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A COMPARISON OF TOOTH WEAR AND BREAKAGE IN RANCHO LA BREA SABERTOOTH CATS AND DIRE WOLVES ACROSS TIME

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ABSTRACT—The carnivores preserved in the late Pleistocene Rancho La Brea tar seep deposits display a remarkably high incidence of teeth broken in life as compared with modern species. In a previous study examining tooth breakage, tooth wear and individual age of *Canis dirus* over different periods in time, we found that Pit 13 *C. dirus* (about 15,000 years before present [ybp]) exhibited heavier tooth wear and fractured their teeth about three times more often than those of the younger Pit 61/67 (about 12,000 ybp). No significant difference was found in the age structure of the population, suggesting this came from differences in feeding behavior, likely bone consumption, at these two times. In this study, we extend this work to the Rancho La Brea sabertooth cat, *Smilodon fatalis*, a hypercarnivore with more specialized teeth and feeding behavior. We looked at tooth breakage, tooth wear, and individual age of *S. fatalis* compared with *C. dirus* from similar time intervals. As in the previous study, the age structure of the *Smilodon* samples did not differ between different time intervals. Interestingly, *S. fatalis* had consistent and higher levels of tooth breakage and apparent average age than *C. dirus* in either location, and tooth wear was similar to that observed in the more worn Pit 13 sample of *C. dirus*. This may demonstrate that *S. fatalis* was consuming more bone, and/or that *S. fatalis* individuals were older, had different relative dentine deposition rates, or might reflect the greater vulnerability of the sabercats' narrow teeth to wear and fracture.

INTRODUCTION

The Rancho La Brea deposits are a unique and substantial glimpse into the late Pleistocene, revealing much about mammalian life and death before the last significant extinction event in North America. Unusually, carnivores are much more well-represented than herbivores (roughly nine to one), which is particularly informative about the life of large predatory mammals during this period. The deposits are made up of “pits” which differ in deposition time, from roughly 40,000 years before present (ybp) to about 12,000 ybp (Harris, 1992; Friscia et al., 2008). The large numbers of specimens taken from these pits give us an opportunity to better understand one of the great extinctions in our continent, the late Pleistocene megafaunal extinction of about 11,500 ybp that eliminated a large percentage of very large carnivores and herbivores in North America (Marcus, 1960; Lyons et al., 2004).

It is well documented that the incidence of tooth breakage among Pleistocene carnivores (members of the Order Carnivora) from Rancho La Brea and elsewhere was greater than that of modern carnivores (Van Valkenburgh and Hertel, 1993; Leonard et al., 2007; Van Valkenburgh, 2009). At present, the most likely explanation is that increased fracture and tooth wear resulted from the need to consume carcasses more rapidly and completely given higher levels of competition among carnivores. Competition is argued to have been more intense in the past due to the greater diversity of large predatory mammals, and their probable higher densities, leading to more numerous encounters over carcasses. However, because both tooth wear and tooth fracture are positively correlated with individual age, an alternative

explanation is that Pleistocene individuals lived longer on average than their living counterparts. This hypothesis was falsified for Rancho La Brea dire wolves by using standardized pulp cavity width of the lower canine tooth as an estimate of relative age, a method that measures age without reference to tooth wear (Smuts et al., 1978; Zapata et al., 1997; Binder et al., 2002). Samples of dire wolves from two distinct time periods differed significantly in rates of tooth wear and fracture, but had similar age distributions. Thus the difference between the two was ascribed to heavier carcass utilization during one interval of time. Interestingly, tooth fracture and wear were appreciably higher in the older (circa 14,500 ybp) than the younger sample, the latter of which sampled a time (circa 12,000 to 11,000 ybp) close to the late Pleistocene megafaunal extinction at roughly 11,500 ybp. Thus the extinction of large herbivores was not reflected in increased food stress among the dire wolves, at least during the represented time window.

To investigate potential temporal shifts in dental attrition further, we decided to extend our analysis to the second most common carnivore at the La Brea tar seeps, *Smilodon fatalis*, a sabertooth felid hypercarnivore. As well as having knife-like upper canines, *S. fatalis* had more specialized, blade-like cheek teeth than the dire wolf and perhaps a more limited diet, and thus might be expected to be more sensitive to changes in prey availability. Despite its narrow premolars and molars, *S. fatalis* consumed bones regularly as evidenced by high rates of tooth breakage at Rancho La Brea (Van Valkenburgh and Hertel, 1993). If the difference in dire wolf fracture frequencies over time reflects shifts in the availability of large herbivore prey, then *Smilodon* might exhibit parallel differences. However, the skulls and teeth of sabertooth cats and dire wolves are very different, and undoubtedly this affected their feeding behaviors and perhaps their responses to food stress.

