significantly different from one indicates geometric similarity (isometry). To assess possible interspecific allometric scaling of each variable, log-transformed measurements were regressed against log GM score

Table 1. Felid species used in analyses, their preferred prey sizes (small, large, and mixed) and cat mass ranges

Sp. No.	Species	Common name	*N*	Prey size	Cat mass range (kg)	Cat lineage
1	*Acinonyx jubatus*	Cheetah	11	Large	40–65	Puma
2	*Caracal aurata*	African golden cat	3	Mixed	5–16	Caracal
3	*Caracal caracal*	Caracal	9	Mixed	7–20	Caracal
4	*Caracal serval*	Serval	9	Small	8–18	Caracal
5	*Felis chaus*	Jungle cat	10	Small	2–13	Domestic
6	*Felis margarita*	Sand cat	4	Small	1–4	Domestic
7	*Felis nigripes*	Black-footed cat	4	Small	1–3	Domestic
8	*Felis silvestris lybica*	African wildcat	10	Small	3–6	Domestic
9	*Leopardus colocolo*	Pampas cat	10	Small	2–4	Ocelot
10	*Leopardus geoffroyi*	Geoffroy's cat	10	Small	2–8	Ocelot
11	*Leopardus guigna*	Kodkod	2	Small	1–3	Ocelot
12	*Leopardus jacobita*	Andean mountain cat	1	Small	4–8	Ocelot
13	*Leopardus pardalis*	Ocelot	9	Mixed	6–16	Ocelot
14	*Leopardus tigrinus*	Tigrina or oncilla	8	Small	2–4	Ocelot
15	*Leopardus wiedii*	Margay	10	Small	2–4	Ocelot
16	*Lynx canadensis*	Canadian lynx	9	Mixed	5–17	Lynx
17	*Lynx lynx*	Eurasian lynx	4	Large	11–30	Lynx
18	*Lynx pardinus*	Iberian lynx	2	Small	7–16	Lynx
19	*Lynx rufus*	Bobcat	14	Mixed	4–16	Lynx
20	*Neofelis nebulosa*	Clouded leopard	10	Mixed	11–25	Panthera
21	*Otocolobus manul*	Manul or Pallas's cat	10	Small	2–5	Leopard Cat
22	*Panthera leo*	Lion	11	Large	110–250	Panthera
23	*Panthera onca*	Jaguar	11	Large	36–120	Panthera
24	*Panthera pardus*	Leopard	11	Large	28–65	Panthera
25	*Panthera tigris*	Tiger	14	Large	75–325*	Panthera
26	*Panthera uncia*	Snow leopard	10	Large	22–52	Panthera
27	*Pardofelis badia*	Bay cat	2	Small	2–4	Bay Cat
28	*Pardofelis marmorata*	Marbled cat	8	Small	2–4	Bay Cat
29	*Pardofelis temminckii*	Asian golden cat	9	Mixed	8–16	Bay Cat
30	*Prionailurus bengalensis*	Leopard cat	10	Small	2–9	Leopard Cat
31	*Prionailurus planiceps*	Flat-headed cat	13	Small	1–3	Leopard Cat
32	*Prionailurus rubiginosa*	Rusty spotted cat	5	Small	0.5–2	Leopard Cat
33	*Prionailurus viverrinus*	Fishing cat	9	Small	5–16	Leopard Cat
34	*Puma concolor*	Puma or Mountain lion	55	Large	23–80	Puma
35	*Puma yaguarondi*	Jaguarundi	10	Small	3–7	Puma

*The present study includes primarily southern Asian tigers; the size range given includes all tiger subspecies. Mass ranges from Sunquist & Sunquist (2002) and Nowak (1999). Species names and cat lineages *sensu* Johnson *et al.* (2006).

in a least squares regression, with equations in the form of: $\log y = \log a + b \log x$ (where $x = \log \mathrm{GM}$, y = measurement, a = y-intercept, and b = slope). 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 & Tolley, 1997). The null hypothesis of $b = 1$ was tested with a t-test in the form of: $t_s = b - 1/\mathrm{SE_b}$ (where b = slope, $\mathrm{SE_b}$ = standard error of the slope, d.f. = $N - 2$, and $\alpha = 0.05$) (Zar, 1996).

Typical prey species (Young & Goldman, 1946; Schaller, 1972; Ewer, 1973; Leyhausen, 1979; Kitchener, 1991; Sunquist & Sunquist, 2002; Hunter, 2005) and prey masses (Nowak, 1999) were compiled from several sources for each cat species. Relative prey size preference, and not cat size, was assessed in the present study because the two are correlated but do not wholly overlap. All cats over 25 kg kill large prey, and all cats under 15 kg kill small prey; however, within the size range 15–25 kg, cats may kill only small prey, only large prey, or a mixture of both, to varying degrees, and prey size is not only determined by cat size. Three relative prey size categories for the analysis were based on Carbone *et al.* (2007) and compiled for the present study from the literature:

