Radiographs reveal exceptional forelimb strength in the sabertooth cat, Smilodon fatalis.

Permalink
https://escholarship.org/uc/item/0rc3418z

Journal
PloS one, 5(7)

ISSN
1932-6203

Authors
Meachen-Samuels, Julie A
Van Valkenburgh, Blaire

Publication Date
2010

DOI
10.1371/journal.pone.0011412

Peer reviewed
Radiographs Reveal Exceptional Forelimb Strength in the Sabertooth Cat, *Smilodon fatalis*

Julie A. Meachen-Samuels*†, Blaire Van Valkenburgh

Department of Ecology and Evolutionary Biology, University of California Los Angeles, Los Angeles, California, United States of America

Abstract

**Background:** The sabertooth cat, *Smilodon fatalis*, was an enigmatic predator without a true living analog. Their elongate canine teeth were more vulnerable to fracture than those of modern felids, making it imperative for them to immobilize prey with their forelimbs when making a kill. As a result, their need for heavily muscled forelimbs likely exceeded that of modern felids and thus should be reflected in their skeletons. Previous studies on forelimb bones of *S. fatalis* found them to be relatively robust but did not quantify their ability to withstand loading.

**Methodology/Principal Findings:** Using radiographs of the sabertooth cat, *Smilodon fatalis*, 28 extant felid species, and the larger, extinct American lion *Panthera atrox*, we measured cross-sectional properties of the humerus and femur to provide the first estimates of limb bone strength in bending and torsion. We found that the humeri of *Smilodon* were reinforced by cortical thickening to a greater degree than those observed in any living felid, or the much larger *P. atrox*. The femur of *Smilodon* also was thickened but not beyond the normal variation found in any other felid measured.

**Conclusions/Significance:** Based on the cross-sectional properties of its humerus, we interpret that *Smilodon* was a powerful predator that differed from extant felids in its greater ability to subdue prey using the forelimbs. This enhanced forelimb strength was part of an adaptive complex driven by the need to minimize the struggles of prey in order to protect the elongate canines from fracture and position the bite for a quick kill.

Introduction

Few extinct predators are as well-known as the saber tooth cats, which are touted for their prowess as ultimate mammalian predators [1,2]. Numerous studies of the skull, teeth, and neck of saber tooth cats have examined how they may have dispatched their prey, e.g. [1,3–10]. A consensus has emerged that the saber tooth cat *Smilodon fatalis* probably differed from modern big cats in making relatively quick kills using directed slashing bites to the throat rather than a suffocating bite, as is typical of extant big cats such as lions. In association with this, *Smilodon* had robust forelimbs that were instrumental in restraining prey so that the killing bite or bites could be made with minimal risk of breaking the elongate canine teeth [11–13]. From external measurements of the forelimb bones, it appears that they were relatively thick for their length [2,12,13] and therefore probably more resistant to bending and compressive loads; however, more accurate estimates of strength require data on both external diameters and cortical bone thickness.

Radiographs allow the measurement, in any plane of interest, of moments of area that reflect resistance to bending and torsion. Previous workers have used cross-sectional properties of mammalian limb bones in various species to identify differences in the pattern of forelimb versus hind limb use, e.g. [14,15], to estimate body mass in extant and extinct taxa, e.g. [16–18], to document significant declines in human bone strength over time despite relatively constant external bone dimensions [19], and even to document asymmetries in left vs. right arm strength in modern human athletes [20].

Despite the many uses of cross-sectional properties in the literature, there is substantial debate about the straightforwardness of these measurements. Studies [21–23] warn that cross-sections of limb midshafts do not always indicate repeated loading patterns in all animals in the same way and cross-sectional geometry of long bones does not correlate well with strain patterns. These authors recommend that *in vivo* data be used whenever possible to get accurate assessments of strain patterns and bone loading. With these caveats, there is still evidence that strain does play a role in documenting asymmetries in left vs. right arm strength in modern human athletes [20].