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TABLE 1. Dire wolf (*C. dirus*) and sabertooth cat (*S. fatalis*) tooth breakage data from Rancho La Brea, California, including the total number of teeth examined, number of teeth broken in life, and percent broken (with ± 95% confidence intervals), for each locality. *S. fatalis*: $\chi^2 = 6.593$, $P = 0.037$; *C. dirus*: $\chi^2 = 32.109$, $P < 0.0005$.

| Species | Locality | Total teeth | Broken teeth | % Broken teeth | <i>P</i> value |
|-------------------|-----------|-------------|--------------|----------------|----------------|
| <i>S. fatalis</i> | Pit 3 | 480 | 40 | 8.33(±2.5) | 0.037* |
| | Pit 13 | 337 | 18 | 5.34(±2.4) | |
| | Pit 61/67 | 1138 | 58 | 5.10(±1.3) | |
| <i>C. dirus</i> | Pit 3 | 1530 | 46 | 3.01(±0.9) | <0.0005** |
| | Pit 13 | 797 | 55 | 6.90(±1.8) | |
| | Pit 61/67 | 1120 | 25 | 2.23(±0.9) | |

*All three groups differ significantly from one another, but Pit 13 doesn't differ individually from the other two pits.

**All three groups differ significantly from one another, as do paired comparisons, except for Pits 3 and 61/67.

Here we compare the rates of tooth wear, fracture, and sample age distribution between and among dire wolves and sabertooth cats from three "pits" (3, 13, 61/67) that represent different time intervals. Pit dates are derived from radiocarbon dates on multiple specimens at different depths of each pit, and we use radiocarbon years before present (rcybp) to indicate this, along with the standard error for each date. The youngest pit is 61/67 and spans a short interval between 12,200 ± 200 to 11,130 ± 275 rcybp based on bone collagen amino acids from four long bones (Marcus and Berger, 1984). Pit 13 spans a similarly short, but older interval, between 15,360 ± 480 to 14,310 ± 920 rcybp, whereas Pit 3 is complex, with at least two periods of deposition, one that overlaps with that of Pit 13, ranging from 15,300 ± 230 to 12,650 ± 160 rcybp, and a second deeper and older deposit that has yielded bones dated between 21,400 ± 560 and 19,300 ± 395 rcybp (Marcus and Berger, 1984). Recently a bone was dated in between the two deposits, and found to have a date of 17,293 rcybp, suggesting that deposition in Pit 3 may have been more continuous than was previously believed (unpublished date, pers. comm., C. Shaw, Jan. 2006).

MATERIALS AND METHODS

Tooth Fracture Analysis

All well-preserved cranial and mandibular specimens of *Smilodon fatalis* and *Canis dirus* in Pits 3, 13, and 61/67 were examined. This resulted in a total of 3447 *C. dirus* teeth for the three localities and 1955 *S. fatalis* teeth for the three localities (Table 1). Teeth were counted as broken only if they showed evidence of subsequent wear in life in the form of distinct wear facets formed by tooth-tooth or tooth-food contact (Van Valkenburgh, 1988; Van Valkenburgh and Hertel, 1993). Fracture rates should be considered minimal estimates because it is difficult to distinguish broken from heavily worn teeth in partial jaws, because right and left teeth cannot be compared to verify that one was clearly injured and subsequently worn in an irregular fashion. Counts were performed by BVV for Pit 3, and by

BVV and F. Hertel for Pits 13 and 61/67. As in Van Valkenburgh and Hertel (1993), fracture frequencies and 95% confidence intervals were included, and comparisons of tooth fracture frequency between pits were done using 3 × 3 contingency tests.

Tooth Wear and Pulp Cavity Analyses

The *C. dirus* sample consisted of 685 mandibles and mandibular fragments, whereas *S. fatalis* sample consisted of 323 mandibles and mandibular fragments distributed unevenly among the three pits (Table 2). Both the *C. dirus* and the *S. fatalis* samples used for the pulp cavity analyses are a subset of that used for the tooth wear analysis because they required the presence of at least one canine tooth. The total numbers of specimens available for pulp cavity analysis for *C. dirus* and for *S. fatalis* are also unevenly distributed among the three pits (Table 2).

Tooth wear stages were estimated for all specimens and compared between the pits. Tooth wear stage was determined by visual inspection and individuals were classified from 1 to 5, from least to most worn. A similar classification was used in Van Valkenburgh (1988) and Van Valkenburgh and Hertel (1993) and produced consistent results with different observers. In all cases, two observers made estimates of wear and their estimates were identical over 95% of the time. Although most samples used for tooth wear could also be used for pulp cavity analysis, this wasn't always the case, so the totals are not identical between samples (Table 2).

