

Parallels between playbacks and Pleistocene tar seeps suggest sociality in an extinct sabretooth cat, *Smilodon*

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Inferences concerning the lives of extinct animals are difficult to obtain from the fossil record. Here we present a novel approach to the study of extinct carnivores, using a comparison between fossil records ($n=3324$) found in Late Pleistocene tar seeps at Rancho La Brea in North America and counts ($n=4491$) from playback experiments used to estimate carnivore abundance in Africa. Playbacks and tar seep deposits represent competitive, potentially dangerous encounters where multiple predators are lured by dying herbivores. Consequently, in both records predatory mammals and birds far outnumber herbivores. In playbacks, two large social species, lions, *Panthera leo*, and spotted hyenas, *Crocuta crocuta*, actively moved towards the sounds of distressed prey and made up 84 per cent of individuals attending. Small social species (jackals) were next most common and solitary species of all sizes were rare. In the La Brea record, two species dominated, the presumably social dire wolf *Canis dirus* (51%), and the sabretooth cat *Smilodon fatalis* (33%). As in the playbacks, a smaller social canid, the coyote *Canis latrans*, was third most common (8%), and known solitary species were rare (<4%). The predominance of *Smilodon* and other striking similarities between playbacks and the fossil record support the conclusion that *Smilodon* was social.

Keywords: Rancho La Brea; competition; *Smilodon*; carnivore sociality

1. INTRODUCTION

An icon of the North American Pleistocene, the sabretooth (*Smilodon fatalis*), was a formidable predator with robust forelimbs and elongate upper canine teeth. Although usually portrayed as solitary, controversy persists over its possible sociality (McCall *et al.* 2003). The strongest evidence for sociality comes from the late

Pleistocene tar seep deposits of Rancho La Brea, California (44 000–9000 YBP; Stock & Harris 1992), where high ratios of *Smilodon* and the presumably social dire wolf (*Canis dirus*) relative to prey species suggest that both hunted in groups.

Here we present additional evidence supporting sociality in *Smilodon* using a comparison between playback experiments carried out in eastern and southern Africa to estimate carnivore abundance (Mills *et al.* 2001) and the fossil record from Rancho La Brea (Marcus 1960; Stock & Harris 1992; Spencer *et al.* 2003). Both playbacks (Cooper 1991; Fanshawe & Fitzgibbon 1993) and the tar seeps represent highly competitive scenarios, in that a dying or dead animal drew in multiple predators, that then potentially competed for food. In the playbacks, sounds of dying herbivores combined with the sounds of lions (*Panthera leo*) and hyenas (*Crocuta crocuta*) were used to attract carnivores for population estimation (Mills *et al.* 2001). At La Brea, carnivores appear to have been similarly lured by dying herbivores and trapped in sticky asphalt. The tar pit deposits represent an accumulation of these events. Carnivores outnumber herbivores nine to one in the La Brea record and commonly several individual carnivores attended playbacks. The parallels between these records, and their broader significance for understanding carnivore competition, led us to explore this in greater detail.

2. MATERIAL AND METHODS

(a) Size and social categories

We grouped carnivore species into four categories (table 1), based on size and social status: 'small' (<21 kg) and 'large' (≥21 kg), following previous studies on carnivore diets (Carbone *et al.* 1999), 'solitary' (mostly found alone) or 'social' (typically in monogamous pairs or larger groups). Extant species in the fossil record (table 1) are assumed to be similar in social category to the present. Extinct species belonging to families with consistent social systems are assumed to be similar to extant relatives (Wrangham *et al.* 1993). Thus, bears (*Ursidae*) are classified as solitary and dogs (*Canidae*) as social. However, *Smilodon*, a felid, has both solitary and social relatives and we focus our analysis on examining the evidence pertaining to its social status.

(b) Playback data

We based our estimates of carnivores attending potential kill sites from substantial playback surveys using broadly similar methods (Mills *et al.* 2001; Maddox 2003; Ferreira & Funston submitted) (Kruger National Park, $n=578$; Serengeti Region, $n=232$). Pre-recorded sounds of herbivore prey species in distress, sometimes in association with lions at a kill and hyenas mobbing, were played for 30–120 min, at night, dawn and dusk and all individuals that approached were identified (Mills *et al.* 2001; Maddox 2003; Ferreira & Funston submitted).

(c) Community density

We used published estimates of species' densities (table 1, electronic supplementary material S1) to calculate the percentage of individuals found in the community for comparison with the percentage attending playbacks. Estimates of age ratios (juvenile to adult) for lion in the playbacks were compared with the La Brea record. Estimates of numbers of individuals for the La Brea tar seeps were based on the minimum numbers of individuals from all excavations. Juveniles were identified by the presence of deciduous teeth (electronic supplementary material S2).

