Assessing Behavior in Extinct Animals: Was *Smilodon* Social?

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Abstract

It has been suggested that saber-tooth species such as *Smilodon fatalis* were social because partially healed skeletal injuries were found at Rancho La Brea, California. This conclusion assumes injured animals would die without help. This paper will rebut assertions of sociality. First, cats use metabolic reserves to heal quickly without feeding. Second, dehydration is a more profound limitation than starvation as prey carcasses only provide a quarter of necessary water. Injured animals must be mobile enough to find water or die of dehydration. Their presence in a tar pit also strongly suggests locomotion. Finally, the relatively small brain found in *Smilodon* is not consistent with sociality. Another argument for sociality has been the large ratio of *Smilodon* to other species in the La Brea tar pits. However, the remains of a non-social species, the Golden eagle *(Aquila chrysaetus)*, are about as common as *Smilodon*. Contrariwise, the highly social grey wolf *(Canis lupus)* and coyote *(Canis latrans)* are extremely rare. Available evidence does not support sociality in *Smilodon*.

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Introduction

Humans are highly social animals who eagerly seek sociality in other species, even making inferences about extinct animals. Speculation on co-operative hunting in predators has been especially popular [Paul, 1988]. Evolutionary patterns in other species could provide clues to the mystery of our own social and neurologic development. The question of sociality is enthralling, especially when applied to spectacular mammalian carnivores such as saber-toothed cats. However, how can we infer the behavior of dead organisms? In this paper, we examine the case for sociality in an extinct mammal.

Paleontological Methods to Assess Behavior

In this paper, we examine the case for sociality in the saber tooth cat *Smilodon* as an example of how one may interpret the evidence for sociality in an extinct mammal. Some evidence is inferred from phylogeny. The feline ancestry of *Smilodon* has been confirmed by DNA [Janczewski et al., 1992], so we should expect fundamentally cat-like behavior.

When taxa are phylogenetically distant we might postulate behavior if they share behavior-specific morphology. Like many vertebrates, mammals have such tightly-

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fitting skulls that endocranial casts reveal the brain's superficial anatomy. Living vertebrate studies relate some behaviors to specific brain regions and the relative importance of these behaviors to the prominence of those regions [Jerison, 1970a, b, 1971]. Endocranial casts might therefore shed light on behavior [Radinsky, 1969]. Relative brain size also pertains to some behaviors [Jerison, 1970b]. Citing the large numbers of *Smilodon* at La Brea, some authors postulate mass entrapment of social groups. Others, citing *Smilodon's* small brain and short legs, conclude that it was a solitary ambush predator [Kurten, 1988].

Behavior can be inferred from specific pathologies. Once other causes were excluded, fossil avascular necrosis suggested decompression sickness ('bends') from diving by extinct giant lizards (mosasaurs) [Rothschild and Martin, 1992]. Social care-giving has been suggested for extinct hominids (Neanderthals) on the basis of healed injuries [Brown, 1990]. Some now likewise argue that pathologies found in *Smilodon* would have been fatal without group support. Because of differing biomechanics, the killing techniques of the two major groups of saber-toothed cats (scimitar-toothed cats; e.g., *Homotherium* and dirk-toothed cats; e.g., *Smilodon*) probably differed, and sociality should be addressed separately. We will limit this discussion to *Smilodon*.

Advantages of social hunting include relay pursuit, driving prey into ambush like lions [Schaller, 1972; Seidensticker and McDougall, 1993; Caro, 1994], and defending a kill from scavengers and other predators. The last technique might sustain infirm individuals if the group allows sharing. However, with the exceptions of wild dogs such as dholes *(Cuon alpinus)* in Indian forests, modern social hunting among large carnivores is restricted to specialized cursorial predators in open habitats [Sacco and Valkenburgh, 2000].

Among cats only lions *(Panthera leo)* hunt cooperatively [McBride, 1977]. Dirk-toothed cats have short legs and heavy forequarter musculature compared to longer-legged scimitar-toothed felids such as *Homotherium* [Rawn-Schatzinger, 1992]. This stocky body habitus suggests close quarter attack rather than high speed or endurance [Van Valkenburgh and Hertel, 1993]. Ambushes at game trails and water sources are likely solo endeavors [Packer and Ruttan, 1988].

Cooperative hunting requires strategy and communication. Hemmer showed social hunters have larger relative brain sizes than their solitary competitors [Hemmer, 1976, 1978]. The relatively small brain of *Smilodon* makes socialty unlikely [Radinsky, 1975].