Pulp cavity diameter was measured from radiographs of lower canine teeth. All radiographs were taken with a portable x-ray machine using radiographic film in rare-earth cassettes, which magnify and clarify the images. Mandibles were placed buccal side down on the cassettes for measurement consistency. Pulp cavities of the canine teeth were measured with digital calipers directly from the developed radiographs placed on a light table. As in Landon et al. (1998) and Binder et al. (2002), tooth and pulp cavity diameter measurements were taken perpendicular to tooth height between the distal and mesial edges of the lower canine at the point where the tooth emerges from the alveolus and

TABLE 2. Sample sizes of dire wolf (*C. dirus*) and sabertooth cat (*S. fatalis*) tooth wear and age data from Rancho La Brea, California, for each locality.

| Species | Locality | Total numbers of specimens | Total specimens for tooth wear | Total specimens for age analysis |
|-------------------|-----------|----------------------------|--------------------------------|----------------------------------|
| <i>S. fatalis</i> | Pit 3 | 105 | 103 | 38 |
| | Pit 13 | 14 | 12 | 5 |
| | Pit 61/67 | 204 | 204 | 42 |
| <i>C. dirus</i> | Pit 3 | 543 | 542 | 108 |
| | Pit 13 | 37 | 37 | 33 |
| | Pit 61/67 | 105 | 105 | 96 |

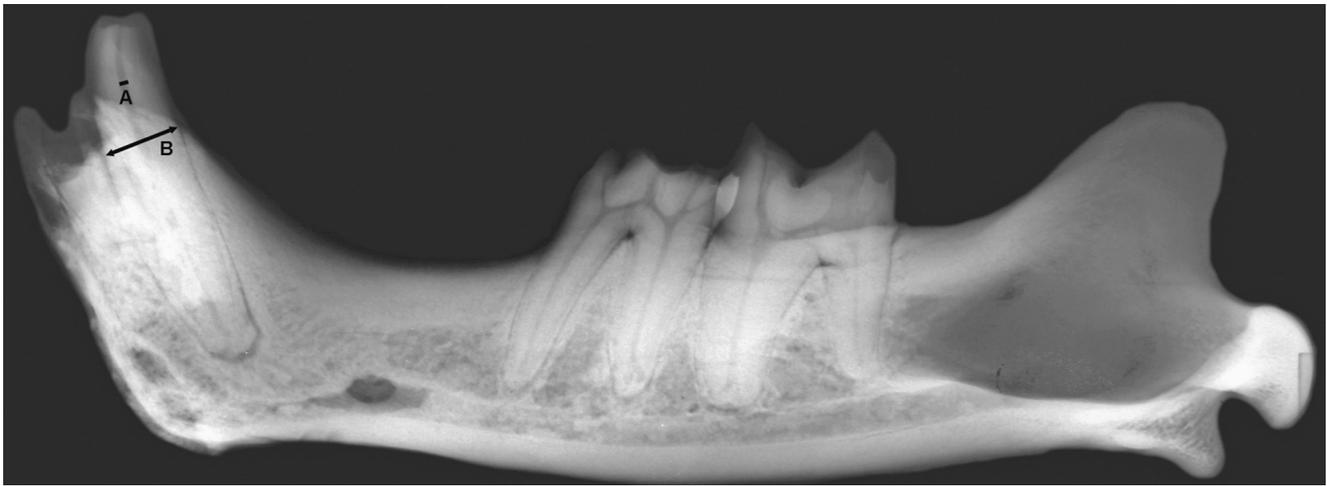


FIGURE 1. Radiograph of a left dentary of a *S. fatalis* specimen, indicating the inner and outer diameters from which pulp cavity measurements are taken. **A**, the pulp cavity diameter; **B**, the canine diameter. Note that measurement **B** is taken from where the tooth emerges from the alveolus.

is generally widest (Fig. 1). Pulp cavity width was measured as a percent of the total pulp cavity closure for standardization and to allow for comparison between different sized animals and different species. Percent pulp cavity width is measured as:

$$100 \times (\text{canine diameter} - \text{pulp cavity diameter}) / (\text{canine diameter})$$

Thus smaller cavity widths (associated with older individuals) have higher values. Measurements were taken to the nearest 0.01 mm. To test for differences among the pits, the non-parametric Kolmogorov-Smirnov test was used (Zar, 1998).

