

CRANIAL EVIDENCE FOR SEXUAL DIMORPHISM AND GROUP LIVING IN THE EXTINCT AMERICAN LION (*PANTHERA LEO ATROX*)

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This study examined whether the extinct American lion (*Panthera leo atrox*) may have exhibited polygamous group mating patterns similar to their modern African relatives. Dimensions of five skeletal elements of *P. l. atrox* from Rancho La Brea were measured. Ratios from these measurements were converted into histograms to try to determine the number of males and females. A statistical test called the mean method was then applied to the canine teeth and the skull; studies have suggested that this test offers insight into the breeding system of mammalian carnivores. While no postcranial dimorphism could be determined with the available tests, there was marked dimorphism in the skull and teeth which surpassed any extant felid. This suggests that the American lion did indeed hunt in polygamous groups similar to modern lions, contrary to previous studies of the Rancho La Brea specimens.

Perhaps the greatest boon in 20th century paleontology was the shift from collecting fossils as geological wonders to examining them as the remains of dynamic, living organisms. Yet determining how extinct animals—often quite unlike anything alive today—could have behaved is often a daunting if not impossible task. Therefore, whenever prehistoric species present themselves as examples that can be readily studied for past behavior, the potential exists to make a great leap in our understanding. The American lion (*Panthera leo atrox*) entered the continent from Asia several million years ago and traveled as far South as Peru before going extinct at the end of the last ice age (Turner and Anton 1997). It was the largest member of the cat family known,

approximately 25 percent larger than the largest male African lion (Harris 2001).

Because of its close relationship to extant lions of today, and because of the extraordinary preservation and quantity of *P. l. atrox* fossils from the tar pits of Rancho La Brea, the American lion has been a subject of intense speculation regarding its behavior. A large brain size has been used to suggest that *P. l. atrox* hunted in groups similar to modern African lions (Kurten and Anderson 1980), and a paleoecological study suggested that the earliest fossil lions lived in sexually dimorphic prides and that this behavior would not have likely been lost (Yamaguchi 2004). However, previous research conducted on the Rancho La Brea specimens found a higher ratio of males to females, which suggested that the cats did not exhibit prides (Jefferson 1991).

Most previous publications based on the materials housed at the George C. Page Museum at the La Brea Tar Pits (see Harris and Jefferson 1985, Jefferson 2001, Stock and Harris 2001) have reported a distinct, sexually dimorphic population among *P. l. atrox*. It is true that all living big cats, including the closest living relative of *P. l. atrox* the African lion (*Panthera leo leo*), exhibit some degree of dimorphism between the sexes (Mazak 2004, Turner 1997). Still, any difference between male and female American lions has yet to be quantified. If sexual dimorphism is found in the postcranial elements and skull, calculations by Jefferson (1991) of the male to female ratio can be confirmed or denied; if no dimorphism is discovered, then any claims about male-female ratios would be unsubstantiated.

One novel method of helping quell this debate is to look for extreme sexual dimorphism in the canine tooth, which has been shown in 45 living mammalian carnivores to be solely linked to a polygamous group breeding system (Gittleman and

Van Valkenburgh 1997). A study based on this canine hypothesis was tested on the Rancho La Brea dire wolf (*Canis dirus*) and saber toothed cat (*Smilodon fatalis*); a lack of canine dimorphism confirmed earlier studies which suggested that the two animals did not form polygamous groups (VanValkenburgh and Sacco 2002). Such a method applied to *Panthera leo atrox* may offer insight into possible polygamous group behavior.

One problem in attempting to determine sexual dimorphism from a fossil collection is the inability to divide the disassociated skeletons into male and female subpopulations for standard statistical analysis (Simpson et. al. 1960, Plavcan 1994). Traditionally, the only absolute way to find multiple populations in a single sample is to look for a non-overlapping bimodal distribution (Simpson et. al. 1960). This is typically rare to discover, for there will be a fair deal of size overlap between males and females in any given population. More recently, several other methods have yielded successful results; one of these will be implemented here (see the Materials and Methods below).

A second problem is that the American lion makes up only 2% of the fossils in the Rancho La Brea fauna (Marcus and Berger 1984), so the remains used in this study were recovered from multiple deposits that span across 30,000 years (Akersten et. al. 1983). It is therefore conceivable that a bimodal distribution in the lions could be concealed if the cats changed in size during this time. Conversely, a rapid evolutionary size change in *Panthera leo atrox* could suggest a sexual bimodal distribution when it does not in fact exist. However, since individual asphalt deposits do cover specific slices of geological time (Marcus and Berger 1984), analysis of individual sites could be used not only to avoid such confounding variables, but also to look for any microevolutionary trends *P. l. atrox* may have gone through.

