Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa

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We provide the first predictions of bite force (B_S) in a wide sample of living and fossil mammalian predators. To compare between taxa, we calculated an estimated bite force quotient (BFQ) as the residual of B_S regressed on body mass. Estimated B_S adjusted for body mass was higher for marsupials than placental predators and the Tasmanian devil (Sarcophilus harrisii) had the highest relative B_S among extant taxa. The highest overall B_S was in two extinct marsupial lions. BFQ in hyaenas were similar to those of related, non-osteophagous taxa challenging the common assumption that osteophagy necessitates extreme jaw muscle forces. High BFQ in living carnivores was associated with greater maximal prey size and hypercarnivory. For fossil taxa anatomically similar to living relatives, BFQ can be directly compared, and high values in the dire wolf (Canis dirus) and thylacine (Thylacinus cynocephalus) suggest that they took relatively large prey. Direct inference may not be appropriate where morphologies depart widely from biomechanical models evident in living predators and must be considered together with evidence from other morphological indicators. Relatively low BFQ values in two extinct carnivores with morphologies not represented among extant species, the sabrecat, Smilodon fatalis, and marsupial sabretooth, Thylacosmilus atrox, support arguments that their killing techniques also differed from extant species and are consistent with ‘canine-shear bite’ and ‘stabbing’ models, respectively. Extremely high BFQ in the marsupial lion, Thylacoleo carnifex, indicates that it filled a large-prey hunting niche.

**Keywords:** bite force; prey size; osteophagy; Carnivora; Dasyuromorphia; Thylacoleonidae

1. INTRODUCTION

Bite force (B_S) is an important aspect of carnivore ecology, with the potential to shed light on the evolution of community structure and prey size in fossil taxa (Meers 2002; Vizzaino & de Iuliis 2003; Rayfield 2004). However, empirical data are not easily obtained; B_S has been measured in only three mammalian carnivore species (Thomason 1991; Dessem & Druzinisky 1992; Binder & Van Valkenburgh 2000) and the comparative biology of B_S in mammals has remained largely unexplored. Important unanswered questions are: is bite force (i) allometrically related to body mass, (ii) phylogenetically constrained, (iii) more strongly influenced by skull length or skull width, (iv) relatively higher in bone-cracking specialists and (v) related to prey size in extant taxa? Answers will define the limits of using B_S estimate as a predictor of behaviour and prey size in fossil species.

2. MATERIAL AND METHODS

We calculated theoretical maximum bite forces using the ‘dry skull’ method (Thomason 1991; Electronic Appendices, sections A and B). Our sample comprised 49 specimens representing 39 taxa (31 extant and eight extinct). The dry skull method, derived from relationships between skull dimensions and jaw muscle cross-sectional areas, models the jaw as a simple lever. It is most applicable to the anterior-most portion of the jaw, where the caniniform teeth are located (Electronic Appendix, section A). Consequently, and because morphology of the canines has long been considered a significant predictor of predatory behaviour in mamalian carnivores (Wroe et al. 1998; Farlow & Pianka 2002), we have largely restricted our discussion to estimates of force for static bites at the canines (CBS). However, analyses of B_S at the carnassial showed the same qualitative trends as for CBS (Electronic Appendix, section C). A further advantage of the ‘dry skull’ method is that because results are derived solely from skull morphology, comparisons can be made between fossil and extant taxa.

The relationship between CBS and body mass between species is allometric (figure 1; Meers 2002; $r^2=0.85$). To compare bite forces in taxa of greatly differing body masses an estimated bite force quotient (BFQ) was calculated using the residuals of regression (table 1; Electronic Appendix, section A). ‘Average’ BFQ was set at 100. Variance in allometry adjusted bite force is small relative to that for absolute BS (Thomason 1991; Electronic Appendix, section D) and a second advantage of using BFQ is that it allows more meaningful comparisons based on small datasets. This quality is particularly valuable in analyses incorporating fossil taxa where sample sizes are limited.