RESULTS

Dire Wolf

Binder et al. (2002) documented a significantly higher fracture frequency in Pit 13 wolves (Table 1) than those from Pit 61/67. Here we add data from Pit 3 that includes wolves that lived both before and after those from Pit 13. Again, Pit 13 wolves have significantly higher fracture rates than Pit 3 wolves, despite the fact that some of the Pit 3 wolves may have been contemporaneous with Pit 13 wolves. Although the Pit 3 fracture frequency (3.01 ± 0.086) is slightly above that of Pit 61/67, the difference is not significant, and this illustrates that Pit 13 represents an unusual interval.

The wear stage data are largely consistent with higher fracture rates being associated with heavier tooth wear as was found in Binder et al. (2002). All of the pits are dominated by individuals with slight tooth wear, but Pit 61/67 includes relatively fewer individuals with moderate to heavy tooth wear than do Pits 3 and 13, respectively (Pit 3, $P < 0.005$, $Z = 1.823$; Pit 13, $P < 0.011$, $Z = 1.634$). Although Pit 13 wolves exhibit somewhat heavier wear than those of Pit 3 (Fig. 2), they do not differ significantly ($P = 0.06$, $Z = 1.337$). As in Binder et al. (2002), the higher fracture rates and wear observed in *C. dirus* in Pit 13 relative to the other two is not associated with a predominance of older individuals. There are no significant between-pit differences in the sample age distributions as estimated by pulp cavity diameter (in all cases $P > 0.6$) (Fig. 3).

Sabertooth Cat

As was found in Van Valkenburgh and Hertel (1993) for a larger sample of pits, on average, the sabertooth cat broke its teeth significantly more often than the dire wolf across all three pits (Table 1). Only in Pit 13 did the dire wolf exceed the sabertooth cat in tooth fracture frequency. Unlike the dire wolf, fracture rates for *Smilodon* are similar in Pit 13 and Pit 61/67, but are significantly higher in Pit 3 than Pit 61/67 ($P < 0.02$, $\chi^2 = 5.66$). Unfortunately, the numbers of *Smilodon* in Pit 13 are too small to perform statistical comparisons of fracture frequency with the other two samples.

In contrast to the dire wolf data, there is no association between increased fracture frequency and heavier tooth wear (Fig. 4). Instead, we find no significant differences in the distributions of tooth wear among all three samples with ($P = 0.932$, $Z = 0.540$), despite the fact that Pit 3 *Smilodon* broke their teeth more frequently than those of Pit 61/67. In the dire wolf sample, there is a preponderance of young, relatively unworn individuals that dominate the samples. Although the *Smilodon* sample is also dominated by individuals with wear stages 1–2, it is slightly more worn than the dire wolf sample. Pit 13 visually appears to have a different distribution, but is such a small data set (sample size is 12 compared with 103 and 204 in Pits 3 and 61/67, respectively) that comparisons are not meaningful. Comparing the wear distributions for *Smilodon* in each pit with their dire wolf counterparts reveals no significant differences between them for Pits 3 and 13 ($P = 0.504$, $Z = 0.825$; and $P = 0.179$, $Z = 1.098$, respectively). However, they do differ for Pit 61/67 ($P < 0.03$, $Z = 1.441$), with *S. fatalis* having more wear.

Finally, the age distribution between the pits using percent pulp cavity width as a relative indicator of age followed the wear data closely, with very similar distributions for all three samples (Fig. 5; $P = 0.525$, $Z = 0.812$) as in the dire wolf. Interestingly, when the data from the three pits of each species are pooled, the difference between the species is significantly different ($P < 0.0005$, $Z = 5.493$), with *Smilodon* including relatively more individuals with closed or near-closed pulp cavities.

DISCUSSION

Our initial intention was to replicate the previous analysis of temporal shifts in tooth fracture in Rancho La Brea dire wolves