Citation: Meachen-Samuels JA, Van Valkenburgh B (2010) Radiographs Reveal Exceptional Forelimb Strength in the Sabertooth Cat, *Smilodon fatalis*. PLoS ONE 5(7): e11412. doi:10.1371/journal.pone.0011412

* E-mail: meachensamuels@nescent.org

* Current address: National Evolutionary Synthesis Center, Durham, North Carolina, United States of America
species [27]. Comparisons of bone cross-sectional properties can also be good estimators of mechanical ability, if the comparisons are kept to closely related groups that share similar body plans and locomotor ecologies, such as living and extinct felids [27].

Quadrapedal limbs are used for weight-bearing as well as other activities, such as climbing, digging, swimming and grappling with prey. In the case of large cats, the hind limb functions primarily in weight-bearing and propulsion, whereas the forelimb functions in weight-bearing, climbing, and prey killing [28,29]. Of course, the hind limbs contribute during climbing but their role is still largely propulsive whereas the forelimbs both grasp the trunk and pull the body upwards. Thus, it might be expected that the humeri of cats that are arboreal or take prey larger than themselves would exhibit greater cortical thickening than expected based on body mass alone. Surprisingly, this does not appear to be the case, as a recent study found that humeral cross-sectional properties were better predictors of body mass than prey size or locomotor habits in extant felids [30].

Results

When Smilodon fatalis was compared with all extant felids and the larger, extinct lion, Panthera atrox, it had humeri that were more resistant to non-axial bending (J/2) and more resistant to bending specifically in both the mediolateral and craniocaudal planes relative to bone length (Table 1, Fig. 1a–c). Although P. atrox is similar to S. fatalis with regards to bending in the craniocaudal and mediolateral planes, and average bending resistance (Ix, Iy and J/2 values respectively), its humerus is much longer. The greater rigidity of Smilodon humeri largely reflects a greater external diameter relative to bone length, but is also due to thicker cortical bone in Smilodon, suggesting that their bones were loaded more heavily in bending and axial compression than would be expected for similar-sized extant cats. The relative thickening of Smilodon humeri is apparent in radiographs (Fig. 2) and in comparisons of K-values (Table 2). Low K-values indicate a small marrow cavity diameter relative to external diameter. In most cats, K_int is less than K_c, indicating the humerus is loaded more heavily in the mediolateral direction. However, Smilodon exhibits the lowest K_c and greatest relative thickening of humeral cortical bone in the craniocaudal plane, and also ranks among the lowest values for K_int as well (Table 2).

The femur of S. fatalis also shows cortical thickening as evidenced by low K-values (Table 2). In both extant cats and Smilodon, values of K_c and K_int are similar for the femur. Despite the cortical thickening, the femur of Smilodon is similar to other cats in estimates of compressive and bending strength (Table 1, Fig. 1d).

Large values for humerus thickness in Smilodon were also demonstrated by CA measurements (Table 2). Both femora and humeri showed significantly higher CA when compared with all cats, or with pantherins only. However, the disparity between Smilodon and other groups was always greater for humeral measurements (0.995 all cats, 0.325 pantherins) than for femoral measurements (0.704 all cats, 0.212 pantherins).

All of the calculated estimates of bone strength and rigidity (CA, Ix, Iy, J/2) were positively allometric with respect to bone length in both the humerus and femur (Table 1). As also found by Doubé et al. [29], the humerus shows a stronger positive allometry than the femur, perhaps because larger cats utilize their forelimbs to kill relatively larger prey [28].

Discussion

Smilodon humeri were distinct from those of non-sabertooth cats: they were thicker and more resistant to bending in both the mediolateral and craniocaudal planes. Although large felids tend to have a minor advantage over smaller felids, with slightly more resistance to bending in the proximal forelimbs [28,29], for its size, S. fatalis had exceptional resistance to bending in the humerus. Sorkin [32] found similar results for external measurements of the humeri of both S. fatalis and P. atrox, with both of them having relatively robust humeri, but with Smilodon showing increased thickening relative to length. Although the femur also exhibits cortical thickening, it falls within the range of variation seen in extant cats, and thus follows scaling expectations.