Based on my understanding of the current available literature, I would expect that *Panthera leo atrox* did not undergo any substantial microevolution, exhibited a large level of sexual dimorphism, and subsequently lived in polygamous group structures similar to modern lions. However, none of this is well established. As a hypothesis, I should expect to see an uneven male to female ratio in favor of females, and a particularly large bimodal distribution in the canine teeth of *P. l. atrox*.

MATERIALS AND METHODS

The skeletal elements that were included in this study are the astragalus, calcaneum, femur, humerus, and the skull. The first two elements were chosen because of quantity and completeness, while the later elements offer good insight into overall body size. Additional measurements in the skull included the fourth premolar (P4), which is a good indicator of overall skull proportions, and the occipital condyles, which offer a good estimate of overall body size (Martin 1980). Each specimen was recorded by its catalogue number, and dial slide gauge calipers were used to take two to seven measurements based on the anatomical recommendations set forth by Angela von den Dreisch (1976) where possible. Although up to seven measurements were taken, only two (a length and breadth measurement) were used for further testing. Each individual measurement was also repeated three or more times to correct for any measurement errors. The following describes which measurements were used in this study and the measuring points are illustrated in Figure 1:

- A. Femur: the greatest length proximal to distal from the head of the femur (1); the least diameter medio-lateral of the mid-shaft (2).

- B. Astragalus: the greatest length (1); from the lateral process, across the articular facets to the medial articulation notch (2).
- C. Calcaneum: the greatest length proximal to distal (1); the greatest breadth across the sustentaculum (2).
- D. Humerus: the greatest length proximal to distal (2); the least diameter medio-lateral of the mid-shaft (1).
- E. Skull (Dorsal): the overall length from anterior to posterior (1); the breadth across the zygomatic arches (2).
- F. Skull (Ventral): the length (1) and breadth (2) of the canines directly below where the enamel ended; 4th premolar breadth (3) and length (4).
- G. Occipital Condyles: the breadth (F5) and length (06).

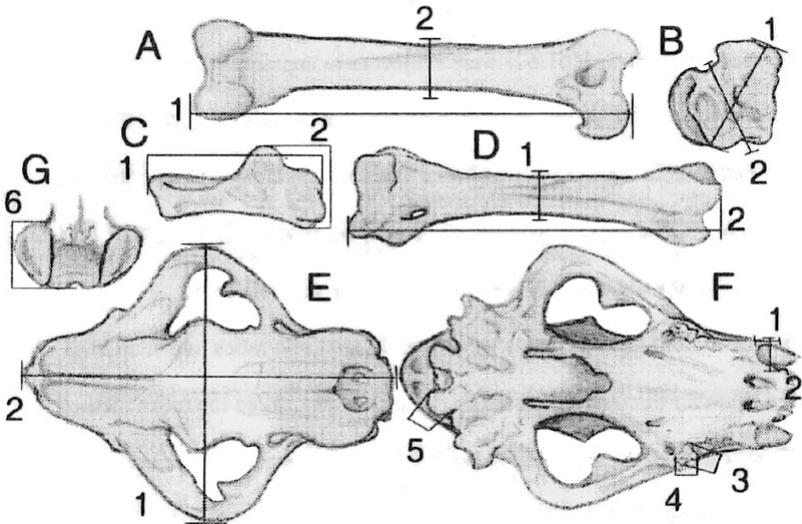


Fig 1. This picture illustrates the measurements that were used in this study. See the above paragraph for a more detailed explanation of each fossil and what each measurement entails.

A total of 83 astragali, 94 calcanei, 32 humeri, 64 femora, and 36 skulls were measured. Some of these fossils were broken, worn, or belonged to a juvenile individual. If for any of these reasons, a proper measurement could not be taken, it was not included in the sample. For the four postcranial elements, left and right examples were found in every site, but because the fossils are jumbled in the deposit none could be linked back to the same individual. For this reason, either left or right samples were chosen from each site, depending on which sample had the largest number of elements. If the case arose that a fossil unique in size or morphology was found in the smaller sample that could not belong to any individual from the larger, it was added to the sample. Individual teeth that could not have belonged to any skull were also measured in the same manner as teeth in the skull.

Measurements of specimens from particularly old deposits (pits 60 and 77) and particularly young deposits (pit 61/67) were subjected to unpaired two tailed t-tests, with equal variances assumed. This tested the hypothesis that the dimensions of the younger specimens became either significantly larger or smaller than their older counterparts. This method could not be applied to study the skulls, because too few could be measured from these sites (for the old deposits $N=1$, for the young deposits $N=3$).