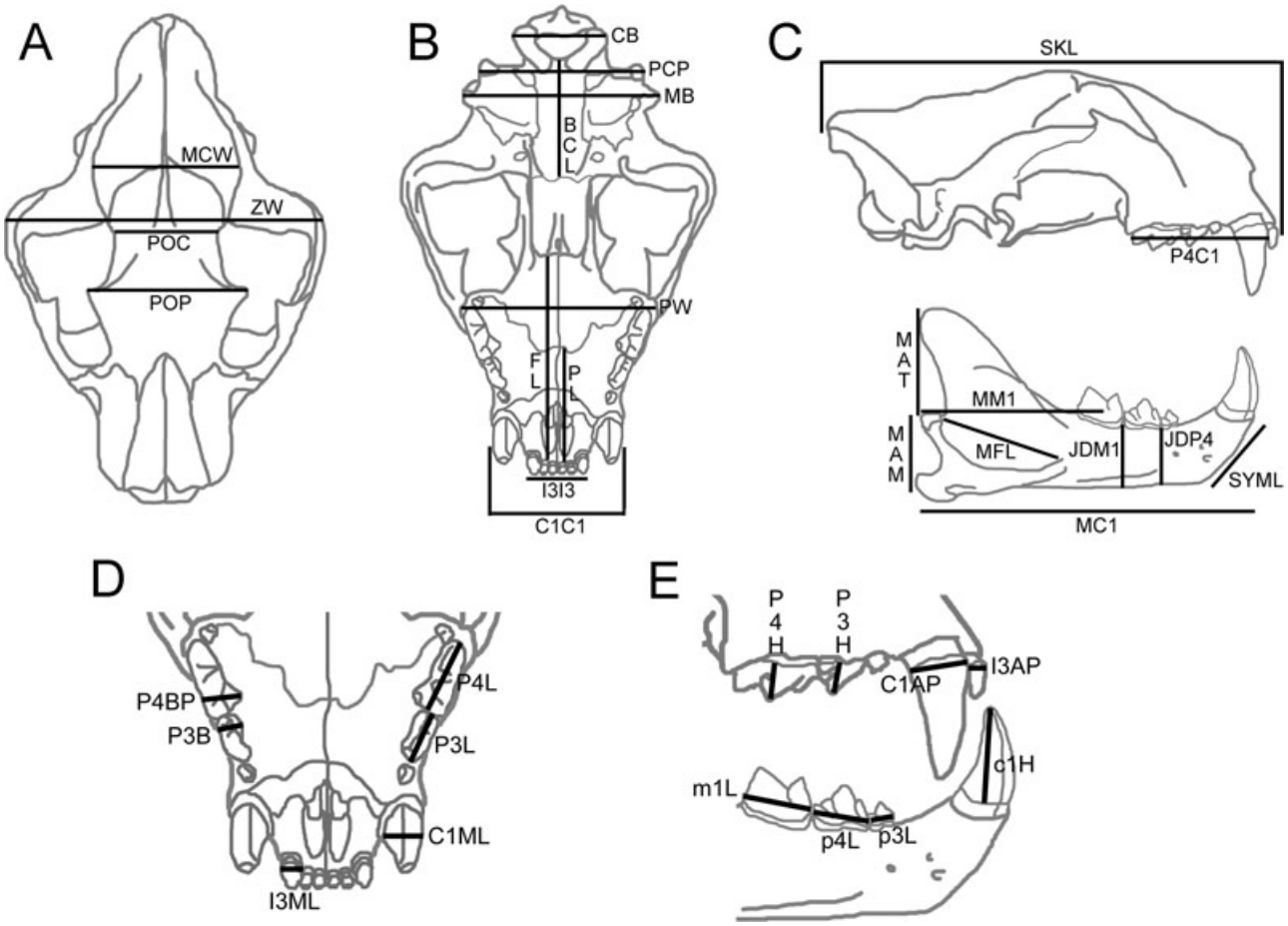

Figure 1. Cranial, mandibular and dental measurements (*sensu* Van Valkenburgh & Koepfli, 1993) shown on a line drawing of a lion skull; A, dorsal view of skull; B, ventral view of skull; C, lateral view of skull and right mandible; D, enlarged ventral view of palate showing dental measurements; E, lateral view of skull and mandible with the dentition enlarged to illustrate measurements. For abbreviations, see Table 2.

cats that predominantly kill prey smaller than themselves (small prey); cats that predominantly kill prey their own size or larger (large prey); and cats that readily kill both sizes of prey depending on what prey is preferred, available, or convenient (mixed prey).

Data were analysed using multivariate analysis of variance (MANOVA) using Scheffe's F and Tamhane's $T2$ procedures for post-hoc comparisons, principal component analysis (PCA) and discriminant function analysis (DFA). MANOVA tested for significant differences in morphology between prey size categories. PCA was used to explore and visualize shape variations. Stepwise discriminant function analysis was performed to identify variables that discriminate among cats that take different prey sizes. All statistical analyses were performed using SPSS, version 13.0 (SPPS Inc.).

The effect of phylogeny was explored with independent contrasts (Felsenstein, 1985) and a recent molecular phylogeny of the Felidae (Johnson *et al.*, 2006). The log of the GM transformed variables and log mean prey sizes were compared using the PDAP module in Mesquite, version 2.5; (Maddison & Maddison, 2006). Contrasts were regressed against log mean prey size through the origin using linear regression to determine whether phylogeny had a significant effect on any of the transformed variables used. Notably, each of the prey size categories included members of at least three of the eight felid clades defined by the Johnson *et al.* (2006) tree, revealing multiple instances of shifts in prey choice. The small prey category encompassed seven lineages, the mixed prey included five, and the large prey category included three (Table 1).

RESULTS

MANOVA

The mean ± SD of each GM transformed variable were calculated for each prey size category (Table 3).

Table 2. Cranial, mandibular, and dental measurements (*sensu* Van Valkenburgh & Koepfli, 1993)

Cranial categories	Abbreviation	Measurement
Skull	SKL	Maximum skull length: most anterior margin to posterior most point of sagittal crest
	BCL	Length of basioccipital and basisphenoid
	FL	Midsagittal hard palate length
	PL	Midsagittal premaxilla and maxilla length along palate
	PW	Palatal width measured posterior to the P4
	ZW	Maximum width of the zygomatic arches
	POP	Maximum skull width at post-orbital process
	POC	Minimum skull width at post-orbital constriction
	MCW	Maximum braincase width
	PCP	Maximum width of the paracondylar processes
	CB	Maximum occipital condylar breadth
	MB	Maximum width of the mastoid processes
Anterior dentition	I3I3	Width across the lateral margins of upper incisors
	I3AP	Anteroposterior width of I3 at the enamel/dentine junction
	I3ML	Mediolateral width of I3 at the enamel/dentine junction
	C1C1	Width across lateral margins of upper canines
	C1AP	Anteroposterior diameter of upper canine at the enamel dentine junction
	C1ML	Mediolateral diameter of upper canine at the enamel/dentine junction
Cheek teeth	P3H	Height of enamel of P3
	P3L	Anteroposterior length of P3
	P4BP	Mediolateral width across the protocone of P4
	P4L	Anteroposterior length of P4
	P4C1	Posterior P4 to anterior C1
	c1H	Height of enamel of c1
	c1AP	Anteroposterior diameter of c1
	c1ML	Mediolateral diameter of c1
	p3H	Height of enamel of p3
	p3L	Anteroposterior length of p3
	p3B	Mediolateral width of p3
	p4H	Height of enamel of p4
	p4L	Anteroposterior length of p4
	p4B	Mediolateral width of p4
	m1L	Anteroposterior length of m1
	m1B	Mediolateral width of m1
Dentary	MAT	Length from glenoid to coronoid process apex: Moment arm of temporalis
	MAM	Glenoid to angle of the dentary: Moment arm of the masseter
	MFL	Maximum masseteric fossa length
	MM1	Moment arm of resistance at carnassial (m1)
	MC1	Moment arm of resistance at canines (full length of jaw from the condyloid process to the canine)
	JDM1	Jaw depth at p4/m1 junction
	JBM1	Jaw mediolateral width at p4/m1 junction
	JDP4	Jaw depth at p3/p4 junction
	JBP4	Jaw mediolateral width at p3/p4 junction
	SYML	Maximum symphysis length at anteroventral margin

Measurements illustrated in Fig 1.

The MANOVA found all three groups to be significantly different ($P < 0.001$). Differences for individual indices were assessed by univariate ANOVAs with Scheffe's F and Tamhane's $T2$ procedures for post-hoc comparisons. All three prey size categories were mutually distinct for 20 of 44 characters. Skull variables included: FL, PL, ZW, POP, POC, MCW, and CB. Anterior dentition variables included: I3I3, I3AP,

Table 3. Mean values and standard deviations (SD) of geometric mean transformed measurements for each prey size category