Relative fossil abundance is cited in support of sociality [Gonyea, 1976]. However, both the highly social gray wolf *(Canis lupus)* and the commonly social coyote *(Canis latrans)* are uncommon at Rancho La Brea. The La Brea lion *(Panthera atrox)*, closely related to the modern social lion, is also rare. The sociality of La Brea's most abundant predator, the dire wolf *(Canis dirus)*, is unknown [Kurten and Anderson, 1980]. The Golden eagle *(Aquila chrysaetos)*, which hunts alone or in pairs over large home territories, is almost as common as *Smilodon* in the tar pits. Tolerating one another while feeding does not prove flock behavior in this Pleistocene bird species. *Smilodon* abundance probably represents excessive sampling of solitary predators lured by a carcass. In fact, predators comprise 90% of Rancho la Brea specimens, but only five percent of wild populations [Stock, 1929, 1992; Marcus, 1960].

Social Care for the Injured

Group care of injured and ailing members is essentially absent in modern social animals outside hominids. More often infirm animals are allowed to feed on group kills [Bertram, 1978; Schaller, 1972], as observed in spotted hyaenas [Kruuk, 1972] and African wild dogs [Estes and Goddard, 1967]. This feeding tolerance meets only a restricted definition of sociality. Even if a pride allows access and deters competitors, injured animals must still be mobile enough to move to the carcass. Canids regurgitate food to feed pups, but not injured adults. Cats entirely lack regurgitation feeding.

Because *Smilodon* was a likely ambush predator, impaired mobility would be less critical than for cursorial predators. Alternatively, the intimidating appearance of *Smilodon* might have allowed it to scavenge alongside dire wolves. Indeed, some see in the large numbers of both *Smilodon* and *Canis dirus* a tight co-evolutionary relationship between saber-toothed cats and bone-crushing, scavenger-predators [Ewer, 1973; Van Valkenburgh, 1991]. Injured animals trapped in tar pits were either injured there or, more likely, were mobile enough to scavenge food and water.

The principal pathological evidence for *Smilodon* sociality is healed injuries. 'Survival of individuals long after grievous injury is indisputable proof of social behavior in S*milodon*' [Heald, 1989]. However, the injury data itself argues against sociality as the majority of luxations occur in the presumably social dire wolves, not *Smilodon* [Moodie, 1930]. One La Brea study of *Smilodon* found

only one fracture, one septic hip, one case of pressure atrophy, three cases of arthritis deformans and ten subperiosteal exostoses and some subluxations [Shaw, 1989]. Other catalogued injuries were vertebral compressions, torsion and flexion fractures, rib fractures and osteophytes caused by tendon injury [Moodie, 1923; Heald, 1989]. Of more than 1,000 *Smilodon* examined, twenty-five had paraspinous muscle calcifications attributed to myositis ossificans progressiva [Moodie, 1923, 1927], a chronic disease of muscular inflammation [Aegerter and Kirkpatrick, 1968]. Moodie [1930] examined 1,945 *Smilodon* femora plus thousands limb bones and metapodials and found osteopathologies in only 1.64% [Moodie, 1930].

To make a human comparison, the rate of new fractures and dislocations in Americans is 2.7% annually [Bureau of the Census, 1993]. Random occurrence over 75 years predicts an average cumulative lifetime risk of 87%. *Smilodon* undoubtedly had a shorter life expectancy, but it was also more combative, making the fracture rate at La Brea strikingly low [Moodie, 1930]. The paucity of injuries suggests La Brea fossils represent the subset of walking wounded. If *Smilodon* received effective social support, we would expect a greater variety and proportion of healed injuries in the tar pits.

Fracture Healing

Fracture healing is best documented in experimental animals. Fracture hematoma forms in six to eight hours and connective tissue cells enter the site in 48–72 h. Granulation tissue replaces the hematoma in one week, even earlier for small fractures [Vaughan, 1966; Gartland, 1987]. Calcification begins in 14–17 days [Gartland, 1987] and is visible on conventional radiography by 20 days [Sweet, 1995]. Healing fractures produce tremendous bone and fibrous proliferation. Notwithstanding the disuse and stress shielding caused by rigid plate fixation, bone density in human tibial fractures is actually greater than normal bone within two weeks [Janes et al., 1993]. Cats *(Felis domesticus)* achieve clinical union in 3–4 weeks, with secondary callus complete in six to twelve weeks [Turnbull, 1966; Vaughan, 1966]. Thus, although full remodeling and strengthening is delayed, functional recovery is prompt.

Individual healing rates vary, with some animals recovering more rapidly than average. Some fractures (e.g., ribs) are naturally splinted by adjacent bones and heal easily. Even multiple metacarpal, metatarsal and phalangeal fractures have good healing when treated by simple immobilization without interventional fracture realignment [Carter, 1966; Singleton, 1966]. Oblique and spiral fractures heal quickly because of their large contact area and impacted fractures heal more rapidly than dislocated ones [Vaughan, 1966]. Fractures in young animals, and in small or cancellous bones also have expedited healing. Even a fraction of injured animals recovering under favorable circumstances explain the La Brea findings without sociality.

