



Bite Forces and Evolutionary Adaptations to Feeding Ecology in Carnivores

Author(s): Per Christiansen and Stephen Wroe

Source: *Ecology*, Vol. 88, No. 2 (Feb., 2007), pp. 347-358

Published by: [Ecological Society of America](#)

Stable URL: <http://www.jstor.org/stable/27651108>

Accessed: 22/04/2013 12:28

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at
<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

BITE FORCES AND EVOLUTIONARY ADAPTATIONS TO FEEDING ECOLOGY IN CARNIVORES

PER CHRISTIANSEN^{1,3} AND STEPHEN WROE²

¹Zoological Museum, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

²School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia, 2052

Abstract. The Carnivora spans the largest ecological and body size diversity of any mammalian order, making it an ideal basis for studies of evolutionary ecology and functional morphology. For animals with different feeding ecologies, it may be expected that bite force represents an important evolutionary adaptation, but studies have been constrained by a lack of bite force data. In this study we present predictions of bite forces for 151 species of extant carnivores, comprising representatives from all eight families and the entire size and ecological spectrum within the order. We show that, when normalized for body size, bite forces differ significantly between the various feeding categories. At opposing extremes and independent of genealogy, consumers of tough fibrous plant material and carnivores preying on large prey both have high bite forces for their size, while bite force adjusted for body mass is low among specialized insectivores. Omnivores and carnivores preying on small prey have more moderate bite forces for their size. These findings indicate that differences in bite force represent important adaptations to and indicators of differing feeding ecologies throughout carnivoran evolution. Our results suggest that the incorporation of bite force data may assist in the construction of more robust evolutionary and palaeontological analyses of feeding ecology.

Key words: adaptation; bite force; bite force quotients; Carnivora; evolution; feeding ecology.

INTRODUCTION

Members of the Carnivora are more ecologically diverse than any other mammalian order, and span more than three orders of magnitude in body size, from 100-g weasels to polar and brown bears weighing up to 800 kg (Nowak 1991, Stirling 1993). In popular imagination, carnivores are defined by their sharp teeth, powerful jaws, and a predilection for meat (Rayfield et al. 2001), but in reality, they encompass the entire feeding spectrum, from hypercarnivorous felids and certain canids and mustelids, to almost exclusively herbivorous species, such as pandas (Nowak 1991). This great variety provides an excellent basis for comparative studies of bite forces and feeding ecology (see Plate 1).

Previous research into the vector mechanics of carnivore skulls has indicated that there should be significant differences in bite forces between species and groups (e.g., Emerson and Radinsky 1980, Miller 1984, Van Valkenburgh and Ruff 1987, Biknevicius and Van Valkenburgh 1996). These findings strongly suggest that, among the various evolutionary adaptations to different feeding ecologies, we might expect bite force to be particularly important. For instance, Radinsky (1981a, b) found that mustelids and felids appear to have a relatively more powerful bite than canids and ursids. It is, however, noteworthy that felids and many

mustelids, especially large genera such as *Mustela* and to some extent *Martes*, also are more carnivorous than the latter two groups. Jaw joint to carnassial distance appear highly constrained among carnivores (Greaves 1982, 1983, 1988, Christiansen and Adolfssen 2005), indicating that efficient biting has been of importance in carnivore evolution.

However, previous studies have been limited by a lack of inferred bite force data with which to examine evolutionary models such as canine bending strengths (Van Valkenburg and Ruff 1987), proposed differences between the carnivoran families (Radinsky 1981a, b), or the suggestion that extant predators of relatively large prey have evolved higher bite forces (Wroe et al. 2005). In this paper, we provide the first comprehensive database of estimated bite forces for all eight traditionally recognized carnivoran families (Gittleman 1989, Nowak 1991, Binida-Emonds et al. 1999) based on estimated muscle cross-sectional areas and lever mechanics on dry skulls and investigate relationships between bite forces and feeding ecology using a recently developed method for comparison of estimated bite forces among species with different body sizes (Wroe et al. 2005).

MATERIALS AND METHODS

Bite forces were estimated using cross-sectional areas for the major jaw adductors: the temporalis and masseteral pterygoideus muscle complexes (Thomason 1991; see also Christiansen and Adolfssen 2005, Wroe et al.

Manuscript received 18 August 2006; accepted 25 August 2006. Corresponding Editor: T. D. Williams.

³ E-mail: p2christiansen@zmuc.ku.dk



PLATE 1. Cranial morphology of a hypercarnivorous canid (Grey wolf [*Canis lupis*]) and an omnivorous ursid (Malayan sun bear [*Ursus malayanus*]). Photo credit: Geert Brovad.

2005). These were computed from digital images of 609 specimens, representing 151 species (~63% of all extant species) from all eight families of extant carnivores (Table 1, Fig. 1), in posterodorsal, direct lateral, and direct ventral views (Fig. 2). The resulting areas were multiplied by the estimated maximal isometric force generated by mammalian muscle (see next paragraph). It was assumed that the resultant force vectors about the temporomandibular joint (T for the temporalis and M for the masseter-ptyergoideus groups, respectively) acted through their respective centroids perpendicular to the plane of the muscle cross-sectional area (Fig. 2). The inlever moment arms about the temporomandibular joints (TMJ) for the temporalis (I_t) were computed from photographs of the skulls in direct lateral view and the inlever moment arms for the masseter (I_m) about the TMJ was computed from photographs of the skulls in direct ventral (palatal) view. Bite force (BF) can be estimated as

$$BF = (T \times I_t + M \times I_m) / I_o$$

where I_o is the outlever moment arm to the center (eocone) of the upper carnassial and upper canine, as appropriate. All measurements are in SI units.

Traditionally, the value of 300 KPa has been applied as an estimate for maximal isometric contractile force of

vertebrate striated muscle (Thomason 1991). However, this has resulted in lower than actual bite force values, when compared with muscle dissections on *Didelphis* skulls (Thomason 1991), probably because actual maximal contractile forces of muscles should ideally be computed from the physiological cross-sectional area (Weijs and Hillen 1984, 1985, Sinclair and Alexander 1987, Koolstra et al. 1988, Cleuren et al. 1995), rather than from estimates of physical cross-sectional areas. Also, the present model does not include other, smaller jaw adductors, such as the zygomaticomandibularis. Accordingly, a slightly higher value of 370 KPa (Weijs and Hillen 1985, Koolstra et al. 1988) was used in the present study.

Average body masses for each species were taken from the literature (Nowak 1991, Stirling 1993, Silva and Downing 1995, Kingdon 1997, Reid 1997, Sunquist and Sunquist 2002, MacDonald and Sillero-Zubiri 2004). For sexually dimorphic species, assignment of average body masses was influenced by the proportion of males and females of each species. The relationship between bite force and body mass in carnivores is allometric and comparisons were, accordingly, made through computation of a bite force quotient or BFQ (Wroe et al. 2005). This value allows comparisons of bite forces across species with different body sizes. Species with BFQs around 100 may be regarded as having near "average" bite force for their body size (Wroe et al. 2005). BFQ equations were computed from the residuals of regression analyses on estimated bite forces at the canine tip and carnassial eocone, respectively, to estimated body masses, and are as follows:

$$BFQ_{ca} = [BF_{ca} / 10^{(0.663 \pm 0.028 \times \log(BM) + 1.561 \pm 0.027)}] \times 100$$

$$r = 0.967 \pm 0.009 \quad SE = 0.109$$

$$F_{1,149} = 2157.955 \quad P \ll 0.000$$

$$BFQ_{cam} = [BF_{cam} / 10^{(0.650 \pm 0.028 \times \log(BM) + 1.762 \pm 0.028)}] \times 100$$

$$r = 0.966 \pm 0.009 \quad SE = 0.109$$

$$F_{1,149} = 2088.379 \quad P \ll 0.000$$

where BF_{ca} and BF_{cam} are the estimated bite forces at the canines and carnassials, respectively, in Newtons (N), and BM is body mass in kilograms (kg). These equations were used to assign a BFQ to each of the 609 specimens, from which species averages were then computed.