3. RESULTS

The highest B_S estimate adjusted for body mass were

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However, relative to body mass, CBS was significantly canids, and thylacoleonids were similar to felids (figure 2). Masses in dasyuromorphians were similar to those of heads—relationships between head lengths and body (158 versus 98), although marsupials do not have larger cats ( \( p < 0.01 \) ) and significantly higher in thylacoleonids than in cats (\( F_{1,11} = 33.51, p < 0.01 \)) and significantly higher in thylacoleonids than in canids (\( F_{1,13} = 11.84, p < 0.01 \)). The average BFQ for Felidae (104) was slightly less than in Canidae (110) and dogs had greater head to body size (figure 2), but the difference in this instance was not significant. Across all taxa, skull width was a better predictor of CBS than skull length (\( r^2 = 0.92 \) and 0.78, respectively; Thomason 1991).

CBS was considerable for specialist bone-crackers included in our study, the spotted and brown hyaenas (Crocuta crocuta and Hyaena hyaena) and the Tasmanian devil (S. harrisii). However, in the two hyaenids, BFQ at the canine was exceeded by several non-osteophagous carnivorans (figure 1; table 1) and BFQ for the Tasmanian devil was not much above average for dasyuromorphians and less than in two marsupial lions. BFQ at the carnassial teeth followed a similar pattern (Electronic Appendix, section C), an expected result because the position of the carnassial varies little among mammalian predators (Greaves 1983).

As an upper restriction on niche, a predator’s maximal prey size is an important component of its ecology and is likely to be strongly influenced by its biomechanical limits. Predator body mass has been shown to correlate with maximal prey size in mammals (Meers 2002). Among extant canids, the four hypercarnivores that often prey on animals larger than themselves, the grey wolf (Canis lupus lupus), dingo (C. l. dingo), African hunting dog (L. pictus) and the dhole (Cu. alpinus), have the highest BFQ (108–142). BFQ was consistently lower in the five more solitary, omnivorous foxes, jackals and coyote characterized by relatively low maximal prey sizes (80–97). Thus, although the ability to bring down large prey in canids is related to cooperative hunting, it is still reflected in a higher BFQ. Within living Felidae, BFQ values were 57 and 75 for the two species that specialize in relatively small prey, while BFQ was 94 or greater for the seven known to take relatively large prey (table 2).

Results suggest that, relative to body mass, calculated canine \( B_S \) is considerably higher in marsupials than in two extinct marsupial lions, Thylacoleo carnifex (194) and Priscileo roskellyae (196). The lowest was also in a fossil marsupial, Thylacosmilus atrox (41). Among extant carnivorous mammals the highest BFQ was in the Tasmanian devil, Sarcophilus harrisii (181). For placental fus, BFQ was greatest in the Pleistocene dire wolf, Canis dirus (163). Another canid, the African hunting dog, Lycaon pictus, had the highest BFQ for living Carnivora (142).

Mean BFQ was higher in marsupials than placental (158 versus 98), although marsupials do not have larger heads—relationships between head lengths and body masses in dasyuromorphians were similar to those of canids, and thylacoleonids were similar to felids (figure 2). However, relative to body mass, CBS was significantly higher in dasyuromorphians than in canids (\( F_{1,11} = 33.51, p < 0.01 \)) and significantly higher in thylacoleonids than in cats (\( F_{1,11} = 11.84, p < 0.01 \)).

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4. DISCUSSION

(a) Comparisons between extant taxa

Results suggest that, relative to body mass, calculated canine \( B_S \) is considerably higher in marsupials than in...
placental and this cannot simply be explained by differences in head size. The presence of the superfast myosin isoform in both carnivorans and dasyuromorphians suggests that their muscle microphysiology is similar (Hoh et al. 2001). Differences between these two groups may relate to brain volumes, which, in carnivorans, are around two and a half times that of marsupial counterparts (Ewer 1969) and through greater efficiency may be able to accomplish similar results with less BS. Because mean BFQ in marsupials is much higher than in placental...

finding that the relatively omnivorous D. viverrinus has a BFQ well within the range of hypercarnivorous placental and is consistent with this interpretation. If in vivo testing shows that placental produce bite forces that are similar, after adjustment for body mass, to marsupials, it will probably be a result of differences in jaw muscle anatomy, such as muscle pennation or microphysiology, although none have been clearly identified to date.