All length/width measurements were then divided into ratios and charted as histograms to look for bimodal distributions. A second test called the mean method (Plavcan 1994, VanValkenburgh and Sacco 2002) was employed for the length of the skull, as well as the length and width of the canines. The reason only these select portions were subjected to the mean method is that it requires additional data from extant organisms, and data for the other portions could not be found in the literature. In the

mean method each set of measurements is divided at the mean, and the two sub-samples are treated as separate sexes. A ratio between the means of these sub-samples is generated and a degree of dimorphism is compared to known ratios from extant relatives. While this method offers a more precise measurement of dimorphism than the histogram method, the mean method only offers an upper bound to the potential distribution, and so it is unable to detect low or moderate levels of sexual dimorphism.

RESULTS

Table 1 shows the sample sizes, standard deviation, means, degrees of freedom, and p-values from the t-tests of the post cranial elements (Fig. 1). These measurements were then converted into ratios and plotted out as histograms (Fig. 2). The postcranial distributions of the astragali (2C) and the calcanea (2D) exhibited outliers, but none revealed a bimodal distribution. In contrast, unusual histograms were generated for the skull, as seen in the ratio between the length of the skull and the width across the zygomatic arches (Fig. 3). Similar charts made from other components of the skull (P4 teeth, canine teeth, skull length) were less clear in their distribution, but were distinctly non-normal. However, the occipital condyles (Fig. 4), showed one of the clearest normal distributions in this study.

Finally, the mean method was applied to both dimensions of the canine teeth and to the length of the skull (Table 2). The results were compared to 11 extant felids, as well as the extinct *Smilodon fatalis*. In all three categories, the American lion exhibited higher levels of sexual dimorphism than any other felid, significantly more than even the modern African lion *Panthera leo leo*.

Element	Measurement	N	Mean	SD	Df	P-Value
Astraglaus	1	24	63.99	5.575	22	0.152
	2	20	49.22	5.886	18	0.399
Calcaneum	1	20	123.1	8.872	18	0.029
	2	21	60.86	6.162	19	0.001
Humerus	1	11	36.95	2.374	9	0.476
	2	11	357.73	16.912	9	0.717
Femur	1	13	35.87	2.098	11	0.859
	2	7	35.97	12.589	5	0.189

Table 1: A list of sample sizes (N), means, degrees of freedom (Df), standard deviations (SD), and p-values determined from t-tests of the postcranial elements. Measurements 1 and 2 are explained in detail in Figure 1 in Materials and Methods.

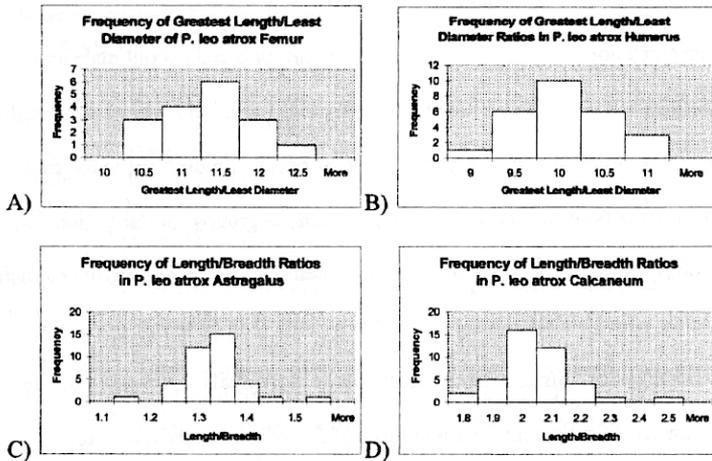


Figure 2: These histograms show length to width ratios of four elements of *Panthera leo atrox*. Although several exhibit an outlier, none of the elements generate a bimodal distribution.

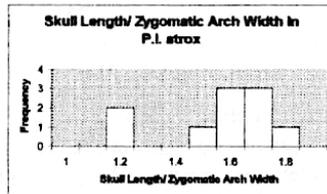


Figure 3: This histogram suggests a bimodal distribution generated from the skull of *Panthera leo atrox* (skull length versus length of the zygomatic arches). While histograms of the P4 and canine teeth did not show such a distinct distribution, they did not exhibit a normal distribution either.

