ELECTRONIC APPENDIX

This is the Electronic Appendix to the article

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

by

Stephen Wroe, Colin McHenry & Jeffrey Thomason

Proc. R. Soc. B (doi:10.1098/rspb.2004.2986)

Electronic appendix

Section A.

Estimates of bite force. Carnivores may use the cheek-teeth on only one side of the mandible when processing food, in which case the opposing jaw joint may become the fulcrum (Greaves 1983). In this model, absolute maximum bite force is typically achieved at the carnassial tooth. The 'dry-skull' method may underestimate maximum bite force at the canine ($\mathbf{CB_S}$) by a factor ranging between 1.3 and 1.5. More posteriorly within the jaw this discrepancy increases and may exceed a factor of two (Thomason 1991). Consistent with this finding, we found that $\mathbf{B_S}$ at the carnassial in a spotted-hyaena, was around half that given as an absolute maximum from empirical data (Binder & Van Valkenburgh 2000). The 'dry-skull' method assumes that bite force correlates with muscle cross-sectional areas and lever arm lengths, and does not take into account any interspecific differences in jaw muscle pennation. We have not applied correction factors to account for underestimations because these make additional assumptions and, as the focus of our study is comparative, it is relative not absolute values that are important.

For a full account of the dry skull method see Thomason (1991); the jaw was treated as a lever, and the torque applied by the jaw musculature was divided by the distance from the bite point to the fulcrum (outlever) to give $\mathbf{B_S}$ (Section B). The torque was given by an estimate of the force developed by each jaw muscle, multiplied by the distance from its point of action upon the lever to the fulcrum (inlever). The jaw adductor musculature was considered to involve two components, the temporalis and masseter systems (including the medial pterygoid). For each muscle, osteological landmarks were used to map the maximal cross sectional area onto a photograph of the skull taken from an angle normal to the plane of the cross section (Section B).

Maximum cross-sectional areas and their centroids were calculated using AutoCAD 2004. Force estimates for each muscle are equal to maximal cross-sectional area multiplied by 300 KPa (30 N/cm^2), the tension developed by mammalian muscle tissue. Distance from the centroid to the jaw hinge, measured in the plane of the maximal cross section, gave the inlever for each muscle.

Bite point. This was designated as being the centre of the tooth, at the base of the crown (Thomason 1991). The bite point was measured at the posterior-most of the opposing caniniform teeth. For carnivorans and dasyuromorphians this is the upper canine, in thylacoleonids this is the lower first incisor. In two thylacoleonids the lower first incisor is unknown and this measurement was an approximation wherein we assumed that I_1 was in the same relative position as for *Thylacoleo carnifex*.

Body mass estimates: Ideally, body mass would be taken from actual recorded values. However, for the great majority of extant specimens available to us these data were not available and most of these were restricted to crania only. Consequently, for all extant taxa body masses were calculated from skull lengths using the most appropriate equations available (Van Valkenburgh 1990, Myers 2001). This may produce overestimates of body mass in relatively large-headed taxa and underestimates in small-headed ones. The influence on **BFQ** would be to dampen differences between large and small-headed species and underestimate disparity within taxa, e.g., the already low **BFQ** in the extant felids with small heads relative to body mass (Felinae) may be an overestimate and the high **BFQ** in the relatively large headed pantherines, an underestimate.

For fossil taxa estimates based on cranial dimensions may be inappropriate, where morphologies diverge greatly from those of living relatives. In these instances predictions based on minimal proximal limb bone circumferences (MPLC) are probably the most reliable (Anderson *et al*. 1985), but for fossil specimens available to us postcranial data were known only for *Thylacosmilus atrox*. Wroe *et al*. (2003) demonstrated that for marsupials, estimates based on endocranial volume corresponded closely with those based on MPLC and this method was applied in the case of *Thylacoleo carnifex*. Neither proximal limb bones nor endocranial volumes were available for remaining fossil taxa and here we were restricted to predictions based on skull length. Because it was considerably more robust than any living cat (Janis 1994), our body mass estimate from skull length for *S. fatalis,* in particular, is likely to be an underestimate, meaning that our calculations may overestimate **BFQ** for this species. We point out that although body mass estimates using any method are clearly inexact, **BFQ** values showed some resistance to variation in this factor. For example, raising or lowering the body mass estimate by 20% in *T. carnifex* produced a 10% increase or decrease in **BFQ**.