The combination of thickened cortical bone and expanded external diameter in the humerus of S. fatalis suggests an unusual adaptation for both large bending and compressive loads on the forelimbs. Cortical thickening helps resist buckling due to axial compression, while higher moments of area distribute bone farther from the neutral axis, increasing resistance to bending [27,33,34]. This is consistent with the probable presence of relatively large and forceful forelimb flexor and extensor musculature in S. fatalis as evidenced by prominent muscle scars and expanded attachment areas positioned to improve mechanical advantage [2,12,35,36]. Like modern big cats, S. fatalis used its forelimbs to both apprehend and position prey for a killing bite. However, unlike modern big cats, Smilodon may have had to rely more heavily on its forelimbs to hold prey because of its elongate canines. Salesa et al. [37] arrived at a similar conclusion in their recent study of an early Old World ancestor of Smilodon, Promegantereon ogygia, (age 9.7–8.7 million years ago). This early sabertooth also had robust forelimbs, intermediate in strength between less-robust conical tooth cats and later sabertooth species and the authors suggested that the greater forelimb strength co-evolved with elongated saber teeth as an adaptation to protect the sabers.

Extant large cats, when killing large prey, use a prolonged suffocating bite to the throat or nose. This crushing bite adds a third point of contact and supports the forelimbs in immobilizing prey [38]. By contrast, sabertooth cats would have killed more quickly with slashing bites to the throat [1,39] that could not have assisted greatly or at all in holding the prey [8]. Additionally,

### Table 1. Regression coefficients of log_{10} humeral or femoral cortical variables against the respective log_{10} bone (humerus or femur) length.

| variable     | R²   | slope | intercept | SEE  |
|--------------|------|-------|-----------|------|
| CA humerus   | 0.970| 2.635 | −3.888    | 0.083|
| Ix humerus   | 0.974| 5.434 | −8.792    | 0.160|
| Iy humerus   | 0.976| 5.148 | −8.348    | 0.145|
| J/2 humerus  | 0.975| 5.323 | −8.630    | 0.153|
| J/2 femur    | 0.966| 4.694 | −7.526    | 0.169|

(SEE, standard error of the estimate. S. fatalis was not included in any regression equations.)

doi:10.1371/journal.pone.0011412.t001
because the elongate canines were relatively vulnerable to fracture [40], it would have been critical to minimize prey struggling and position the killing bite carefully to avoid contact with bone. This likely selected for enhanced forelimb strength in *S. fatalis*.

Cross-sectional limb bone properties have been explored in only a few orders of mammals, including primates, rodents, ungulates, and carnivores, e.g. [14,15,17,19,20,29,33,41–44]. Among these, there are two interesting partial analogs to the pattern of much greater forelimb than hind limb strength seen in *Smilodon*. The first is in a distantly related group that also uses its forelimbs in a specialized way, fossorial caviomorph rodents. The humerus of the Highland tuco-tuco (*Ctenomys opimus*) differs from other caviomorph rodents, in having thicker cortices and a higher resistance to non-axial bending (high J/2); but its femur is similar to other species [44]. Like *S. fatalis*, the tuco-tuco has enlarged forelimb muscles and its forelimbs are loaded heavily, but for different reasons. Rather than grappling with prey, tuco-tucos use their forelimbs to excavate burrows, cutting dirt with powerful movements of their forefeet. Among caviomorphs, moderate or occasional diggers do not show such extreme adaptation. Thus, in both *C. opimus* and *S. fatalis*, greater differences in forelimb and hind limb use result in parallel differences in limb structure. A second example can be found in the bush dog; this small, rarely seen South American forest canid shows thickened cortical bone in the humerus relative to other dogs, and relative to its mass [30]. Bush dogs are excellent swimmers with partially webbed feet [45,46]; this habit might explain the increased cortical thickness in the humerus relative to the femur.

It is unlikely that the enhanced forelimb strength of *Smilodon* represents an adaptation to either digging or swimming, rather than prey-killing, given that its distal unguals are retractile and shaped like those of felids rather than diggers [47] and a specialization for swimming would be quite surprising among felids. Another alternative explanation for enhanced forelimb strength in *Smilodon* might be as an adaptation to climbing given that skeletal adaptations of the forelimbs for climbing and prey-killing are similar in felids [28]. However, the largest extant felids (lions, tigers) and ursid (*U. arctos*) rarely climb as adults, probably because their mass makes climbing too difficult and dangerous [48–50].