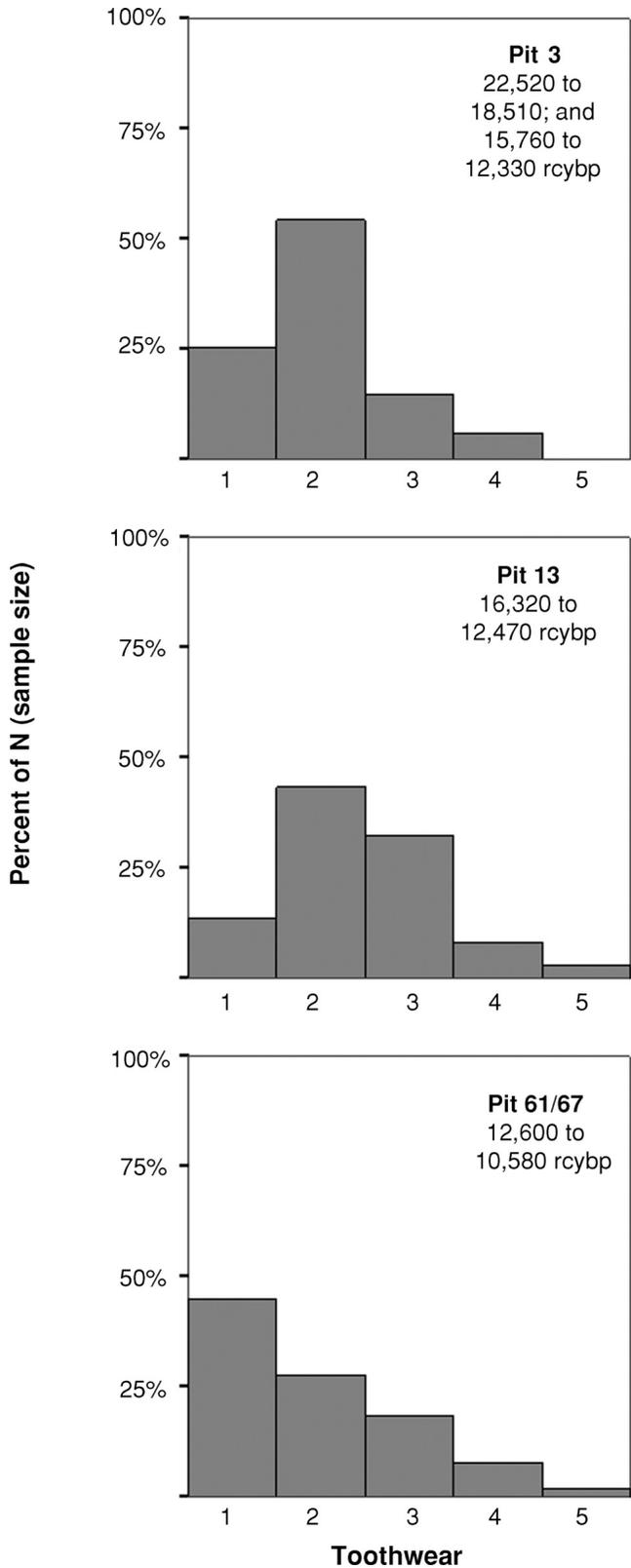


FIGURE 2. Histograms of *C. dirus* tooth wear for three Rancho La Brea localities, Pit 3, Pit 13, and Pit 61/67. Pit dates are maximum (upper) and minimum (lower) 95% confidence intervals for each pit, including both deposits for Pit 3.

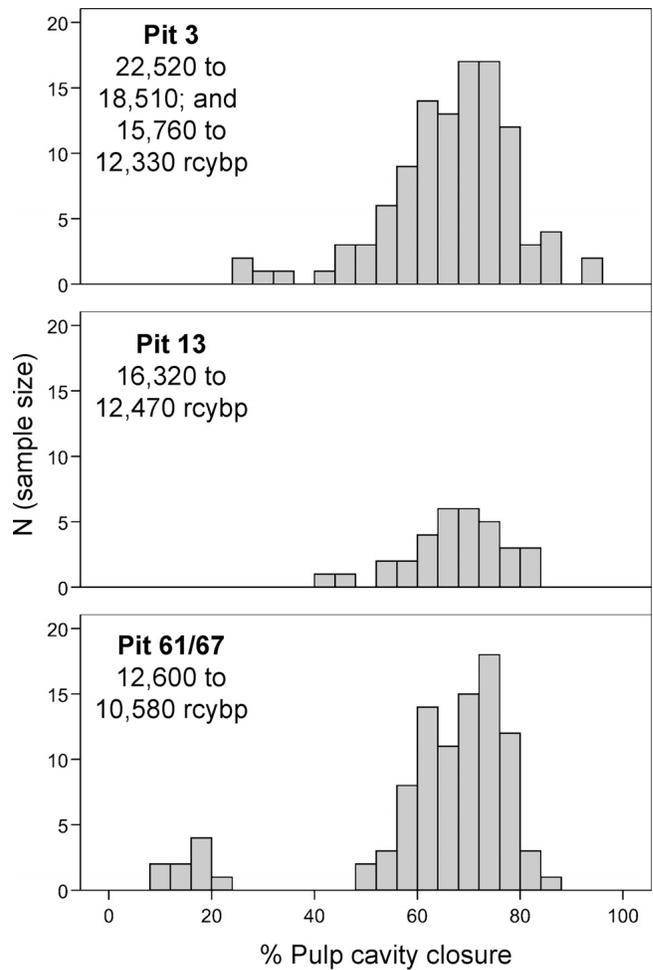


FIGURE 3. Histograms of *C. dirus* percent pulp cavity closure for three Rancho La Brea localities, Pit 3, Pit 13, and Pit 61/67. Pit dates are maximum (upper) and minimum (lower) 95% confidence intervals for each pit, including both deposits for Pit 3.

