Sexual dimorphism and ontogenetic growth in the American lion and sabertoothed cat from Rancho La Brea

J. A. Meachen-Samuels1* & W. J. Binder2

1 Department of Ecology and Evolutionary Biology, University of California, Los Angeles CA, USA
2 Department of Biology, Loyola Marymount University, Los Angeles, CA, USA

Keywords
ontogeny; pulp cavity; dentaries; Panthera leo.

Correspondence
Julie A. Meachen-Samuels, Department of Ecology and Evolutionary Biology, University of California, Los Angeles, 621 Charles E. Young Dr. S., Los Angeles, CA 90095, USA.
Email: meachensamuels@nescent.org

Abstract
Sexual dimorphism has long been purported in the American lion Panthera atrox well-known from the asphalt deposits at Rancho La Brea. However, few studies have quantified this dimorphism. Along with the sabertoothed cat, Smilodon fatalis, we examine sexual dimorphism in dentaries from the Rancho La Brea tar pits using extant Panthera leo as a guide. Although growth rate in large carnivores declines after a certain age, it has been demonstrated to continue well beyond adulthood, therefore age must also be incorporated into a measure of sexual dimorphism in large carnivores. Prior studies demonstrated that tooth wear can be an inaccurate measure of age in Rancho La Breaan carnivores, as it is affected by both diet and age. This study, instead, uses per cent pulp cavity closure of the lower canine tooth which is solely a measure of relative age, combined with linear measurements of the dentaries to separate the sexes of these two extinct cats. Results show that P. atrox has similar, or slightly greater, levels of sexual dimorphism than P. leo, whereas S. fatalis shows little to no sexual dimorphism. Our results also demonstrate that both Panthera species continue to grow into adulthood, strengthening the case that it is necessary to incorporate a measure of age into studies of sexual dimorphism in large carnivores, living or extinct.

Introduction
In carnivores and other larger mammals, male-dominated harem social structure is often accompanied by an increase in sexual dimorphism (Ralls, 1977; Gittleman & Van Valkenburgh, 1997; Weckerly, 1998; Sacco & Van Valkenburgh, 2002). African lions Panthera leo are the only living felid species to demonstrate this type of social structure, in which individuals live in prides with one to a few dominant males and many females (Schaller, 1972; Packer, 1986), and indeed show a high level of sexual dimorphism relative to most other cats (Gittleman & Van Valkenburgh, 1997).

It is particularly difficult to study sociality or dimorphism in extinct species, as determining either trait must be done indirectly. We can use comparisons with extant species that are morphologically similar or related in order to make educated inferences about the extinct species and better understand their ecology and morphology. The sex ratio can give important information about species ecology, such as how a species hunted, mated and morphologically evolved through time. When examining a fossil species, incorrect assumptions about population demographics can lead to erroneous conclusions that may affect the way we perceive an entire extinct ecosystem. Further, morphological analyses, such as growth and mechanics are strongly affected by the ability to divide a population into sex-specific groups (for instance, a growth series may be misinterpreted if sexual size dimorphism is not taken into account).

The extensive collection of large carnivores present at the Rancho La Brea deposits in Los Angeles, California provides a unique sample that many other fossil sites do not offer. Because of the unusual type of deposition that occurred, where one herbivore became mired in the tar and in turn attracted numerous carnivores, the latter outnumber the former 10 to one, and the preservation of the fossils at the tar pits makes studies of carnivores optimal at this locality. The extinct dire wolf Canis dirus is the most prevalent species at the tar pits, followed closely by Smilodon fatalis, with Panthera atrox as the third most common carnivore (Stock & Harris, 1992). This study focuses on these two large cats.

The extinct American lion P. atrox, has been demonstrated to be a close relative of the African lion (Kurten, 1968; Turner & Antón, 1997; Barnett et al., 2006, 2009), and may share important morphological traits with living lions. Prior studies have observed that there may be marked sexual
dimorphism in *P. atrox* (Kurten, 1985; Jefferson, 1992; Yamaguchi et al., 2004), which may or may not be related to their social system, as sexual dimorphism is present in most large cats, including solitary species (Sunquist & Sunquist, 2002). However, there is a dearth of studies which actually quantify the level of sexual dimorphism in the American lion. Prior studies have elucidated sexual dimorphism from prehistoric cave paintings in closely related European lions *Panthera spelaea* (Yamaguchi et al., 2004; Barnett et al., 2009).

