tween the bare water surface tension (72 mN/m) and the measured surface tension. The collapse pressure, π_c, of a monolayer is the highest surface pressure obtainable before the monolayer "collapses," or ejects material into a bulk phase. The minimum surface tension of a monolayer film, γ, is the bare water surface tension minus the collapse pressure (72 mN/m − π_c). For a general discussion of monolayer film behavior including collapse, see A. W. Adamson, *Physical Chemistry of Surfaces* (Wiley, New York, 1990), chap. IV.

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SP-B1-25 (M_w = 2929)

```
           +   ++      +
FPIPLPYCWLCRALIKRIQAMIPKG
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SP-B1-25m (M_w = 2709)

```
FPIPLPYCWLCSALISSIQAMIPSG
1                      25
```

The crude peptides were purified by C4-column (Vydac, Hesperia, CA) reversed-phase high-performance liquid chromatography (HPLC) with a mixture of water, acetonitrile, and 0.1% trifluoroacetic acid. Solvents from HPLC and ion-pairing agents were removed from the purified peptides by vacuum centrifugation, and the expected molecular masses of each peptide were obtained by fast atom bombardment mass spectrometry or electrospray mass spectrometry (UCLA Center for Molecular and Medical Sciences Mass Spectrometry). Quantitative amino acid composition for the peptides was determined at the UCLA Protein Microsequencing Facility.

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30. Single-letter abbreviations for the amino acid residues are as follows: A, Ala; C, Cys; F, Phe; G, Gly; I, Ile; K, Lys; L, Leu; M, Met; P, Pro; Q, Gln; R, Arg; S, Ser; W, Trp; and Y, Tyr.
31. We thank D. K. Schwartz, R. Viswanathan, and J. Israelachvili for helpful discussions. Supported by Office of Naval Research grant N00014-90-J-1551, National Science Foundation grant CTS90-15537, and National Institutes of Health (NIH) grant GM 47334 (J.A.N.Z.); NIH grant HL 40666 (A.J.W.); a Parker B. Francis Foundation fellowship and March of Dimes grant FY92-0360 (R.B.); Research Center in Minority Institutions award G 12 RRO 302607 and R01 HL 40666 (R.B. and A.J.W.); a University of California President's Dissertation Year fellowship (M.L.L.); and the National Consortium for Graduate Degrees for Minorities in Engineering and Sciences (A.M.B.).

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Tough Times at La Brea: Tooth Breakage in Large Carnivores of the Late Pleistocene

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One million to two million years ago, most of today's large, predatory mammals coexisted with larger extinct species, such as saber-toothed cats and giant running bears. Comparisons of tooth fracture frequencies from modern and Pleistocene carnivores imply that predator-prey dynamics and interspecific interactions must have been substantially different 36,000 to 10,000 years ago. Tooth fracture frequencies of four Rancho La Brea species—dire wolf, coyote, saber-toothed cat, and American lion—were about three times that of extant carnivores. Consequently, these findings suggest that these species utilized carcasses more fully and likely competed more intensely for food than present-day large carnivores.

During the late Pleistocene in North America, the species richness of large carnivores and their presumed prey was much greater than at present. There were 56 herbivore species larger than 30 kg and, of those species, 29 (52%) exceeded 300 kg, the size of a moose (*Alces alces*) or larger. At least seven species, such as the mastodon and mammoth, were larger than any extant New World herbivore (*1*). By contrast, 11 herbivores larger than 30 kg (3 of them >300 kg) exist in North America today; even in Africa only 13% of the herbivore species exceed 300 kg (*1*). If Pleistocene herbivores existed at population densities comparable to extant species of similar body size and formed sizable herds as do living zebras (*Equus* spp.) and bison (*Bison bison*), then levels of prey availability would have been comparable to or greater than those of East Africa today. The rich array of large Rancholabrean carnivores is consistent with this hypothesis; for example, 15 species coyote-sized or larger existed in North America during the Pleistocene, whereas today there are 7 (*1*). Because the majority of extant large carnivore species originated more than 500,000 years ago, most of their history has been spent under Pleistocene rather than present-day conditions of predator-prey diversity. Evidence concerning levels of food availability and interspecific competition in the Pleistocene might provide some understanding of the behavior and morphology of living carnivores.