Variable	Small prey mean (N = 20, 145)	Small prey SD	Mixed prey mean (N = 8, 69)	Mixed prey SD	Large prey mean (N = 8, 123)	Large prey SD
SKL	2.772^{L}	0.163	2.793	0.231	2.839^{S}	0.176
BCL	0.923	0.166	0.922	0.134	0.918	0.173
FL	$1.042^{M,L}$	0.073	$1.097^{S,L}$	0.088	$1.188^{S,M}$	0.102
PL	$0.593^{M,L}$	0.052	$0.661^{S,L}$	0.102	$0.735^{S,M}$	0.059
PW	$1.063^{M,L}$	0.054	1.094^{S}	0.101	1.110^{S}	0.045
ZW	$1.897^{M,L}$	0.099	$1.941^{S,L}$	0.070	$1.990^{S,M}$	0.089
POP	$1.349^{M,L}$	0.149	$1.167^{S,L}$	0.177	$1.040^{S,M}$	0.126
POC	$0.864^{M,L}$	0.130	$0.757^{S,L}$	0.123	$0.652^{S,M}$	0.104
MCW	$1.254^{M,L}$	0.074	$1.159^{S,L}$	0.067	$1.043^{S,M}$	0.080
PCP	0.889^{L}	0.047	0.885^{L}	0.049	$0.918^{S,M}$	0.055
CB	$0.672^{M,L}$	0.037	$0.655^{S,L}$	0.034	$0.586^{S,M}$	0.034
MB	1.208	0.077	1.201	0.039	1.203	0.046
I3I3	$0.298^{M,L}$	0.027	$0.314^{S,L}$	0.025	$0.356^{S,M}$	0.034
I3AP	$0.074^{M,L}$	0.010	$0.087^{S,L}$	0.012	$0.099^{S,M}$	0.013
I3ML	$0.063^{M,L}$	0.010	$0.072^{S,L}$	0.012	$0.081^{S,M}$	0.010
C1C1	$0.646^{M,L}$	0.037	$0.685^{S,L}$	0.037	$0.768^{S,M}$	0.043
C1AP	$0.147^{M,L}$	0.017	$0.164^{S,L}$	0.024	$0.198^{S,M}$	0.023
C1ML	$0.113^{M,L}$	0.012	$0.132^{S,L}$	0.016	$0.158^{S,M}$	0.015
P3H	0.145	0.016	0.146	0.011	0.141	0.016
P3L	$0.205^{M,L}$	0.016	$0.213^{S,L}$	0.017	$0.224^{S,M}$	0.014
P4BP	$0.150^{M,L}$	0.019	0.162^{S}	0.014	0.165^{S}	0.017
P4L	0.328^{M}	0.021	0.337^{S}	0.025	0.333	0.023
P4C1	$0.852^{M,L}$	0.050	0.880^{S}	0.079	0.893^{S}	0.044
c1H	1.262^{M}	0.135	1.332^{S}	0.199	1.306	0.177
c1AP	$0.592^{M,L}$	0.050	$0.622^{S,L}$	0.061	$0.684^{S,M}$	0.066
c1ML	$0.450^{M,L}$	0.033	$0.469^{S,L}$	0.036	$0.513^{S,M}$	0.044
p3H	$0.529^{M,L}$	0.061	$0.476^{S,L}$	0.071	$0.421^{S,M}$	0.074
p3L	$0.706^{M,L}$	0.052	0.653^{S}	0.059	0.664^{S}	0.069
p3B	0.344	0.022	0.346	0.028	0.343	0.038
p4H	0.619^{L}	0.060	0.601^{L}	0.056	$0.576^{S,M}$	0.052
p4L	$0.920^{M,L}$	0.071	0.883^{S}	0.056	0.859^{S}	0.064
p4B	0.409^{L}	0.031	0.416	0.023	0.422^{S}	0.031
m1L	1.046^{L}	0.092	1.020^{L}	0.073	$0.941^{S,M}$	0.078
m1B	0.450	0.038	0.453	0.022	0.445	0.031
MAT	1.993^{L}	0.186	2.032	0.170	2.091^{S}	0.188
MAM	1.171	0.154	1.203	0.149	1.218	0.165
MFL	3.010^{L}	0.234	2.988	0.184	2.929^{S}	0.251
MM1	$3.924^{M,L}$	0.258	$3.741^{S,L}$	0.199	$3.651^{S,M}$	0.251
MC1	$7.278^{M,L}$	0.374	$7.054^{S,L}$	0.286	$6.802^{S,M}$	0.619
JDM1	$1.287^{M,L}$	0.082	1.345^{S}	0.076	1.330^{S}	0.080
JBM1	0.691	0.545	0.636	0.051	0.677	0.052
JDP4	$1.222^{M,L}$	0.079	1.291^{S}	0.082	1.283^{S}	0.094
JBP4	0.597^{L}	0.048	0.604^{L}	0.048	$0.639^{S,M}$	0.046
SYML	$1.847^{M,L}$	0.204	$1.974^{S,L}$	0.186	$2.108^{S,M}$	0.205

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

Table 4. Variable loadings, eigenvalues and percent variance explained for PC1 and PC2

Variable	PC1	PC2*	Variable	1	2*
C1AP	0.934	0.081	MFL	–0.141	–0.651
C1ML	0.917	0.104	MM1	–0.470	–0.636
MCW	–0.908	0.123	P3H	–0.230	0.586
C1C1	0.896	–0.011	p4B	0.160	0.583
POC	–0.867	0.084	p3L	0.499	0.580
FL	0.849	–0.099	P3B	–0.261	0.558
I3AP	0.827	0.292	MAT	0.249	–0.551
c1AP	0.821	0.174	P4BP	0.487	0.520
PL	0.812	–0.047	JDM1	0.307	–0.516
POP	–0.800	–0.197	MC1	–0.294	–0.466
p3H	–0.774	0.198	ZW	0.444	–0.453
I3I3	0.767	0.279	SKL	0.472	–0.075
c1ML	0.766	0.095	PW	0.203	0.254
I3ML	0.734	0.322	JBP4	0.378	–0.125
CB	–0.717	0.191	BCL	–0.033	–0.147
SYML	0.701	–0.090	MB	0.058	–0.146
m1L	–0.686	0.311	MAM	0.130	–0.438
P4C1	0.634	0.158	m1B	–0.178	0.457
p3L	–0.511	0.444	c1H	0.315	0.071
p4H	–0.497	0.466	JDP4	0.398	–0.321
p4L	–0.424	0.397	PCP	0.299	0.186
P4L	0.114	0.652	JBM1	0.064	–0.121
Eigenvalue	14.8	5.7			
% Variance	32.2	12.4			

*This principal component does not explain significant variance in the data set and is shown for illustrative purposes only (Figure 2).

I3ML, C1C1, C1AP, C1ML, c1AP, and c1ML. Cheek teeth variables included: P3L and p3H. Dentary variables included: SYML, MM1, and MC1. Large prey specialists had highest means for all values except, POP, POC, MCW, CB, p3H, MM1, and MC1, for which small prey specialists had the highest means. Mixed prey feeders were intermediate for all means.

PCA

PCA performed on all cranial data yielded ten principal components (eigenvalues > 1), which accounted for 76% of the total variance in the data set (Table 4). Some of the principal components were related to ecological characters, whereas others were related to phylogenetic affinities or allometry; only those components associated with prey size will be discussed here. Univariate ANOVA tests were used to assess whether prey size categories displayed significantly different PC scores. Only PC1 displayed significant differences between prey size groups. Principal component 1 accounted for 32.2% of the variance, and partially separated all three prey categories (Fig. 2). Cats that kill predominantly large prey, with the exception of the cheetah and European lynx, were well separated from other groups, and had positive PC1 scores associated with larger anterior dentition (I3AP, C1AP, C1ML, C1C1), longer palates and symphyses (FL, SYML), as well as a relatively smaller braincase (MCW, POP, POC). Mixed prey and small prey categories overlap, but mixed prey feeders generally had higher PC1 scores than small prey specialists. PC1 was plotted against PC2 for illustrative purposes, however, PC2, accounting for 12.4% of the variance, was not meaningful in regards to prey size preference or other behaviours. Heavily weighted variables include those that describe cheek tooth size (P4L, P3L,p4B, p3B), as well as jaw muscle size and leverage (MFL, MAT, MM1; Table 4), only one of which, MM1, had a slight association with large prey specialization in the discriminant function analysis discussed below.

DFA

Stepwise DFA was performed on all GM transformed data using the three a priori groups for prey size. Using 18 of the 44 variables, separation of the groups was significant (Wilks' lambda = 0.087, $P < 0.001$). The analysis yielded two discriminant functions,