While extant mammals can be easily sexed, extinct animals are often compared using statistical analyses in order to determine the sexes of the individuals, and thus the presence of dimorphism, if any. However, in studies on spotted hyenas (Binder & Van Valkenburgh, 2000) and living lions (Benoit, 2006, 2007) it has been demonstrated that bones of adult individuals may continue to grow in size even past sexual maturity, possibly continuing to grow into senescence, albeit at a slower rate. Therefore, age may be a complicating factor in sex determination that must be considered. If this is the case in the American lion and sabertoothed cat, then these samples should be treated in a similar fashion to animals that continue to grow asymptotically after sexual maturity, and a method must be sought that takes into account age at death as well as size of the individual before an accurate assessment of sexual dimorphism can be obtained (Stamps, 1993).

An earlier study on *P. atrox*, the only one which quantified dimorphism (Jefferson, 1992), used an estimation of ontogenetic age through molar tooth wear along with size to determine the level of sexual dimorphism in *P. atrox* from Rancho La Brea. However, using tooth wear as an ontogenetic indicator can be problematic. Van Valkenburgh & Hertel (1993) found that tooth breakage frequencies were three times as high in large carnivores (dire wolf, American lion and *Smilodon*) at Rancho la Brea as in extant carnivore populations, and this may correlate with tooth wear, resulting in an erroneously older age estimation (Van Valkenburgh, 1988). Additionally, in a study of dire wolves from Rancho La Brea, Binder, Thompson & Van Valkenburgh (2002) found there were significant differences in tooth wear and breakage between different pits at the fossil site, while there were no differences in ontogenetic ages of individuals between the same pits. Using wear as a proxy for age would give incorrect age assignments to individuals that may have been the same ontogenetic age at death, therefore it is an inaccurate method to assess age in carnivores at Rancho La Brea. Even in the case of extant *P. leo*, Smuts, Anderson & Austin (1978) found tooth wear to be a less accurate method in determining ontogenetic age of known aged specimens than radiographic analysis. Here, we use pulp cavity closure as a better estimator of ontogenetic age.

Unlike tooth wear, pulp cavity closure is a function of ontogeny and does not relate to diet or tooth wear patterns (Burns & Maples, 1976; Morse et al., 1991). Measuring the pulp cavity closure of the lower canine, via X-rays, is a non-destructive way to assess ontogenetic age in modern and extinct carnivores that is also fast, simple and inexpensive. As the animal ages, secondary dentine is deposited within the pulp cavity, which fills it in, reducing the diameter over time. Hence, the more filled the pulp cavity, the older the individual (Gustafson, 1950; Woods, Robinson & Harris, 1990; Drusini, Toso & Ranzato, 1997; Landon et al., 1998). This technique has been used with success on many extant species including: humans (Woods et al., 1990), grey foxes (Tumlinson & McDaniel, 1984), lions (Smuts et al., 1978) and wolves (Landon et al., 1998). Binder et al., (2002) using coyotes, tested it against the well-established methodology of cementum annuli, where teeth are sectioned and rings of cementum are stained and counted (a much more expensive and destructive method) and found the results to be fundamentally similar. Therefore both *P. leo* and *P. atrox* could be aged successfully with this method, given the presence of at least one undamaged lower canine.

Living alongside the American lion in the Rancho La Brea deposits was the sabertoothed cat *S. fatalis*. A study by Sacco & Van Valkenburgh (2002) found little to no sexual dimorphism in the crania of *S. fatalis*, however they did not include ontogenetic age in their analysis to account for any growth pattern differential. Since sabertoothed cats have no close living relatives, using a large conical-toothed cat such as the extant African lion to examine the ecology of *Smilodon* is the best available option.

We hypothesize that by using linear bone measures while controlling for age with pulp cavity width, we will be able to more accurately determine the presence of sexual dimorphism in the extant African lion and make accurate determinations of the presence of sexual dimorphism in the extinct American lion and sabertoothed cat.

**Materials and methods**

For this study, we used *P. leo* as the closest living comparator species for both *P. atrox* and also for *S. fatalis*. For known-sex adult *P. leo*, we took a linear measurement of dentary length, from the anterior tip below the lower first incisor to the posterior end of the condyloid process at the jaw joint, and radiographed the mandible, allowing a clear image of the lower canine tooth and confirming the presence of fully erupted permanent dentition. For maximum accuracy (of radiograph measurements) we only used complete hemimandibles with a complete lower canine. Digital radiographs were taken of *P. leo* hemimandibles at the United States National Museum of Natural History in Washington, DC. All other radiographs were taken by placing the mandibles, lateral side down, directly on a Dupont Quanta Rapid X-ray cassette (Dupont Corporation, Wilmington, DE, USA) containing 3M green light-sensitive UVL film using a portable X-ray machine.