When food is limited, carnivores are likely to feed more rapidly, guard their kills more aggressively, and more completely consume their prey, often ingesting bone in the process (*2, 3*). All these activities involve the risk of tooth breakage, an event carnivores are expected to avoid given the importance of teeth for

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feeding and defense. However, a study of nine extant species of large carnivores revealed that an average of one out of four adults had broken at least one tooth in life (4). The spotted hyena (*Crocuta crocuta*), a habitual bone-cracker, had the highest fracture frequency (approaching 40% of all individuals) as would be expected in a carnivore that fully consumes its kills. Because of its relation to carcass utilization behavior, tooth breakage may provide evidence of past predator-prey dynamics. We therefore studied tooth fracture frequencies in late Pleistocene [36,000 to 10,000 years before present (B.P.)] carnivores preserved in the Rancho La Brea tar pits in Los Angeles, California (5). The tar pits are an exceptional fossil deposit, having preserved over 3400 individuals of large mammals, including six predator species (Table 1) whose numbers are sufficient to compare their patterns of dental wear and fracture with those of living large carnivores.

Our analysis of extant carnivores is based on an earlier study of the skulls and mandibles of over 700 adult, wild-caught individuals of nine species (Table 1) (4). We also studied 82 extant coyotes for comparison with the coyote's Pleistocene representatives (6). For each individual, the number and position of broken teeth and a qualitative estimate of wear stage were recorded. A tooth was counted as broken only if it showed subsequent wear in life, that is, the presence of distinct wear facets that were a result of tooth-tooth or tooth-food contact. Wear stage was assumed to reflect age, with heavier wear characterizing older individuals (2, 7). Because the probability of having a broken tooth increases with age (4), species differences in fracture frequency can result from disparities among samples in age distributions.

The proportion of all teeth broken in life ranged from 5 to 11% in four of the Rancholabrean species: dire wolf, coyote, American lion, and saber-toothed cat (Table 1). When we excluded incisors from our calculations, the values ranged from 5.5 to 17%. In sharp contrast, the proportions of broken teeth exhibited by 10 extant predators were much smaller, ranging from 0.5 to 2.7% when we included incisors in the calculations and 1 to 3% when incisors were not included (Table 1). Although their sample sizes were small, the Pleistocene bobcat and puma tooth samples exhibited no fractures. For their fracture frequency to be comparable to that of the other Pleistocene species (9%), four or five teeth should have been broken rather than the zero observed. The striking difference in breakage frequencies between the four extinct species and all others is not due to a preponderance of old individuals in the four Pleistocene species (4, 8). As in the Holocene samples of carnivores, slightly and moderately worn teeth predominated over heavily worn teeth for those extinct species (4, 8). Older individuals of *Smilodon* and *Panthera atrox* are underrepresented at the pits relative to the sample of extant lion (8). Among the canids, no significant differences in wear stage distribution are apparent between fossil and recent samples (8). Thus, the higher fracture frequencies exhibited by these species are not a result of a bias toward the entombment of older individuals.

Table 1. Observed number of teeth (broken and total) for the 10 extant and 6 Rancholabrean species and the per tooth fracture frequencies calculated with and without incisors (*17*). Fracture frequency is equal to the weighted average (*18*) of tooth breakage frequencies for each tooth position. A weighted average is used because the relative representation of different tooth types, such as incisors or canines, differs between fossil and recent species. For example, incisors make up 46% (12 out of 26) of a complete tooth row in *Smilodon* but are only 31% (544 out of 1773) of its preserved tooth sample. Fracture frequency is the sum across tooth types of the product of the observed fracture frequency per tooth type (Table 2) and the proportion of the tooth row represented by that tooth type in a complete dentition. For example, in *Smilodon* the fraction of incisors that were broken (52 out of 544) was multiplied by 0.46 (the proportion of a complete tooth row represented by incisors), and this product was added to comparable figures for the other tooth types to estimate the per tooth fracture frequency for the species. Shown in parentheses are 95% confidence intervals multiplied by 0.001 (*19*).