(d) Statistical analysis

To compare the observed frequencies of carnivores in the four size/sociality categories with the frequencies expected based on relative densities, we used Pearson chi-squared goodness-of-fit tests (electronic supplementary material S2). To examine the importance of size and sociality in explaining the observed patterns, we used negative binomial regression with the number of individuals of each carnivore species attending as the dependent variable, size/sociality categories as the independent variables, and density as an offset

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2008.0526> or via <http://journals.royalsociety.org>.

Table 1. Carnivore species present in region and those observed (numbers and percentages) attending playbacks in eastern and southern Africa and found in La Brea tar seeps in the late Pleistocene of western North America. (References for body mass, social status and population density estimates are in electronic supplementary material S1 and S2; see also text for details. *The social status of *Homotherium* and American lion were set as solitary and social, respectively. In the former species, its rarity in the fossil record suggests that it may have been solitary, in the American lion the nearest relatives were social. Since the two species make up less than 3% of the record, their classification has only a marginal influence on the overall pattern.)

African playbacks		North American Late Pleistocene tar seeps								
common name	scientific name	mass (kg)	South Africa	East Africa	ave. perc. (%)	common name	scientific name	mass (kg)	no. all pits	perc. all pits (%)
<i>small solitary</i>						<i>small solitary</i>				
striped polecat	<i>Ictonyx striatus</i>	0.8	0	0	0	long-tailed weasel	<i>Mustela frenata</i>	0.191	19	0.6
small-spotted genet	<i>Genetta genetta</i>	1.8	0	0	0	eastern spotted skunk	<i>Spilogale putorius</i>	0.569	6	0.2
large-spotted genet	<i>Genetta tigrina</i>	2.1	0	0	0	striped skunk	<i>Mephitis mephitis</i>	2.4	32	1.0
white-tailed mongoose	<i>Ichneumia albicauda</i>	3.7	1	0	0.02	ringtail	<i>Bassariscus astutus</i>	1.02	0	0.0
African civet	<i>Civettictis civetta</i>	12.1	0	0	0	northern raccoon	<i>Procyon lotor</i>	6.37	0	0.0
honey badger	<i>Mellivora capensis</i>	9.0	0	0	0	American badger	<i>Taxidea taxus</i>	7.84	13	0.4
wild cat	<i>Felis silvestris</i>	4.5	1	0	0.02	bobcat	<i>Lynx rufus</i>	6.39	9	0.3
serval	<i>Leptailurus serval</i>	11.8	0	0	0					
caracal	<i>Caracal caracal</i>	12.0	0	0	0					
<i>small social</i>						<i>small social</i>				
black-backed jackal	<i>Canis mesomelas</i>	8.3	284	205	10.9	grey fox	<i>Urocyon cinereoargenteus</i>	3.83	16	0.5
golden jackal	<i>Canis aureus</i>	9.7	0	90	2.0	coyote	<i>Canis latrans</i>	12	255	7.7
side-striped jackal	<i>Canis adustus</i>	10.4	46	3	1.1					
<i>large solitary</i>						<i>large solitary</i>				
striped hyena	<i>Hyaena hyaena</i>	35.1	0	3	0.07	puma	<i>Puma concolor</i>	53.9	15	0.5
cheetah	<i>Acinonyx jubatus</i>	50.5	0	0	0	jaguar	<i>Panthera onca</i>	84.9	5	0.2
leopard	<i>Panthera pardus</i>	52.4	42	0	0.9	<i>Homotherium*</i>	<i>Homotherium serum</i>	190	5	0.2
						black bear	<i>Ursus americanus</i>	111	1	0.03
						grizzly bear	<i>Ursus arctos</i>	196	1	0.03
						short-faced bear	<i>Arctodus simus</i>	650	33	1.0
<i>large social</i>						<i>large social</i>				
African wild dog	<i>Lycyaon pictus</i>	22.0	44	0	1.0	grey wolf	<i>Canis lupus</i>	35	18	0.5
spotted hyena	<i>Crocotta crocuta</i>	64.0	1345	1541	64.3	dire wolf	<i>Canis dirus</i>	50	1702	51.2
						<i>Smilodon</i>	<i>Smilodon fatalis</i>	230	1108	33.3
African lion	<i>Panthera leo</i>	159.0	698	188	19.7	American lion*	<i>Panthera atrox</i>	430	86	2.6
total			2461	2030					3324	