The various species were assigned to seven feeding categories based on literature sources (Lyneborg 1970, Nowak 1991, Stirling 1993, Kingdon 1997, Sunquist and Sunquist 2002, MacDonald and Sillero-Zubiri 2004). Assignments were necessarily broad based, and overlaps were evident between some categories, most notably for omnivores and carnivores predominately feeding on small prey (categories listed in the next paragraph). Moreover, seasonal fluctuations occur in many species (Nowak 1991), and only a few examples will be given

TABLE 1. Average bite forces at the canine tips (BF_{ca}) and carnassial eocone (BF_{carn}), body mass (BM), bite force quotients at the canine tip (BFQ_{ca}) and carnassial eocone (BFQ_{carn}), and dietary category (D) in 151 species of carnivores.

Species	BM (kg)	BF_{ca} (N)	BF_{carn} (N)	BFQ_{ca}	BFQ_{carn}	D
Canidae						
<i>Alopex lagopus</i>	4.8	82.3	138.0	80.1	86.2	4
<i>Atelocynus microtis</i>	10.2	197.5	295.5	116.1	112.7	4
<i>Canis adustus</i>	9.5	142.1	233.2	87.5	93.0	2
<i>Canis aureus</i>	9.1	138.2	217.9	87.7	89.6	4
<i>Canis familiaris</i> †	25.0	351.5	549.8	114.3	117.4	5
<i>Canis latrans</i>	10.7	173.4	289.6	98.9	107.2	4
<i>Canis lupus</i>	35.5	493.5	773.9	127.3	131.6	6
<i>Canis mesomelas</i>	8.5	117.8	187.5	78.3	80.6	2
<i>Cerdocyon thous</i>	6.8	114.6	178.2	88.7	89.0	4
<i>Chrysocyon brachyurus</i>	23.4	323.0	510.8	109.6	113.7	2
<i>Cuon alpinus</i>	12.9	261.5	397.9	132.0	130.7	6
<i>Fennecus zerda</i>	1.0	39.0	64.8	107.2	112.2	4
<i>Lycalopex vetulus</i>	4.1	85.3	133.5	92.4	92.7	2
<i>Lycaon pictus</i>	22.4	374.6	556.8	131.1	127.7	6
<i>Nyctereutes procynoides</i>	5.1	98.0	145.9	91.1	87.2	2
<i>Otocyon megalotis</i>	5.2	76.2	111.3	69.7	65.5	7
<i>Pseudalopex culpaeus</i>	11.5	158.4	258.5	86.3	91.5	4
<i>Pseudalopex griseus</i>	5.9	131.0	223.4	111.2	122.1	4
<i>Pseudalopex gymnocerus</i>	5.6	111.4	177.5	97.4	99.9	2
<i>Speothos venaticus</i>	6.0	150.0	233.5	125.8	125.7	5
<i>Urocyon cinereoargenteus</i>	4.8	85.8	134.1	83.5	83.8	2
<i>Vulpes bengalensis</i>	3.8	75.8	127.6	85.9	92.7	2
<i>Vulpes chama</i>	4.3	78.4	134.0	82.4	90.3	4
<i>Vulpes ferrilata</i>	4.9	113.3	214.5	108.6	132.1	4
<i>Vulpes pallida</i>	3.0	60.3	94.9	79.6	80.1	4
<i>Vulpes rueppelli</i>	2.5	57.4	99.6	85.6	94.7	4
<i>Vulpes velox</i>	3.4	78.5	141.5	96.0	110.8	4
<i>Vulpes vulpes</i>	7.9	144.0	239.0	100.2	107.5	4
Felidae						
<i>Acinonyx jubatus</i>	46.8	338.8	509.1	72.7	72.3	5
<i>Caracal caracal</i>	11.5	168.5	251.4	91.8	89.0	5
<i>Catopuma temminckii</i>	12.6	194.2	309.0	99.5	103.0	5
<i>Felis catus</i>	3.7	73.3	118.1	84.4	87.1	4
<i>Felis chaus</i>	6.8	112.2	181.7	86.9	90.7	4
<i>Felis margarita</i>	3.0	102.0	155.4	136.7	133.1	4
<i>Felis nigripes</i>	1.9	54.3	92.9	98.9	107.3	4
<i>Felis silvestris</i>	4.8	98.4	152.6	95.8	95.4	4
<i>Herpailurus yagouaroundi</i>	5.2	87.5	129.7	80.1	76.4	4
<i>Leopardus pardalis</i>	10.7	199.5	306.0	113.8	113.3	4
<i>Leopardus tigrinus</i>	3.5	63.0	97.2	75.9	74.9	4
<i>Leopardus wiedii</i>	3.5	63.4	101.4	75.2	77.0	4
<i>Leptailurus serval</i>	10.2	165.6	263.3	97.3	100.5	4
<i>Lynx canadensis</i>	9.8	139.6	225.3	84.6	88.6	4
<i>Lynx lynx</i>	17.0	201.6	310.2	84.7	85.1	6
<i>Lynx rufus</i>	10.5	184.5	289.1	106.8	108.7	5
<i>Neofelis nebulosa</i>	20.9	334.2	544.3	122.4	130.6	6
<i>Oncifelis colocolo</i>	4.1	124.2	196.9	134.5	136.7	4
<i>Oncifelis geoffroyi</i>	4.9	110.9	169.4	106.3	104.3	4
<i>Oncifelis guigna</i>	2.2	72.6	114.6	116.9	117.4	4
<i>Otocolobus manul</i>	3.5	94.4	155.4	113.8	119.8	4
<i>Panthera leo</i>	162.2	1314.7	2023.7	123.8	128.1	6
<i>Panthera onca</i>	95.5	887.0	1361.2	118.6	121.6	6
<i>Panthera pardus</i>	55.0	621.1	964.4	119.8	123.4	6
<i>Panthera tigris</i>	177.8	1472.1	2164.7	130.4	129.1	6
<i>Panthera uncia</i>	35.5	387.6	603.5	99.9	102.6	6
<i>Pardofelis marmorata</i>	4.5	117.2	185.3	119.4	121.2	4
<i>Prionailurus bengalensis</i>	3.1	61.2	94.4	80.2	79.0	4
<i>Prionailurus planiceps</i>	3.0	87.3	145.1	115.3	122.3	3
<i>Prionailurus rubiginosus</i>	2.2	68.2	108.6	111.6	112.9	4
<i>Prionailurus viverrinus</i>	8.3	166.0	255.6	112.0	111.6	5
<i>Profelis aurata</i>	11.0	216.2	336.6	121.5	122.8	5
<i>Puma concolor</i>	39.8	497.1	773.2	118.8	122.0	6
Herpestidae						
<i>Bdeogale crassicauda</i>	2.8	56.2	90.2	79.0	80.7	7
<i>Crossarchus platycephalus</i>	1.4	39.4	63.0	84.7	85.7	2
<i>Cynictis penicillata</i>	0.9	33.7	56.6	95.9	101.4	7
<i>Galidia elegans</i>	1.0	35.5	58.4	96.9	100.2	4

TABLE 1. Continued.