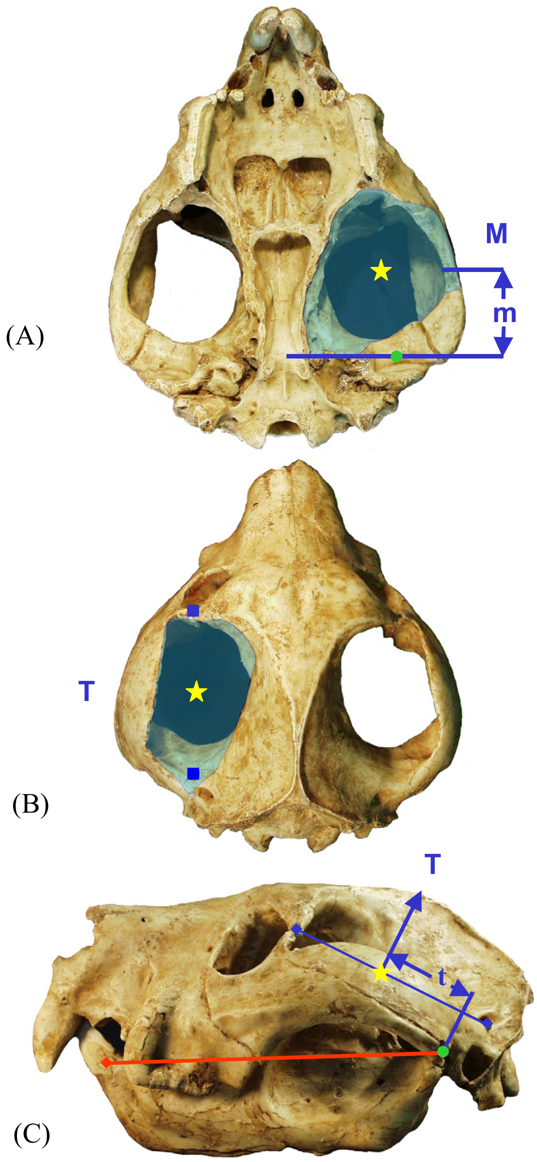
Bite Force Quotient (***BFQ***). **BFQ** was derived using the residuals of regression for bite force and body mass based on our sub-sample of 31 extant carnivores.

$\mathbf{BFQ} = [\mathbf{CB_S} / 10\hat{}(0.6014 \times \text{Log}_{10}\, \mathbf{BoM} + 1.7137)] \times 100$, $r^2 = 0.85$.

Prey size (data for additional taxa). For *C. l. dingo* (Corbett 1995), *C. l. hallstromi* (Koler-Matznick *et al*. 2003), *M. meles* (Nowak & Paradiso 1983), and *D. maculatus* and *S. harrisii* (M. Jones Pers. Commun.).

Statistics. Analysis of covariance was used to compare bite forces with body mass treated as the covariate. Systat 9 (SPSS 1999) was used for all statistical comparisons.

Section B. Calculation of bite forces at the canine (**CB$_s$**) in the marsupial lion (*Thylacoleo carnifex*). (A) 'Masseter' (ventral) view, from point perpendicular to longitudinal plane through the anteriormost tip of premaxillae and posterior apex of occipital condyle; estimated cross-sectional area of masseter and medial pterygoid shaded light blue; resultant force vector (**M**) acts normal to this plane through centroid (yellow star) with lever-arm (**m**) acting about jaw joint (closed green circle). (B) 'Temporalis' (dorsoposterior) view from point perpendicular to line through two markers (closed blue squares); estimated cross-sectional area of temporalis shaded light blue; resultant force vector (**T**) acts through centroid. (C) In lateral view marker dots as in (A & B); moment arm (**t**) of force (**T**) operates about jaw joint. Lever-arm (red) measured from jaw joint to base of posterior-most caniniform tooth.



Section C. BFQ at the carnassial. Carnassial Bite force (**CaB_S**); Basal Skull Length (**BSL**); maximum Skull Width at the Zygoma (**SWZ**); and estimates of Body Mass (**BoM**) for 39 taxa of Recent and fossil mammals. Measurements and calculations were taken from prepared skulls.

