

Sociality in Rancho La Brea *Smilodon*: arguments favour 'evidence' over 'coincidence'

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Biol. Lett. published online 14 May 2009
doi: 10.1098/rsbl.2009.0261

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Invited reply

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Kiffner (in press) questions the comparability of the Pleistocene tar seep records and those derived from predator playback experiments. While we acknowledge that they are not identical, the differences are not sufficient to overturn our inference of sociality in Rancho La Brea (RLB) *Smilodon*. He suggests that a greater likelihood of heavier animals becoming trapped might have significantly biased our results. However, carnivores far outnumber (by 9 : 1) the much heavier herbivores (bison, horse) at RLB. There were also differences in preservation among the carnivores themselves. The most abundant species, the dire wolf, was ranked fourth largest in body mass, and the second most abundant species, *Smilodon*, was ranked third in body mass. Size bias clearly does not explain the pattern of fossilization at RLB. Kiffner suggests that social carnivores would be less likely to be trapped at RLB, because their larger brain size and presumed greater intelligence would lead them to avoid this when they witnessed trapped fellow group members. Arguing against this are: (i) the large numbers of preserved dire wolves, a species that is assumed to have been social given its ancestry and (ii) little or no support for larger brain size among large, social carnivores (Perez-Barberia *et al.* 2007).

Several criticisms raised by Kiffner (in press) concern issues of comparing responses to playback experiments with responses to an actual carcass with associated predators. We agree that the two differ significantly; the tar seep events went on for hours or days until the carcass was gone, whereas the playbacks ran for brief intervals of time. This would be expected to result in a greater species diversity at RLB, as subordinate species could visit the carcass after the larger, dominant species had left. Indeed, this is the case, with weasels, badgers, skunks, bobcats and foxes present at RLB but with very few similar species observed in the playback experiments. Kiffner points out that a carcass would provide olfactory cues as well as auditory and visual cues, whereas playbacks would supply only the latter two, but does not suggest how this might have biased the RLB records. We do not see how this is relevant to the question of *Smilodon* sociality.

He also notes that the response of species to playbacks is affected by how long a recording is played, and the 'type of audio lure', which we assume to

mean the content of the recording (hyena calls versus herbivore in distress). Lions may be slower than hyenas to show up at playbacks, in part because lions walk and hyenas lope. Given this, the open-ended RLB events should have done an excellent job of attracting both quicker and slower species, and this supports our hypothesis that some species, such as pumas and jaguars, and possibly grey wolves, avoided attending, just as cheetahs avoid playbacks. Similarly, if 'type of audio lure' influences the proportion of species at playbacks, this would not have been an issue at RLB, as both types of calls, those of distressed prey and their squabbling predators, would have been present. Notably, the African playback experiments we used differed from one another in type of audio lure, time of day and duration, but there was no significant difference between them in the distribution of species that responded by size and sociality (Carbone *et al.* 2009).

Finally, Kiffner (in press) questions our assumption of broad similarity between the African savannah predator guild and that of the late Pleistocene of Los Angeles, California, and suggests that other modern carnivore guilds, such as those that include tigers, might be more appropriate. Unfortunately, there are no playback data for regions that include tigers but we would be interested in comparing such results, especially for regions where the social dhole is abundant. Nevertheless, African savannah or open woodland ecosystems are a more suitable choice for comparison with RLB than any extant forest ecosystem of the Indian subcontinent or elsewhere. In both Africa and RLB, the dominant large herbivores are herd-forming grazers, such as antelope, zebra and buffalo in Africa versus camel, horse and bison in California. These ungulates indicate that RLB was an open woodland, and this is consistent with palaeobotanical and isotopic evidence (Stock & Harris 1992; Coltrain *et al.* 2004). Although difficult to quantify, it appears likely that encounters over carcasses such as those which occurred at RLB are more likely in relatively open environments with greater visibility and soaring vultures that signal the presence of a carcass. We note that the diversity of large, soaring, scavenging birds is similar at RLB and in African savannah (Stock & Harris 1992). It is difficult to know how tigers would behave in an open environment, where they are part of a more diverse predator guild that includes species larger than themselves as well as a hyena analogue. Clearly, tigers exhibit some social flexibility under extreme scenarios, but, like many carnivores, might be expected to alter their behaviour according to circumstances affecting resource availability and levels of competition. *Smilodon* may have been solitary in parts of its range, but it seems unlikely that it was so in the highly competitive setting found at RLB in the late Pleistocene.

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The accompanying comment can be viewed at <http://dx.doi.org/doi:10.1098/rsbl.2009.0008>.

Received 1 April 2009
Accepted 20 April 2009



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