Species	Total teeth (no.)	Broken teeth (no.)	Fracture frequency	
			With incisors	Without incisors
Extant				
Lion, *Panthera leo*	3146	49	0.016 (6)	0.026 (10)
Jaguar, *P. onca*	1846	17	0.009 (6)	0.011 (9)
Leopard, *P. pardus*	2236	27	0.012 (6)	0.022 (11)
Cheetah, *Acinonyx jubatus*	1196	9	0.008 (7)	0.014 (12)
Puma, *Puma concolor*	2990	30	0.010 (5)	0.019 (9)
Spotted hyena, *Crocuta crocuta*	2464	50	0.020 (3)	0.027 (11)
Striped hyena, *Hyaena hyaena*	1767	34	0.019 (8)	0.027 (13)
Gray wolf, *Canis lupus*	4704	49	0.010 (4)	0.015 (5)
Coyote, *Canis latrans*	3444	93	0.027 (7)	0.035 (10)
Wild dog, *Lycaon pictus*	1848	10	0.005 (4)	0.007 (6)
Rancho La Brea				
Coyote, *Canis latrans*	1280	66	0.05 (20)	0.068 (20)
American lion, *Panthera atrox*	275	30	0.11 (50)	0.17 (67)
Saber-toothed cat, *Smilodon fatalis*	1775	127	0.08 (20)	0.069 (19)
Bobcat, *Lynx rufus*	54	0	0	0
Puma, *Puma concolor*	40	0	0	0
Dire wolf, *Canis dirus*	949	39	0.08 (20)	0.055 (20)
San Josecito, Mexico				
Dire wolf, *Canis dirus*	212	11	0.04 (34)	0.10 (55)
Talara, Peru				
Dire wolf, *Canis dirus*	329	17	0.05 (31)	0.065 (35)

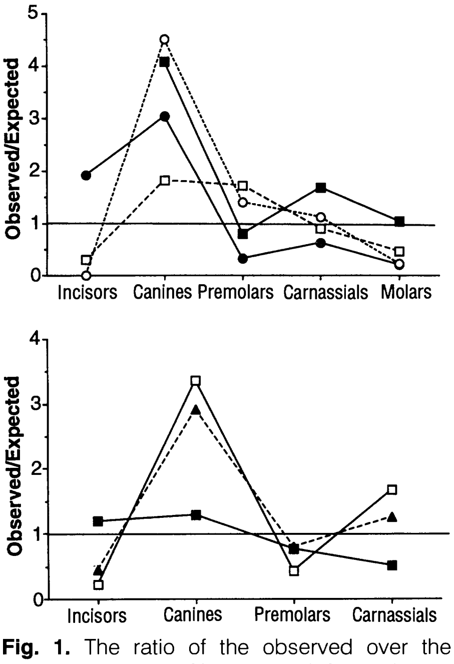

Fig. 1. The ratio of the observed over the expected number of broken teeth for each type of tooth within each species. Top: *Canis dirus* (●), Pleistocene *C. latrans* (RLB) (■), extant *C. latrans* (□), *C. lupus* (○). Bottom: *Panthera leo* (□), *Panthera atrox* (▲), *Smilodon fatalis* (■). For each species, the expected values were calculated as the product of the overall fracture frequency (Table 1) and the number of teeth represented in the sample for each position (Table 2). A value of 1 indicates the observed rate was equal to the expected rate. Tooth types as described in Table 2.

The higher fracture frequencies exhibited by the four Rancholabrean species are not a result of particular teeth (for example, upper canines) being broken more often. Instead, almost all teeth in each species exhibited higher fracture frequencies than were found in their modern counterparts, and in all but one case the differences were significant (Table 2). The sole exception was the slightly lower fracture frequency of premolars in the Pleistocene coyote relative to the present-day coyote.