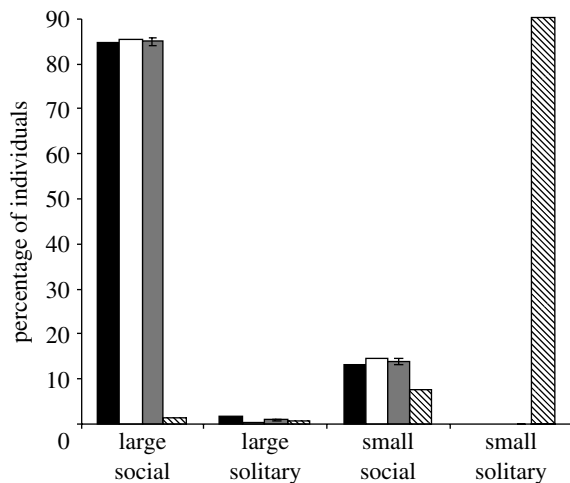


Figure 1. Comparison of percentages of African carnivores attending playbacks from Kruger National Park (black bars), South Africa, the Serengeti region (white bars), Tanzania and the mean of all playbacks (grey bars; \pm confidence intervals), against the percentages based on typical densities (hatched bars) of African carnivores for four size/social structure categories (See also table 1, electronic supplementary material S1).

(exposure) term to control for the relative densities of species. A Wald test was used to compare the coefficients for size and sociality. To obtain 95 per cent bootstrap confidence intervals for the proportions of individuals in each size/sociality category (see figures 1 and 2), the data were re-sampled 10 000 times with replacement. To compare the La Brea and playback datasets depending on whether *Smilodon* was social or solitary, we used the following Monte Carlo simulation. Expected frequencies were generated by multiplying the tar seep sample size ($n=3324$) by the proportions of individuals in the four size/sociality categories in the Africa playback dataset and this distribution was re-sampled with replacement 10 000 times. In each replicate a chi-squared goodness-of-fit value was calculated for each model, and a paired t -test was used to compare the means of the two distributions of chi-square values. The proportions of juvenile large carnivores found at La Brea were compared with the proportion of juvenile lions at playbacks using chi-squared tests. For non-significant tests, *post hoc* power analyses were carried out to estimate the probability of finding a significant difference (at $\alpha=0.05$) if the true proportion of juveniles in the pits was 50 per cent lower than the observed proportion of juvenile lions in playbacks. The chi-squared results for coyote (*Canis latrans*) and American lion are questionable due to small samples, but Fisher's exact tests (not shown) yielded similar results. Statistical analyses were conducted using STATA 10.0 (Stata Corp., College Station, TX, USA).

3. RESULTS

A comparison of the number of individuals attracted to playbacks to the expected number based on community densities reveals a consistent pattern. Large social carnivores make up approximately 85 per cent of all individuals attending playbacks. This differs markedly from the percentages expected based on community densities, where most individuals are from small solitary species (figure 1; table 1, electronic supplementary material S1; $\chi^2_3=23\,3061$, $p<0.0001$, $n=4491$). When analysed separately by sociality category, large species are overrepresented compared with small species (social: $\chi^2_1=18509$, $p<0.0001$, $n=4444$; solitary: $\chi^2_1>358$, $p<0.0001$, $n=47$); and when analysed separately by size category, social species are overrepresented compared with solitary species (small: $\chi^2_1=6864$, $p<0.0001$, $n=630$; large: $\chi^2_1=1405$, $p<0.0001$, $n=3861$)

