

Costs of carnivory: tooth fracture in Pleistocene and Recent carnivorans

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Large, carnivorous mammals often break their teeth, probably as a result of tooth to bone contact that occurs when carcasses are consumed more fully, a behaviour likely to occur under conditions of food stress. Recent studies of Pleistocene predators revealed high numbers of teeth broken in life, suggesting that carcass utilization and, consequently, food competition was more intense in the past than at present. However, the putative association between diet and tooth fracture frequency was based on a small sample of large, highly carnivorous species. In the present study, a greater diversity of extant carnivorans is sampled, including insectivorous, omnivorous, and carnivorous forms, ranging in size from weasels to tigers. Species that habitually consume hard foods (bones, shells) had the highest fracture frequencies, followed by carnivores, and then insectivorous and/or omnivorous species. Predator and prey sizes were not associated with tooth fracture frequency, but more aggressive species did break their teeth more often. Comparison of the modern sample with five Pleistocene species confirms the previous finding of higher tooth breakage in the past, although some extant species have fracture frequencies that approach those of extinct species. Thus, the Pleistocene predator guild appears to have been characterized by relatively high levels of competition that are rarely observed today. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 68–81.

ADDITIONAL KEYWORDS: Carnivora – diet – feeding behaviour – paleoecology – skeletal injury.

INTRODUCTION

Injury rates of vertebrate bones and teeth as well as invertebrate shells have provided novel windows into the behaviour of extinct species and past ecosystems. Among the best-known studies are those of Vermeij (Vermeij, Zipser & Dudley, 1980; Vermeij, Schindel & Zipser, 1981) who examined shell-boring traces in marine invertebrates to study the evolution of predator–prey interactions over the Phanerozoic. Among vertebrates, evidence from tooth fracture and wear has provided insight into feeding behaviour of several extant and extinct species, including the infamous man-eating lions of Tsavo (Patterson, Neiburger & Kasiki, 2003), tyrannosaurid dinosaurs (Schubert & Ungar, 2005), Tasmanian wolves, *Thylacinus*

cynocephalus (Jones & Stoddart, 1998), and two sabertooth cats, *Homotherium serum* (Marean & Ehrhardt, 1995) and *Smilodon fatalis* (Van Valkenburgh & Hertel, 1993). In addition, the study of injury rate or type can reveal previously unknown features of past communities. For example, Dietl, Herbert & Vermeij (2004) documented a long-term shift in predation styles (location of drill holes) among marine snail predators between the Pliocene and the present in response to reduced levels of interspecific competition and predation following an extinction event. Similarly, Van Valkenburgh & Hertel (1993) and Leonard *et al.* (2007) recorded a post-Pleistocene drop in tooth fracture incidence among large, terrestrial, mammalian carnivores that appeared to reflect a lessening of competition intensity with a consequent diminished need for heavy carcass utilization. Together, these studies suggest that the dynamics of present-day ecosystems and species interactions have undergone significant changes in the recent past.

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A correct inference concerning the ecological implications of differences in injury rate or type in extinct faunas depends on a confident assessment of injury cause. In the case of Pleistocene mammalian predators, it was argued that higher tooth fracture frequencies were a result of frequent tooth to bone contact when feeding (Van Valkenburgh & Hertel, 1993). This was based on a survey of tooth breakage in extant species of carnivorans, in which habitual bone-crackers (grey wolves, hyenas) had significantly more broken teeth (Van Valkenburgh, 1988). However, that study included nine species only, all of which were of large size (mass > 20 kg) and predominantly carnivorous. Subsequently, Fenton *et al.* (1998) compared tooth fracture frequencies between bats (13 species) and carnivorans (ten species) with a wider range of sizes and diets and found no significant relationship between diet and fracture incidence, unless the nine large carnivoran taxa from Van Valkenburgh (1988) were included. Alternative explanations for frequent tooth breakage such as body size, prey size, or intraspecific aggression levels were suggested. To clarify the causes of tooth fracture, a comparative analysis of tooth fracture data from 36 species of extant and five Pleistocene carnivoran species was conducted. For the comparative study, over 3500 individual skulls that included more than 120 000 teeth were examined for dental wear and fracture. The extant species range in size from weasels (< 0.5 kg) to tigers (> 150 kg) and include insectivorous, omnivorous, carnivorous, and durophagous (hard object) feeders. The paleontological sample includes five late Pleistocene species (spanning approximately 50–11 000 years ago) and is dominated by specimens from three predator traps in which numerous carnivores were lured to their death by dying or dead herbivores: Rancho La Brea, California tar seeps, San Josecito Cave, Mexico, and the Talara tar seeps of Peru. The fourth Pleistocene sample represents attritional deaths of grey wolves and American lions in the permafrost deposits of Alaska. The predominance of predator trap samples reflects the need for large samples of 20 or more individuals from the same geographic region spanning a relatively short period of geologic time for comparison with modern samples. Carnivores are usually poorly represented in single fossil deposits, except in the case of predator traps. Importantly, there is no evidence that the predator traps used here were biased towards the entrapment of old or injured predators. By contrast, most of the individuals in the three deposits appear to have been young adults (Miller, 1968; Harris, 1992; Van Valkenburgh & Hertel, 1993; Binder, Thompson & Van Valkenburgh, 2002). Thus, it is reasonable to compare their tooth fracture patterns with those of extant species in museum collections.

MATERIAL AND METHODS

Skulls and jaws of 36 species of extant adult, wild-caught carnivorans were examined with sample sizes per species in the range 28–366 (mean = 103; Table 1). Whenever possible, approximately even numbers of males and females from a single, relatively limited geographic distribution were sampled. In some species, individuals from multiple distinct localities were included, and these data were analysed to assess levels of intraspecific variation (Table 2). The Pleistocene sample includes five species, sabertooth cat (*S. fatalis*), American lion (*Panthera atrox*), dire wolf (*Canis dirus*), grey wolf (*Canis lupus*), and coyote (*Canis latrans*). Relatively few complete skulls were available for the fossil sample so tooth fracture incidence was assessed on a per tooth (rather than per individual) basis as in Van Valkenburgh & Hertel (1993). The numbers of teeth examined for each fossil species were: *S. fatalis* ($N = 1777$); *P. atrox* ($N = 400$); *C. dirus* ($N = 4830$); *C. lupus* ($N = 373$); and *C. latrans* ($N = 1248$). All modern and fossil specimens represent part of the collections of various museums, a list of which is available from the author upon request.