Species	BM (kg)	BF _{ca} (N)	BF _{carn} (N)	BFQ _{ca}	BFQ _{carn}	D
<i>Herpestes auropunctatus</i>	1.1	33.7	46.8	87.0	76.2	4
<i>Herpestes edwardsi</i>	1.6	46.2	75.2	93.6	96.5	4
<i>Herpestes fuscus</i>	1.7	49.7	80.9	96.1	99.2	4
<i>Herpestes ichneumon</i>	3.1	90.6	148.5	117.9	123.4	4
<i>Herpestes pulverulentus</i>	1.7	31.5	54.3	60.2	65.7	4
<i>Ichneumia albicauda</i>	3.9	65.8	104.7	75.5	74.9	2
<i>Mungos mungo</i>	1.9	34.0	53.7	61.8	62.0	7
<i>Rhynchogale melleri</i>	2.5	55.7	86.0	83.1	81.8	2
<i>Salanoia concolor</i>	1.0	31.8	52.4	90.1	93.3	2
Hyaenidae						
<i>Crocuta crocuta</i>	63.1	565.7	985.5	99.6	115.3	6
<i>Hyaena brunnea</i>	38.9	560.1	1029.6	135.9	164.9	6
<i>Hyaena hyaena</i>	36.3	507.8	889.2	128.9	148.9	6
<i>Proteles cristatus</i>	13.2	122.2	...	60.7	...	7
Mustelidae						
<i>Aonyx capensis</i>	14.1	238.3	348.0	113.1	107.7	3
<i>Aonyx cinerea</i>	3.1	71.2	113.3	92.6	94.1	3
<i>Conepatus humboldti</i>	3.2	52.7	76.1	67.5	62.2	7
<i>Conepatus semistriatus</i>	3.6	60.3	80.2	70.5	60.0	7
<i>Eira barbara</i>	5.2	169.3	243.4	155.0	143.3	4
<i>Enhydra lutris</i>	34.7	281.0	394.2	73.6	68.0	3
<i>Galictis cuja</i>	1.4	58.2	85.8	129.2	120.4	4
<i>Gulo gulo</i>	14.5	223.6	348.5	104.6	106.2	6
<i>Ictonyx striatus</i>	1.3	47.6	72.2	108.9	104.3	4
<i>Lutra canadensis</i>	7.8	144.3	219.7	101.9	100.3	3
<i>Lutra felina</i>	4.2	100.9	152.0	107.6	103.9	3
<i>Lutra longicaudis</i>	7.8	129.1	189.8	90.9	86.4	3
<i>Lutra lutra</i>	8.3	147.8	216.0	99.7	94.3	3
<i>Lutra maculicollis</i>	5.2	92.5	141.8	84.7	83.5	3
<i>Lutra perspicillata</i>	9.8	202.6	306.8	122.8	120.6	3
<i>Lutra sumatrana</i>	5.5	99.2	151.6	88.1	86.6	3
<i>Martes americana</i>	1.1	42.4	70.0	113.1	117.5	4
<i>Martes flavigula</i>	2.8	78.0	121.5	109.5	108.8	4
<i>Martes foina</i>	2.2	62.3	98.9	101.9	102.9	2
<i>Martes martes</i>	2.0	73.2	116.6	125.3	126.8	4
<i>Martes pennanti</i>	4.0	113.1	184.3	124.3	129.8	4
<i>Meles meles</i>	13.8	207.0	282.2	99.8	88.6	2
<i>Mellivora capensis</i>	11.7	216.9	317.7	116.4	110.8	2
<i>Melogale everetti</i>	2.0	47.8	71.4	83.1	78.9	4
<i>Mephitis macrura</i>	1.7	44.3	61.9	85.6	75.9	2
<i>Mephitis mephitis</i>	2.4	73.3	99.9	112.8	97.8	2
<i>Mustela africana</i>	0.3	14.0	21.1	80.3	74.9	6
<i>Mustela altaica</i>	0.2	21.5	32.2	159.5	147.2	6
<i>Mustela erminea</i>	0.2	19.9	30.4	146.2	138.2	6
<i>Mustela frenata</i>	0.3	14.5	22.8	99.6	96.8	6
<i>Mustela lutreola</i>	0.6	28.2	46.0	108.6	110.6	5
<i>Mustela nivalis</i>	0.1	12.0	18.4	164.0	152.9	6
<i>Mustela putorius</i>	1.2	60.4	88.0	149.0	137.0	5
<i>Mustela vison</i>	1.1	37.4	58.5	96.7	95.3	5
<i>Mydaus javanensis</i>	3.2	41.3	58.2	52.9	47.6	2
<i>Poecilictis libyca</i>	0.6	19.0	28.4	75.2	70.4	4
<i>Pteronura brasiliensis</i>	31.6	414.6	614.3	115.4	112.6	3
<i>Taxidea taxus</i>	8.7	221.6	316.6	145.0	134.1	4
Procyonidae						
<i>Ailurus fulgens</i>	5.2	167.8	244.9	153.6	144.2	1
<i>Bassaricyon alleni</i>	1.3	58.7	87.5	138.4	130.3	2
<i>Bassaricyon gabbii</i>	1.0	59.2	91.7	162.6	158.6	2
<i>Bassariscus astutus</i>	1.7	54.7	87.1	105.8	106.8	2
<i>Bassariscus sumichrasti</i>	1.9	79.7	116.3	142.8	132.3	2
<i>Nasua nasua</i>	4.4	83.7	133.4	86.6	88.5	2
<i>Nasuella olivacea</i>	1.9	38.9	64.1	70.8	74.0	2
<i>Potos flavus</i>	3.3	99.9	128.3	123.8	101.7	1
<i>Procyon cancrivorus</i>	7.8	164.7	237.7	116.3	108.5	2
<i>Procyon lotor</i>	8.9	121.4	176.7	78.2	73.7	2
Ursidae						
<i>Ailuropoda melanoleuca</i>	117.5	1298.9	1815.9	151.4	141.8	1
<i>Tremarctos ornatus</i>	100.0	795.1	946.6	103.1	82.1	1
<i>Ursus americanus</i>	140.0	744.3	1003.6	77.2	69.9	2

TABLE 1. Continued.

Species	BM (kg)	BF _{ca} (N)	BF _{carn} (N)	BFQ _{ca}	BFQ _{carn}	D
<i>Ursus arctos</i>	251.2	1409.7	1894.9	99.3	90.3	2
<i>Ursus malayanus</i>	60.1	883.2	1189.6	160.5	143.6	2
<i>Ursus maritimus</i>	354.8	1646.7	2349.6	92.3	89.4	6
<i>Ursus thibetanus</i>	125.9	858.3	1135.7	95.6	84.8	2
<i>Ursus ursinus</i>	120.2	522.1	712.0	59.9	54.7	7
Viverridae						
<i>Arctictis binturong</i>	15.8	249.2	351.2	109.6	100.8	2
<i>Arctogalidia trivirgata</i>	2.4	89.8	139.8	138.2	136.9	2
<i>Civettictis civetta</i>	13.5	145.3	231.3	71.1	73.7	2
<i>Cryptoprocta ferox</i>	7.8	145.0	239.7	102.3	109.3	5
<i>Cynogale bennettii</i>	4.6	110.3	192.8	110.7	124.2	3
<i>Eupleres goudotti</i>	3.0	28.6	50.0	37.8	42.1	7
<i>Fossa fossa</i>	2.2	64.7	110.8	105.9	115.3	4
<i>Genetta genetta</i>	2.8	81.7	132.3	112.9	116.7	4
<i>Macrogalidia musschenbroeki</i>	5.6	184.3	270.5	161.1	152.3	2
<i>Nandinia binotata</i>	2.6	72.1	116.4	104.3	107.4	1
<i>Paguma larvata</i>	4.5	140.4	177.6	142.4	115.6	2
<i>Paradoxurus hermaphroditus</i>	4.5	80.8	123.2	95.9	93.6	2
<i>Prionodon linsang</i>	0.9	31.8	57.9	95.8	109.6	4
<i>Viverra megaspila</i>	8.9	130.0	226.9	83.8	94.7	4
<i>Viverra zibetha</i>	5.6	96.3	163.3	84.2	91.9	4
<i>Viverricula indica</i>	8.7	114.1	192.3	74.6	81.5	4
	2.5	57.9	101.1	87.7	97.5	4

Note: Dietary categories: 1, herbivores (including frugivores); 2, omnivores; 3, piscivores; 4, carnivores, small prey; 5, carnivores, medium-sized prey; 6, carnivores, large prey; 7, insectivores.