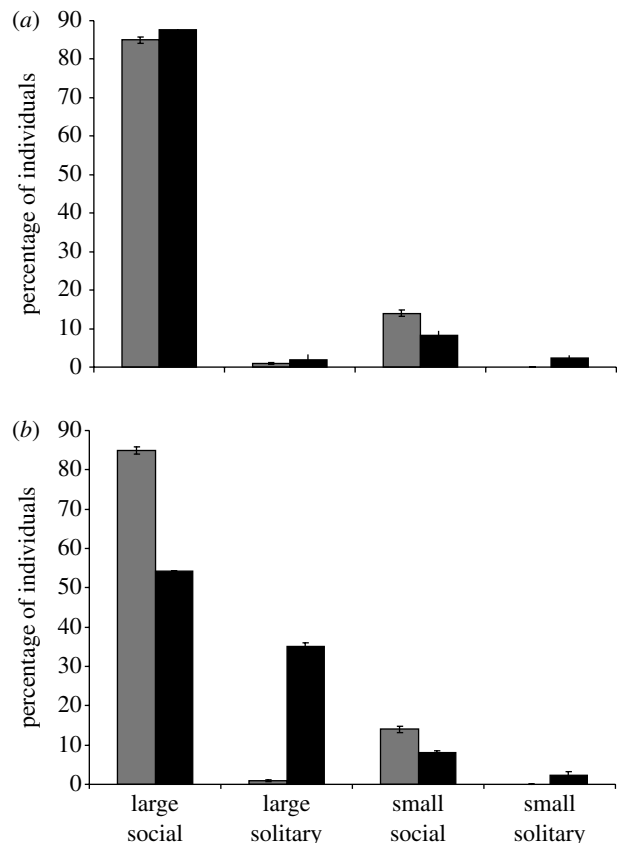


Figure 2. Comparison of mean percentage (\pm confidence intervals) of individual African carnivores attending playbacks (grey bars) against the mean percentage (\pm confidence intervals) of individual North American carnivores recorded in the La Brea tar seeps (black bars) for four size/social structure categories, assuming *Smilodon* was (a) social and (b) solitary (See also table 1, electronic supplementary material S2).

(figure 1). Size and sociality are equally influential (negative binomial regression; size coefficient = 6.07 ± 1.07 , sociality coefficient = 6.22 ± 1.06 ; Wald test: $p=0.88$). Large social carnivores attended approximately 60 times more often than expected.

The Rancho La Brea tar seep records include 17 species of carnivore, 5 of which are extinct (table 1). If we classify *Smilodon* as social (figure 2a), the percentages of specimens in each category are very similar to the percentages attending the playbacks, with the large social species representing approximately 88 per cent (table 1). As in the playbacks, the second most common group comprises coyotes (*C. latrans*), a small social canid. Classifying *Smilodon* as solitary, we find a marked mismatch between playback and La Brea datasets (figure 2b). The difference in fit to the playback data between the two models (*Smilodon* social versus *Smilodon* solitary) is highly significant (Monte Carlo simulation, $p<0.0001$), supporting the view that *Smilodon* was social.

Additional evidence for sociality in *Smilodon* comes from the fact that a number of juvenile sabretooth cats died in the tar pits, indicating that young attended the site with adults. This was also true of La Brea lions, dire wolves and coyotes, but not of the presumably solitary short-faced bears among which only one in 33 was a juvenile. In the playbacks,

lion cubs were observed in the presence of several (2–7) adults (mean = 3.4, $n = 5$; mean = 4.3, $n = 7$, Serengeti and Kruger, respectively). Notably, the proportion of juvenile to adults for four La Brea species, which were likely to be social, *Smilodon*, dire wolves, coyote and American lion (27.4, 28.6, 37.5 and 33.3%, respectively), do not differ significantly from the same proportion observed for African lions at playbacks (34.4%; $p > 0.24$, electronic supplementary material S2). This is not the case for the short-faced bear ($p < 0.0001$).

4. DISCUSSION

Overall we find similarities between playbacks in Africa and the fossil record in the Late Pleistocene of North America. In both the records, there are parallels in the types of species attending. In Africa large social carnivores attended playbacks 60 times more often than expected based on background densities, while large and small solitary carnivores attended less frequently than expected. The African wild dog (*Lycaon pictus*) is an exception, being a large social species that is mostly absent from playbacks. In the tar seep deposits, most of the species for which social status can be reliably inferred show patterns consistent with those in Africa. The large, presumably social, dire wolf is common and the presumably solitary bears and two large cats, the cougar (*Puma concolor*) and jaguar (*Panthera onca*), are rare. The social grey wolves in the fossil record, on the other hand, were rare, but this is similar to African wild dogs in playbacks. For the three remaining large cat species, the social status is unsure, but classifying *Smilodon* as social, we obtain strikingly similar patterns in both the playback and fossil records. This along with the presence of a high juvenile to adult ratio in *Smilodon* (similar to lions today) suggests that this cat was social.

Small social carnivores were the next most abundant group in both the playbacks and fossil record. In the playbacks, jackals made up between 13 and 15 per cent of the individuals attending. At Rancho La Brea, an ecologically similar species, the coyote, represents approximately 8 per cent of the records and probably filled an analogous niche. Unfortunately, in the tar seeps, the interpretation of rare species such as the American lion and *Homotherium* is difficult, because it is hard to determine whether they were avoiding these events because they were solitary, as leopards, or were social but existed at low densities (as African wild dogs). In these two large species of cats, we classified the American lion as social (because of its relatedness to African lions) and *Homotherium* as solitary, owing to its extreme rarity in the fossil record.