Data collected for each individual include: (1) a qualitative estimate of overall wear stage; (2) total number and identity of teeth present; and (3) position of all broken teeth. A tooth was identified as broken in life only if it exhibited clear damage (partially gone or significant loss of a cusp) and showed subsequent wear in life. Missing teeth were noted but are not included as broken in life because it is difficult to determine whether they had been resorbed after fracture or were never present. As in previous studies (Van Valkenburgh, 1988; Van Valkenburgh & Hertel, 1993), wear stage was recorded as one of three categories: (1) 'slight', little or no apparent wear observed on shear facets or blunting of cusps; (2) 'moderate', shear facets apparent on carnassial teeth, cusps blunted on most teeth; or (3) 'heavy', carnassial teeth with strong shear facets and/or blunted cusps, premolars and molars with well-rounded cusps. Wear stage is assumed to increase with age but the rate at which this occurs may vary within and among species, depending on diet (Carlsson, Hugoson and Persson, 1966; Berkovitz & Poole, 1977).

Tooth fracture incidence can be assessed on both a per-individual and per-tooth basis. Because a single individual may have multiple broken teeth, it has been suggested that assessment on a per-individual basis is less biased. Although this may be true, comparisons with fossil material necessitate the use of fracture frequency on a per-tooth basis because complete skulls are very rare and, in some cases, different partial specimens of dentary bones may have belonged to the same individual. In the present study,

Table 1. List of extant and Pleistocene species, their body mass, sample size (N individuals), percent of individuals with one or more broken teeth, weighted average tooth fracture frequency multiplied by 100 with and without incisors included, and behavioural classifications

Species	Body mass (kg)	N	% Individuals with ≥ 1 broken	% Broken teeth		Diet	Prey size	Aggression level
				(all teeth)	(without incisors)			
Felidae								
<i>Panthera leo</i>	162	121	24	1.6	2.6	C	L	HI
<i>Panthera tigris</i>	170	88	36	2.3	3.7	C	L	LO
<i>Panthera pardus</i>	45	120	34	2.3	4.5	C	M	LO
<i>Panthera onca</i>	70	71	15	0.9	1.1	C	M	LO
<i>Acinonyx jubatus</i>	58	54	15	0.6	0.5	C	M	LO
<i>Puma concolor</i>	60	213	34	2.1	3.6	C	L	LO
<i>Caracal caracal</i>	17	50	28	2.1	3.4	C	M	LO
<i>Lynx rufus</i>	10	228	32	2.3	4.3	C	M	LO
Family mean			27.3	1.78	2.96			
Hyaenidae								
<i>Crocuta crocuta</i>	52	120	57	4.6	5.4	B/S	L	HI
<i>Hyaena brunnea</i>	9	39	41	4.1	5.3	B/S	M	LO
<i>Hyaena hyaena</i>	32	57	35	2.0	2.7	B/S	S	LO
Family mean			44.3	3.57	4.47			
Canidae								
<i>Canis lupus</i>	42	334	24	3.8	4.3	B/S	L	HI
<i>Canis latrans</i>	13	366	56	3.6	4.5	C	M	LO
<i>Lycaon pictus</i>	21	98	25	0.7	0.7	C	L	LO
<i>Vulpes vulpes</i>	7	278	56	3.5	4.5	C	M	LO
<i>Vulpes macrotis</i>	2.5	45	27	0.8	1.0	C	S	LO
<i>Alopex lagopus</i>	3.5	132	55	2.3	2.8	C	S	LO
<i>Urocyon cinereoargenteus</i>	4.5	44	61	4.3	5.9	C	S	LO
<i>Urocyon littoralis</i>	2	163	38	1.4	2.0	C	S	LO
<i>Otocyon megalotis</i>	4	45	11	0.5	0.6	O/I	N	LO
<i>Canis mesomelas</i>	7	30	27	1.4	1.9	C	M	LO
<i>Canis aureus</i>	7	31	13	1.2	1.7	C	M	LO
<i>Canis adustus</i>	7	28	7	0.3	0.4	C	M	LO
Family mean			33.3	1.98	2.53			
Mustelidae								
<i>Mustela nivalis</i>	0.1	100	46	2.1	3.0	C	S	HI
<i>Mustela erminea</i>	0.1	72	67	3.4	4.9	C	S	HI
<i>Mustela frenata</i>	0.2	104	44	2.7	3.9	C	S	HI
<i>Martes americana</i>	0.9	60	23	0.9	0.8	C	M	LO
<i>Martes pennanti</i>	3.4	86	41	2.6	2.4	C	S	LO
<i>Gulo gulo</i>	21.5	105	23	1.7	1.4	C	S	LO
<i>Enhydra lutris</i>	21	50	50	3.2	4.3	B/S	M	LO
<i>Taxidea taxus</i>	8.4	57	26	1.5	2.0	C	M	LO
Family mean			40	2.26	2.84			
Mephitidae								
<i>Mephitis macroura</i>	0.8	34	21	1.1	1.7	O/I	S	LO
<i>Mephitis mephitis</i>	3	70	9	0.4	0.7	O/I	S	LO
<i>Spilogale putorius</i>	0.7	61	7	0.2	0.3	O/I	S	LO
Family mean			12.3	0.57	0.90			
Procyonidae								
<i>Procyon lotor</i>	6.5	76	37	1.9	2.4	O/I	N	LO

Table 1. *Continued*

Species	Body mass (kg)	N	% Individuals with ≥ 1 broken	% Broken teeth		Diet	Prey size	Aggression level
				(all teeth)	(without incisors)			
<i>Bassariscus astutus</i>	1	65	26	0.8	1.0	O/I	N	LO
Family mean			31.5	1.35	1.70			
Mean for all extant species				2.00	3.00			
Pleistocene species								
<i>Canis dirus</i>	50			5.0	4.8			
<i>Canis latrans</i>	20			5.0	6.8			
<i>Canis lupus</i>	40			11.0	9.9			
<i>Smilodon fatalis</i>	230			7.0	7.5			
<i>Panthera atrox</i>	400			12.5	17.5			
Pleistocene mean				8.10	9.30			

Diet: C, carnivorous; B/S, bone or shell hard-object feeders; O/I, omnivorous and/or insectivorous. Prey size: L, large; M, moderate; S, small; N, nonpredacious. References for body mass and behavioural classifications include: (Kingdon, 1977; Chapman & Feldhamer, 1982; Gittleman, 1986; Skinner & Smithers, 1990; Nowak, 1999; Sunquist & Sunquist, 2002; King & Powell, 2007), and other references provided in the text for specific species.

fracture frequency is examined on a per-individual basis for comparison of extant carnivorans with the bat species described by Fenton *et al.* (1998) because that is the metric they used. The alternative per-tooth measure is used for all remaining analyses because one of the primary intents of this project was to better understand the apparently high rates of fracture in late Pleistocene predators. As in Van Valkenburgh & Hertel (1998), a weighted average of tooth fracture frequencies for each tooth type or position (e.g. incisors, molars) was calculated for all fossil and extant species to compensate for differences in the distribution of tooth types among species. The probability of fossil preservation of all tooth types is not identical; single-rooted teeth are less likely to be preserved *in situ* in the dentary or maxilla than are multiple-rooted teeth. The weighted average is the sum across tooth types of the product of the observed fracture frequency per tooth type and the proportion of the tooth row represented by that tooth type in a complete dentition. In addition, the incidence of fracture was calculated separately for each tooth position (e.g. number of canines broken/total number of canines observed) to explore differences among species in the distribution of fracture along the tooth row.