† Domestic dogs include only large semi-feral or feral specimens; in this case, two Greenland dogs and three dingos. Some authors (MacDonald and Sillero-Zubiri 2004) consider the dingo to be a separate species.

here. Sloth bears (*Ursus ursinus*) are largely insectivorous, but will ingest large amounts of fruit when in season (Joshi et al. 1997). Hoary foxes (*Lycalopex vetulus*) prey on small vertebrates, but also feed extensively on insects, especially termites (MacDonald and Sillero-Zubiri 2004). The European mink (*Mustela lutreola*) feeds extensively on fish and amphibians, but its staple food is the water vole (*Arvicola terrestris*) (Lyneborg 1970, Nowak 1991). Hog-nosed skunks (*Conepatus* sp.) are omnivores feeding on fruit, carrion, and small vertebrates, but they rely mostly on insects (Nowak 1991). Clawless (*Aonyx* sp.) and river (*Lutra* sp.) otters are both grouped as piscivorous, despite the former relying on crustaceans and amphibians and less on fish than the latter (Nowak 1991). Our categorizations were based on the type of food that made up the majority of the diet.

The dietary categories used are:

- 1) Primarily herbivorous. Two of the included species are primarily frugivorous (*Nandinia binotata* and *Potos flavus*), and the rest are primarily folivorous.
- 2) Omnivorous, vegetable matter constituting a large part of diet.
- 3) Piscivorous, mainly feeding on aquatic prey such as fish, amphibians, mollusks, and crustaceans.
- 4) Carnivorous, primarily taking small prey weighing up to ~20% of the predator's own body mass.
- 5) Carnivorous, primarily taking small to medium-sized prey, up to the predator's own body mass.
- 6) Carnivorous, primarily taking medium-sized to large prey, frequently exceeding the predator's own

body mass. The bone-cracking hyaenas were included in this category, although only the spotted hyaena (*Crocuta crocuta*) is a regular hunter of large vertebrates (Mills 1978, Nowak 1991, Holekamp et al. 1997, Trinkel et al. 2004). We consider that it is both the killing and processing of proportionally large prey that can be expected to covary with high bite forces. In this respect, the largely scavenging *Hyaena* spp. would also need high bite forces for their body size. Moreover, while *H. hyaena* and *H. brunnea* rely heavily on carrion, both are known to occasionally kill prey greatly exceeding their own body masses (Meers 2002).

7) Primarily insectivorous.

For studies of allometry, we performed analyses of log₁₀ values of body masses (kg) and estimated bite forces (N) with Reduced Major Axis Independent Contrasts analyses (Felsenstein 1985, Garland et al. 1992, 1993) in the 2004 program PDTREE (PDAP: Phenotypic Diversity Analysis Programs, T. Garland, Jr., unpublished program). We used a tree topology as in Bininda-Emonds et al. (1999) (Fig. 1). For many clades, especially within Mustelidae and Viverridae-Herpestidae (Bininda-Emonds et al. 1999), clade ages were unavailable. Consequently, we used uniform branch lengths. Contrasts must be standardized in independent contrasts analyses so as to become independent of their respective branch lengths. Standardization is adequate if the coefficient of determination (r^2) of the contrasts and their standard deviations are <0.05 (Diaz-Uriarte and Garland 1998, Garland 2004).

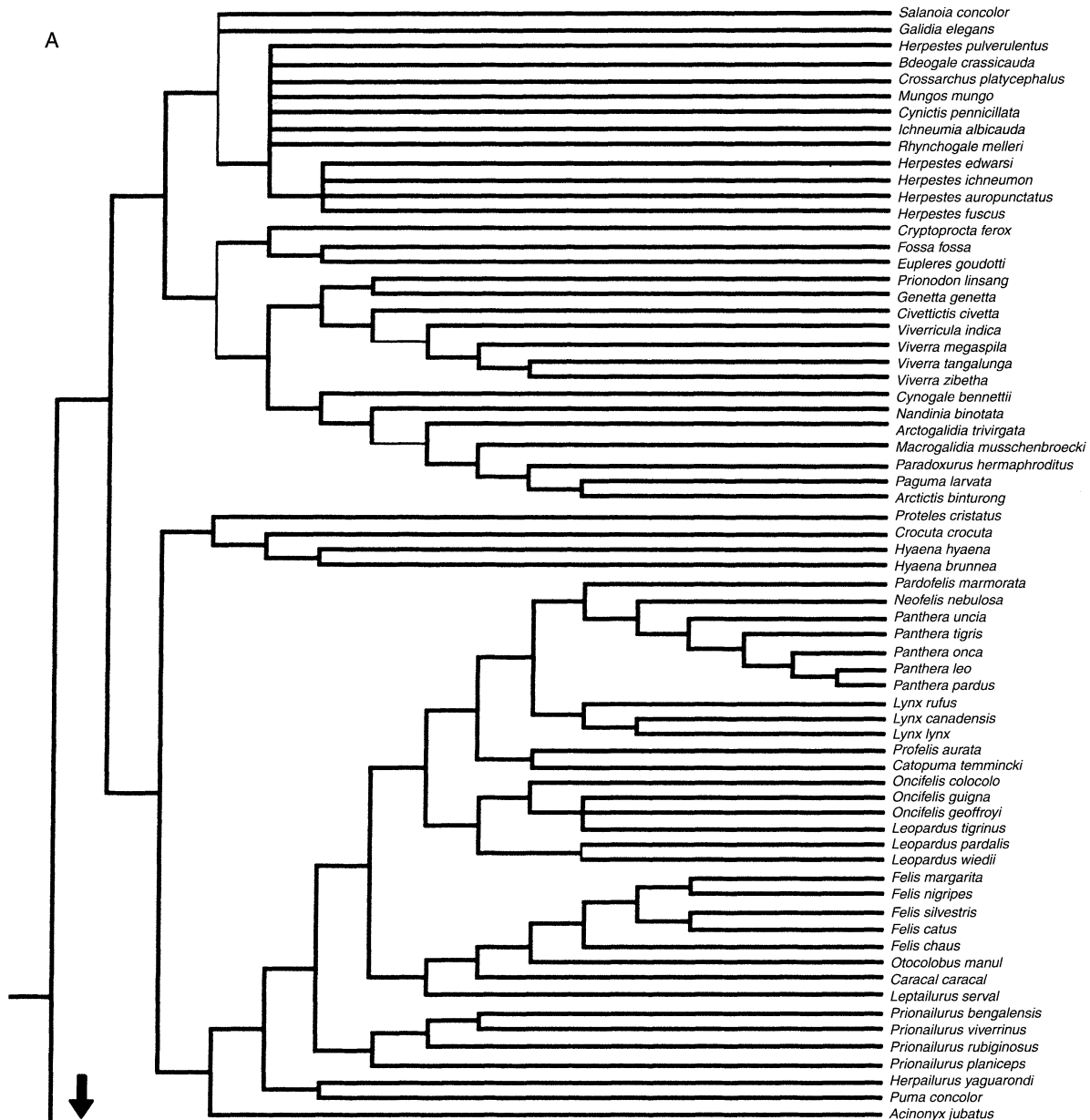


FIG. 1. (A, B) Diagram of the proposed phylogenetic topology of the included species of carnivorans ($n = 151$ species). The two panel parts (A and B) line up at the arrows.

RESULTS AND DISCUSSION

The results are given in Table 1. We found a strong positive relationship between body mass and bite forces. It was not necessary to transform the branch lengths of the tree presented in Fig. 1, as the raw (i.e., unmodified) branch lengths were adequate for contrast standardization. The absolute values of the contrasts to their respective standard deviations of $\log_{10}(\text{body mass})$ to $\log_{10}(\text{bite forces})$ at the canine resulted in a coefficient of determination (r^2) of 0.001 and an $F_{1,149}$ statistic of 0.185 (NS). For $\log_{10}(\text{body mass})$ to $\log_{10}(\text{bite forces})$ at

the carnassial the results were $r^2 = 0.003$ and $F_{1,149} = 0.419$ (NS). A RMA slope of 0.762 ± 0.053 ($r = 0.907$, $F_{1,149} = 683.78$, $P < 0.001$) was found for $\log_{10}(\text{body mass})$ to $\log_{10}(\text{bite forces})$ at the canine, and 0.778 ± 0.059 ($r = 0.901$, $F_{1,149} = 562.72$, $P < 0.001$) for $\log_{10}(\text{body mass})$ to $\log_{10}(\text{bite forces})$ at the carnassial. Both slopes are significantly ($P < 0.001$) different from isometry (1.00), indicating that smaller species have more powerful jaws for their body size than large species. Smaller mustelids and certain felids and procyonids often have high bite forces for their body size.