We analyzed the pattern of breakage across the tooth row within each species by comparing the relative frequencies of breakage of incisors, canines, and cheek teeth with frequencies expected if breakage was distributed evenly among all tooth positions. In extant species, over half of all broken teeth were canines, yet canines compose less than a quarter of the teeth examined (*4*). The higher than expected frequencies of canine breakage in living large carnivores are most likely the result of injury during the act of killing prey because (i) large, unpredictable loads occur as canines are driven into mobile prey and (ii) the elongate shape of canines makes them susceptible to larger bending moments than other teeth. Presumably, canine teeth are broken when they contact the bones of the prey.

In the dire wolf, fossil coyote, and American lion the pattern of increased canine breakage is again apparent (Fig. 1). Among the canids, the frequency of canine breakage is lowest in the modern coyote, an omnivorous species that rarely takes prey larger than itself (9). The higher canine fracture frequency in the Pleistocene coyote is close to that of the predaceous gray wolf, suggesting that in the past the coyote might have fed on large prey more often. Although breakage patterns in the dire wolf and gray wolf are comparable, dire wolves broke their incisors more than expected and gray wolves showed the converse. The difference between these two species is similar to that observed between the extant spotted hyena and gray wolf (*4*), suggesting that *C. dirus* utilized its incisors regularly to feed close to the bone.

Smilodon did not break its dagger-like canines at a significantly higher frequency than other teeth (Fig. 1), suggesting that the saber-toothed cat was not killing its prey in the same manner as living big cats do. The forelimbs of *Smilodon* were more massive than those of extant big cats, implying that it was critical to hold prey still while the killing bites were applied. In this way, *Smilodon* might have reduced the risk of canine tooth–bone contact (*10, 11*). Nevertheless, the proportion of canine teeth broken was greater than that observed for living cats (10 versus 5% in the lion); thus, the canines of *Smilodon* were often subjected to injurious loads. Given their knife-like shape, the upper canines of *Smilodon* were more vulnerable than the rounded canines of living cats to fracture across their narrow axis (*12*). Several studies have suggested that saber-toothed cats avoided bone when feeding, presumably to protect their exposed, yet crucial, sabers from fracture (*10, 12, 13*).

Table 2. Frequency of broken teeth (number of broken teeth/total number of teeth) among tooth positions in four extant species and four Rancholabrean species. I, incisors; C, canines; P, premolars except upper P4; P4-M1, upper P4 and lower M1 (carnassials); M, postcarnassial molars. The cats do not have postcarnassial molars or these teeth are vestigial and were not considered.

Species	Frequency of broken teeth				
	I	C	P	P4-M1	M
Extant					
Canis lupus	0 (0/1344)	0.045 (20/448)	0.014 (22/1568)	0.011 (5/448)	0.002 (2/896)
Canis latrans	0.008 (8/984)	0.049 (16/328)	0.046 (53/1148)	0.024 (8/328)	0.012 (8/656)
Panthera leo	0.003 (5/1452)	0.054 (26/484)	0.007 (5/726)	0.027 (13/484)	
Rancho La Brea					
Canis latrans	0 (0/3)	0.188* (3/16)	0.037 (21/575)	0.077* (24/310)	0.048* (18/376)
Panthera atrox	0.048† (3/63)	0.32† (6/19)	0.088† (10/114)	0.139† (11/79)	
Smilodon fatalis	0.096† (52/544)	0.1† (26/251)	0.062† (27/437)	0.041 (22/543)	
Canis dirus	0.15‡ (6/39)	0.24‡ (9/37)	0.03 (9/347)	0.05‡ (10/203)	0.016 (5/323)
San Josecito, Mexico					
Canis dirus	0 (0/13)	0.25 (4/16)	0.03 (2/80)	0.11 (4/36)	0.015 (1/67)
Talara, Peru					
Canis dirus	0 (0/5)	0.20 (1/5)	0.044 (5/114)	0.12 (10/84)	0.008 (1/121)

*Significantly different ($P < 0.05$) from the comparable value for recent *Canis latrans* χ^2 values: C, 5.739; P4-M1, 9.407; M, 11.793. †Significantly different ($P < 0.05$) from the comparable value for *Panthera leo*. The χ^2 values for *Smilodon* comparisons are I, 121.12; C, 6.252; and P, 30.725. The χ^2 values for *Panthera atrox* comparisons are I, 22.433; C, 21.078; P, 36.707; and P4-M1, 21.017. ‡Significantly different ($P < 0.01$) from the comparable value for *Canis lupus*. The χ^2 values are I, 207.67; C, 23.978; P4-M1, 9.009; and M, 7.298.