To assess possible causes of tooth fracture, each extant species was assigned to one of the following dietary categories that reflect typical food texture: (1) carnivorous, flesh-eaters that rarely consume large bones or other hard foods; (2) bone/shell, flesh-eaters that regularly consume large bones or hard-shelled invertebrates, or (3) omnivorous or insectivorous, species that rarely consume hard foods (abbreviated as

'C', 'B/S', and 'O/I', respectively). They were also assigned to one of four categories that reflected typical prey size: (1) large, at least 45% of predator mass; (2) moderate, 25–45% of predator mass, (3) small, less than 25% of predator mass; and (4) predominantly nonpredacious or insectivorous. Because it could be expected that species with high levels of intraspecific aggression might engage more often in battles that result in tooth fracture, each species was also assigned to one of two aggression level categories, high or low ('HI' or 'LO'). Unfortunately, behavioural data for this last category were relatively limited for many species, and only a few species were placed in the 'HI' category based on field documentation of repeated instances of intraspecific combat that resulted in injury or death. Consequently, the results of the aggression comparisons must be considered as tentative. Species assignments to each of the above categories and references are listed in Table 1.

The relationship between categorical variables and tooth fracture incidence (both total and by tooth position) in the extant sample were explored with both analysis of variance and nonparametric (Kruskal–Wallis, Mann–Whitney *U*-test) statistics. Both produced very similar results and, because some comparisons did violate assumptions of normality among samples, only results of nonparametric tests are presented here. Linear regression and Pearson correlation coefficients were used to look for associations between body mass and fracture frequency, and wear stage (proportion of each species sample in each of the wear stages) and fracture frequency, respectively.

Table 2. Percent broken teeth (weighted average tooth fracture frequencies [incisors included] multiplied by 100), provenance, and sample sizes for subspecies or populations analysed within seven extant and one extinct species

Species	Locality	<i>N</i>	Percent broken teeth
<i>Alopex lagopus</i>			
<i>A. l. lagopus</i>	Alaska	66	2.5 (0.08)
<i>A. l. pribilofensis</i>	Pribilof Islands	66	2.1 (0.07)
<i>Canis latrans</i>			
<i>C. l. mearnsi</i>	Arizona	88	2.8 (0.07)
<i>C. l. incolatus</i>	Alaska	52	3.3 (0.1)
<i>C. l. frustror</i>	Southeastern USA	94	2.9 (0.07)
<i>C. l. lestes</i>	Washington	66	4.5 (0.1)
<i>C. l. lestes</i>	Wyoming	66	5 (1.1)
<i>Canis lupus</i>			
<i>C. l. lycaon</i>	Isle Royale National Park	26	7.5 (2.6)
<i>C. l. lycaon</i>	Minnesota, Michigan	65	6.3 (1.3)
<i>C. l. irremotus</i>	Idaho, Canada	66	2 (0.07)
<i>C. l. mongollensis</i>	New Mexico, Texas	83	3.9 (0.09)
<i>C. l. pambasileus</i>	Alaska	74	4.1 (0.09)
<i>C. l. irremotus</i>	Yellowstone National Park	20	1.2 (0.06)
<i>Urocyon littoralis</i>			
<i>U. l. santarosae</i>	Santa Rosa Island	38	0.6 (0.05)
<i>U. l. clementae</i>	San Clemente Island	17	1.8 (1.5)
<i>U. l. littoralis</i>	San Miguel Island	22	1.6 (1.2)
<i>U. l. santacruzae</i>	Santa Cruz Island	36	1.7 (0.09)
<i>U. l. dickeyi</i>	San Nicolas Island	50	1.7 (0.07)
<i>Vulpes vulpes</i>			
<i>V. v. alascensis</i>	Alaska	89	5.8 (1)
<i>V. v. regalis</i>	Iowa	88	2.4 (0.07)
<i>V. v. niloticus</i>	Egypt	51	3.7 (1.1)
<i>V. v. fulva</i>	New York	50	0.9 (0.05)
<i>Lynx rufus</i>			
<i>L. r. floridanus</i>	Florida	54	1.3 (0.08)
<i>L. r. rufus</i>	New England	42	4.1 (1.8)
<i>L. r. texensis</i>	Texas	66	1.7 (0.08)
<i>L. r. fasciatus</i>	Oregon	66	3.1 (1.1)
<i>Puma concolor</i>			
<i>P. c. coryi</i>	Florida	48	3.3 (1.4)
<i>P. c. stanleyana</i>	Texas	93	1.9 (0.07)
<i>P. c. oregonensis</i>	Oregon, Washington	72	1.7 (0.08)
<i>Canis dirus</i>			
Rancho La Brea	All pits		5 (0.09)
Rancho La Brea	Pit 13		7 (2.3)
Rancho La Brea	Pit 61/67		2 (1.1)
San Josecito Cave	Mexico		4.6 (3.7)
Talara	Peru		5 (3.1)

Shown in parentheses are the 95% confidence intervals for the fracture frequencies.

RESULTS

CARNIVORANS VERSUS BATS

Contra Fenton *et al.* (1998), carnivorans break their teeth significantly more often than do bats, based on a comparison of the bat species ($N = 13$) from their

study and the 36 species of extant carnivorans in the present study ($P < 0.001$, $t = 5.457$, d.f. = 47) (Fig. 1, Table 1). On average, 33% of individuals had at least one broken tooth among carnivorans, whereas the same figure is only 8% for bats. This difference is not simply due to the inclusion of large species (mass

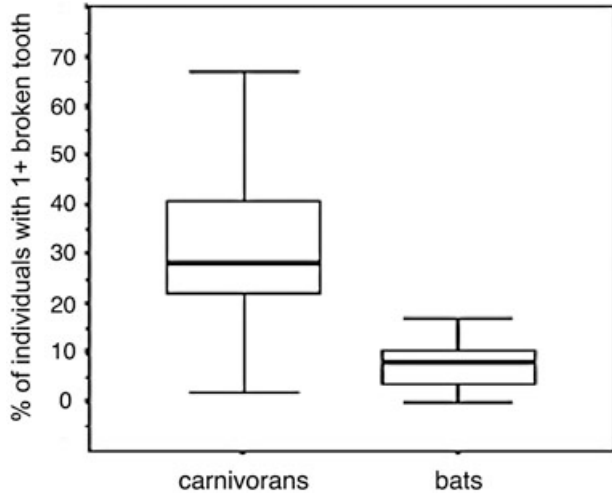


Figure 1. Box plot of the percent of all individuals observed with at least one broken tooth for 36 carnivoran and 13 bat species. Data for bats are from Fenton *et al.* (1998).