Pulp cavities of the canine teeth and mandibular lengths were measured in ImageJ (Rasband, 2007) for digital radiographs; and directly, using digital calipers and a light table, for film radiographs. All measurements were taken to the nearest 0.01 mm. As in Binder et al., (2002) and Landon et al., (1998) tooth and pulp cavity diameter measurements were taken perpendicular to tooth height at the point where
the tooth emerges from the alveolus at its widest. Per cent pulp cavity closure was calculated as

\[
100 \times \frac{\text{canine diameter} - \text{pulp cavity diameter}}{\text{canine diameter}}
\]

with smaller cavity widths (associated with older individuals) indicating higher percentage values.

To assess the level of sexual dimorphism in these three species, we performed a linear regression of jaw length (mm), against per cent pulp cavity closure for each species separately. For extant lions, we also performed separate regressions for known sex males and females. In *P. atrox* and *S. fatalis*, to test for a bimodal distribution of jaw length versus pulp cavity closure, we used the species regression line as delineation between hypothesized male and hypothesized female individuals, and reran a linear regression using the hypothesized *a priori* categories.

Additionally, we used a \( \chi^2 \)-test to determine the fit of our *P. leo* data to the regression line estimate, and we ran a mixed model analysis of variance (ANOVA) on the slopes of each of the actual (*P. leo*) or hypothesized (*P. atrox* and *S. fatalis*) sex assignments to test for homogeneity of variance between sex categories within and between each species. Finally, we performed an AIC analysis to compare the different regressions to determine whether two separate regressions separating the sexes improved the fit over a single linear regression, and if two regressions of different slopes would improve upon regressions with the same slopes.

**Results**

Plots of jaw length and per cent pulp cavity width as a proxy for age (hereafter referred to as age) (Fig. 1), show a positive trend for all species, which demonstrates increasing jaw length with increasing age. Correlation coefficient \( (R^2) \) values were not very high (*P. atrox*, \( R^2 = 0.095 \); *P. leo*, \( R^2 = 0.156 \); and *S. fatalis*, \( R^2 = 0.15 \)) and only the *S. fatalis* correlation was significant (Spearman’s \( P = 0.016 \) (Table 1). Species were also separated in the plot vertically by size, with *P. atrox* on top and clearly larger than *P. leo*. *Smilodon fatalis* had the smallest mandibles, falling below both *Panthera* species (Fig. 1).

If sex-specific growth is important as a function of age, the fit of regression lines for each sex should be closer than one line for all individuals. To look at the effect of separating the sexes on the fit of the regression line, the *P. leo* data were used alone, as these were the only known sex individuals. The first comparison was with all individuals together (Fig. 2a), and next to it the same figure separated into known sex individuals with individual regression lines (Fig. 2b).

Upon looking closely at the dataset separated by sex, it is clear that males tend to be larger for a given age than females (Fig. 2a and b), an expected result in this dimorphic species. A simple technique was then used to try to separate sexes of the extinct species; after placing a regression line for all individuals; those above the line are classified as male and below are classified as female. While this did not separate the sexes with 100% accuracy, it was overwhelmingly accurate (of our known sex lions, when compared with a random distribution, the result of a \( \chi^2 \)-test demonstrated the sexes were distributed above and below the line correctly, \( \chi^2 = 9.308, P = 0.002 \) (Fig. 3a). To further test the accuracy of this method, we re-analyzed the *P. leo* data using the regression method. We attempted this with all of the unknown sex *P. leo* individuals (Fig. 3b), and compared it with the previous known sex comparisons (Fig. 3a). The improvements in \( R^2 \) values were similar in both cases (Table 1).

Given that the technique appears to work in terms of a similar increase in \( R^2 \) values of regression lines when separating by sex, we applied this technique to *P. atrox*. In Fig. 4a, the \( R^2 \) value regression of all individuals is not significantly different from zero, indicating that the line does not explain any variation in the dataset, but when sexes were separated into two distinct clusters, above and below the original regression line (Fig. 4b), \( R^2 \) values of putative sexes were far higher, which would not necessarily be the case if the technique randomly grouped data. Finally, in Fig. 5 there is a comparison of all three species with separate regression lines for each sex.