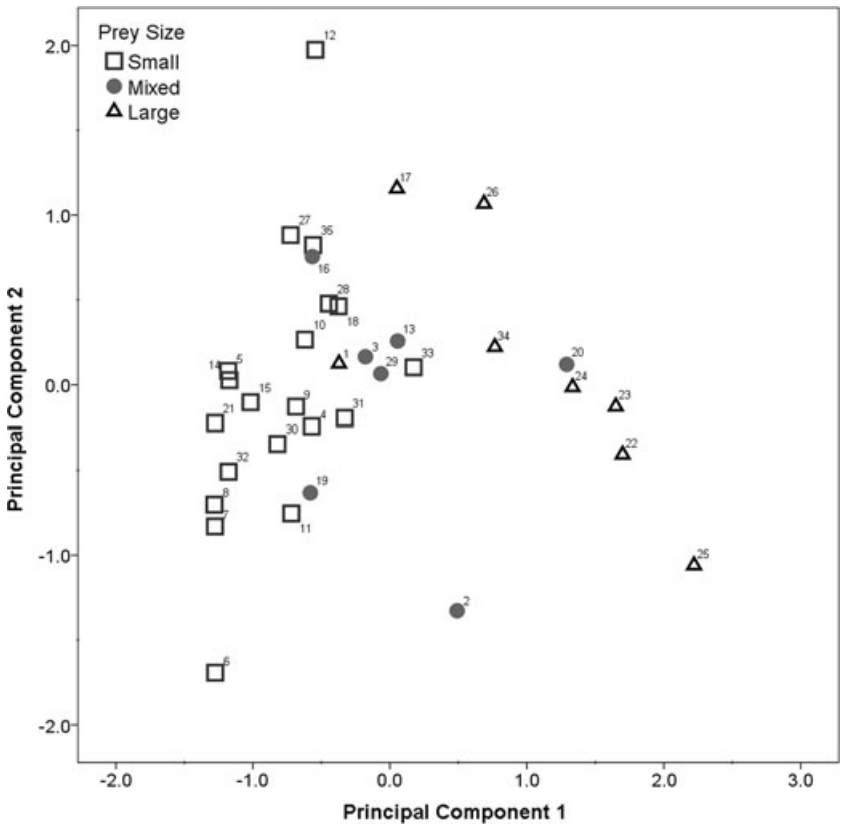

Figure 2. Plot of PC1 and PC2 for principal component analysis of felid crania. Individual specimens for each species were collapsed to single points. Numbers refer to individual species identified in Table 1. For an explanation of PC2, see Table 4.

accounting for 100% of the total variance in the data (Fig. 3; Table 5).

The first discriminant function (DF1) accounted for 91.2% of the total variance and separated all three groups. Cats that kill predominantly large prey had negative scores on DF1 and were characterized by relatively small braincases (POP, MCW, CB) and enlarged anterior dentition (I3AP, I3I3, C1C1, C1AP, C1ML). Small prey specialists had positive scores on DF1 and mixed prey species fell in between the other two groups.

The second discriminant function (DF2) accounted for a much smaller portion of the total variance (8.8%) and distinguished mixed prey feeders from the other two categories. The most important variables were dentary shape (JBM1, JDM1), p3 anteroposterior length (p3L), and condylar breadth (CB). Mixed prey specialist tended to have relatively narrower dentaries and condylar breadths, as well as shorter p3s than the other two groups although these differences were minimal based on the MANOVA results.

The classification showed 92.9% correct classification of individuals, and 90.9% correct classification when cases were cross-validated, a method used to further validate classifications by jackknifing. All species were correctly assigned to their respective prey categories, except the Iberian lynx, *Lynx pardinus* (Temminck, 1827), which was categorized as a small prey specialist by us but as a mixed prey feeder by the DFA.

When body size was regressed against the first discriminant function a strong correlation ($r^2 = 0.897$) was found (Fig. 4), suggesting that body mass alone is an excellent predictor of relative prey size. Although large and small prey specialists do not overlap in body size, both show some overlap with mixed prey cats. However, it is also clear that similarly sized species do not always fall in the same prey size categories. For example, the clouded leopard and the Eurasian lynx both weigh approximately 21 kg and yet differ in prey size preference as was reflected by their different craniodental shapes. In addition, species with a mass of approximately 10 kg may be either small prey specialists (e.g. serval, fishing cat and Iberian lynx) or mixed prey feeders (e.g. African golden cat, caracal, ocelot, Canadian lynx, bobcat, and Asian golden cat) and, for these taxa, prey choice was better predicted by craniodental shape (DF1) than body size. The

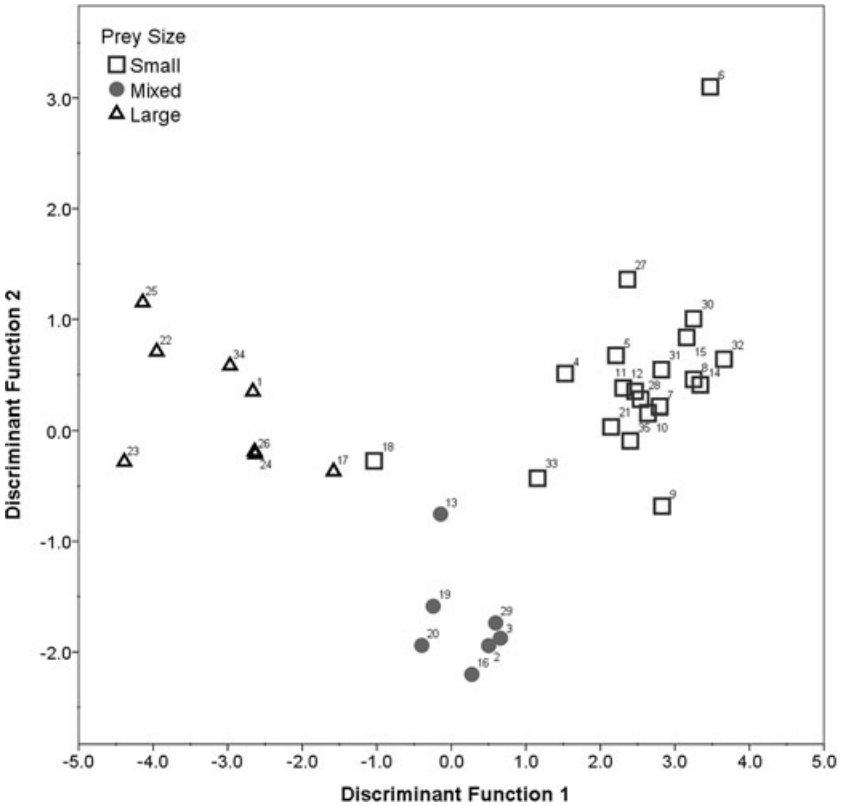

Figure 3. Plot of DF1 and DF2 for discriminant function analysis of felid crania relating to prey preference. Individual specimens for each species were collapsed to single points. Numbers refer to individual species identified in Table 1.

possible exception to this was the Iberian lynx that had DF1 scores more similar to that of mixed prey than small prey species and may be misclassified as noted above.

Allometry

Allometric trends were assessed by regression of log-transformed variables against the respective log geometric mean for variables that were shown to best discriminate between cats of different prey sizes using the DFA (Table 6). Features that were positively associated with killing large prey (I3I3, C1C1, I3AP, C1AP, C1ML, P4C1, JBP4, JBM1, and JDM1) also tended to be positively allometric ($b > 1$). In association with this, estimates of the moment arms of resistance for a bite at the carnassial (MM1) scaled negatively ($b < 1$), enhancing the mechanical advantage of jaw adductors by shortening the length of the jaw from the condyloid process to the m1, at the same time as increasing the velocity advantage of smaller cats by having a relatively elongated MM1. Estimates of braincase volume (MCW, POP, and CB) were negatively allometric, which is consistent with previous studies demonstrating a decline in relative brain size with body size in mammals (Jerison, 1973; Radinsky, 1981; Wayne, 1986; Schoenemann, 2004). Skull length (SKL), basicranial length (BCL), width across paracondylar processes (PCP), and length of the P4 (P4L) all scaled isometrically ($b = 1$).