> 7 kg) in the carnivoran sample. If the analysis is confined to a comparison of the 13 bats with the 18 carnivorans weighing less than 7 kg in my sample, the difference is still significant (mean for small carnivorans = 30.4%, $P < 0.001$, $t = 4.033$, d.f. = 29). Notably, if only those carnivorans classified here as rarely taking vertebrate prey ('OI') or as insectivorous in Fenton *et al.* (1998) are compared with the 13 bat species, there is no significant difference ($P = 0.09$, $t = 1.767$, d.f. = 19).

PLEISTOCENE VERSUS RECENT CARNIVORANS

Mean fracture frequency for the five sampled Pleistocene species is 8% (with incisors included) and 9% (without incisors) and significantly exceeds that of all 36 extant species (mean = 2–3%), with or without incisors included ($P < 0.01$, Mann–Whitney U -test; Table 1). The Pleistocene sample includes three canids and two felids that had 5–17.5% of their teeth broken (excluding incisors), whereas the more diverse modern sample ranged from 0.3% (*Spilogale putorius*) to 5.9% (*Urocyon cinereaargenteus*). When all teeth are considered, there is no overlap between mean fracture frequencies of recent and Pleistocene species, and the American lion and permafrost grey wolf samples exhibit very high numbers of broken teeth (Fig. 2A). When incisors are excluded, the dire wolf falls within the upper range of the recent sample, and only the lion appears as an outlier (Fig. 2B). Two species, coyote and grey wolf, are represented by both fossil and modern samples and in both instances, modern samples exhibit significantly reduced fracture frequencies (incisors excluded), 4% versus 10% in wolf

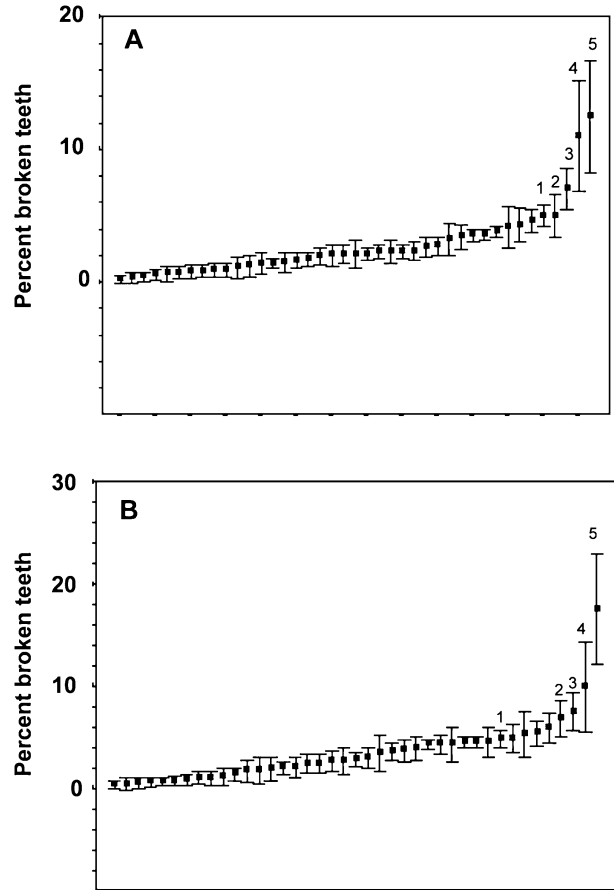


Figure 2. Percent broken teeth (weighted average tooth fracture frequency multiplied by 100) for sampled extant and Pleistocene carnivorans, including incisors (A) and without them (B), arranged in order of fracture frequency. Error bars represent 95% confidence intervals based on the binomial distribution (Wonnacott & Wonnacott, 1985). Pleistocene species: 1, dire wolf, *Canis dirus*; 2, coyote, *Canis latrans*; 3, sabertooth cat, *Smilodon fatalis*; 4, grey wolf, *Canis lupus*; and 5, American lion, *Panthera atrox*.

($P < 0.001$, $\chi^2 = 22.66$) and 5% versus 7% in coyote ($P < 0.001$, $\chi^2 = 13.27$). Notably, there are some populations of extant carnivorans that overlapped the low end of the Pleistocene fracture frequency distribution (Table 2). For example, grey wolves from Isle Royale and northern Minnesota and Michigan exhibited relatively high fracture frequencies in the range of 6–8%, as do Alaskan red foxes. However, none of the extant populations or species sampled had a fracture frequency above 8%, with or without incisors included.

The high incidence of fracture in Pleistocene species relative to the extant sample is spread across the entire tooth row; canines, premolars and post-carnassial molars are broken approximately three times more often and incisors and carnassials are broken six times more frequently (Table 3). The

Table 3. Percentage of each sample assigned to each of the three wear stages and the percent of tooth fracture for each tooth type (number broken/number observed multiplied by 100) for extant and Pleistocene species