Why did some carnivores from La Brea break their teeth so frequently? Four explanations are apparent: (i) demographic bias, (ii) preservational bias, (iii) local bias, and (iv) behavioral differences between past and present large carnivores. The possibility that demographic or preservational biases created the pattern of high fracture frequencies seems improbable. The fossil samples were not biased toward a greater representation of older individuals, nor were the fractures the result of abrasion within the pits. This latter conclusion is supported by the absence of breakage in the fossil bobcat and puma.

The higher frequencies of tooth breakage at the tar pits might reflect a local bias of the Los Angeles region during the late Pleistocene. However, fracture frequencies in two other, smaller accumulations of Pleistocene dire wolves in Mexico and Peru are nearly the same as those from La Brea, indicating that tooth breakage frequencies of dire wolves at Rancho La Brea are not unusually high for the late Pleistocene (Table 2) (*14*). On the basis of the well-sampled tooth types (all but incisors), the three dire wolf samples show similar frequencies of dental fracture ($P > 0.08$, χ^2 tests) that exceed those observed in modern wolves (Tables 1 and 2).

On the basis of their dental morphology, all four fossil species were moderately to highly carnivorous (*15*); thus, tooth-bone contact is the probable cause of breakage. Considering the association between higher breakage frequencies and bone eating in modern carnivores, the elevated frequencies of tooth fracture in the dire wolf, coyote, American lion, and saber-toothed cat imply that contact between teeth and bones occurred more frequently in these species than in the smaller sympatric puma and bobcat or in their extant counterparts. Prey capture techniques differed among the four fossil species, which suggests that increased carcass utilization is the most likely explanation for the higher fracture frequencies. The explanation that teeth were broken more often as a result of larger prey size is unsatisfactory given that the fossil carnivores were also larger than their living counterparts.

Our hypothesis of increased carcass utilization among late Pleistocene large carnivores compared with extant species has several implications. It suggests that times were tough for these Pleistocene species; prey must have been difficult to acquire or retain. Prey availability could have been low, at least seasonally, forcing predators to fully consume their prey. Alternatively, predator densities might have been relatively high, resulting in intense competition over kills. Higher probabilities of carcass theft would favor their rapid and complete consumption. The relatively rare puma and bobcat at La Brea probably existed on the fringes of that community and had few interactions with larger carnivores. We have little data on carnivore or herbivore abundance in the Pleistocene; population densities are difficult to infer from collections because of preservational biases (*16*). Despite the more diverse array of prey species for the La Brea carnivores, it would seem that food was limited, at least seasonally. The Pleistocene fracture frequencies might even reflect tough times for the big carnivores as their presumed prey approached extinction 8,000 to 10,000 years ago. Of the four Pleistocene predators examined, only the omnivorous coyote survived.

Finally, our results question the wisdom of interpreting present-day behaviors and morphological features without consideration of the past. If high tooth breakage rates are typical of past conditions and reflect increased competition for food, then most, if not all, extant and recently extinct large carnivores evolved under conditions of coexistence more interactive than at present. Selective forces that molded their behavioral and morphological evolution probably differed in magnitude, if not in kind, from those observed today. A conclusion that the skulls and teeth of extant carnivores are too strong (that is, have large safety factors) for the typical loads they bear might overlook adaptations for past feeding behaviors. Given the recency of New World Pleistocene extinctions, we should expect incongruencies between behavior and morphology that are inexplicable when considering present conditions alone.