Independent contrasts

For each variable found to be important in the DFA (Table 5), we used independent contrasts to analyse whether ecomorphological variables showed significant phylogenetic influence. Prey size preference was transformed into a continuous variable by entering log mean prey size for each species using the phylogeny of Johnson *et al.* (2006). Branch lengths were assigned using the supplementary material provided in Johnson *et al.* (2006). All of the variable contrasts were regressed against log mean prey size through the origin using linear regression to examine correlations between the contrasts and mean prey size (Table 7). The results of the regressions indicate that phylogeny does not have a significant effect on the following variables: post-orbital process (POP), maximum braincase width (MCW), occipital condyle breadth (CB), width of paracondylar processes (PCP), muzzle width (C1C1), length of the upper tooth row

Table 5. Discriminant analysis structure matrix, including eigenvalues, proportion of variance explained by each function, and Wilks' lambda

	Discriminant function	
Variable	1	2
C1ML	**–0.581**	0.097
C1C1	**–0.574**	0.217
MCW	**0.521**	0.004
CB	**0.450**	**–0.299**
C1AP	**–0.436**	0.146
I3AP	**–0.391**	–0.074
POP	**0.380**	0.157
I3I3	**–0.357**	0.191
MM1	0.202	0.125
JBP4	–0.157	0.139
P4C1	–0.134	–0.078
SKL	–0.074	0.003
BCL	0.007	0.005
p3L	0.116	**0.294**
JBM1	–0.106	0.241
JDM1	–0.097	–0.223
PCP	–0.105	0.168
P4L	–0.042	–0.157
Eigenvalues	6.202	0.600
% Variance	91.2	8.8
Wilks' λ	0.087	0.625

Values in bold indicate correlations between individual indices and the discriminant model that are 0.25 or greater. Only variables listed were included in the stepwise discriminant model.

Table 6. Interspecific allometric relationships for log transformed measurements regressed against body size (log GM)

Variable (y)	a	b	r^2	SE_b	$b = 1$
SKL	0.393	1.032	0.992	0.023	1
BCL	–0.140	1.059	0.915	0.056	1
POP	0.651	0.655	0.835	0.051	< 1
MCW	0.724	0.525	0.979	0.018	< 1
PCP	–0.808	1.019	0.991	0.017	1
CB	0.107	0.819	0.983	0.019	< 1
I3-I3	–0.867	1.224	0.985	0.037	> 1
I3AP	–1.722	1.389	0.978	0.052	> 1
C1-C1	–0.515	1.212	0.994	0.016	> 1
C1AP	–1.437	1.393	0.989	0.037	> 1
C1ML	–1.554	1.399	0.991	0.033	> 1
P4L	–0.514	1.023	0.979	0.026	1
P4C1	–0.223	1.098	0.984	0.025	> 1
p3L	–0.052	0.888	0.973	0.026	< 1
MM1	0.670	0.914	0.984	0.021	< 1
JBP4	–0.269	1.053	0.991	0.018	> 1
JBM1	–0.238	1.052	0.985	0.023	> 1
JDM1	0.060	1.055	0.992	0.017	> 1

Regression equations were calculated in the form $\log y = \log a + b \log x$ (where x = GM score, y = measurement, $a = y$ intercept, b = slope, r^2 = correlation coefficient, SE_b = standard error). Significant deviations from isometry ($b = 1$) at the $P \leq 0.05$ level are indicated by $b > 1$ for positive allometry and $b < 1$ for negative allometry.

(P4C1), moment arm of the temporalis at the carnassial (MM1), and anterioposterior and mediolateral diameters of the anterior teeth (I3AP, C1AP, C1ML). This indicates that many of the variables important in large prey specialization, such as muzzle width and robustness of the anterior teeth are not well-correlated with phylogeny ($\alpha = 0.05$). However, phylogeny was found to have a significant effect in the following variables: skull length (SKL), basicranial length (BCL), width across upper incisors (I3I3), length of premolars (P4L, p3L), jaw depth at P4/M1 junction (JDM1), jaw breadth at P3/P4 junction (JBP4), and jaw breadth at P4/M1 junction (JBM1).

Using five values from the original DFA that were found not be phylogenetically influenced, C1AP, C1ML, C1C1, I3AP, and MM1, we ran a subsequent DFA to determine whether these variables alone could discriminate prey size categories. There was an 80.2% correct classification, with a 79.6% cross-validation. Although the percentage of individuals correctly classified was not as high as when all variables were included (92.9%), these five variables alone were still able to correctly classify prey-size groups. Even with the effects of size removed through geometric mean transformation and with allometric and phylogenic effects taken into account, muzzle width (C1C1) and anterior dental robustness (C1AP, C1ML, and I3AP) were important cranial variables that distinguish large prey specialists from all other cats.

Some functionally significant variables, such as jaw depth and jaw breadth, were not significantly correlated with prey size when the data were corrected for phylogenetic effects. However, this does not mean that these variables may not still be functionally important. Due to many of the large prey specialists in the present study belonging to one lineage, the Panthera group, tests of independent contrasts may not be able to discern all of the functionally important variables that characterize this group.

DISCUSSION

Felids that kill prey near or above their own body size can be distinguished from those that take prey smaller than themselves by their relatively robust canines, in both mediolateral and anteroposterior dimensions and relatively wide muzzles, in addition

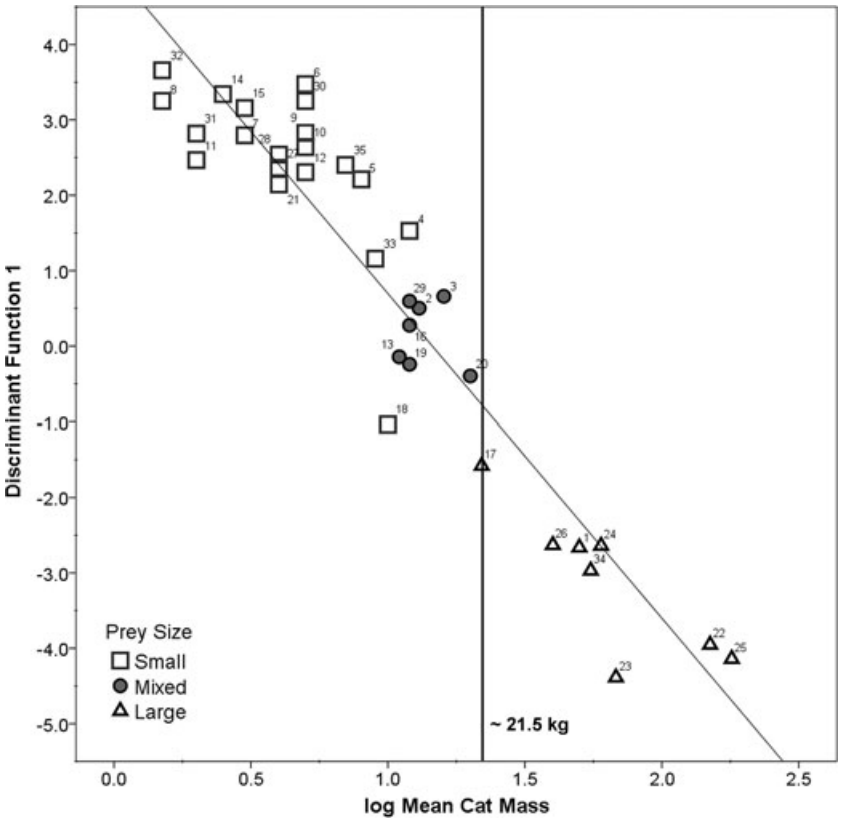

Figure 4. Log_{10} mean cat mass plotted against DF1 from a discriminant function analysis of Felidae measured in the present study. The highlighted line represents the 21.5 kg threshold discussed in the text, $r^2 = 0.897$. Individual specimens for each species were collapsed to single points. Numbers refer to individual species identified in Table 1.

to body masses that exceed 21 kg. These features probably evolved multiple times within the family given that large prey specialists include representatives from three of the eight primary felid clades. In addition to enlarged canine teeth, large prey specialists also had relatively deep and broad dentaries (JBM1, JDM1) and reduced relative braincase dimensions (MCW, CB, POP). Although large prey specialists were distinct in all these variables, the small prey specialists and the mixed prey feeders showed some overlap in morphospace, with the mixed prey group generally intermediate to small and large prey specialists.

This prey size separation is well illustrated by several cat species approximately 10 kg in size. For example, the caracal and the serval are approximately the same mass and are very closely related. The caracal will occasionally kill a small wild or domestic ungulate (Pringle & Pringle, 1979; Sunquist & Sunquist, 2002) but the serval kills larger prey much less frequently (Smithers, 1983). This difference is reflected in their skulls in the results of both the PCA and DFA. These two species are clearly separated, with the caracal grouping with the mixed prey feeders and the serval grouping with the small prey specialists. Many other cats in the 10 kg range also vary greatly in their typical prey choices and, with the exception of the Iberian lynx, these choices are reflected in their skull morphology.