Mean BFQ was lower in cats than canids, reflecting the smaller head size of cats relative to body mass, but relative to skull length, CBS in felids was greater, possibly because of their greater skull width relative to length (Electronic Appendices, sections E and F). Although extant canids and dasyuromorphians have higher mean BFQ than felids, the shorter skull of cats may confer greater resistance to forces produced by struggling prey. Cats also have more powerful, flexible forelimbs, of critical utility in violent, close quarter interactions and may recruit ventral cervical
musculature to assist in jaw closure (Van Valkenburgh et al. 2003; Antón et al. 2004).

(b) Bite force and osteophagy
Our finding that BFQ at both the canine and carnassial in osteophages were often comparable to, and sometimes less than, many non-osteophagous relatives was unexpected. This may have important implications regarding the biomechanics of osteophagy.

In most carnivores, maximal bite forces are used in the killing bite at the canines where maximal loads will be distributed between adjacent teeth in the anterior region of
the jaw. In contrast, osteophagy requires the concentration of high loads on a limited part of the food item in order to produce material failure. The highest bite forces are typically achievable in carnassial biting, which is restricted to one side of the mandible rather than distributed between left and right jaws (Greaves 1983). In hyaenids, maximum forces may be generated immediately anterior to the carnassial (Werdelin 1989). Moreover, from observation, osteophages may use kinetic, rather than static bites to crack bones, further increasing loads. Consequently, theoretical forces that can be achieved are far greater than those experienced during a canine bite. The application of maximal bite forces at post-canine teeth on hard materials requires very robust dentitions, as evidenced in specialized bone-crackers such as C. crocuta, H. hyaena and S. harrisii. Our results suggest that although the capacity of teeth (and probably crania) to resist high stresses on hard substances in the cheek-tooth row is an essential adaptation to specialized osteophagy in mammals, particularly high bite strength relative to body size is not. The flipside of this argument is that many felids and canids could theoretically apply relatively greater bite forces at a single point in the cheek-tooth row than could a same-sized hyaenid. However, we posit that in practice, non-osteophagous taxa will not voluntarily develop maximal bite forces in a post-canine bite because neither their dentitia nor their crania are optimized to resist such high stresses in this region. Unused capacity at the carnassial in non-osteophages may be an incidental product of the requirement for high B_S at the canines as part of their killing strategy.

(c) Bite force and the prediction of feeding ecology

(i) Extant carnivores

Our results demonstrate that among living mammalian carnivores, B_FQ is a broad indicator of relative prey size and feeding ecology. However, considered in isolation, B_S adjusted for body mass is not an infallible predictor. In the aardwolf (Proteus cristatus), B_FQ is low (77), but higher than in some bears, a viverrid and two small cat species (table 2). Although this finding is consistent in that all take relatively small prey, it does not reflect the fact that P. cristatus subsists largely on termites. Interestingly, the unusual, hypotrophied post-canine morphology of the aardwolf unambiguously suggests that vertebratae are rarely taken, but the canines are quite well developed. Together with moderate B_FQ, this indicates that it is physically capable of killing much larger prey than it does. The retention of functional canines and moderate B_FQ in P. cristatus may be related to intra and/or interspecific defence. Either way, the aardwolf clearly lies outside generalized biomechanical subcategories, such as the cat and dog types, which themselves differ in details including head shape, canine cross-sectional morphologies and killing behaviour. This example demonstrates well that B_FQ may not directly reflect feeding ecology for morphologically atypical taxa that do not fit within generalized biomechanical models. Consequently, in the reconstruction of ecology for fossil carnivores, B_FQ must be qualified against the type and extent of morphological departure from biomechanical subcategories observable in living species. For example, predictions incorporating B_FQ for fossil cats, or taxa with cat-like morphologies, are best made on the basis of comparisons with extant felids.

(ii) Extinct taxa with morphologically similar extant relatives

Neither cranial, nor post-cranial morphology of the thylacine, Thylacinus cynocephalus, differ greatly from those of living dasyuromorphians (Wroe 2003). Based on low rates of canine tooth breakage and snout morphology, it has been argued that thylacines may have been restricted to small or medium sized prey (Jones 2003; Johnson & Wroe 2003). Our finding that B_FQ was comparable to extant dasyuromorphians known to take relatively large prey is contra these interpretations (table 1). Similarly, high B_FQ in the Miocene thylacinid, Nimbasinicus dicksoni, suggests that relatively large prey were accessible to this anatomically conservative species.