To determine whether the use of two linear regressions (rather than a single one) was an improvement, an AIC analysis was performed using the *P. leo* data of known sex only, the *P. leo* data including individuals of unknown sex, and the regressions of *P. atrox* and *S. fatalis* with the presumed sexes included. In each case, the AIC plot was most optimal for two regressions separating sexes. This indicates that the addition of the parameter which allows for separation of sexes in each case is justified.
Unlike the previous two species, results from the Smilodon data suggest that this species did not show the same pattern of sexual dimorphism as in *P. leo* or *P. atrox*. The $R^2$ values did not increase in the same fashion, and the data points did not separate bimodally (Table 1).

Finally, we wanted to know if there were any differences between sexes or species in these relationships. In order to determine if there were differences between slopes of jaw length correlated with pulp cavity width between males and females of each species, we ran a mixed model ANOVA. We found no significant differences between putative males and females of any species (*P. leo*, $F = 1.09$; *P. atrox*, $F = 0.061$; *S. fatalis*, $F = 0.576$). In addition, we wanted to see if there were any differences in these trends between species, and found none in the combined dataset of any comparison (Table 2). We also ran an AIC analysis for two regressions allowing for different slopes, and this also resulted in a less optimal AIC result, further reinforcing that growth rate does not differ between sexes.

### Discussion

The results of our study demonstrate that *P. atrox* showed strong sexual dimorphism. The clearly bimodal distribution of data points, similar to (if not more exaggerated than) *P. leo*, suggests that our classifications are realistic. Additionally, compared with the regressions of all individuals, when the sexes are separated, in both *P. leo* and *P. atrox*, the

<table>
<thead>
<tr>
<th>Species</th>
<th>Pooled sexes $R^2$</th>
<th>Pooled Spearman’s $\rho$ values</th>
<th>Separate sexes $R^2$</th>
<th>Separate Spearman’s $\rho$ values</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Panthera atrox</em></td>
<td>0.095</td>
<td>0.266</td>
<td>M 7 0.75</td>
<td>0.857</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>F 6 0.55</td>
<td>0.886</td>
</tr>
<tr>
<td><em>Panthera leo</em></td>
<td>0.156 all, 0.233 known sex</td>
<td>0.311 all, 0.313 known sex</td>
<td>M 5 0.42</td>
<td>0.771</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>F 8 0.70</td>
<td>0.714</td>
</tr>
<tr>
<td><em>Smilodon fatalis</em></td>
<td>0.150</td>
<td>0.546</td>
<td>M 10 0.50</td>
<td>0.952</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>F 9 0.54</td>
<td>0.517</td>
</tr>
</tbody>
</table>

Figure 2 (a) Regression of jaw length and age (as per cent pulp cavity closure) in *Panthera leo*, with known sex individuals indicated (all individuals: $R^2 = 0.156$; only known sex individuals: $R^2 = 0.233$). (b) Regression of jaw length and age (as per cent pulp cavity closure) by sex in *P. leo*, with known sex individuals indicated (all individuals: $R^2 = 0.233$; females: $R^2 = 0.695$; males: $R^2 = 0.419$).
$R^2$ values increase similarly and significantly for both sexes, and the AIC analysis confirms this result. If *P. atrox* was not sexually dimorphic, the regression scatter would likely look more like the graph of *S. fatalis*, with a tighter cluster of points rather than a bimodal distribution. It is curious however, that the $P$-values are only significant for *P. atrox* and not for *P. leo*, where sexes are known. This may suggest that *P. atrox* may be more dimorphic than *P. leo*. This is not a wholly unexpected result because previous studies have shown that the level of sexual size dimorphism increases as
species get larger (Gittleman & Van Valkenburgh, 1997; Weckerly, 1998). Despite the trend of the data, sample sizes are quite small, which makes achieving significance difficult, even with non-parametric statistics.

In addition to indicating the presence (or lack thereof) for sexual dimorphism in the three species, this analysis has the additional benefit of identifying the sex of the individual specimens of each species (Table 3). This allows for comparisons of individual morphological features of males and females, giving greater insight and understanding of extinct species (and even the analysis of extant species of indeterminate sex, common in large collections).