Our findings are similar to those of Van Valkenburgh & Koepfli (1993), who found that canids that specialize on large prey have more robust canines and incisors, as well as wider muzzles. As in the present study, they also found that large prey specialists are the most morphologically distinct group of canids. These findings are also similar to those of Werdelin's (1983) morphometric analysis of felid skulls Although his focus was phylogenetic relationships among felids rather than prey size, he found a consistent grouping of *Puma concolor* (Linnaeus, 1771) and the pantherines in regards to robustness of the canines and muzzle width. He also found a distinct division between small and large cats, with *Neofelis nebulosa* (Griffiths, 1821) and *Lynx lynx* (Linnaeus, 1758) falling in between.

Although a wider muzzle (C1C1) reduces the force applied by the bite, it also reduces cranial torsion from struggling prey (Covey & Greaves, 1994). Small

Table 7. Results of phylogenetically independent contrasts of log morphological variables versus log mean prey size preference

Variable	*P* (two-tailed)	*F*	Slope	r^2
SKL	0.957	0.002	1.005×10^{-4}	8.87×10^{-4}
BCL	0.076	3.360	–0.013	0.095
POP	0.020	5.990	–0.016	0.157
MCW	0.001	12.277	–0.015	0.277
PCP	0.004	9.335	0.007	0.225
CB	5.23×10^{-4}	14.873	–0.012	0.317
I3I3	0.290	1.153	0.004	0.034
I3AP	0.028	5.230	0.009	0.140
C1C1	1.75×10^{-8}	55.542	0.024	0.634
C1AP	3.28×10^{-8}	52.240	0.038	0.620
C1ML	4.22×10^{-12}	114.470	0.048	0.781
P4L	0.147	2.200	0.006	0.064
P4C1	0.001	12.094	0.007	0.274
p3L	0.339	0.941	–0.005	0.028
MM1	2.18×10^{-4}	17.360	–0.147	0.351
JDM1	0.393	0.748	0.002	0.022
JBP4	0.172	1.950	0.005	0.057
JBM1	0.739	0.112	–0.001	0.003

Listed variables were included in the stepwise discriminant model. Variables in bold were found to be significant at the $\alpha = 0.05$ level.

prey specialists also use their anterior dentition to kill prey, but they do so by using a swift bite to the nape of the neck, which requires more speed than force (Ewer, 1973) and, consequently, this method of dispatching prey results in different loads than in large prey specialists. Small prey cats have relatively less robust canines with a smaller area of contact, which increases the force per unit area during biting compared to large-prey cats with more rounded canines (Frazzetta, 1988; Freeman & Lemen, 2007); therefore, a smaller cat's bite, would more easily penetrate the skin of prey with less force than would that of a larger cat. This is indeed the case observed by Leyhausen (1979) where small prey specialists slice through the nape of the neck, severing the spinal cord, whereas large prey-specialists use a trachea hold that suffocates the prey animal, but might not break the skin.

One interesting species of note is the cheetah, *Acinonyx jubatus* (Schreber, 1776). Although cheetahs mainly consume medium-sized ungulates (e.g. Thompson's gazelles or impalas) in the majority of their range (Sunquist & Sunquist, 2002), they have also been observed specializing on prey as small as springhares and hares in South Africa and Namibia (M. G. L. Mills, pers. comm.; Wachter, Jauernig & Breitenmoser, 2006) and occasionally will kill prey as large as wildebeest and buffalo (male cheetah coalitions; Caro, 1994). In the present study, cheetahs are unique because they group with the small or mixed prey feeders in the PCA and with the large prey specialists in the DFA. Because cheetahs consistently prefer smaller prey (e.g. Thomson's gazelle) than other large prey cats, they may not need the very robust muzzles and canines that characterize large prey specialists (Caro, 1994). However, because cheetahs occasionally kill prey much larger than themselves, their skulls and teeth should be able to withstand greater forces than those of small prey specialists. The intermediate position of the cheetah in our statistical tests is indicative of their preferred intermediate prey size, and notably is not similar to their closest extant relative (i.e. the puma) that consistently groups with the other large-prey pantherines.

Another interesting large prey specialist is the jaguar, *Panthera onca* (Linnaeus, 1758). Jaguars were found to have the most robust canines relative to size out of all cats measured. This may be because jaguars utilize their canines in different ways than do other large prey specialists. Observations have shown that jaguars will occasionally kill some prey (usually capybaras) by a braincase piercing bite with the canines and will also kill large tortoises by cracking open their shells with their canines (Schaller & Vasconcelos, 1978; Emmons, 1989; Sunquist & Sunquist, 2002). These habits require reinforcement of the canines both anteroposteriorly and mediolaterally to

reduce the risk of fracture when biting these hard tissues.

Neofelis nebulosa, the clouded leopard, is a mixed prey cat that has also received much recent focus because it is a smaller, mixed-prey pantherine and because of its anomalously long canines relative to skull size (Therrien, 2005; Christiansen, 2006; Christiansen, 2007; Slater & Van Valkenburgh, 2008). Upper canine lengths were not measured in the present study; however, we found that *Neofelis* has robust (both anteroposteriorly and mediolaterally) canines for its size, perhaps to provide the needed reinforcement to reduce the risk of breakage when killing larger prey. The functional significance of the enlarged canines in clouded leopards remains unclear, but our data suggest they are not compressed mediolaterally as is true of most saber-tooth cats. These findings concur with the results obtained in several other studies (Werdelin, 1983; Van Valkenburgh & Ruff, 1987; Salesa *et al.*, 2005). *Neofelis* also grouped with the large-prey specialists in the PCA (Fig. 2). This may be due to the shape of its canines, or because, despite killing smaller prey, it resembles its large-prey specialist *Panthera* relatives as a consequence of phylogenetic affinity.

One interesting small prey specialist (misclassified by the DFA) is the Iberian lynx, *L. pardinus*. Although Iberian lynx most often kill ducks and lagomorphs (Sunquist & Sunquist, 2002), they are found in a very limited area, and this may reflect a lack of large prey. Their body mass (7–16 kg) overlaps with two sister taxa, bobcat and Canada lynx, that are mixed prey feeders, and historically Iberian lynx brought down larger prey as well (Gil-Sánchez, Ballesteros-Duperón & Bueno-Segura, 2006).

As reported in Werdelin (1983), we found that variables related to braincase size, maximum braincase width (MCW), occipital condyle breadth (CB), and length across the post-orbital process (POP) are all negatively allometric. Larger cats have relatively smaller brains. A similar result was also found in small dog breeds, such as the Chihuahua, when compared to larger dog breeds and also between domestic dogs and wild canids (Wayne, 1986). Other studies have also shown the well established negative allometry of the mammalian brain and other neurocranial components (Jerison, 1973; Radinsky, 1975, 1981). This negative allometry may be explained by the relationship between brain size and metabolic rate. It has been suggested that, as mammal body size increases, metabolic rate will decrease. This decrease in metabolic rate is then translated to a developing fetus from its mother who may constrain the size of the metabolically expensive brain tissue in her developing fetus, ultimately limiting brain size in the adult (Martin, 1981; Schoenemann, 2004).