Species	% Slight	% Moderate	% Heavy	I	C	PM	CR	M
Felidae								
<i>Panthera leo</i>	0.67	0.24	0.09	0.3	5.4	5.4	2.7	
<i>Panthera tigris</i>	0.66	0.33	0.01	1.4	9.2	9.2	1.5	
<i>Panthera pardus</i>	0.63	0.34	0.03	0.6	9.8	9.8	2.5	
<i>Panthera onca</i>	0.73	0.23	0.04	0.7	3.2	3.2	0.7	
<i>Acinonyx jubatus</i>	0.85	0.11	0.04	0	3.3	3.3	1.6	
<i>Puma concolor</i>	0.59	0.36	0.05	0.5	8.4	8.4	1.7	
<i>Caracal caracal</i>	0.88	0.12	0.00	0.2	6.8	6.8	1.5	
<i>Lynx rufus</i>	0.53	0.43	0.04	0.2	6.8	6.8	1.5	
Family mean	0.69	0.27	0.04	0.49	6.61	6.61	0.02	
Hyaenidae								
<i>Crocuta crocuta</i>	0.25	0.63	0.12	3.1	9.6	9.6	1.7	
<i>Hyaena brunnea</i>	0.33	0.48	0.19	1.9	8.9	8.3	4.2	
<i>Hyaena hyaena</i>	0.40	0.42	0.18	0.7	8.3	8.3	1.3	
Family mean	0.33	0.51	0.16	1.90	8.93	8.73	0.02	
Canidae								
<i>Canis lupus</i>	0.56	0.36	0.08	2.8	9.8	9.8	3.6	1.7
<i>Canis latrans</i>	0.51	0.43	0.06	1.3	9.8	9.8	2.5	0.2
<i>Lycaon pictus</i>	0.52	0.44	0.04	0.8	4.2	4.2	1.5	0.3
<i>Vulpes vulpes</i>	0.47	0.44	0.09	0.8	14.4	14.4	5.1	0.4
<i>Vulpes macrotis</i>	0.53	0.42	0.05	0.2	6.3	6.3	0.6	0
<i>Alopex lagopus</i>	0.62	0.34	0.04	1.1	10.4	10.4	2.1	0.3
<i>Urocyon cinereoargenteus</i>	0.26	0.64	0.10	0.2	8.9	8.9	7.6	0.3
<i>Urocyon littoralis</i>	0.32	0.48	0.20	0.2	8.7	8.7	0.9	0.4
<i>Otocyon megalotis</i>	0.49	0.38	0.13	0.4	1.8	1.8	0	0.2
<i>Canis mesomelas</i>	0.47	0.44	0.10	0	7.5	7.5	0.8	0
<i>Canis aureus</i>	0.49	0.42	0.09	0	5.1	5.1	4.0	1.7
<i>Canis adustus</i>	0.61	0.32	0.07	0	2.8	2.8	0	1.7
Family mean	0.49	0.43	0.09	0.65	7.48	7.48	2.39	0.6
Mustelidae								
<i>Mustela nivalis</i>	0.49	0.50	0.02	0.6	9.2	0.1	2.3	0
<i>Mustela erminea</i>	0.44	0.49	0.08	0.5	17.3	0.2	1.7	0
<i>Mustela frenata</i>	0.48	0.42	0.10	0.5	12.0	0.1	1.5	0.2
<i>Martes americana</i>	0.53	0.46	0.01	0.5	0.6	0	0	0
<i>Martes pennanti</i>	0.56	0.36	0.08	1.1	12.7	0.1	6.3	2.7
<i>Gulo gulo</i>	0.70	0.27	0.03	1.1	5.9	0.1	1.2	0
<i>Enhydra lutris</i>	0.50	0.37	0.13	1.7	15.6	0.2	4.0	0.5
<i>Taxidea taxus</i>	0.20	0.60	0.20	0.5	7.3	0.1	0	0.9
Family mean	0.49	0.43	0.08	0.81	10.1	0.11	2.13	0.54
Mephitidae								
<i>Mephitis macroura</i>	0.08	0.44	0.48	0	0.1	0	0	0.8
<i>Mephitis mephitis</i>	0.30	0.51	0.19	0	1.4	0	0.3	0
<i>Spilogale putorius</i>	0.25	0.42	0.33	0	0.8	0	0	0
Family mean	0.21	0.46	0.33	0	0.77	0	0	0
Procyonidae								
<i>Procyon lotor</i>	0.32	0.50	0.18	0.6	0.8	0.8	1.3	0.4
<i>Bassariscus astutus</i>	0.34	0.52	0.14	0.4	0.4	0.4	0.4	0.5
Family mean	0.33	0.51	0.16	0.50	0.58	0.60	0.9	0.5
Mean for all extant species	0.49	0.41	0.11	0.7	7	2	2	0.5
Pleistocene species								
<i>Canis dirus</i>	0.50	0.44	0.06	6.8	18.8	3.5	4.3	2.7
<i>Canis latrans</i>	0.12	0.77	0.11	0	19	3	3.2	5.1
<i>Canis lupus</i>	0.01	0.62	0.37	14.5	22.7	2.8	3	4.9
<i>Smilodon fatalis</i>	0.62	0.36	0.02	7.2	11.2	3	4	
<i>Panthera atrox</i>	0.56	0.33	0.11	6.4	36	3	4	
Pleistocene mean	0.36	0.5	0.13	6.98	21.5	3	3.53	4

I, incisors; C, canines, PM, pre-carnassial premolars; CR, carnassials, M, post-carnassial molars.

absence of broken incisors in Pleistocene coyotes is not significant because only three incisors were preserved in place in either jaws or skulls. Apparently, these small peg-like teeth tended to slip out of their sockets in the asphalt medium. In the modern sample of coyotes, approximately 1% of the incisors were broken, which is similar to the mean incisor breakage for all extant species (Table 2).

FRACTURE FREQUENCY, BODY MASS, AND WEAR STAGE

Although Fenton *et al.* (1998) suggested that larger species might be expected to have more broken teeth than smaller species because they have longer life spans, this appears not to be the case for carnivorans. There is no significant correlation between body mass and dental fracture frequency in the sample of 36 carnivorans ($r^2 = 0.02$, $P = 0.47$). Although there are large species with relatively high fracture frequencies, there are also small species, such as weasels, that display many broken teeth and large species, such as felids, that have many fewer (Fig. 3).

The incidence of tooth fracture should be positively correlated with the degree of tooth wear. The correlations between tooth fracture frequency and the proportion of individuals (recent sample) or specimens (fossil sample) assigned to each of the three wear stage categories, respectively, were not significant ($P > 0.05$, two-tailed test). However, the proportion in the moderate wear category approached significance ($P = 0.07$) and achieved significance when reanalysed as a one-tailed test ($P < 0.05$). The positive association between tooth breakage and dental wear stage was more apparent when insectivorous forms were excluded because they tended to show low fracture frequencies despite a high proportion of moderately to heavily worn individuals. Thus, there does appear to be a positive association between wear stage and fracture frequency among species that consume vertebrates, although the relationship is not tight ($r^2 = 0.2$, $P = 0.01$, Fig. 3).

FRACTURE FREQUENCY AND THE CATEGORICAL VARIABLES

Of the four categorical variables, diet, prey size, aggression level, and family membership, only diet and aggression level were significantly correlated with tooth fracture frequency (Table 4). In the case of diet, extant hard object feeders (B/S) displayed significantly more broken teeth than either flesh-eaters (C) or omnivore/insectivores (O/I). Species deemed to have higher levels of intraspecific aggression had a significantly higher mean fracture frequency than that of species classified as less aggressive ($P < 0.05$, $\chi^2 = 5.073$).