Since *P. leo* is one of the most sexually dimorphic extant felid species and also has the most social behavior, it is also likely that *P. atrox* which is also very sexually dimorphic and even larger may have had a similar social structure to *P. leo* based on the level of sexual dimorphism that our results suggest. Although sexual dimorphism alone is not

Table 2 Comparisons of *P*-values of slopes of mandible length versus per cent pulp cavity closure using a mixed model ANOVA

<table>
<thead>
<tr>
<th>Species</th>
<th>Panthera atrox</th>
<th>Panthera leo</th>
<th>Smilodon fatalis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Panthera atrox</td>
<td>0.860&lt;sup&gt;MF&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Panthera leo</td>
<td>0.750</td>
<td>0.372&lt;sup&gt;MF&lt;/sup&gt;</td>
<td>–</td>
</tr>
<tr>
<td>Smilodon fatalis</td>
<td>0.134</td>
<td>0.637</td>
<td>0.460&lt;sup&gt;MF&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>MF</sup>, male/female comparisons within species. All other values are pooled sex between species comparisons.

Table 3 Sex assignment of *Panthera atrox* using mandible length (mm) and per cent pulp cavity closure of the lower canine tooth

<table>
<thead>
<tr>
<th>Museum collection number</th>
<th>Mandible length (mm)</th>
<th>Per cent pulp cavity closure</th>
<th>Sex assignment</th>
</tr>
</thead>
<tbody>
<tr>
<td>LACMHC 285</td>
<td>251.10</td>
<td>31</td>
<td>M</td>
</tr>
<tr>
<td>LACMHC 17488</td>
<td>271.10</td>
<td>85</td>
<td>M</td>
</tr>
<tr>
<td>LACMHC 593</td>
<td>267.67</td>
<td>49</td>
<td>M</td>
</tr>
<tr>
<td>LACMHC 6988</td>
<td>202.00</td>
<td>38</td>
<td>F</td>
</tr>
<tr>
<td>LACMHC 6987</td>
<td>224.50</td>
<td>44</td>
<td>F</td>
</tr>
<tr>
<td>LACMHC 6981</td>
<td>224.80</td>
<td>87</td>
<td>F</td>
</tr>
<tr>
<td>LACMHC 17460</td>
<td>241.55</td>
<td>85</td>
<td>F</td>
</tr>
<tr>
<td>LACMHC 594</td>
<td>258.50</td>
<td>21</td>
<td>M</td>
</tr>
<tr>
<td>LACMHC 597</td>
<td>268.60</td>
<td>50</td>
<td>M</td>
</tr>
<tr>
<td>LACMHC 594</td>
<td>278.40</td>
<td>82</td>
<td>M</td>
</tr>
<tr>
<td>UCMP 21548</td>
<td>217.60</td>
<td>15</td>
<td>F</td>
</tr>
<tr>
<td>UCMP 114904</td>
<td>245.00</td>
<td>91</td>
<td>F</td>
</tr>
<tr>
<td>LACMHC 600</td>
<td>272.63</td>
<td>70</td>
<td>M</td>
</tr>
</tbody>
</table>

LACMHC, George C. Page Museum of La Brea Tar Pits Discoveries; UCMP, University of California Museum of Paleontology, Berkeley.

Figure 5 Regression of jaw length and age (as per cent pulp cavity closure) by sex in *Panthera atrox*, *Panthera leo* and *Smilodon fatalis*, using above and below the regression line sex determination for all individuals by sex (see Table 1 for regression values).
necessarily a basis for social behavior (i.e. social behavior occurs in vertebrate species with relatively little sexual dimorphism, wolves (Mech, 1970), beavers (Müller-Schwartz & Sun, 2003) and ravens and crows [[Heinrich, 1989] to name a few] sexual size dimorphism is often more pronounced in polygonous mating systems than in monogamous mating systems (Ralls, 1977; Harvey, Kavanagh & Clutton-Brock, 1978; Kay et al., 1988; Plavcan & van Schaik, 1992; Weckerly, 1998). Since there is evidence that the two closest relatives of P. atrox, P. spelaea and P. leo show high levels of sexual dimorphism and traveled in groups, it is most likely that P. atrox did as well (Schaller, 1972; Yamaguchi et al., 2004).