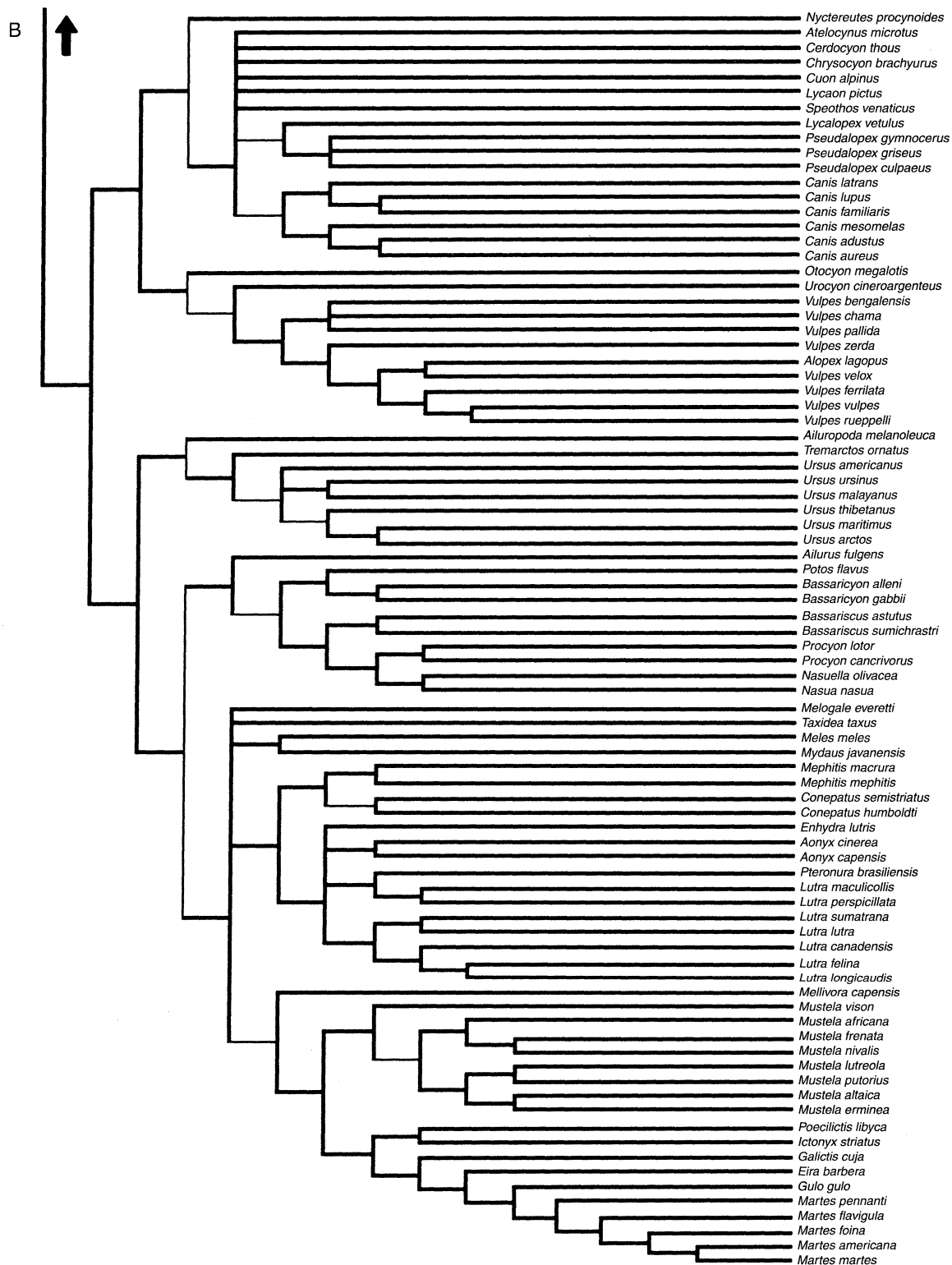


FIG. 1. Continued.

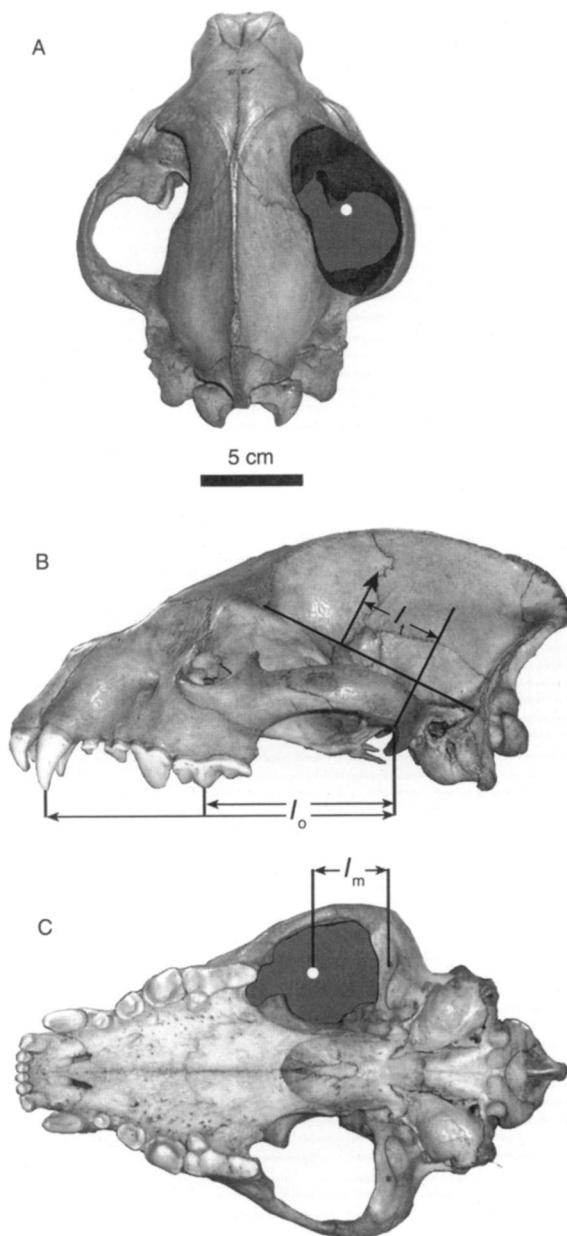


FIG. 2. Skull of spotted hyaena (*Crocota crocuta*) CN138 in (A) posterodorsal, (B) lateral, and (C) palatal views, showing computation of muscle areas and force vectors. Shaded areas are reconstructed muscle cross-sectional areas of the (A) temporalis and (C) masseter-ptyergoideus group. White dots represent the centroids of the resultant force vectors of the (A) temporalis and (C) masseter-ptyergoideus. Abbreviations are: I_m = inlever moment arm of masseter muscle; I_t = inlever moment arm of the temporalis muscle; I_o , outlever moment arms to the carnassial eocone and canine tip, respectively.

The average BFQs at the canine tips among the various taxonomic categories vary relatively little, and only the procyonids are significantly different from the herpestids (Table 2). However, if the insectivorous aardwolf (*Proteles cristatus*) is removed from Hyaeni-

dae, the remaining three large, bone-cracking forms have a BFQ average of 121.5. However, the low sample size (three species) precludes assumptions of significance from other groups, despite the average being higher than in any other group. This pattern is mirrored in BFQs at the carnassials, which are only significantly different in hyenids (three species, owing to the lack of a carnassial in *Proteles*) and herpestids. Accordingly, although several averages appear different among the taxonomic groups, few are, in effect, significantly different, which is also evident from the ANOVA F values, which are barely (carnassial) or not (canine) statistically significant.