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6. The sample of recent coyotes (*C. latrans*) is based on 82 (37 females, 42 males, and 3 unknown) wild-caught specimens in the collections of the Division of Mammals within the U.S. National Museum of Natural History, Washington, DC. The fossil specimens are all part of the vertebrate paleontology collections of the Los Angeles County Museum of Natural History and are housed at the George C. Page Museum, Los Angeles. Within the Rancholabrean coyote sample, there were only two specimens with associated incisors; thus, fracture frequencies of incisors could not be accurately assessed. The relatively poor preservation of associated incisors in the coyote, compared with those of the dire wolf, saber-toothed cat, and American lion, probably reflects their small size and greater vulnerability to loss.
7. Wear stage was recorded as one of three categories: (i) slight, little, or no apparent wear observed as facets or blunting of cusps; (ii) moderate, shear facets apparent on carnassial teeth, cusps blunted on most teeth; and (iii) heavy, carnassial teeth with strong shear facets or blunted cusps and premolars and molars with well-rounded cusps. The tooth positions we examined were incisors, canines, premolars exclusive of the upper carnassial (fourth premolar), carnassials, and postcarnassial molars. The carnassials were treated separately in both this and the earlier study (*4*) because of their functional importance as the primary meat-slicing teeth in carnivores. For fossil specimens, the locality (pit number) was recorded in addition to the wear stage and the number of broken and unbroken teeth; G. L. Smuts, J. L. Anderson, J. C. Austin, *J. Zool.* (*London*) **185**, 115 (1978); M. G. L. Mills, *Koedoe* **25**, 55 (1982); M. Lindeque and J. D. Skinner, *S. Afr. J. Zool.* **19**, 291 (1984).
8. Percent distribution by wear stage (slight, moderate, heavy) of the fossil specimens: *Canis dirus* (44, 46, 10), *Canis latrans* (66, 32, 2), *Smilodon fatalis* (69, 29, 2), and *Panthera atrox* (83, 17, 0). For recent individuals the percent distributions were *Canis lupus* (46, 40, 13), *C. latrans* (70, 24, 6), and *Panthera leo* (67, 24, 9). The number of specimens for the fossil taxa must be considered a maximum estimate of the number of individuals. Most fossil specimens represent a partial individual, and in some cases two or more specimens could represent parts of the same individual. Comparison of wear stage distributions between the following extinct and extant species: *Smilodon fatalis* and *Panthera leo*, $P < 0.001$, $\chi^2 = 14.793$; *Panthera atrox* and *P. leo*, $P < 0.001$, $\chi^2 = 14.04$; *Canis dirus* and *C. lupus*, $P = 0.59$, $\chi^2 = 1.048$; Rancholabrean *C. latrans* and recent *C. latrans*, $P = 0.11$, $\chi^2 = 4.501$.
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14. The two sites are San Josecito Cave, Mexico (~10,000 to 50,000 years B.P.), and Talara Tar Seeps, Peru (~13,900 years B.P.). The San Josecito Cave deposits are believed to represent a trap-fall cave site into which individuals accidentally fell. The tar seeps at Talara appear to have been analogous to Rancho La Brea. Individuals were trapped in a viscous mixture of tar and sediment, and their deaths attracted large carnivores. [See K. Campbell, *R. Ont. Mus. Life Sci. Contrib.* **118**, 1 (1979); and B. Kurtén and E. Anderson, *Pleistocene Mammals of North America* (Columbia Univ. Press, New York, 1980)].
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17. Because fossil species were represented by portions of individuals, such as a mandibular fragment with three teeth, tooth fracture frequencies were quantified on a per tooth rather than per individual basis. Incisors, as the smallest single-rooted teeth, tended to be missing in both fossil and recent skulls, so calculations were done with and without their inclusion.
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19. Confidence intervals (*CI*) for the fracture frequencies were calculated as follows: $CI = 2.576 \{[X(1 - X)]/N\}^{1/2}$, where *CI* is the 95% confidence interval, *X* is the observed fracture frequency, and *N* is the total number of teeth examined for that species [R. Wonnacott and T. Wonnacott, *Introductory Statistics* (Wiley, New York, 1985)].

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