from Pits 13 and 61/67 with the co-occurring sabertooth cat, *S. fatalis*. However, due to the limited numbers of *Smilodon* dentaries in Pit 13, we expanded our study to include Pit 3, a pit that included the Pit 13 time interval of about 15,000–14,000 ybp, but also extended before and after that fairly narrow window. As results did not differ if we treated the older and younger samples from Pit 3 separately, we used the entire range of Pit 3 to maximize sample size. Our hypothesis was that both the dire wolves and sabertooth cats of Pit 3 would exhibit greater tooth wear and higher tooth fracture rates, similar to those of the Pit 13 samples and significantly greater than those from the youngest sample, Pit 61/67. Compared to equivalent sized modern species, wear in *C. dirus* and *S. fatalis* is higher as well (Van Valkenburgh, 2009). Moreover, we expected there to be no significant differences among pits in the age distributions of the sampled populations as estimated by pulp cavity diameter. Our expectations were met in part, but there were clear differences between the species that may reflect differences in their behavior and dental anatomy.

Looking at the pulp cavity data, within each species, the age distributions of the populations sampled in each pit did not differ among pits. In all cases, the populations are dominated by young adults with relatively open pulp cavities. This indicates that there

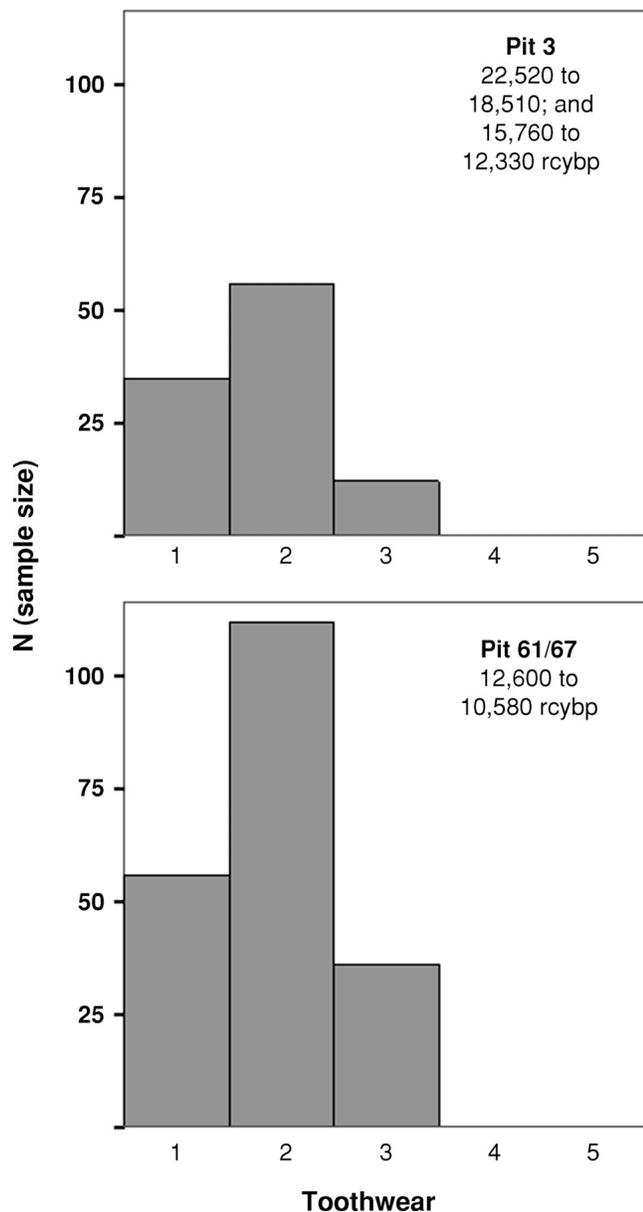


FIGURE 4. Histograms of *S. fatalis* tooth wear for two Rancho La Brea localities, Pit 3 and Pit 61/67. Pit dates are maximum (upper) and minimum (lower) 95% confidence intervals for each pit, including both deposits for Pit 3.

is no reason to suspect that individuals trapped were primarily older in age, nor could the age-structure of any of the trapped populations account for any other differences found. This also confirms the results of Binder et al. (2002), which found the same distribution for two pits did not differ in two pits for *C. dirus*.