Much greater differences are found when analyzing BFQs for different feeding categories across the taxonomic groups, as indicated by markedly greater ANOVA F values (Table 3). Specialized herbivorous carnivores such as the giant panda (*Ailuropoda melanoleuca*) and the lesser panda (*Ailurus fulgens*) have some of the highest bite forces for their body size (Table 1). However, there are few truly herbivorous carnivores, and low sample size (five species) preclude assumptions of significance from other dietary categories, despite their having the highest BFQs at the canines and the second-highest at the carnassials, surpassed only by carnivores regularly killing and/or consuming large prey (Table 3), which may require large bite forces to subdue and process their quarry (see Wroe et al. 2005).

The spectacled bear (*Tremarctos ornatus*), although almost exclusively herbivorous, has a much more varied diet than the pandas (Peyton 1980, Schaller et al. 1985, 1989, Nowak 1991), and its skull is less morphologically adapted for dealing with tough vegetation than are the pandas. Accordingly, it has much lower BFQs (Table 1). The giant pandas skull is remarkably heavy and has very thick skull bones (Chorn and Hoffman 1978; P. Christiansen and S. Wroe, *personal observations*), and is morphologically well adapted for generating high bite forces (Sacco and Van Valkenburgh 2004). This is in accord with our results. With similar feeding ecology to the giant panda, the lesser panda also has a robust skull. Both panda species are characterized by markedly molarized dentitia (Davis 1964, Schaller et al. 1985, see also Gittleman 1994). In contrast, the African palm civet (*Nandinia binotata*) feeds extensively on fruit (Nowak 1991), which is much less demanding to process orally than bamboo. Accordingly, this species has lower BFQs, despite being herbivorous (as classified in this study). The frugivorous kinkajou (*Potos flavus*) has a higher BFQ at the canine tip, which may be an adaptation for tearing into fruit. Its bite force at the carnassial (i.e., for mastication) is average.

The BFQs of omnivores, piscivores, and carnivores feeding on small prey (feeding categories 2–4), are similar, but all are significantly below the values of carnivores feeding on large prey (Tables 1 and 3). This is consistent with the proposal that smaller prey requires less force to kill and process orally than large, powerful

TABLE 2. Bite force quotients (BFQ) at the (A) canine tips and (B) carnassial eocone, by taxonomic category of carnivores.

Taxonomic category	Ca	Fe	He	Hy	Mu	Pr	Ur	Vi
A) BFQ (N) at canine tip								
Ca	1.000							
Fe	0.974	1.000						
He	0.802	0.274	1.000					
Hy	0.999	1.000	0.827	1.000				
Mu	0.817	1.000	0.114	1.000	1.000			
Pr	0.345	0.786	0.035	0.992	0.917	1.000		
Ur	0.999	1.000	0.731	1.000	1.000	0.948	1.000	
Vi	1.000	1.000	0.698	1.000	0.988	0.648	1.000	1.000
B) BFQ (N) at carnassial eocone								
Ca	1.000							
Fe	0.998	1.000						
He	0.499	0.201	1.000					
Hy	0.258	0.394	0.023	1.000				
Mu	1.000	0.983	0.587	0.190	1.000			
Pr	0.952	0.998	0.192	0.433	0.947	1.000		
Ur	0.936	0.755	0.999	0.089	0.968	0.753	1.000	
Vi	1.000	0.999	0.667	0.274	1.000	0.986	0.966	1.000

Notes: Table entries are *P* values, based on one-way ANOVA and post hoc Tukey hsd tests. Abbreviations for taxonomic category are: Ca, Canidae (28 species); Fe, Felidae (33 species); He, Herpestidae (13 species); Hy, Hyaenidae (4 species); Mu, Mustelidae (38 species); Pr, Procyonidae (10 species); Ur, Ursidae (8 species); Vi, Viverridae (17 species). The taxonomic category averages \pm SD for canine tips are: Ca, 98.3 ± 17.3 ; Fe, 104.6 ± 18.3 ; He, 86.1 ± 15.5 ; Hy, 106.3 ± 34.2 (Hyaenid average, excluding the insectivorous *Proteles*, is 121.5 ± 19.3); Mu, 107.2 ± 26.5 ; Pr, 119.6 ± 32.9 ; Ur, 104.9 ± 34.5 ; and Vi, 101.1 ± 29.0 ($F_{7,143} = 1.841$; $P = 0.084$). The taxonomic category averages \pm SD for carnassial eocones are: Ca, 102.4 ± 18.2 ; Fe, 106.3 ± 19.1 ; He, 87.8 ± 16.8 ; Hy, 143.0 ± 25.3 ; Mu, 102.6 ± 25.6 ; Pr, 113.3 ± 28.8 ; Ur, 94.6 ± 31.9 ; and Vi, 103.7 ± 24.9 ($F_{7,143} = 2.615$; $P = 0.014$).

mammalian prey, with thick hides and large bones. Carnivores feeding on medium-sized prey have BFQs that are, on average, intermediate between those of small- and large-prey carnivores, and, accordingly, nonsignificantly different from either. Predators of large prey must be equipped to both subdue large animals and dismember their carcasses. Thus, their high BFQs are consistent with the proposal that the additional effort required should be reflected in proportionately higher

bite forces (Wroe et al. 2005). Brown and striped hyenas rarely hunt large prey, but are similar to consistent predators of large prey, in that they need powerful bite forces to dismember large carcasses. While their BFQs are higher than that of the spotted hyena, their estimated bite forces are similar, suggesting selection for uniformly high bite forces to efficiently process similar sized carcasses, in accord with their cranio-dental morphology, regardless of differences in body mass.

TABLE 3. Bite force quotients (BFQ) at the (A) canine tips and (B) carnassial eocone compared to diet in 151 species of carnivores.

Dietary category	1	2	3	4	5	6	7
A) BFQ (N) at canine tip							
1	1.000						
2	0.192	1.000					
3	0.258	1.000	1.000				
4	0.100	0.999	1.000	1.000			
5	0.664	0.971	0.978	0.854	1.000		
6	0.994	0.046	0.183	0.006	0.757	1.000	
7	0.000	0.000	0.005	0.001	0.000	0.000	1.000
B) BFQ (N) at carnassial eocone							
1	1.000						
2	0.605	1.000					
3	0.819	1.000	1.000				
4	0.858	0.952	1.000	1.000			
5	0.996	0.701	0.944	0.966	1.000		
6	0.995	0.001	0.048	0.006	0.542	1.000	
7	0.000	0.002	0.005	0.000	0.000	0.000	1.000

Notes: Table entries are *P* values, based on one-way ANOVA and post hoc Tukey hsd tests. Abbreviations for dietary category are as in Table 1. Feeding category averages \pm SD for canine tips are: 1, 127.2 ± 24.5 ; 2, 102.2 ± 27.5 ; 3, 101.3 ± 14.5 ; 4, 99.9 ± 19.7 ; 5, 108.6 ± 18.2 ; 6, 120.0 ± 22.4 ; and 7, 67.0 ± 15.7 ($F_{6,144} = 7.637$; $P < 0.001$). Feeding category averages \pm SD for carnassial eocones are: 1, 115.4 ± 26.9 ; 2, 98.3 ± 24.5 ; 3, 100.3 ± 17.0 ; 4, 102.8 ± 19.0 ; 5, 108.9 ± 16.6 ; 6, 122.2 ± 23.2 ; and 7, 66.1 ± 17.8 ($F_{6,144} = 7.888$; $P < 0.001$).

Omnivore/small-prey feeding ecologies are probably closer to those of primitive carnivores, suggesting that a selection for higher bite forces accompanied evolutionary adaptations to both specialized herbivory and large-prey carnivory in members of all carnivore groups, which became evolutionarily adapted for such feeding ecologies. Specialization on fish, amphibians, and crustaceans may simply represent a lateral shift from one kind of small prey (e.g., reptiles, small mammals, and birds) to another, and thus did not require evolutionary selection for higher bite forces. This is corroborated by the absence of any morphological features for piscivory in the flat-headed cat (*Prionailurus planiceps*) and the fishing cat (*P. viverrinus*) (Sunquist and Sunquist 2002; P. Christiansen and S. Wroe, *personal observations*), the only piscivorous felids. However, since the latter also feeds on small mammals and birds besides aquatic food, it is here classified as a small-prey carnivore (Table 1).