Because *Smilodon* was well armed with enormous canine teeth, perhaps single individuals could have dominated competitive interactions with social carnivores. Indeed, during contests, exceptionally large species can dominate groups of smaller species (Cooper 1991; McNulty *et al.* 2001). However, *Smilodon* was substantially smaller than American lion and the short-faced bear also present at La Brea

(table 1). In addition, the African lion is social despite the fact that it represents the largest and most dominant species in the African carnivore guild. In this species, larger lion prides dominate smaller ones and intraspecific competition is seen as a major factor driving the evolution of coalitions (Packer *et al.* 1990). In *Smilodon*, therefore, given the potential for high levels of competition with other very large carnivores, including members of its own species, it seems very unlikely that as a solitary species, it would have approached these events with such a high frequency.

Our results also have broader implications for understanding the evolution of social behaviour. Carnivores have been used as a model group for developing an understanding of other meat-eating species, including early hominids (Schaller & Lowther 1969). Scavenging was an important food source for early hominids, being linked with many important adaptations, including larger body size and bipedalism (Plummer 2004). In early humans and in other carnivorous species, sociality, through greater coordination and strength in numbers, would probably have significantly enhanced their ability to compete with other species, thereby increasing caloric intake. These results support the idea that social organization and size are important factors influencing status within competitive predatory guilds.

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- Carbone, C., Mace, G. M., Roberts, S. C. & Macdonald, D. W. 1999 Energetic constraints on the diet of terrestrial carnivores. *Nature* **402**, 286–288. (doi:10.1038/46266)
- Cooper, S. M. 1991 Optimal hunting group-size—the need for lions to defend their kills against loss to spotted hyaenas. *Afr. J. Ecol.* **29**, 130–136. (doi:10.1111/j.1365-2028.1991.tb00993.x)
- Fanshawe, J. H. & Fitzgibbon, C. D. 1993 Factors influencing the hunting success of an African wild dog pack. *Anim. Behav.* **45**, 479–490. (doi:10.1006/anbe.1993.1059)
- Ferreira, S. M. & Funston, P. J. Submitted. Variability in lion density and survival in Kruger National Park.
- Maddox, T. M. 2003 The ecology of cheetahs and other large carnivores in a pastoralist-dominated buffer zone. PhD Thesis, University College, London.
- Marcus, L. F. 1960 A census of the abundant large Pleistocene mammals from Rancho La Brea. *Contributions in science*, pp. 1–11. Los Angeles, CA: Los Angeles County Museum.
- McCall, S., Naples, V. & Martin, L. 2003 Assessing behavior in extinct animals: was *Smilodon* social? *Brain Behav. Evol.* **61**, 159–164. (doi:10.1159/000069752)
- McNulty, D. R., Varley, N. & Smith, D. W. 2001 Grizzly bear *Ursus arctos*, usurps bison calf, *Bison bison*, captured by wolves, *Canis lupus*, in Yellowstone National Park, Wyoming. *Can. Field Nat.* **115**, 495–498.
- Mills, M. G. L., Juritz, J. M. & Zucchini, W. 2001 Estimating the size of spotted hyaena (*Crocuta crocuta*) populations through playback recordings allowing for non-response. *Anim. Conserv.* **4**, 335–343.

- Packer, C., Scheel, D. & Pusey, A. E. 1990 Why lions form groups: food is not enough. *Am. Nat.* **136**, 1–19. (doi:10.1086/285079)
- Plummer, T. 2004 Flaked stones and old bones: biological and cultural evolution at the dawn of technology. *Yearb. Phys. Anthropol.* **47**, 118–164. (doi:10.1002/ajpa.20157)
- Schaller, G. B. & Lowther, G. R. 1969 The relevance of carnivore behavior to the study of early hominids. *Southwest. J. Anthropol.* **25**, 307–341.
- Spencer, L. M., Van Valkenburgh, B. & Harris, J. M. 2003 Taphonomic analysis of large mammals recovered from the Pleistocene Rancho La Brea tar seeps. *Paleobiology* **29**, 561–575. (doi:10.1666/0094-8373(2003)029<0561:TAOLMR>2.0.CO;2)
- Stock, C. & Harris, J. M. 1992 *Rancho La Brea: a record of Pleistocene life in California*. Los Angeles, CA: Natural History Museum of Los Angeles County Museum.
- Wrangham, R. W., Gittleman, J. L. & Chapman, C. A. 1993 Constraints on group size in primates and carnivores: population density and day-range as assays of exploitation competition. *Behav. Ecol. Sociobiol.* **32**, 199–209. (doi:10.1007/BF00173778)