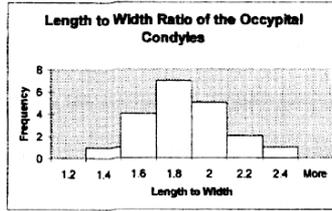


Figure 4: This histogram was generated from measurements of the occipital condyles. While the rest of the skulls' dimensions generated non-normal distributions, the occipital condyles created a normal one.

	Canine Length	Canine Breadth	Skull Length
<i>Panthera leo atrox</i> (American Lion)	1.27	1.26	1.21
<i>Panthera leo</i> (lion)	1.25	1.23	1.12
<i>Panthera tigris</i> (tiger)	1.16	1.08	1.16
<i>Panthera pardus</i> (leopard)	1.24	1.26	1.13
<i>Panthera onca</i> (jaguar)	1.12	1.11	1.06
<i>Puma concolor</i> (puma)	1.14	1.09	1.08
<i>Caracal caracal</i> (caracal)	1.06	1.03	1.08
<i>Lynx rufus</i> (bobcat)	1.16	1.11	1.1
<i>Felis silvestris</i> (wild cat)	1.15	1.13	1.1
<i>Felis chaus</i> (jungle cat)	1.16	1.15	1.07
<i>Leptailurus serval</i> (serval)	1.1	1.14	1.08
<i>Acinonyx jubatus</i> (cheetah)	1.15	1.11	1.1
<i>Smilodon fatalis</i> (sabertooth)	1.09	1.12	1.06

Table 2: The mean method was applied to *Panthera leo atrox* and is compared in this chart to 11 extant felids and one extinct one (*Smilodon fatalis*). In all three categories, *P. l. atrox* shows the highest levels of dimorphism. Data for the other cat species and the significance of the size difference was taken from Van Valkenburgh and Sacco (2002).

DISCUSSION

The t-tests suggest that little evolutionary change took place in *Panthera leo atrox* morphology at Rancho La Brea. Three of the four postcranial elements (the astragalus, femur and humerus) all exhibited large p-values. Interestingly enough, this was not the case for the calcaneum. Either this was caused by an odd sampling bias, or perhaps there actually was some sort of selective pressure on the ankles of these cats. This anomaly

could offer an interesting future study, but it is of little importance here since the calcaneum is not a significant indicator of overall body size (Von den Driesch 1976).

The results of the histograms suggest that significant sexual dimorphism existed in the size and shape of the skull of the American lion, while no significant dimorphism could be found in the size of the postcranial skeleton. The four elements studied all exhibited normal or near normal distributions. These results were further supported by the normal curve of the occipital condyles, which is a good indicator for overall body size. This does not mean that no sexual dimorphism existed between the overall body sizes of the males and females, but that the test used did not distinguish a quantifiable distribution. Additionally, many studies have shown that felid skulls generally show more extreme sexual dimorphism than the rest of the animal (Mazak 2004, Turner and Anton 1997).

When all skulls available (including the individuals that could not be measured) were sexed via the bimodal distribution, I did find the same 3:2 ratio of males to females that Jefferson found in his study (Stock and Harris 2001). In my study the skull sample size ($N = 12$) was simply too small to make any presumptions about mating dynamics or male to female ratios. There could be other explanations for why there are three male skulls found for every two female skulls. For example, the Rancho La Brea tar asphalt traps exhibit an unnatural 9: 1 ratio of carnivores to herbivores, which may be the result of the entrapment of a large herbivore acting as a lure for predators, which in turn became mired in the asphalt themselves (Harris and Jefferson 1985, Stock and Harris 2001). On savannas today, when female lions are harassed by other predators, such as hyenas, the much larger male will often step in to drive off the competition. If female lions were

threatened at the tar seeps by other carnivores such as wolves, saber toothed cats, and bears, the males may have come to protect the females in a similar fashion. Such behavior could have increased the chance of a male lion being killed or trapped in an asphalt seep, and may explain the high percentage of male lions found. It is also true that packs of male African lions sometimes band together (Turner and Anton 1997). Although whether or not the American lion would exhibit similar behavior is mere speculation, it could have potentially taken the members of only one unfortunate male pack to create the male to female ratio we see today.

This research does not definitively show that current beliefs about male and female populations at the tar pits are wrong, but only that I found no way of meaningfully corroborating them. Additionally, the great degree of sexual dimorphism in the canine teeth suggests that the lions did indeed hunt in polygamous groups similar to lions of today. As a future study I hope to get data on the dimensions of the postcranial elements for modern felids; perhaps a significant dimorphism could then be teased out of the *Panthera leo atrox* bones. Since there are many more individuals represented by the postcranial elements (I found a minimum number of 56 individuals based on the calcaneum), the potential exists for calculating a much stronger male to female ratio.

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