Likewise, among fossil placental morphologies, morphology of the dire wolf (C. dirus) is similar to that of living relatives. If C. dirus was a social hunter, then its high B_FQ (163) relative to extant canids suggests that it preyed on relatively large animals.

(iii) Extinct taxa without morphologically similar living relatives

Some fossil taxa included in our analyses clearly fell well outside extant morphotypes. Major differences between the sabrecat Smilodon fatalis and all extant felids, including extreme hypertrophy of the canines, very powerful forelimbs, lengthening of the neck and shortening of the lumbar region, leave little doubt that it used killing techniques not represented among living carnivores and regularly took large prey (Janis 1994; Antón & Galobart 1999; Antón et al. 2004; Argot 2004). Notwithstanding its high absolute C_B_S compared with large living felids, B_FQ in S. fatalis was low (78). Having secured large prey with its muscular forelimbs, S. fatalis used its hypertrophied canines to effect fatal trauma (Antón et al. 2004; Argot 2004). The reduced cross-sectional area of the canines in sabrecats may require relatively less bite force than that used by living Panthera (M. Meers, personal communication). In the marsupial sabretooth, T. atrox, both B_FQ (41) and absolute B_S were extremely low, but as with S. fatalis, post-cranial adaptations and canine morphology indicate a killing technique without present day analogy and systematic predation on relatively large taxa (Argot 2004).

Current functional models of sabretooth killing behaviour include: (i) the ‘stabbing’ model in which the force applied to the canines is primarily neck-driven (Antón & Galobart 1999; Argot 2004) and (ii) a ‘canine-shear bite’, in which significant absolute force is required of the jaw adductors in conjunction with input from neck muscles (Akersten 1985). Because absolute C_B_S in S. fatalis is high, and B_FQ is considerably higher than in T. atrox, our results are consistent with the ‘canine shear-bite’ model for the sabrecat, with significant force required of the jaw adductors in conjunction with cervical musculature. From estimates of bending strength in the mandibular corpus, Biknevicius & Van Valkenburgh (1996) posit that S. fatalis may have applied a sustained throat clamping bite. Our results do not rule out this possibility, but are contra the conclusion that bite
force in *S. fatalis* was comparable to that of similar sized pantherines. However, in the marsupial sabretooth, CB₃ and BFQ are both so low that we consider our result supportive of a primarily neck-driven use of the canines and strongly contra the possibility that *T. atrox* applied a sustained throat bite to dispatch large prey.

For the marsupial lion, *T. carnifex*, BFQ was the highest of any large predator and its CB₃ approached that of a lion (*Panthera leo*) more than twice its size (table 1). If the killing mechanism of *T. carnifex* was functionally equivalent to that of extant felids, our results suggest that it could take prey much larger than itself. However, although cat-like in many respects, its dentition is unusual and interpretation of feeding ecology in the marsupial lion has long attracted controversy (Wells et al. 1982; Wroe et al. 2004a). Our findings confirm that short outlever arms and anteriorly placed muscle resultants conferred high mechanical efficiency (Wells et al. 1982). The marsupial lion’s vertical shearing ‘carnassial’ cheek-teeth are relatively larger than in any other mammalian carnivore (Wells et al. 1982; Werdelin 1988). Brought together with a very high BS₃ these carnassials may have enabled *T. carnifex* to rapidly slice through tracheas or vital blood vessels and quickly dispatch large, potentially dangerous prey, although mechanical simulation will be required to confirm this. When CB₃ and BFQ are considered together with forelimb, cervical and lumbar morphology that converges on that of marsupial and placental sabretooths, as well as taphonomic data (Janis 1994; Wroe 2003; Argot 2004), the marsupial lion may have been capable of taking sub-adults of the heaviest available prey (Wroe et al. 2004b).

5. CONCLUSIONS

The dry skull method, because it takes into account subtle changes in the shape of the skull and jaws, provides estimates of BS that can be applied across unrelated taxa and strongly shows that placental produce bite forces that are similar after allometric adjustment to marsupials, it will be because of differences in muscle anatomy and organization.

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