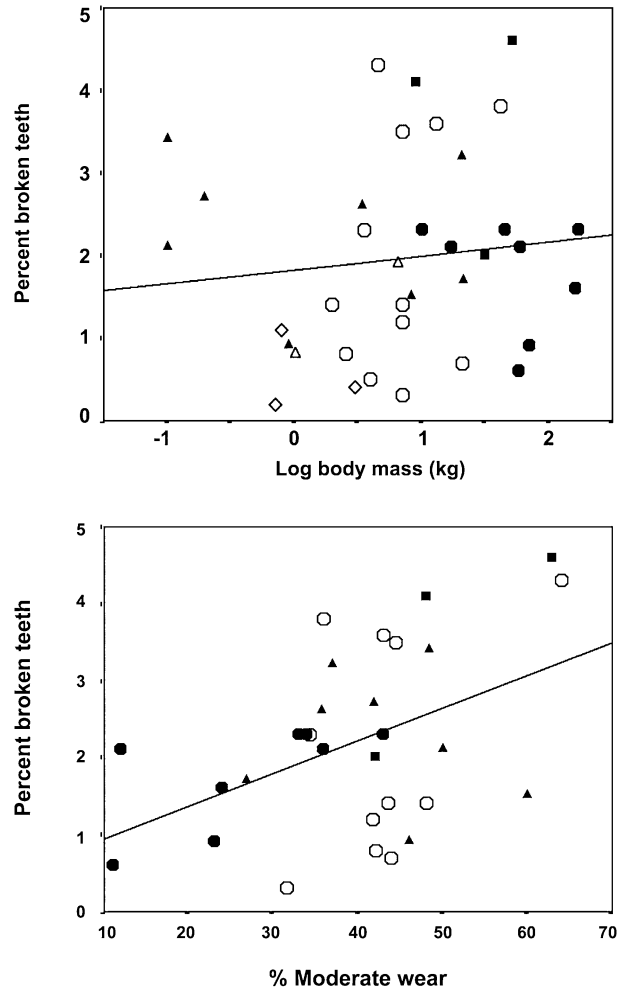


Figure 3. (Top) Scatterplot of percent broken teeth (weighted average tooth fracture frequency multiplied by 100 for all teeth) against log body mass for the extant sample. Filled circles, Felidae; filled squares, Hyaenidae; filled triangles, Mustelidae; open circles, Canidae; open diamonds, Mephitidae; open triangles, Procyonidae. The line represents a least-square fitted linear regression ($P = 0.47$, $r^2 = 0.02$). (Bottom) Scatterplot of percent broken teeth (weighted average tooth fracture frequency multiplied by 100 for all teeth) against percent of individuals assigned to the moderate wear category for species classified as carnivorous (C) or durophagous (B/S). The line represents a least-square fitted linear regression ($P = 0.01$, $r^2 = 0.2$, $y = 0.0005x + 0.004$).

Although typical prey size did not show a significant correlation with mean fracture frequency ($P = 0.21$), the rank order of means declined with typical prey size, suggesting a weak effect that might become significant with larger sample size (Table 4). Because carnivoran families are often diagnosed by aspects of their dentition (dental formula, carnassial and post-carnassial molar shape), it might be

Table 4. Percent broken teeth (mean average weighted tooth fracture frequencies and standard deviations in parentheses multiplied by 100) for extant species within each of the behavioural categories and by family

Category	<i>N</i>	Mean percent fracture frequency (SD)	χ^2	<i>P</i>
Diet			12.857	0.002*
C	25	2 (1)		
B/S	5	4 (1)		
O/I	6	1 (1)		
Prey size			8.99	0.29
L	6	2.5 (1.4)		
M	15	2.1 (1)		
S	12	1.9 (1.4)		
N	3	1.1 (7.4)		
Aggression level			5.073	0.024
HI	6	3 (1.1)		
LO	30	1.8 (1)		
Family			10.11	0.079
Felidae	8	1.8 (0.7)		
Hyaenidae	3	3.6 (1.4)		
Canidae	12	2 (1.4)		
Mustelidae	8	2.3 (0.9)		
Mephitidae	3	0.6 (0.5)		
Procyonidae	2	1.4 (1.2)		

*All three groups differ significantly from one another. *N*, number of species per category, chi-square and *P*-values are shown for a Kruskal–Wallis test for significant differences among groups.

Diet: C, carnivorous; B/S, bone or shell hard-object feeders; O/I, omnivorous and/or insectivorous. Prey size: L, large; M, moderate; S, small; N, nonpredacious.

expected that there would be a significant association between family identity and the likelihood of fracture. This was not the case; instead, there was considerable overlap among families in the range of fracture frequencies, with the hyaenids (all durophagous) at the high end and the mephitids (all relatively nonpredacious) at the low end (Table 4).

FRACTURE FREQUENCY AND TOOTH POSITION

As found in Van Valkenburgh (1988), all teeth are not equally likely to fracture. Comparing the percentages of observed teeth broken for each of the five tooth types (incisors, canines, premolars, carnassials, and post-carnassial molars) among the extant species reveals that canine teeth suffer much higher rates of fracture (mean = 7%) than any other teeth (means = 1–2%) (Table 3). Some of this difference can be explained by tooth fracture variation within diet

and aggression level categories. Both meat-eating groups (C, B/S) significantly exceeded the least predacious group (O/I) in both canine and carnassial tooth fracture incidence ($P < 0.01$), and the B/S group exhibited significantly higher mean incisor fracture frequency than either of the other two groups ($P < 0.01$; Table 5). In a comparison of fracture incidence by position and intraspecific aggression level, only canine tooth fracture incidence differed significantly, with more aggressive species breaking their canines approximately twice as often ($P < 0.05$; Table 5). There were no significant associations between fracture frequencies by tooth position and prey size categories. Relative to family membership, a single difference appeared significant; mephitids were never observed to have broken an incisor (total incisors = 1977) whereas all other families did. However, due to considerable variance within families in incisor fracture frequency, this difference was only significant between mustelids and mephitids ($P = 0.03$, $\chi^2 = 12.431$; Table 5).

DISCUSSION

THE COMPARATIVE STUDY: EXTANT CARNIVORANS

Diet appears to be the fundamental factor determining rates of tooth fracture in carnivorans, and probably mammals, in general. Species that include bones or hard-shelled invertebrates in their diet break teeth more often than those that rarely or never do and, among these species, those that consume tough foods most often tend to have the highest rates of dental damage. This was apparent in both the comparison of tooth breakage incidence between bats and carnivorans and that within the carnivoran sample itself. Largely insectivorous carnivorans did not differ significantly from bats in dental fracture incidence, but a larger sample of 36 carnivorans dominated by species that eat some vertebrate flesh showed much higher rates of dental fracture than bats. Moreover, comparisons among the carnivorans also revealed the positive influence of carnivory on tooth breakage.

The sample of 36 extant carnivorans used in the present study includes species with a wide range of diets including meat-specialists (felids, weasels), omnivores (foxes, martens), durophagous feeders (hyenas, sea otter), and largely insectivorous forms (bat-eared fox, skunks). Rates of dental fracture on a per tooth basis spanned an order of magnitude, from 0.2% in the largely insectivorous spotted skunk to 4.6% in the durophagous spotted hyena. This variation was not related to body mass; fracture frequencies among species smaller than 7 kg ranged from 0.2% (spotted skunk, *S. putorius*) to 4.3% (grey fox, *Urocyon cinereoargenteus*), whereas the range among

Table 5. Mean (standard deviation) tooth fracture frequency multiplied by 100 by tooth type for each of the behavioural categories (including extant species only)