In marked contrast to large-prey carnivores and specialized herbivores are the insectivores, which have highly significantly lower BFQs than all other groups (Table 3). Small mustelids are probably insectivorous through size-related factors (Carbone et al. 1999). Hence, the truly specialized carnivorous insectivores are the larger species, such as the aardwolf, bat-eared fox (*Otocyon megalotis*), and sloth bear (*Ursus ursinus*), all of which have low BFQs (Table 1). The sloth bear has lower BFQs at both the canine and carnassial than all other ursids (both $P < 0.001$). Similarly, the bat-eared fox has lower BFQs at the canine and carnassial than omnivorous canids (both $P < 0.001$), canids preying on small prey (both $P < 0.001$), and canids preying on large prey ($P = 0.001$ and $P < 0.001$, respectively), but only in part than canids preying on medium-sized prey ($P = 0.070$ and $P = 0.047$, respectively), owing to small sample size (two species; Table 1). As expected, the latter have much higher BFQs than the bat-eared fox, however. This trend is also apparent in some omnivores, such as the stink badger (*Mydaus javanensis*), whose long, mobile snout is well adapted for feeding on worms. The coatimundis (*Nasua* and *Nasua*) also reportedly feed extensively on insects, and have low BFQs among omnivores.

If higher bite force at any given body size (among taxa exhibiting carnassialized dentition) is an evolutionary adaptation for killing and processing prey that is large compared to the carnivores' own body size, convergent adaptation towards increased BFQ might be expected among unrelated species preying on relatively large prey (Wroe et al. 2005). Within Carnivora, this includes representatives of Canidae, Mustelidae, and Felidae.

Among canids, there are five hypercarnivorous species (*Canis familiaris*, *C. lupus*, *Cuon alpinus*, *Lycan pictus*, *Speothos venaticus*), i.e., species that feed on large mammalian prey and possess carnassial teeth that are more highly adapted for shearing meat (Van Valkenburgh 1991). Of these, *C. lupus*, *C. alpinus*, and *L. pictus*

frequently take prey that is larger than themselves (category 6). There is a clear trend in canine BFQs, from omnivores to consumers of progressively larger mammalian prey, in that omnivores have the lowest average BFQ (90.7), followed by small- (94.9), medium- (119.8), and large-prey (130.1) species. Confidence is limited by sample size, however, large-prey species have significantly higher canine BFQs than omnivores ($P = 0.001$) and small-prey ($P = 0.026$), but not medium-prey ($P = 0.299$) species. Conversely, medium-prey species have significantly higher canine BFQs than omnivores ($P = 0.032$), but not small-prey ($P = 0.138$) species. This is mirrored in carnassial BFQs, again going from omnivores through large-prey carnivores (averages 93.0, 101.9, 121.5, and 130.0, respectively). Canids specializing in large prey have significantly higher carnassial BFQs than omnivores ($P = 0.001$), and small-prey ($P = 0.008$) species, but not medium-prey species ($P = 0.212$).

All felids are hypercarnivores, feeding almost exclusively on meat, and this is unambiguously reflected in their highly derived shearing carnassial teeth. However, despite this relatively narrow ecological breadth, the same general trend is apparent in felids as in canids, with species feeding on small prey having lower BFQs than large-prey species, but the difference is less marked (small-prey, 100.0 and 101.3 [canine and carnassial, respectively]; medium-prey, 102.3 and 103.0, respectively; and large-prey, 114.8 and 117.8, respectively). The cheetah (*Acinonyx jubatus*) is an outlier, having much lower BFQs than other species in the medium-sized prey category (Table 1), in accord with its domed, rather gracile skull and weak muscle attachment sites compared to the puma and the pantherines (including *Neofelis*). Although the cheetah occasionally subdues prey comparable in mass to itself, most of its prey is small (Kruuk and Turner 1967, Schaller 1972, Sunquist and Sunquist 2002). Excluding the cheetah, the BFQ averages in the medium-prey category become 107.2 and 108.0, respectively. Large-prey species have significantly higher BFQs at the canines ($P = 0.032$) and carnassials ($P = 0.031$) than small-prey species, but there are no significant differences between species preying on small- or medium-sized prey, or medium-sized or large prey.

This indicates an evolutionary increase in BFQs with increased prey size for felids. It is notable that this trend toward increasing BFQ with relative prey size is evidenced in both felids and canids, despite the fact that large-prey specialists in these two families exhibit markedly different killing behaviors. The typically solitary felids kill large prey using an asphyxiating throat or muzzle bite, while the canids that concentrate on large prey are universally social and dispatch such prey through repeated slashing bites.

Similar trends are also apparent among mustelids. Average BFQs at the canines and carnassials, respectively, are 94.9 and 87.3 (omnivores), 99.1 and 96.2 (piscivores), 116.9 and 113.4 (small prey), 118.1 and 114.3 (medium prey), and 125.7 and 119.4 (large prey).

When carnivores (categories 3–6) are compared to omnivores, differences in BFQ at the canines and carnassials, respectively, approach ($P = 0.051$) or exceed significance ($P = 0.008$), and mustelids also show an increase in BFQs with increased carnivory, although for this taxon prey size appears to have less influence. Since mammalian and reptilian prey is typically more mechanically resistant than fish, it is not surprising that piscivores have, on average, moderate BFQs despite being faunivorous (Tables 1, 3). However, variation among individual species in the same feeding category and small sample sizes (six omnivores, six large-prey specialists and three medium-prey specialists) limit confidence in the results of statistical analyses for this family.

No herpestids or viverrids are adapted to large-prey predatory ecologies, and only the fossa (*Cryptoprocta ferox*) occasionally takes prey approaching its own body size. However, this group also shows increasing BFQ with increasing carnivory. Among herpestids, omnivores have lower BFQs at the canines and carnassials (82.8 and 83.9, respectively) than small-prey predators (92.0 and 93.5, respectively). In viverrids, some omnivores (*Arctogalidia* and *Macrogalidia*) have unexpectedly high BFQs and small-prey *Viverra* and *Viverricula* have moderate BFQs. This results in omnivores on average having higher BFQs than small-prey carnivores (119.7 and 112.1 at canines and carnassials, respectively, to 92.1 and 101.0, respectively). Neither groups are, however, statistically different. Viverrid feeding ecology is not well recorded and, consequently, we are less certain of the veracity of our allocations to feeding category for this family. In addition, most viverrids are less derived for specialized carnivory than are predators in other taxonomic groups. As previously noted, some herpestids and viverrids are insectivores, with most species eating at least some invertebrates, probably as a result of their small body size.

We conclude that, among carnivoran lineages, a trend toward the evolution of increased bite force relative to body mass has characterized increasing specialization toward both larger prey carnivory and herbivory on tough, fibrous plant material. Specialization on relatively large prey is accompanied by advanced carnassialization of the check–tooth row, while species concentrating on mechanically resistant plants are characterized by heavily molarized dentitia. Thus, while bite force is clearly informative, it must be considered in combination with other morphological indicators, particularly dental anatomy. Living viverrids superficially resemble primitive fossil miacid and viverravid (sensu lato) carnivorans (Gittleman 1989) both morphologically and, presumably, ecologically. In other carnivore groups, both dietary and size differences appear to have evolved further than in most viverrids. In contrast, insectivory in larger species has involved selection for specialized structures, e.g., the mobile lips, vaulted palate, and lack of incisors in the sloth bear (Nowak

1991, Joshi et al. 1997), while high bite forces appear to have been relatively unimportant, perhaps even undesirable.

Our findings suggest that selection for different bite forces relative to body size accompanied evolutionary trends in carnivore dietary specialization and that analyses of bite force adjusted for body mass may represent powerful adjuncts in the separation of living carnivorans into feeding guilds. Bite force estimates may also be of value with respect to the elucidation of killing behavior and feeding ecology in extinct taxa. However, while BFQ is informative with respect to generalized extant morphotypes, for fossil taxa, inference must be weighed against morphological and phylogenetic proximity to living species of known habitus (Wroe et al. 2005).