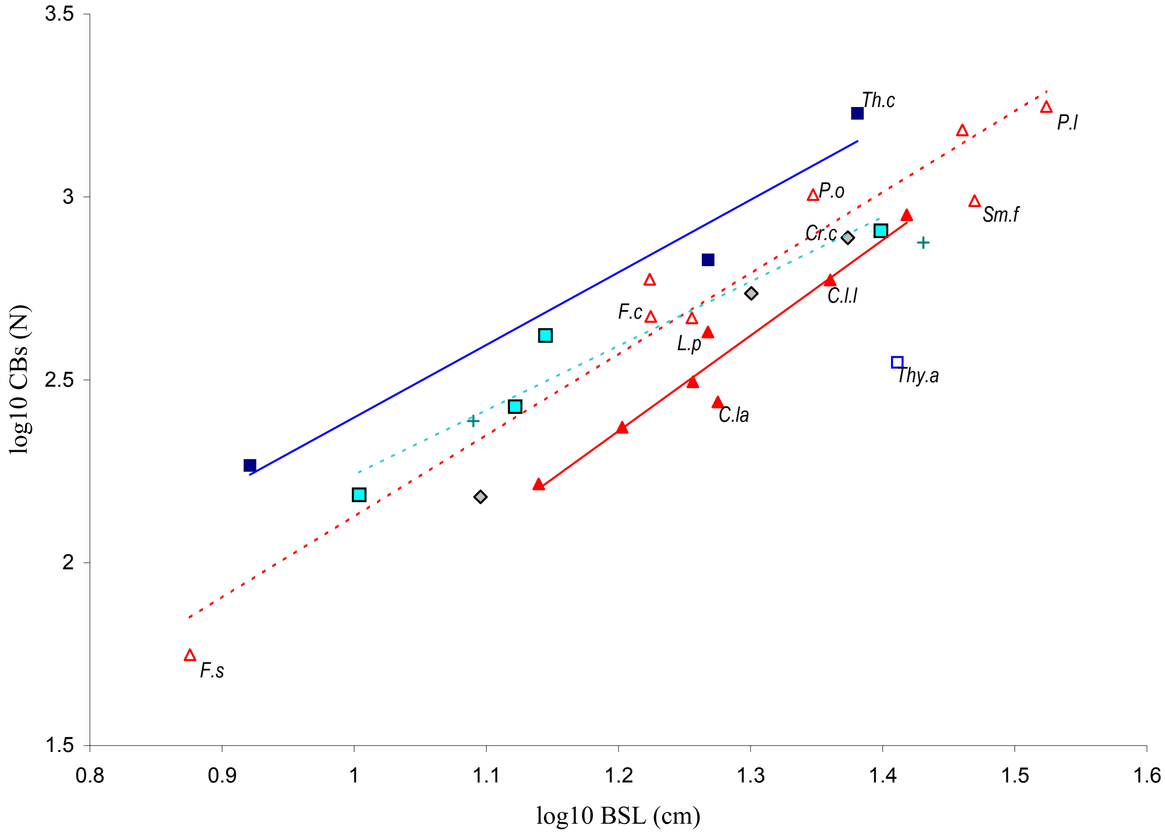
Species	Family	**BSL (cm)**	**SWZ (cm)**	**BoM (kg)**	**CaB_S (N)**	**BFQ**
Alopex lagopus	Canidae	13.86	8.05	8.3	322	103
Canis alpinus	Canidae	17.69	10.78	16.5	541	114
Canis aureus	Canidae	13.53	8.12	7.7	280	93
Canis lupus dingo (*C l.d*)	Canidae	18.04	9.97	17.5	555	113
Canis lupus hallstromi	Canidae	15.95	9.41	12.3	487	122
Lycaon pictus (L.p)	Canidae	18.52	13.18	18.9	694	135
Vulpes vulpes (*V.v*)	Canidae	13.79	7.35	8.1	304	97
Urocyon cineroargentus	Canidae	11.91	6.14	5.3	198	80
Canis latrans (*C.la*)	Canidae	18.85	9.86	19.8	554	97
Canis lupus lupus (*C.l.l*)	Canidae	22.92	13.22	34.7	1033	141
Canis dirus †	Canidae	26.19	17.58	50.8	1577	171
Ursus americanus	Ursidae	24.39	17.20	105.2	758	53
Ursus arctos	Ursidae	26.96	16.28	128.8	1180	74
Ursus thibetanus	Ursidae	20.92	11.07	77.2	706	33
Meles meles	Mustelidae	12.31	8.05	11.4	349	92
Gennetta tigrinus	Viverridae	10.93	5.19	6.2	265	45
Crocuta crocuta (*Cr.c*)	Hyaenidae	23.64	16.73	69.1	1569	142
Hyaena hyaena	Hyaenidae	19.98	15.18	40.8	1097	135
Proteles cristatus	Hyaenidae	12.46	7.22	9.3	1824	54
Panthera onca (P.o)	Felidae	22.25	18.63	83.2	1755	142
Panthera tigris	Felidae	28.86	22.73	186.9	2789	140
Acinonyx jubatus	Felidae	15.93	12.30	29.5	736	110
Felis yagouaroundi	Felidae	10.09	6.94	7.1	227	79
Lynx rufus	Felidae	7.58	5.93	2.9	162	95
Felis concolor (F.c)	Felidae	16.77	12.92	34.5	864	118
Felis sylvestris (*F.s*)	Felidae	7.51	5.39	2.8	105	63
Neofelis nebulosa	Felidae	16.74	11.88	34.4	1051	144
Panthera leo (*P.l*)	Felidae	33.41	24.81	294.6	3085	118
Panthera pardus	Felidae	18.01	13.02	43.1	837	100
Smilodon fatalis † (*Sm.f*)	Felidae	29.48	19.53	199.6	1933	93
Dasyurus maculatus (*D.m*)	Dasyuridae	10.09	6.01	3.0	308	187
Dasyurus viverrinus	Dasyuridae	7.27	4.15	0.9	123	148