Bones with thick cortices are heavier and are energetically more costly to build, maintain, and move. Their presence in *S. fatalis*...
strongly suggests a forelimb dominated predation strategy that differed from that of modern felids, and hence corroborates conclusions based on craniodental and neck anatomy [1,6,9,39,51]. The extreme specialization of the skull, teeth, neck and forelimbs of *Smilodon* probably made it an efficient predator of large ungulate prey, such as bison and camels [52], and, perhaps, juvenile proboscideans. Unfortunately, this specialization may also have led to *Smilodon’s* extinction, as the cat may have been too specialized to switch to alternative, perhaps more agile prey, such as cervids during the ice age megafaunal extinctions [53].

**Materials and Methods**

Humeral and femoral cortical areas were calculated using radiographic procedures following previous studies [15,16], with radiographs taken in both craniocaudal and mediolateral planes.
JMS radiographed humeri of 26 of 28 extant species at the Natural History Museum of the Smithsonian Institution (USNM) using a digital x-ray machine. The remaining two extant species humeri, all extinct species, and all femora were x-rayed by placing bones directly on a DuPont Quanta Rapid x-ray cassette containing 3M green light sensitive UVL film and using a portable x-ray machine. To equalize the effects of parallax for all specimens using the latter method, the x-ray machine was placed at a constant height above the film and external measurements were also taken directly from the bone. A measured difference of less than 4% (~<3 mm) was found between the radiograph and the actual bone using this method for Panthera atrox.

Cortical thicknesses and, when possible, lengths were measured from digital radiographs using ImageJ [54] and from traditional radiographs to the nearest 0.1 mm using a light box and digital calipers. Table S1 includes a list of species measured and individual radiographic measurements and calculations.

Measurements of internal and external diameters were taken for both humerus and femur approximately at the midshaft, taking humerus measurements immediately distal to the deltopectoral crest to minimize interference from this muscle insertion area. These measures were used to estimate aspects of long bone strength in axial compression (CA), bending about mediolateral and craniocaudal planes (Ix, Iy, respectively), and average rigidity in non-axial loading (J/2), [15,16,18,42,43]. Values were calculated using the following formulas:

\[
CA = \pi (AB - ab)/4
\]

\[
Ix = \pi (A^2B - a^2b)/64
\]

\[
Iy = \pi (AB^3 - ab^3)/64
\]

\[
J = Ix + Iy
\]

where A = external cranio-caudal diameter, B = external mediolateral diameter, a = cranio-caudal diameter of the medullary cavity, and b = mediolateral diameter of the medullary cavity [15,16,43].

One additional measure of relative cortical thickness (K) was assessed that is independent of bone length, measured in the craniocaudal (cc) and mediolateral directions (ml) as:

\[
K = \text{internal diameter/external diameter}
\]

where values closer to one signify relatively thinner cortical bone and values closer to zero signify relatively thicker cortical bone [55].

To assess differences between species, species averages were calculated for CA, Ix, Iy, J/2, Kcc, Kml, and lengths. All measurements except K were log transformed and regressed against respective log10 bone (humerus or femur) length. Differences between Smilodon and all other felids, and Smilodon and the clade that includes only large felids (pantherins) were analyzed using non-parametric Mann-Whitney U-tests.

Supporting Information

Table S1 List of species/specimens measured; number and letter abbreviations for Figure 1; sex, specimen number, limb element, raw measurement data and calculations of CA, Ix, Iy, and J. Found at: doi:10.1371/journal.pone.0011412.s001 (0.23 MB DOC)

Acknowledgments

We thank S. Cox, J. Dines, A. Farrell, L. Gordon, J. Harris, J. Jacobs, K. Molina and C. Shaw for access to equipment and specimens in their care, as well as W. Binder, K. Carlson, M. Lajeunesse, J. Logdson, G. McClain, M. Salesa, J. Samuels, and G. Slater for assistance and critical feedback on our manuscript.

Author Contributions

Conceived and designed the experiments: JAMS. Performed the experiments: JAMS. Analyzed the data: JAMS. Contributed reagents/materials/analysis tools: BVV. Wrote the paper: JAMS BVV.