ACKNOWLEDGMENTS

We thank Christine Janis for comments on a previous draft, and Daphne Hills and Paula Jenkins (Natural History Museum, London) for access to collections. This work was supported by an Australian Research Council Discovery Grant and an ARC QE2 Research Fellowship (to S. Wroe), the University of New South Wales, and a long-term travel grant from the Danish Research Agency (to P. Christiansen).

LITERATURE CITED

- Biknevicius, A. R., and B. Van Volkenburg. 1996. Design for killing: craniodental adaptations of predators. Pages 393–428 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Cornell University Press, Ithaca, New York, USA.
- Bininda-Emonds, O. R. P., J. L. Gittleman, and A. Purvis. 1999. Building large trees by combining phylogenetic information: A complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* 74:143–175.
- Carbone, C., G. M. Mace, S. C. Roberts, and D. W. MacDonald. 1999. Energetic constraints on the diet of terrestrial carnivores. *Nature* 402:286–288.
- Chorn, J., and R. S. Hoffman. 1978. *Ailuropoda melanoleuca*. *Mammalian Species* 110:1–6.
- Christiansen, P., and J. S. Adolfssen. 2005. Bite forces, canine strengths and skull allometry in extant carnivores (Mammalia, Carnivora). *Journal of Zoology, London* 266:1–19.
- Cleuren, J., P. Aerts, and F. de Vree. 1995. Bite and joint force analysis in *Caiman crocodilus*. *Belgian Journal of Zoology* 125:79–94.
- Davis, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. *Fieldiana Zoology Memoirs* 3:1–339.
- Diaz-Uriarte, R., and T. Garland, Jr. 1998. Effects of branch length errors on the performance of phylogenetically independent contrasts. *Systematic Biology* 47:654–672.
- Emerson, S. B., and L. B. Radinsky. 1980. Functional analysis of sabertooth cranial morphology. *Paleobiology* 6:295–312.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* 42:265–292.
- Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetic independent contrasts. *Systematic Biology* 41:18–32.
- Gittleman, J. L., editor. 1989. *Carnivore behavior, ecology, and evolution*. Cornell University Press, Ithaca, New York, USA.
- Gittleman, J. L. 1994. Are the pandas successful specialists or evolutionary failures? *Bioscience* 44:456–464.

- Greaves, W. S. 1982. A mechanical limitation on the position of the jaw muscles of mammals: the one-third rule. *Journal of Mammalogy* 63:261–266.
- Greaves, W. S. 1983. A functional analysis of carnassial biting. *Biological Journal of the Linnean Society* 20:353–363.
- Greaves, W. S. 1988. The generalized carnivore jaw. *Zoological Journal of the Linnean Society* 85:267–274.
- Holekamp, K. E., L. Smale, R. Berg, and S. M. Cooper. 1997. Hunting rates and hunting success in the Spotted Hyaena (*Crocuta crocuta*). *Journal of Zoology, London* 242:1–15.
- Joshi, A. R., D. L. Garshelis, and J. L. D. Smith. 1997. Seasonal and habitat-related diets of sloth bears in Nepal. *Journal of Mammalogy* 78:584–597.
- Kingdon, J. 1997. *The Kingdon field guide to African mammals*. Academic Press, San Diego, California, USA.
- Koolstra, J. H., T. M. G. J. van Euden, W. A. Weijs, and M. Naeije. 1988. A three-dimensional mathematical model of the human masticatory system predicting maximum possible bite forces. *Journal of Biomechanics* 21:563–576.
- Kruuk, H., and M. Turner. 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti area, East Africa. *Mammalia* 31:1–27.
- Lyneborg, L. 1970. *Mammals in colour*. [In Danish.] Politiken, Copenhagen, Denmark.
- MacDonald, D. W., and C. Sillero-Zubiri, editors. 2004. *The biology and conservation of wild canids*. Oxford University Press, Oxford, UK.
- Meers, M. B. 2002. Maximum bite force and prey size of *Tyrannosaurus rex* and their relationships to the inference of feeding behavior. *Historical Biology* 16:1–12.
- Miller, G. J. 1984. One the jaw mechanism of *Smilodon californicus* Bovard and some other carnivores. Imperial Valley College Museum Society Occasional Paper 7:1–107.
- Mills, M. G. L. 1978. Foraging behaviour of the Brown Hyaena (*Hyaena brunnea* Thunberg 1820) in the Southern Kalahari. *Zeitschrift für Tierpsychologie* 48:113–141.
- Nowak, R. M. 1991. *Walker's mammals of the world*. Volumes I and II. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Peyton, B. 1980. Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *Journal of Mammalogy* 61:639–652.
- Radinsky, L. B. 1981a. Evolution of skull shape in carnivores. I. Representative modern carnivores. *Biological Journal of the Linnean Society* 15:369–388.
- Radinsky, L. B. 1981b. Evolution of skull shape in carnivores. II. Additional modern carnivores. *Biological Journal of the Linnean Society* 16:337–355.
- Rayfield, E. J., D. B. Norman, C. C. Horner, J. R. Horner, P. M. Smith, J. J. Thomason, and P. Upchurch. 2001. Cranial design and function in a large theropod dinosaur. *Nature* 409:1033–1037.
- Reid, F. A. 1997. *A field guide to the mammals of Central America and southeast Mexico*. Oxford University Press, Oxford, UK.
- Sacco, T., and B. Van Valkenburgh. 2004. Ecomorphological indicators of feeding behaviour in the bears (Carnivora: Ursidae). *Journal of Zoology, London* 263:41–54.
- Schaller, G. B. 1972. *The Serengeti lion*. University of Chicago Press, Chicago, Illinois, USA.
- Schaller, G. B., J. Hu, W. Pan, and J. Zhu. 1985. *The giant pandas of Wolong*. University of Chicago Press, Chicago, Illinois, USA.
- Schaller, G. B., T. Qitao, K. G. Johnson, X. Wang, H. Shen, and J. Hu. 1989. The feeding ecology of giant pandas and Asiatic black bears in the Tangjiahe Reserve, China. Pages 212–241 in J. L. Gittleman, editor. *Carnivore behavior, ecology, and evolution*. Volume I. Cornell University Press, Ithaca, New York, USA.
- Silva, M., and J. A. Downing. 1995. *CRC handbook of mammalian body masses*. CRC Press, Boca Raton, Florida, USA.
- Sinclair, A. G., and R. N. McAleander. 1987. Estimates of forces exerted by the jaw muscles of some reptiles. *Journal of Zoology, London* 213:107–115.
- Stirling, I., editor. 1993. *Bears. Majestic creatures of the wild*. HarperCollins, London, UK.
- Sunquist, M., and F. Sunquist. 2002. *Wild cats of the world*. Chicago. University of Chicago Press, Chicago, Illinois, USA.
- Thomason, J. J. 1991. Cranial strength in relation to estimated biting forces in some mammals. *Canadian Journal of Zoology* 69:2326–2333.
- Trinkel, M., P. H. Fleischmann, A. F. Steindorfer, and G. Kastberger. 2004. Spotted hyaenas (*Crocuta crocuta*) follow migratory prey. Seasonal expansion of a clan territory in Etosha, Namibia. *Journal of Zoology, London* 264:125–133.
- Van Valkenburgh, B. 1991. Iterative evolution of hypercarnivory in canids (Mammalia, Carnivora): Evolutionary interactions among sympatric predators. *Paleobiology* 17:340–362.
- Van Valkenburgh, B., and C. B. Ruff. 1987. Canine tooth strength and killing behaviour in large carnivores. *Journal of Zoology, London* 212:379–397.
- Weijs, W. A., and B. Hillen. 1984. Relationship between the physiological cross-section of the human jaw muscles and their cross-sectional area in computer tomograms. *Acta Anatomica* 118:129–138.
- Weijs, W. A., and B. Hillen. 1985. Cross-sectional areas and estimated intrinsic strength of the human jaw muscles. *Acta Morphologicae Neerlandiae-Scandinavicae* 23:267–274.
- Wroe, S., C. McHenry, and J. J. Thomason. 2005. Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. *Proceedings of the Royal Society of London Series B* 272:619–625.