Category	<i>N</i>	I	C	PM	CR	M
Diet						
C	25	0.53 (0.42)*	7.8 (3.81)†	2.1 (2.06)	2.1 (1.88)†	0.4 (0.73)
B/S	5	2.04 (0.95)†	10 (2.95)†	3.4 (2.44)	3 (1.36)†	1.1 (0.85)
O/I	6	0.23 (0.27)	2.6 (3)	0.7 (0.64)	0.3 (0.5)	0.3 (0.31)
Prey size						
L	6	1.5 (1.19)	7.8 (2.38)	2.9 (2.06)	2.1 (0.85)	1 (0.99)
M	15	0.5 (0.44)	8.4 (4.3)	2.3 (2.04)	2.2 (1.71)	0.5 (0.93)
S	12	0.6 (0.66)	6.4 (4.8)	1.7 (2.29)	1.78 (2.37)	0.3 (0.34)
N	3	0.7 (0.74)	1 (0.75)	1 (0.75)	0.6 (0.67)	0.4 (0.15)
Aggression level						
HI	6	1.3 (1.29)	10.6 (3.94)‡	3.3 (1.92)	2.3 (0.8)	0.5 (0.82)
LO	30	0.6 (0.53)	6.7 (3.99)	1.8 (2.02)	1.8 (1.95)	0.5 (0.65)
Family						
Felidae	8	0.5 (0.44)	6.6 (2.51)	1.3 (1.04)	1.7 (0.63)	
Hyaenidae	3	1.9 (1.2)	8.9 (0.65)	3.6 (2.29)	2.4 (1.57)	
Canidae	12	0.7 (0.81)	7.5 (3.6)	2.6 (2.65)	2.4 (2.31)	0.5 (0.6)
Mustelidae	8	0.8 (0.44)§	10.1 (5.64)	2.26 (0.19)	2.1 (2.12)	0.5 (0.94)
Mephitidae	3	0	0.8 (0.67)	0.3 (0.35)	0.1 (0.17)	0.27 (0.46)
Procyonidae	2	0.5 (0.14)	5.9 (3.25)	1.3 (0.92)	0.9 (0.64)	0.5 (0.07)

*Significantly different from the 'B/S' group mean ($P < 0.01$).

†Significantly different from the 'O/I' group mean ($P < 0.01$).

‡Significantly different from the 'LO' group mean ($P < 0.05$).

§Significantly different from the Mephitidae group mean ($P < 0.05$).

I, incisors; C, canines, PM, pre-carnassial premolars; CR, carnassials, M, post-carnassial molars. Diet: C, carnivorous; B/S, bone or shell hard-object feeders; O/I, omnivorous and/or insectivorous. Prey size: L, large; M, moderate; S, small; N, nonpredacious.

larger species was 0.6% (cheetah, *Acinonyx jubatus*) to 4.6% (spotted hyena, *Crocuta crocuta*). Variation also was not well explained by family membership, nor did it correlate significantly with typical prey size, as defined by the categories used in the present study. However, there was a significant difference in rates of dental fracture among species categorized by diet and level of intraspecific aggression, respectively.

The three dietary groups were designed to reflect the potential quantity of bone consumed. Results indicated that on average, the hard-object (B/S) feeders broke their teeth more often than flesh-eaters (C) or relatively nonpredacious species (O/I). Hard-object feeders include three hyena species, the grey wolf (*C. lupus*), and sea otter (*Enhydra lutris*). The hyenas and wolf all consume relatively large bones, but wolves, spotted (*C. crocuta*) and brown hyenas (*Hyaena brunnea*) do so more frequently than striped hyenas (*Hyaena hyaena*) (Kruuk, 1976; Haynes, 1982; Macdonald, 1988; Mills, 1990), and their tooth fracture rates are slightly higher. Sea otters consume tough sea urchins, snails, crabs, and bivalves regularly and, although they are known to use rocks to

crack shells, their tooth fracture rates suggest that they are using their teeth to process them as well (Kenyon, 1969; Tinker *et al.*, 2007). As a group, these five species tended to fracture incisors significantly more than either of the other two groups, indicating a relatively important role in feeding for these small teeth. This is supported by feeding observations in the wild of the spotted hyena, in which the anterior dentition (canines and incisors) was used frequently in feeding on bone as well as flesh (Van Valkenburgh, 1996). Notably, the enamel microstructure of spotted hyena teeth, from incisors to the anterior cusps of the upper carnassial, is highly specialized to resist crack propagation, indicating that tooth to bone contact is not confined to the enlarged premolars (Stefen & Rensberger, 1999; Rensberger & Stefen, 2006).

Species defined here as carnivorous (C) had diets that were dominated by vertebrate prey, but the relative proportions of meat to non-meat varied from pure hypercarnivores (felids) to those that consume considerable quantities of plant matter as well (e.g. foxes). It might be expected that the hypercarnivores would tend to break their teeth more often than the more

omnivorous taxa because they encounter more bone but this was not the case. Although not shown here, these two groups did not differ significantly in mean fracture frequency ($P = 0.1$, $\chi^2 = 4.564$). Notably, red foxes and grey foxes, both omnivorous, had higher rates of tooth fracture than any felid species sampled. The red fox was sampled extensively over its geographic range and showed a wide variation in fracture frequencies among populations (Table 2). Red foxes from New York had the lowest incidence of damage (1%), whereas those from Alaska had the highest (6%). It may be that differences among red fox populations reflect dietary differences. Perhaps Alaskan foxes include more carrion (occasionally frozen) in their diet, thus contributing to higher tooth fracture, but data to confirm this are not available. Nevertheless, it is not surprising to find variation both within and among omnivorous species in fracture frequencies given their eclectic diets and the likelihood that they will emphasize different foods in different localities. Determining the causes of increased fracture frequency in omnivores will require more detailed information on diets of individuals in association with dental damage than are available at present.

The least predacious category (O/I) included six species that were judged to feed on more nonvertebrate than vertebrate prey, as well as plant matter: bat-eared fox, three skunks, raccoon, and ring-tailed 'cat'. This group exhibits the least variation in fracture frequency, ranging from less than 1% to 2%. As is true of all sampled species, they broke their canine teeth most frequently but still at a mean frequency that was significantly less than that observed for either of the more carnivorous groups (C, B/S), as was also true of their carnassials.

Estimated levels of intraspecific aggression were correlated positively with tooth fracture frequency. Based on behavioural data, six species were characterized as having relatively high levels of aggression: lion, spotted hyena, grey wolf, short-tailed weasel, ermine, and mink. As might be expected if tooth fracture is sustained in battle, putatively aggressive species broke canines more often than putatively non-aggressive species. Although this result is promising, caution is advised as many species were placed in the less aggressive category simply because of a lack of available data.

THE PALEOECOLOGICAL STUDY: LATE PLEISTOCENE LARGE CARNIVORANS

Confirming previous results, late Pleistocene large carnivorans exhibit significantly higher fracture frequencies than their extant counterparts. However, in the previous work, there was a substantial gap

between fossil and recent species, with Pleistocene species displaying two to four times the maximum frequency observed in the recent species. This is no longer the case; instead, the Pleistocene species form the upper end of a continuum of fracture frequencies, and may overlap with a few extant species (Fig. 2).