References

1. McHenry C, Wroe S, Clausen PD, Moreno K, Cunningham E (2007) Supermoderated sabretooth, predatory behavior in Smilodon fatalis revealed by high-resolution 3D computer simulation. Proc Nat Acad Sci U S A 104: 16010–16015.
2. Wroe S, Lowry MB, Antón M (2008) How to build a mammalian super-predator. Zoology 111: 196–203.
3. Akersten WA (1985) Canine function in Smilodon (Mammalia: Felidae: Machairodontidae). Contributions in Science (Los Angeles) 356: 1–22.
4. Bryant HN (1996) Force generation by the jaw adductor musculature at different loading conditions. J Zool Lond 238: 395–413.
5. Martin LD (1998) Felidae. In: Janis CM, Scott KM, Jacobs LL, eds. Evolution of Anatomies of Carnivorous Mammals. Toronto: University of Toronto Press. pp 283–299.
6. Antón M, Galobart A (2005) Co-existence of scimitar-toothed cats, lions and hominins in the European Pleistocene. Implications of the post-cranial anatomy of Homotherium latidens (Owen). J Vertebr Paleontol 19: 847–853.
7. Antón M, Galobart A, Turner A (2005) Sabertooth characters in the clouded leopard (Neofelis nebulosa Griffiths 1821). J Morphol 267: 1186–1198.
8. Therrien F (2005) Feeding behaviour and bite force of sabretoothed predators. Zool J Linn Soc-Lond 145: 393–426.
9. Wroe S, McHenry C, Thomason J (2005) Bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. Proc Roy Soc, B 272: 619–625.
10. Christiansen P (2006) Sabertooth characters in the clouded leopard (Neofelis nebulosa Griffiths 1821). J Morphol 267: 1186–1198.
11. Schultz CB, Martin LD (1970) Machairodont cats from the early Pleistocene of Broadwater and Liso local fauna. Bull Univ Nebraska State Mus 9: 33–38.
12. Zawoyny WJ (1976) Behavioral implications of saber-toothed felid morphology. Paleobiology 2: 332–342.
13. Anyonge W (1996) Locomotor behaviour in Plio-Pliocenete sabre-tooth cats: A biomechanical analysis. J Zool Lond 238: 395–413.
14. Demes B, Jungers WL, Selpien K (1991) Body size, locomotion, and long bone cross-sectional geometry in indrid primates. Am J Phys Anthropol 86: 537–547.
15. Heinrich R, Biknevicius A (1998) Skeletal allometry and interlimb scaling patterns in musidid carnivorous. J Morphol 235: 121–134.
16. Anyonge W (1993) Body mass in large extant and extinct carnivores. J Zool Lond 231: 339–350.
17. Jungers WL, Barr DB (1994) Body size, long bone geometry and locomotion in quadrupedal monkeys. Z Morphol Anthropol 88: 89–97.
18. Ruff CB (2006) Body size, body shape, and long bone strength in modern humans. J Hum Evol 5: 209–219.
19. Ruff CB, Trinkaus E, Walker A, Larsen CS (1993) Postcranial robusticity in Homo, I: Temporal trends and mechanical interpretation. Am J Phys Anthropol 90: 21–53.
20. Trinkaus E, Churchill SE, Ruff CB (1994) Postcranial robusticity in Homo, II: humeral bilateral asymmetry and bone plasticity. Am J Phys Anthropol 93: 1–34.
21. Lieberman DE, Polk JD, Demes B (2004) Predicting long bone loading from cross-sectional geometry. Am J Phys Anthropol 123: 156–171.
22. Demes B, Stern JT, Jr., Hausman MR, Larson SG, McLeod KJ, et al. (1998) Patterns of strain in the macaque ulna during functional activity. Am J Phys Anthropol 106: 87–100.
23. Demes B, Qin Y-X, Stern JT, Jr., Hausman MR, Larson SG, Rubin CT (2001) Patterns of strain in the macaque tibia during functional activity. Am J Phys Anthropol 116: 257–265.
24. Rubin CT, Gross TS, McLeod KJ, Bain SD (1995) Morphologic stages in lamellar bone formation stimulated by a potent mechanical stimulus. J Bone Miner Res 10: 488-495.
25. Martin RB, Burr DB, Sharkey NA (1998) Skeletal Tissue Mechanics. New York: Springer. 392 p.