For *S. fatalis*, there was also minimal difference in tooth wear stage between pits. Thus the differences in fracture frequency between the pits is the only evidence of differences in the samples. The Pit 3 sample exhibited significantly higher fracture frequency than that of Pit 61/67. Wear stage reflects age, as the longer an individual lives, the more likely they are to have broken a tooth. Among extant carnivorans, the probability of tooth fracture tends to increase with tooth wear (Van Valkenburgh, 2009), and this relationship appears to hold for the dire wolf as well. Pit

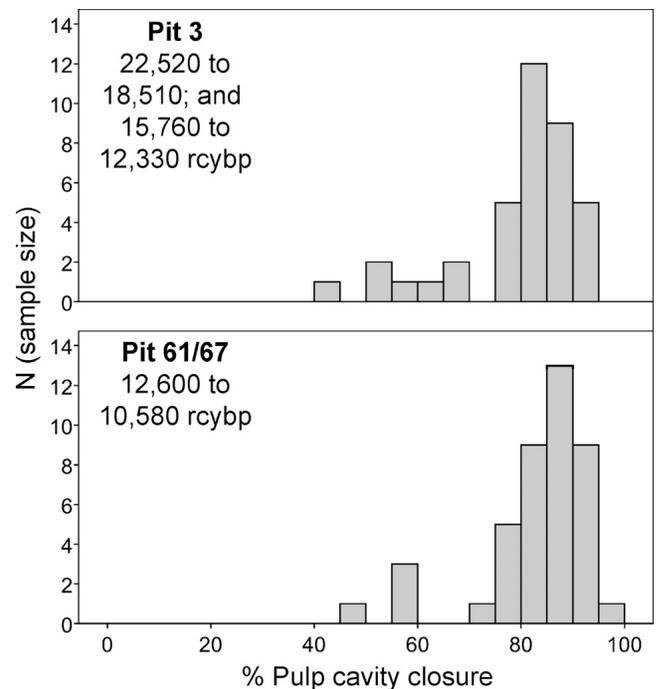


FIGURE 5. Histograms of *S. fatalis* percent pulp cavity closure for two Rancho La Brea localities, Pit 3 and Pit 61/67. Pit dates are maximum (upper) and minimum (lower) 95% confidence intervals for each pit, including both deposits for Pit 3.

13 dire wolves had significantly more broken teeth and the largest proportion of individuals with moderate to heavy tooth wear.

The pattern of tooth fracture frequency over time was not identical in the two species. For *C. dirus*, the similarly low fracture frequencies of Pit 3 and Pit 61/67 wolves, and their difference from those of Pit 13 wolves was not expected, because Pit 3 includes the time interval sampled by Pit 13. This is difficult to explain, but may reflect the fact that Pit 3 samples a longer time interval. Perhaps Pit 13, which spans about 1000 years between 15 and 14 ypb, represents a particularly stressful time for dire wolves. Preliminary morphometric analyses indicate that these wolves are unusually small as well (O'Keefe, 2008). This requires further investigation and more extensive dating of Pit 3 and Pit 13 to better understand the temporal overlap between them.

Smilodon exhibits a different pattern of shifting fracture frequencies, with Pit 3, spanning about 22,000–12,600 ypb, displaying high rates of fracture frequency relative to both the older Pit 13 and younger Pit 61/67, which are similar to one another. This implies that there may be different causes of tooth fracture in different species. If tooth fracture frequency reflects food stress, the dire wolves and sabertooth cats do not appear to be responding similarly. However, it is possible that a larger sample of *Smilodon* from the same 15,000–14,000-ybp time window would show a spike in tooth fracture rates. Unfortunately, our current sample is too small for reliable statistical comparisons, and all that can be concluded is that both species show significant fluctuations in fracture frequency that cannot be explained by differences in population age structure.

However, the differences between species cannot be explained by a simple spike in the time frame for Pit 13. In addition to having different fracture frequencies in different pits, tooth fracture in *S. fatalis* was higher than that of *C. dirus* in both early and later pits (at the same time, tooth wear was equivalent to the higher level of wear found in the older Pit 13 in *C. dirus*), a result also

seen in Van Valkenburgh and Hertel (1993). There are several possible explanations for this result. One is the possibility that *S. fatalis* was consuming more bone on average than *C. dirus*. Although this is somewhat counterintuitive, the sabertooth cats were likely to have been more limited in prey choice than dire wolves; this is reflected in studies of extant sympatric canids and felids, which demonstrated that canids have a more varied diet, whereas felids are limited to hypercarnivory (Kok and Nel, 2004; Fox-Dobbs et al., 2007). In fact, the diets of dire wolves appeared to have been broader than those of *Smilodon*, which is reflected in isotope values (Coltrain et al., 2004).