Wayne *et al.* (1989) found a positive allometric trend in anteroposterior diameters of canid canines, relative to skull length. This agrees with our assessment of a positive allometric trend in the canine teeth and other skull features of felids that are correlated with large prey specialization. However, skull length in canids is negatively allometric compared to body mass, whereas this same relationship is isometric in felids (Van Valkenburgh, 1990). The fact that larger canids tend to have shorter skulls likely relates to an increased need for greater bite forces in canids that take prey as large as or larger than themselves (Maynard Smith & Savage, 1959; Van Valkenburgh & Koepfli, 1993). Unlike felids, canids must kill with jaws alone and, consequently, those that take large prey have relatively short snouts and enhanced moment arms of their masseter and temporalis muscles (Turnbull, 1970; Van Valkenburgh & Koepfli, 1993) Canids that take smaller prey have more elongate snouts that probably favor speed of jaw closure over bite force (Turnbull, 1970). This result is also seen somewhat in felids through the negative allometry in the moment arm of the temporalis at the carnassial (MM1). A relatively longer mandible affords a slight velocity advantage to smaller cats that catch small, quick prey and a shorter distance between the jaw joint and the carnassial in large prey specialists proffers increased mechanical advantage. Although MM1 was not significant in the DFA, it was found to be significantly different in all three prey categories by the MANOVA, with the proportionately shortest lengths in large prey specialists. Additionally, this shortening trend in the mandible between the jaw joint and the carnassial was found in all large prey specialists, regardless of lineage. However, all felids still use a single, strong killing bite combined with manipulation of the prey by their paws, and therefore all display foreshortened skulls that optimize bite force at the canines.

If the differences found in the present study between large and small cats were due to size alone, then all features of larger cats would be expected to scale with geometric similarity (slope = 1 for log/log regression). This isometric scaling is seen in the length of the skull, the width of the paracondylar processes, and basicranial length, but not in key elements of the prey-killing apparatus, such as canine robustness (mediolateral and anteroposterior widths) and muzzle width. These features scale with positive allometry, giving big cats relatively broader muzzles and thicker canines than smaller cats. Because cats that kill large prey often employ a stranglehold to the throat using a bite from the anterior dental arcade, these teeth are subjected to erratically directed, substantial loads incurred by struggling prey (Biknevicius & Van Valkenburgh, 1996). Accordingly,

the canines must be reinforced to counteract this resistance and reduce the risk of fracture.

Emerson & Bramble (1993) found that vertebrates that kill increasingly large prey show positive allometric scaling of the prey killing apparatus in the skull, and that clades that do not show this positive allometry do not eat relatively large prey. This phenomenon holds true for amphibians (four frog genera), reptiles (varanids), and mammals (Emerson & Bramble, 1993). Given these findings, our data suggest that positive allometry seen in the anterior dentition and muzzle widths of felids is an integral part of their ability to kill large prey, and not a confounding factor obscuring the results.

Christiansen (2007) also found that canine morphology was a variable trait in felids and attributed this difference to feeding ecology. In our analysis, all cats were not equally positively allometric and this may also be informative. As discussed above, the canines of jaguars are relatively more robust for their size than are those of the lion or the tiger, and jaguars are known for using a skull-crushing killing bite. Our data also show that similar sized cats that kill prey of different sizes, such as the caracal and serval, and, to some degree, the cheetah and puma, have canines of different robustness that reflects their choice in prey size (caracals larger than serval, puma larger than cheetah).

A thickening of mandibular breadth and depth between the p4 and m1 and a thickening of the breadth between the p3 and p4 were important variables in large prey specialization, and a deeper mandible without a subsequent mediolateral thickening was important for mixed prey feeders. None of these variables were found to be significant when phylogeny was taken into account. However, a mediolaterally thickened mandible suggests a greater need to resist lateral bending and torsional loads exerted by struggling prey during the killing bite (Hylander, 1984; Biknevicius & Ruff, 1992b). A dorsoventrally thickened mandible is indicative of reinforcement against bending in the sagittal plane when the animal is biting or chewing, especially during a bilateral canine bite, as is made when a cat is delivering a killing bite to large prey (Biknevicius & Ruff, 1992a; Biknevicius & Van Valkenburgh, 1996).

Because they were relatively little affected by phylogeny in the present study, increased muzzle width (C1C1) and anterior dental robustness (C1ML, C1AP, and I3AP) are excellent predictors of large prey specialization in extant Felidae and could be used to predict the prey size of extinct conical-toothed cats. Given the success of this ecomorphological analysis of living felids that specialize on different prey sizes, we look forward to applying this same approach to extinct species, such as *Pseudaelurus* (Gervais, 1850). In addition, because felids use their forelimbs as well as their skulls and jaws to capture prey, we will also incorporate estimates of forelimb strength and leverage in future work. The present study could also be applied to saber-toothed felids. However, given their unusual cranial morphology and probably different prey capture behaviour, our measurements might not be optimal. In addition to dissimilar canine morphology from conical-toothed cats, saber-tooth cats have more mediolaterally compressed skulls and very disparate morphology of the mandible, notably of the coronoid and condyloid processes, which may skew the results (Christiansen, 2008; Slater & Van Valkenburgh, 2008). At a minimum, our approach should help elucidate the ecological differences among extinct conical-toothed felids, a group that has been notoriously difficult to understand given their morphological conservatism.

ACKNOWLEDGEMENTS

The following curators and collection managers kindly allowed access to specimens in their care: J. Dines (Museum of Natural History of Los Angeles County); K. Molina (Donald R. Dickey Collection of the University of California, Los Angeles); E. Lacey (Museum of Vertebrate Zoology, University of California, Berkeley); M. Schulenburg (Field Museum of Natural History); and L. Gordon and J. Jacobs (US National Museum of Natural History). Discussion with and comments by X. Wang, D. Jacobs, R. Wayne, P. J. Brantingham, J. Samuels, G. Slater, K. Koepfli, P. Adam, and two anonymous reviewers greatly improved this paper. This project was partially funded by a UCLA Graduate Assistance in Areas of National Need (GAANN) fellowship.

REFERENCES

Andersson K. 2004. Elbow joint morphology as a guide to forearm function and foraging behaviour in mammalian carnivores. *Zoological Journal of the Linnean Society* **142:** 91–104.

Andersson K, Werdelin L. 2003. The evolution of cursorial carnivores in the Tertiary: implications of elbow-joint morphology. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270:** S163–S165.

Biknevicius AR, Ruff CB. 1992a. Use of biplanar radiographs for estimating cross-sectional geometric properties of mandible. *Anatomical Record* **232:** 157–163.

Biknevicius AR, Ruff CB. 1992b. The structure of the mandibular corpus and its relationship to feeding behaviors in extant carnivorans. *Journal of Zoology* **228:** 479–507.

Biknevicius AR, Van Valkenburgh B. 1996. Design for killing: craniodental adaptations of predators. In: Gittleman

J, ed. *Carnivore behavior, ecology and evolution*, Vol. 2. Ithaca, NY: Cornell University Press, 393–428.

Bryant HN, Russell AP, Laroiya R, Powell GL. 1996. Claw retraction and protraction in the Carnivora: skeletal microvariation in the phalanges of the Felidae. *Journal of Morphology* **229:** 289–308.

Carbone C, Mace GM, Roberts SC, Macdonald DW. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* **402:** 286–288.

Carbone C, Teacher A, Rowcliffe JM. 2007. The costs of carnivory. *Public Library of Science Biology* **5:** 1–6.

Caro TM. 1994. *Cheetahs of the Serengeti plains*. Chicago, IL: University of Chicago Press.

Christiansen P. 2006. Sabertooth characters in the clouded leopard (*Neofelis nebulosa* Griffiths 1821). *Journal of Morphology* **267:** 1186–1198.

Christiansen P. 2007. Canine morphology in the larger Felidae: implications for feeding ecology. *Biological Journal of the Linnean Society* **91:** 573–592.

Christiansen P. 2008. Evolution of skull and mandible shape in cats (Carnivora: Felidae). *PLoS ONE* **3:** e2807.

Covey DS, Greaves WS. 1994. Jaw dimensions and torsion resistance during canine biting in the Carnivora. *Canadian Journal of Zoology* **72:** 1055–1060.