26. Robling AG, Hinant FM, Burr DB, Turner CH (2002) Improved bone structure and strength after long-term mechanical loading is greatest if loading is separated into short bouts. J Bone Miner Res 17: 1545-1554.
27. Ruff CB, Holt BH, Trinkaus E (2006) Who’s afraid of the big bad Wolf? Wolf’s law and bone functional adaptation. Am J Phys Anthropol 129: 484-498.
28. Meachen-Samuels JA, Van Valkenburgh B (2009) Forelimb indicators of prey-size preference in the Felidae. J Morphol 270: 729-744.
29. Double M, Wiktorska-Secony A, Christiansen P, Hutchinson JR, Shefelbine S (2009) Three-dimensional geometric analysis of limb bone allometry. PLoS ONE 4:e7342. Available http://www.plosone.org/article/info:doi/10.1371%2Fjournal.pone.0007342. Accessed 2009 April 1.
30. Meachen-Samuels JA (2010) Comparative scaling of humeral cross-sections of felids and canids using radiographic images. J Mammal Evol, In press.
31. Barnett R, Shapiro B, Barnes I, Ho SYW, Burger J, et al. (2009) Phylogeography of lions (Panthera leo ssp.) reveals three distinct taxa and a late Pliocene reduction in genetic diversity. Mol Ecol 18: 1608-1617.
32. Sorokin B (2008) A biomechanical constraint on body mass in terrestrial mammalian predators. Lethaia 41: 333-347.
33. Rubin CT, Lanyon LE (1982) Limb mechanics as a function of speed and gait: a study of functional strains in the radius and ulna of horse and dog. J Exp Biol 101: 187-211.
34. Bertram JEA, Biewener AA (1988) Bone curvature: sacrificing strength for load predictability? J Theor Biol 131: 75-92.
35. Turner A, Antón M, Turner A, Morales A (2005) Aspects of the functional morphology in the cranial and cervical skeleton of the sabre-toothed cat Paramachairodus aggi (Kaup, 1832) (Felidae, Machairodontinae) from the Late Miocene of Spain: implications for the origins of the machairodont killing bite. Zool J Linn Soc-Lond 144: 363-377.
36. Van Valkenburgh B, Ruff CB (1987) Canine tooth strength and killing behaviour in large carnivores. J Zool Lond 212: 379-397.
37. Ruff CB, Hayes WC (1983) Cross-sectional geometry of premaxillary fangs and teeth: a biomechanical investigation: 1. Method and general patterns of variation. Am J Phys Anthropol 60: 359-381.
38. Polk JD, Demes B, Jungers WL, Biknevicius AR, Heinrich RE, et al. (2009) A comparison of primate, carnivore and rodent limb bone cross-sectional properties: are primates really unique? J Hum Evol 39: 297-325.
39. Runcie JA (1997) Postcranial adaptations for climbing in the Loridae (Primates). J Zool Lond 242: 261–280.
40. Biknevicius AR (1993) Biomechanical scaling of limb bones and differential limb use in caviomorph rodents. J Mammal 74: 95–107.
41. Macdonald DW (1996) Social behaviour of captive bush dogs (Speothos venaticus). J Zool Lond 239: 525–541.
42. Ruff CB, Hayes WC (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vertebr Paleontol 7: 162-192.
43. Schaller GB (1967) The Deer and the Tiger. Chicago: University of Chicago Press. 304 p.
44. Schaller GB (1972) The Serengeti Lion: A Study of Predator Prey Relationships. Chicago University of Chicago Press. 304 p.
45. Sasaki M, Hideki E, Wiig O, Derocher AE, Tsubota T, et al. (2005) Adaptation of the hindlimbs for climbing in bears. Ann Anat 187: 153−160.
46. Antón M, García-Perea R, Turner A (1998) Reconstructed facial appearance of the sabretoothed felid Smilodon. Zool J Linn Soc-Lond 124: 369–386.
47. Coltrain JB, Harris JM, Cerling TE, Ehleringer JR, Dearing M, et al. (2004) Comparison of primate, carnivoran and rodent limb bone cross-sectional variation. Am J Phys Anthropol 60: 359–381.
48. Bieseigel BD, Zuercher GL (2005) Smilodon Forelimb Strength. Mammalian Species 783: 1-6.
49. Van Valkenburgh B (1987) Skeletal indicators of locomotor behavior in living and extinct carnivores. J Vertebr Paleontol 7: 162-192.