Another possibility is that the higher level of tooth breakage may also reflect the differences in cheek tooth morphology between *S. fatalis* and *C. dirus*. The narrower, more blade-like teeth of *S. fatalis* make them more effective slicers, but there is a trade-off in tooth strength. Narrower and sharper structures are physiologically more likely to break under stress (Lucas et al., 1994; Lucas and Teaford, 1994), and thus *S. fatalis* teeth might be more vulnerable to fracture than the broader teeth of *C. dirus*.

Finally, the difference in fracture frequency may reflect another finding, that of the differences in age distribution between the dire wolves and sabertooth cats across all pits. Although age distributions for the three pits of *C. dirus* were very similar, as they were for *S. fatalis*, there was a difference in distribution between *C. dirus* and *S. fatalis*, with the *S. fatalis* sample including individuals of an older average age. This may mean that the *S. fatalis* sample was, in fact, older, which may be due to their being longer-lived on average. Another possibility is that there may have been some tendency for the pits to trap older *S. fatalis* individuals, but not older *C. dirus* ones, which is not supported, but cannot be ruled out. A third alternative is that pulp cavity width is a relative measure and the cavity of *S. fatalis* filled in faster on average than that of *C. dirus*. In this case, age distributions based on pulp cavity widths may be species specific, indicating that that cross-species comparisons should be made with caution. This seems to be a strong possibility, and although there are pulp cavity width data from many species (Smuts et al., 1978; Zapata et al., 1997; Landon et al., 1998), there has yet to be a study that compares these data among species.

In addition to having higher fracture frequencies in comparison with dire wolves, *Smilodon* has a relatively high tooth fracture frequency compared with most modern carnivores, especially extant felids. Comparisons between *S. fatalis* and the extant North American *Puma concolor* show far greater fracture frequencies in *S. fatalis* (Van Valkenburgh, 2009). Although the frequencies of broken teeth for three subspecies of *P. concolor* range from 1.7% to 3.3%, they range from 5.1% to 8.3% in *S. fatalis* ranges (Table 2). The overall mean of percent broken teeth for all extant felids is 1.8 (± 0.7), and the mean for the Hyaenidae (the family with the highest mean breakage) is 3.6 (± 1.4). These data demonstrate that the sabertooth cats broke their teeth two to three times more often than extant pumas and much more often than is typical of all felids and all combined families of extant carnivores, demonstrating a distinct difference in the Pleistocene population compared with modern species. These fracture frequencies are informative about the relative feeding patterns and competition among these species in the Pleistocene, and demonstrate that different species, even two with strong niche overlap such as *Smilodon* and dire wolves, may not experience the same environment similarly. This also supports the possibility that *Smilodon* may have been eating harder foods such as bone due to increased food competition, which combined with the more slender, delicate teeth of *Smilodon* would result in the increase in breakage. If interspecific food competition was more intense, then other similarly large felids should also exhibit high fracture frequencies, and this appears to have been true of the Pleistocene American Lion (*Panthera atrox*). Also found at Rancho La Brea, the extinct lion exhibited the highest observed

percent of broken teeth (12.5%) among all sampled carnivores, past and present (Van Valkenburgh, 2009).

Our results some evidence for sociality in *S. fatalis*. Intraspecific feeding competition is likely to be greater in social than solitary species and this could result in higher fracture frequencies. A recent study by Carbone et al. (2009) also argued for sociality in *Smilodon* based on a comparison of the numbers of extant African carnivore species attending the recorded sounds of dying herbivores to those found in Rancho La Brea. They found a strong similarity between the much larger representation of social carnivores at the African playbacks and that of both *C. dirus* and *S. fatalis* at La Brea compared with the much lower occurrence of the remaining solitary species. Apparently, solitary species in both ecosystems avoid such events due to the risk of dangerous encounters with groups of social species. The large numbers of *S. fatalis* at Rancho La Brea, heavy tooth wear, and large numbers of broken teeth are all consistent with a social species feeding rapidly and thoroughly on large carcasses.

Finally, the analysis of the data reveal that tooth fracture variation is not just a reflection of age differences among sampled populations but instead appears to reflect variation in feeding behavior. The comparison between species, though, provides evidence that caution must be used when comparing species with different dentitions, and that certain measures of aging may be species specific, and may not be reliable across species. Further, the lack of coincidence in the fracture variation between the two La Brea species might be resolved with better dating of specimens.

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