Large veterinary studies find 75–100% of feline fractures occur before age three [Phillips, 1979; Wong, 1984]. Healing is especially rapid in young animals; puppies achieve clinical union of fractures in just ten to fourteen days [Vaughan, 1966]. Femoral fractures in human three-year-olds heal five times faster than in seventy-year-old adults [Buckwalter et al., 1996].

As long as stress is not so strong or early as to disrupt the hematoma or developing callus, exercise and partial weight bearing speed healing. Fractures with surrounding soft tissue and good vascularization heal rapidly even while bone fragments remain mobile [Buckwalter et al., 1996]. Most evidence suggests that fixation devices allowing partial loading and slight fracture motion improve healing [Aro and Chao, 1993; Goodman and Aspenberg, 1993; Goodship et al., 1993; Goodman et al., 1994; Hedstrom et al., 1994; Kostopoulos et al., 1994; O'Sullivan et al., 1994; Prat et al., 1994; Noordeen et al., 1995; Augat et al., 1996; van Laarhoven et al., 1996].

Benign neglect is frequently the treatment of choice in feline trauma. Feline pelvic fractures heal in three to four weeks without treatment [Carter, 1966; Hill, 1977]. Feline fractures of the femoral head and neck recover without surgery because a pseudoarthrosis forms with good function [Carter, 1966; Singleton, 1966]. Fractures of the femur and epiphysis also heal well with cage rest alone [Ormrod, 1966; Hill, 1977].

Among 298 feline fractures, the most frequent were femoral, pelvic and mandibular. Four weeks of cage rest was routine for hip and pelvic fractures, femoral neck fractures, long bone greenstick fractures, multiple rib fractures and minimally displaced fractures as well as some skull, mandibular, and fibular fractures. Success was uniform, with the only reported sequela being a case of urinary incontinence after pelvic fracture. Ten of 13 radial or ulnar fractures were treated successfully with splints or casts. Overall, 53% of the fractures were treated without surgical fixation (i.e., with cage rest, splinting or casting alone) and results were satisfactory in 96.7% of cases [Phillips, 1979]. Similar results were obtained by Wong et al. [1984].

Another study of 108 feline fractures had similar success with three weeks of cage rest. Cats with pelvic fractures were walking in just seven days. Even four cases with inoperable comminuted fractures of the femoral shaft recovered in three weeks without treatment [Hill, 1977]. Medical intervention does not prove an animal would not have healed on its own. Veterinarians are motivated to assure a good result in every case, to speed healing, to alleviate pain, to improve cosmesis, to respond to the concerns of the owners, to forestall litigation, and to justify higher professional fees.

Unlike the potential fatal hemorrhage in human femoral and pelvic fractures, shock rarely supervenes in cats. They are stoic and carry an injured limb so well it is often difficult even to diagnose fracture [Carter, 1964; Fraser, 1991]. Cats readily free stiff joints and seldom need physical therapy [Carter, 1966]. After healing, cats adjust completely to post-fracture shortening of a hind leg [Ormrod, 1966]. Even amputated cats get along well on three legs [Herron, 1975].

Zoos are safe environments that limit veterinary experience with large felid fractures. One caged African lioness, however, suffered a comminuted diaphyseal fracture of the radius and a simple distal ulnar fracture. Internal fixation was attempted, but failed because proper prostheses were unavailable. An additional radial fracture was undetected and untreated. Despite the fact that this animal was six years old and presumably had slower healing, the lioness was standing and eating in three days without fixation or casting. Although she favored the limb for a few weeks, a follow-up radiograph at seven weeks demonstrated complete healing [Clark and Short, 1975].

Nutritional Factors

Implicit in the sociality argument is the assumption that injury prevents hunting, adequate nutrition and healing. Instead, tremendous evolutionary pressure exists for rapid recovery. There is little information on feline starvation. Conditions in the wild are uncontrolled and famine is seldom total, whereas lethal starvation experiments are most unlikely to pass Animal Care and Use Committees. Human hunger strikers are another matter. Despite weakening by a previous fast, the first fatality of the 1981 hunger strike at Ulster's Maize Prison, survived 65 days. Ten hunger strikers survived an average of sixty-two days and some individuals up to 79 days, although debilitation began after 30 days [Facts on File, 1981; Johannes Weir Foundation, 1995].