Sarcophilus harrisii (*S.h*)	Dasyuridae	13.96	11.17	12.0	553	141
Nimbacinus dicksoni †	Thylacinidae	13.24	8.08	5.3	465	191
Thylacinus cynocephalus	Thylacinidae	25.04	14.83	41.7	1176	143
Prisciieo roskellyae †	Thylacoleonidae	8.34	6.34	2.7	227	139
Wakaleo vanderleurei †	Thylacoleonidae	18.53	12.58	41.4	875	107
Thylacoleo carnifex † (*Th.c*)	Thylacoleonidae	24.04	20.15	109.4	2102	145
Thylacosmilus atrox †	Thylacosmilidae	257.71	139.65	106	658	46

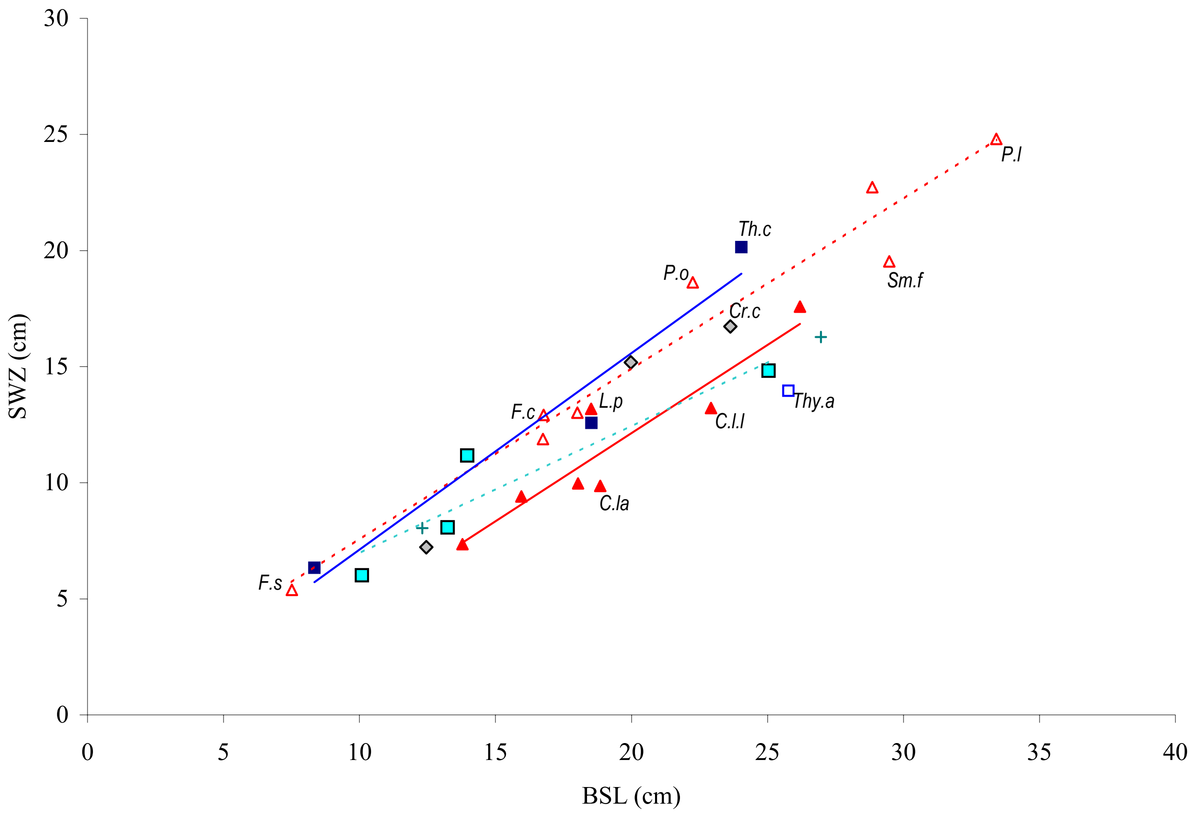
Section D. Basic statistics of variance for bite force quotient (**BFQ**) and predicted canine bite strength (**CB_S**) in samples of adult red fox (*Vulpes vulpes*) and spotted-tailed quoll (*Dasyurus maculatus*). Samples included two males, two females and two individuals of unknown sex in each species. For both, variance is considerably higher for **CB_S** than for **BFQ**.