Emerson SB, Bramble DM. 1993. Scaling, allometry and skull design. In: Hanken J, Hall BK, eds. *The skull*, Vol. 3: *Functional and evolutionary mechanisms*. Chicago, IL: University of Chicago Press, 384–421.

Emmons LH. 1989. Jaguar predation on chelonians. *Journal of Herpetology* **23:** 311–314.

Ewer RF. 1973. *The carnivores*. New York, NY: Cornell University Press.

Felsenstein J. 1985. Phylogenies and the comparative method. *American Naturalist* **125:** 1–15.

Frazzetta TH. 1988. The mechanics of cutting and the form of shark teeth (Chondrichthyes, Elasmobranchii). *Zoomorphology* **108:** 93–107.

Freeman PW, Lemen CA. 2007. The trade-off between tooth strength and tooth penetration: predicting optimal shape of canine teeth. *Journal of Zoology* **273:** 273–280.

Friscia AR, Van Valkenburgh B, Biknevicius AR. 2007. An ecomorphological analysis of extant small carnivores. *Journal of Zoology* **272:** 82–100.

Gil-Sánchez JM, Ballesteros-Duperón E, Bueno-Segura JF. 2006. Feeding ecology of the Iberian lynx *Lynx pardinus* in eastern Sierra Morena (Southern Spain). *Acta Theriologica* **51:** 85–90.

Gittleman JL, Van Valkenburgh B. 1997. Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny and behavioral ecology. *Journal of Zoology* **242:** 97–117.

Gonyea WJ. 1978. Functional implications of felid forelimb morphology. *Acta Anatomica* **102:** 111–121.

Gonyea WJ, Ashworth R. 1975. The form and function of the retractile claws in the Felidae and other representative carnivorans. *Journal of Morphology* **145:** 229–238.

Hunter L. 2005. *Cats of Africa: behavior, ecology and conservation*. Baltimore, MD: Johns Hopkins University Press.

Hylander WL. 1984. Stress and strain in the mandibular symphysis of primates, a test of competing hypotheses. *American Journal of Physical Anthropology* **64:** 1–46.

Jablonski D, Gould SJ, Raup DM. 1986. The nature of the fossil record: a biological perspective. In: Raup DM, Jablonski D, eds. *Patterns and processes in the history of life*. Berlin: Springer-Verlag, 7–22.

Jerison H. 1973. Brain evolution and biological intelligence. *Bulletin of the Psychonomic Society* **2:** 339.

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* **311:** 73–77.

Kitchener A. 1991. *The natural history of the wild cats*. London: A&C Black.

Leyhausen P. 1979. *Cat behavior: the predatory and social behavior of domestic and wild cats*. New York, NY: Garland STMP Press.

Maddison WP, Maddison DR. 2006. *Mesquite: a modular system for evolutionary analysis*, Version 2.5. Available at: http://mesquiteproject.org

Martin RD. 1981. Relative brain size and basal metabolic rate in terrestrial vertebrates. *Nature* **293:** 57–60.

Mattern MY, McLennan DA. 2000. Phylogeny and speciation of felids. *Cladistics* **16:** 232–253.

Maynard Smith J, Savage JRG. 1959. The mechanics of mammalian jaws. *School Science Review* **141:** 289–301.

Mosimann JE, James FC. 1979. New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* **33:** 444–459.

Nowak RM. 1999. *Walker's mammals of the world*, 6th edn. Baltimore, MD: John Hopkins University Press.

Nowak RM. 2005. *Walker's carnivores of the world*, 7th edn. Baltimore, MD: John Hopkins University Press.

Peigné S. 1999. *Proailurus*, l'un des plus anciens Felidae (Carnivora) d'Eurasie: systématique et évolution. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **135:** 125–134.

Pringle JA, Pringle VL. 1979. Observations on the lynx *Felis caracal* in the Bedford district. *South African Journal of Zoology* **14:** 1–4.

Radinsky LB. 1975. Evolution of the felid brain. *Brain, Behavior and Evolution* **11:** 214–254.

Radinsky LB. 1981. Evolution of skull shape in carnivores 1. Representative modern carnivores. *Biological Journal of the Linnean Society* **15:** 369–388.

Read AJ, Tolley KA. 1997. Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Canadian Journal of Zoology* **75:** 122–130.

Russell AP, Bryant HN. 2001. Claw retraction and protraction in the Carnivora: the cheetah (*Acinonyx jubatus*) as an atypical felid. *Journal of Zoology* **254:** 67–76.

Salesa MJ, Antón M, Turner A, Morales J. 2005. Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat *Paramachairodus ogygia* (Kaup, 1832) Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. *Zoological Journal of the Linnean Society* **144:** 363–377.

Schaller GB. 1972. *The Serengeti lion: a study of predator prey relationships*. Chicago, IL: University of Chicago Press.

Schaller GB, Vasconcelos JMC. 1978. Jaguar predation on capybara. *Zeitschrift Säugetierk* **43:** 296–301.

Schmidt-Nielsen K. 1993. *Scaling: why is animal size so important?* Cambridge: Cambridge University Press.

Schoenemann PT. 2004. Brain size scaling and body composition in mammals. *Brain, Behavior and Evolution* **63:** 47–60.

Slater GJ, Van Valkenburgh B. 2008. Long in the tooth: evolution of sabertooth cat cranial shape. *Paleobiology* **34:** 403–419.

Smithers RHN. 1983. *The mammals of the Southern African subregion*. Pretoria: University of Pretoria Press.

Sunquist M, Sunquist F. 2002. *Wildcats of the world*. Chicago, IL: University of Chicago Press.

Therrien F. 2005. Mandibular force profiles of extant Carnivorans and implications for the feeding behaviours of extinct predators. *Journal of Zoology* **267:** 249–270.

Turnbull WD. 1970. Mammalian masticatory apparatus. *Fieldiana Geology* **18:** 149–356.

Turner A, Antón M. 1997. *The big cats and their fossil relatives*. New York, NY: Columbia University Press.

Van Valkenburgh B. 1987. Skeletal indicators of locomotor behavior in living and extinct carnivores. *Journal of Vertebrate Paleontology* **7:** 162–182.

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: Cambridge University Press, 181–206.

Van Valkenburgh B, Koepfli KP. 1993. Cranial and dental adaptations to predation in canids. *Symposium of the Zoological Society of London* **65:** 15–37.

Van Valkenburgh B, Ruff CB. 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology* **212:** 379–397.

Van Valkenburgh B, Sacco T, Wang X. 2003. Pack hunting in Miocene borophagine dogs: evidence from craniodental morphology and body size. *Bulletin of the American Museum of Natural History* **279:** 147–162.

Van Valkenburgh B, Wang X, Damuth J. 2004. Cope's rule, hypercarnivory, and extinction in North American canids. *Science* **306:** 101–104.

Wachter B, Jauernig O, Breitenmoser U. 2006. Determination of prey hair in feces of free-ranging Namibian cheetahs with a simple method. *Cat News* **44:** 8–9.

Wayne RK. 1986. Cranial morphology of domestic and wild canids, the influence of development on morphological change. *Evolution* **40:** 243–261.

Wayne RK, Van Valkenburgh B, Kat PW, Fuller TK, Johnson WE, O'Brien SJ. 1989. Genetic and morphological divergence among sympatric canids. *Journal of Heredity* **80:** 447–454.

Werdelin L. 1983. Morphological patterns in the skulls of cats. *Biological Journal of the Linnean Society* **19:** 375–392.

Young SP, Goldman EA. 1946. *The puma: mysterious American cat*. New York, NY: Dover Publications, Inc.

Zar JH. 1996. *Biostatistical analysis*, 3rd edn. Upper Saddle River, NJ: Prentice Hall.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of individual specimens measured for this study. Museum abbreviations include Field Museum of Natural History (FMNH); Natural History Museum of Los Angeles County (LACM); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); UCLA Donald R. Dickey Collection (UCLA); US National Museum of Natural History (USNM).

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.