As obligate carnivores, cats are adapted to feast or famine. The have an adaptive 1.2°C fall in body temperature during starvation. It took 6–23 weeks of near starvation producing weight losses of 38–55%, before domestic cats failed cold challenge. One cat was well and active with a core temperature of only 32.8°C. As no cats died, these studies did not reach physiologic limits [Clark, 1938, Clark et al., 1968]. Unlike most animals, cats do not curtail enzyme production during starvation and and remain able to digest a kill at any time [Rogers et al., 1977].

Stiffness and tensile strength are proportional to bone density [Gartland, 1987; Marshall et al., 1996]. Bones are little affected in feline starvation studies – unweighted average loss was 13.8% of fresh bone weight, but only 5.3% of fat-free weight with no chemical change [Keys et al., 1950].

Felids maintained exclusively on meat and viscera eventually develop vitamin deficiencies [Griner, 1983]. In the wild, they consume the intestines and partly digested food of herbivore prey, obtaining thereby water-soluble vitamins having limited body reserves [Cotran et al., 1994]. Without this, deficiency still takes six weeks to develop in adult cats [Wallach and Boever, 1983]. Fat-soluble vitamins (e. g., Vitamin D) are stored in the body and deficiencies develop much more slowly [Wilson, 1994].

Serengeti studies show that adults rarely starve to death [Packer et al., 1990]. Famished cubs visibly emaciate in one month, but seldom die unless completely starved eight to ten weeks. Recover was rapid 'Ten days of ample food were sufficient to transform the survivors from staggering skeletons to frisky youngsters whose recent deprivation was not evident' [Schaller, 1972]. Domestic cats took sixteen weeks to lose 50% body weight on 69 kcal daily, but still resisted cold challenge [Clark et al., 1968]. These cats received only a quarter of their requirement of 261 kcal (76 kcal/kg) for weight maintenance [Kendall et al., 1983]. Extrapolating to complete starvation should take 12 weeks to reach cold challenge failure. Long bone fractures increase metabolic requirements by 20–25% and probably speed starvation by the same fraction or about nine weeks to a lack of cold response, let alone mortality [Buckwalter et al., 1996]. A previously healthy animal should therefore have functional fracture healing long before demise. Small animals such as lions cubs and domestic cats have large relative surface areas, whereas the larger *Smilodon* should be more resilient due to a lower metabolic rate and greater metabolic reserves.

Discussion

Arguments that healed fractures are only found in social animals are based on false or unsubstantiated premises. They run counter to evolutionary pressure for rapid bone healing. Second, it is a fallacy that bone healing proves ultimate survival. Much healing would occur even as an animal starves to death. Third, a previously nourished animal has enough metabolic reserve to form a primary fracture callus and achieve functional healing without assistance. Fourth, the paucity of severe fractures suggests that seriously injured animals were simply immobile and never entrapped at La Brea. Fifth, recovery times cited in veterinary studies are for animals provided food and water. Injured animals compelled by thirst and hunger to endure pain would be ambulatory sooner and such activity may even speed healing. Sixth, felids can obtain only 25% of their water from food [Wallach and Boever, 1983]. Because water cannot be provided in the wild by social groups, an immobilized animal will quickly die of dehydration. It is clear that social welfare for *Smilodon* did not include provisioning. It is not clear that sharing the kills would be more successful than solitary scavenging, even assuming the injured animal keeps up with the group. Group hunting might simply result in a greater number of formidable predators at a kill.

In modern cats nondisplaced fractures can be difficult to even diagnose and spontaneous improvement typically occurs within days [Lloyd, 1990]. It is plausible that *Smilodon* would be capable of a brief ambush attack in the latter stages of healing. Animals mobile enough to find water could probably also scavenge food. Even in starvation cats retain normal metabolic function. Sole predation is compatible with the remarkable healing ability of felids subsisting on metabolic reserves. Finally, no wild population should have such a low prevalence of fractures. This suggests that imobilized animals simply did not survive to be mired. On the other hand, mobile animals recovering without assistance would account for the small fraction of healed, minor or moderately serious fractures in the tar pits.

These facts do not conclusively disprove sociality, but do refute evidence hailed as indisputable [Heald, 1989]. Social hunting remains a rare behavior, difficult to document in the fossil record. It seems to be a late development in canid evolution [Radinsky, 1969]. *Smilodon* would be unique in having a smaller brain than its solitary hunting relatives. Its short limbs suggest ambush rather than pursuit, and sociality is unnecessary in ambush hunting [Martin, 1980]. A preponderance of evidence suggests *Smilodon* was solitary.

Social hunting has also been postulated for several dinosaurs with small brains by mammalian standards. We should look carefully at the evidence presented for these claims, bearing in mind that evidence for *Smilodon* sociality fails scrutiny and yet has been extended to other animals.

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