	Vulpes vulpes		*Dasyurus maculatus*	
	BFQ	CB_S	BFQ	CB_S
specimen 1	90.19	164.3	198.44	208.17
specimen 2	90.8	174.63	192.61	215.27
specimen 3	89.31	172.37	158.84	142.74
specimen 4	92.97	170.44	185.67	139.81
specimen 5	101.56	204.37	179.47	193.13
specimen 6	84.63	118.41	183.33	142.8
Mean	91.58	167.42	183.06	173.65
Standard Error	2.29	11.35	5.58	14.55
Standard Deviation	5.61	27.79	13.67	35.65
Variance	31.51	772.52	186.82	1271.12
Coefficient of Variance	6.13%	16.60%	7.47%	20.53%
95(	97.47	96.59	197.40	211.07
95(	85.69	138.25	168.72	136.24

Section E. Log_{10} Canine Bite force (**CB$_S$**) plotted against $\log_{10}$ Basal Skull Length (**BSL**). Data points and linear regression lines are shown using symbols as in Figs. 1 & 2.



Section F. Basal Skull Length (**BSL**) plotted against Skull Width at the Zygoma (**SWZ**). Symbols as in Figs.1 & 2. Note that species with high **BFQ** (Table 1) have skulls that are wide for their length.



REFERENCES

Anderson, J. F., Hall-Martin, A. & Russell, D. A. 1985 Long-bone circumference and weight in mammals, birds, and dinosaurs. *J. Zool. (Lond.)* **207**, 53-61.

Binder, W. J. & Van Valkenburgh, B. 2000 Development of bite strength and feeding behaviour in juvenile spotted hyena (*Crocuta crocuta*). *J. Zool. Lond*. **252**, 273-283.

Corbett, L. 1995 *The dingo in Australia and Asia,* New York: Cornell University Press.

Koler-Matznick, J. Birsbin, I. L., Feinstein, M. & Bulmer, S. 2003 An updated description of the New Guinea singing dog (*Canis hallstromi*, Troughton 1957). *J. Zool. Lond.* **261**, 109-118.

Myers, T. J. 2001 Marsupial body mass prediction. *Aust. J. Zool.* **49**, 99-118.

Nowak, R. M. & Paradiso, J. N. 1983 *Walker's mammals of the world*, Vol. II. 4th Ed. Baltimore: John Hopkins University Press.

Van Valkenburgh, B. 1990 Skeletal and dental predictors of body mass in carnivores. In *Body size in mammalian paleobiology: estimation and biological implications* (eds J. Damuth & B. J. MacFadden), pp. 181-205. Cambridge: Cambridge University Press.