Closer examination of the dire wolf sample exposes some intriguing variation. Dire wolves were sampled from three late Pleistocene localities, San Josecito Cave, Talara tar seeps, and Rancho La Brea tar seeps, all of which exhibited fracture frequencies of approximately 5%. For Rancho La Brea, the total sample of dire wolves includes individuals from several spatially and, in some cases, temporally distinct deposits ('pits'), two of which had sufficient sample sizes of dire wolves for comparison, Pits 13 (approximately 15–14 000 years ago) and 61–67 (approximately 11–12 000 years ago) (Table 2). The older pit contains wolves with significantly heavier dental wear and more broken teeth (7%) than the younger (2%). Using pulp-cavity diameter of a lower canine as an indicator of individual age, Binder *et al.* (2002) demonstrated that the age distributions of dire wolves from the two pits did not differ significantly. Thus, the heavier tooth wear and increased tooth breakage in Pit 13 dire wolves were not a result of a predominance of older individuals. Instead, they likely reflect heavier carcass consumption by dire wolves 15 000 years ago shortly after the last glacial maximum. Thus, dire wolves likely modified their feeding behaviour and thereby altered their risk of tooth fracture as environmental conditions changed, probably in response to food availability. Such trade-offs between risk of injury and caloric return are seen among invertebrate predators, such as crabs, that select smaller prey to minimize risk of claw damage despite a diminished nutritional return (Juanes & Hartwick, 1990; Juanes, 1992; Palmer, Taylor & Barton, 1999).

The pattern of breakage across the tooth row of Pleistocene species differed slightly from that of the combined sample of 36 extant carnivorans, and was most similar to that of hard-object feeders. As was the case for all extant species, canine teeth were broken most often (11–36%). This likely reflects their anterior position in the jaw and the fact their elongate shape that makes them prone to higher bending stresses (Van Valkenburgh, 1988; Rensberger & Wang, 2005). Canines were followed by carnassials (4–18%), incisors (0–15%) and premolars (4–13%), and finally post-carnassial molars (3–5%). Similar to hard-object feeders, Pleistocene species tended to fracture incisors more frequently relative to other teeth than extant flesh-eaters or omnivores. Although it may seem surprising that predators would use incisors to feed on bone, the need to feed rapidly, as occurs often among

social species, can lead to less than optimal tooth use as noted above for spotted hyenas (Van Valkenburgh, 1996). In addition, incisors are used to gnaw on bones, an activity that is likely to incur heavy wear and occasional breakage. The higher incisor fracture incidence along with the overall higher tooth fracture across the tooth row supports the hypothesis that high Pleistocene tooth fracture reflects elevated levels of food competition and greater carcass utilization.

All of the above suggests that late Pleistocene predators were consuming carcasses more completely, and perhaps more rapidly on average, than their modern counterparts. Although these species may have been taking relatively larger prey than their modern counterparts, comparative analysis among extant species does not support a positive relationship between tooth fracture incidence and prey size. Instead, a better explanation is heavy carcass utilization and high levels of intraspecific and interspecific aggression, all of which would be engendered by a high density and diversity of large carnivores. Species diversity within the North American predator guild declined sharply approximately 10 000 years ago, with the loss of the largest species including the short-faced bear (*Arctodus simus*), American lion (*P. atrox*), sabertooth cats (*S. fatalis*, *H. serum*) and dire wolf (*C. dirus*) (Van Valkenburgh & Hertel, 1998). The elimination of these alpha predators must have had a significant impact on the dynamics of interspecific competition that could be reflected by numbers of broken teeth. For example, 20 years of data on feeding success in African wild dogs documented that dogs consumed carcasses more fully when the density of their chief kleptoparasite, the spotted hyena, was high (Carbone *et al.*, 2005).

Alternatively, low prey abundance in the late Pleistocene might also engender increased food competition among carnivores. Although prey densities may have played a role occasionally, they are unlikely to be the full explanation as the fossil deposits span at least 35 000 years and an array of environments. Moreover, studies using the abundance of preserved spores of a dung fungus (*Sporormiella*) as a proxy for herbivore biomass in the late Pleistocene and Holocene of the western USA suggest the contrary. *Sporormiella* spore frequency is high in the late Pleistocene and then plummets around 11 000 years ago in association with the disappearance of the megafauna (Davis & Shafer, 2006).

As noted in the Introduction, because three of the localities (La Brea, Talara, San Josecito cave) are considered predator-traps to which carnivores were lured by dying or dead ungulates, it might be argued that battles over trapped prey occurred frequently, incurring more dental fractures among individuals that regularly attended these events. However, based

on the estimated number of individual herbivores buried at La Brea and the represented timespan, a carcass was only available approximately once every 50–70 years (Marcus & Berger, 1984; Friscia *et al.*, 2008). Comparable data are not available for Talara and San Josecito, although samples are much smaller, suggesting lower frequencies of entrapment. Elevated tooth fracture frequencies appear to be a widespread feature of late Pleistocene large predator guilds that cannot be explained by taphonomy. They are apparent in multiple species from several distinct late Pleistocene localities (Peru, Mexico, California, Alaska) all studied by the myself, as well as a single species of sabertooth cat (*Homotherium*) examined by Marean & Ehrhardt (1995) from a den site, in Texas.

Another alternative explanation for increased dental damage is that Pleistocene predators were living longer (on average) than their extant counterparts. This might explain the higher fracture frequencies observed for living Isle Royale wolves because these individuals are protected from hunting and road kill. Among Rancho La Brea dire wolves, this was ruled out by estimating age distributions from pulp-cavity dimensions (Binder *et al.*, 2002). Unfortunately, this type of analysis requires substantial samples of intact lower canine teeth, which are not available for any of the other fossil species, except the La Brea sabertooth cat, *Smilodon* (W. Binder, unpubl. data). Nevertheless, it is unlikely that late Pleistocene carnivores would have lived longer on average than extant carnivores of similar size. Large carnivores often kill one another, either as an act of predation or more typically, in intra- or interspecific battles over territory or a carcass (Palomares & Caro, 1999; Van Valkenburgh, 2001; Donadio & Buskirk, 2006). Given that anthropogenic influences probably limit the present-day abundance of large predators to levels well below those reached in the late Pleistocene, encounters among and within species must have been frequent and dangerous in the past, making it difficult to survive to old age.

Finally, the fact that dental damage rates among living large carnivores rarely approach or overlap with those of the sampled Pleistocene predators indicates species are not pushing the limits of their tooth strength (and probably other anatomical structures) as often as they did in the Pleistocene. Thus, it would be a mistake to infer behavioural capabilities (e.g. the ability to consume bones) from the relationship between tooth form and observed carcass utilization behaviour in modern predator species. Clearly, North American grey wolves, coyotes, and lions, were consuming carcasses more fully on average in the late Pleistocene than at present. It must be considered that aspects of their anatomy (e.g. tooth dimensions, jaw muscle mass) and behaviour (e.g. sociality,

interspecific aggression levels) might reflect to some degree the ghosts of competition past rather than present conditions.

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