From Fig. 5, we see that P. leo and P. atrox show similar bimodal patterns. S. fatalis, on the other hand, does not demonstrate a clear difference between the groups as in the two Panthera species. This finding concurs with those of Sacco & Van Valkenburgh (2002) that S. fatalis shows little to no sexual dimorphism. Although the P-values indicate that Smilodon males demonstrated a significant trend, the females did not, and the two putative sexes did not show the similar pattern of lowered P-values when placed into different groups that was seen in P. leo or P. atrox. It is also important to note that all Smilodon individuals together have a significant P-value before the sexes are separated, whereas neither Panthera species does (Table 1).

Additionally, many of the S. fatalis specimens that we radiographed showed significant pulp cavity closure (80% or greater). This either indicates that the population at Rancho La Brea was older, or more likely, that the pulp cavity of the canine filled up relatively rapidly compared with either Panthera species. This technique has been used in a species-specific manner for this reason, and direct comparisons between species may not work for this method. This accelerated pulp cavity closure may have been due to the smaller diameter of the lower canine, making accurate age assessment more challenging when using this tooth in S. fatalis.

Even though we find no evidence of size dimorphism in Smilodon, this does not necessarily imply this species was not social. A recent paper by Carbone et al., (2009) suggested that Smilodon may have been social because of the large number of individuals entombed at the tar pits. They based their assessment on playback experiments from the African savanna, where only group-hunting large carnivores responded to the noises of dying herbivores or fighting carnivores at a kill site. In addition, some important similarities in toothwear and breakage were found in Smilodon and C. dirus, also a social species, which give further evidence for sociality in Smilodon (Binder & Van Valkenburgh, in press). We agree with these findings and suggest, based on previous studies on carnivore size dimorphism (Weckerly, 1998), that because of the lack of dimorphism in Smilodon, this species had a social system that was less polygynous than most living cats and possibly monogamous as in wolves, or promiscuous, where females and males both are free to choose their mates. Since Smilodon is morphologically disparate from conical-toothed cats, it is reasonable to suggest their social system may be different as well.

Our findings also agree with previous studies on African lions (Benoit, 2006, 2007) and spotted hyaenas (Binder & Van Valkenburgh, 2000) that demonstrate these animals continue to grow well past reaching adulthood and that it is necessary to incorporate age into a calculation of sexual dimorphism to get an accurate result in large carnivores. Our data show that younger male and older female P. leo have similar jaw lengths and may be indistinguishable from two different tar pits where past environmental conditions cause differential tooth wear. However, it is prudent to note that incorporating a measure of ontogenetic growth is not as important when examining a species with a high level of sexual dimorphism like P. atrox, but is much more essential when dealing with a species with low to no sexual dimorphism, like S. fatalis.

Since our sample of P. atrox was not chosen for any particular character except the presence of a lower canine and a hemimandible for ease of radiographs, our sample is a random cross-section of all of the adult animals trapped in the asphalt at Rancho La Brea. From our data there is no overall entrapment bias based on sex (six estimated females, seven estimated males) or age (five individuals <50% closure, two individuals ~50%, six individuals >50% closure) in P. atrox. However, our sampling is across several pits, so an entrapment bias in any particular pit may have been overlooked.

This technique allowed us to confirm dimorphism in two species, and reject it in a third. For other studies, this type of analysis has the potential for allowing for both the detection of dimorphism along with the separation of specimens into distinct single-sex groups for further study.

In the future, we plan to radiograph P. atrox from other fossil localities, along with its close relative, P. spelaea as well, to examine if this pattern holds true. Since Smilodon is different from living felids in many ways, we would also like to compare this extinct species to other pantherines, such as the clouded leopard Neofelis nebulosa. Neofelis shares some postcranial trends with Smilodon, such as thickened cortical bone and wider articular areas in the humerus (Meachen-Samuels, 2008) that may give some important insights into the behavior of this enigmatic extinct cat.

Acknowledgments

We would like to thank the collection managers who kindly allowed access to specimens and equipment in their care: L. Gordon and J. Jacobs (US Museum of Natural History, Smithsonian Institution), J. Harris, C. Shaw and S. Cox (George C. Page Museum), J. Dines (Natural History Museum of Los Angeles County), K. Molina (UCLA Donald R. Dickey Collection), C. Conroy (Museum of Vertebrate Zoology, UC Berkeley), P. Holroyd (UCMP Berkeley) and J. Phillips (Field Museum of Natural History). This project also benefited greatly from the assistance of J. Samuels, B. Van Valkenburgh and B. Fitzpatrick. Additionally, B. Scrivens assisted with some of the data.
collection. We would also like to thank L. Werdelin and one anonymous reviewer for their helpful comments.

References


