



Estimating the body mass of Pleistocene canids: discussion of some methodological problems and a new ‘taxon free’ approach

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In a recent seminar in *Lethaia*, Kaufman & Smith (2002) indicate a number of statistical problems with the methodology of multiple regression analysis used by Palmqvist *et al.* (1999) for predicting the body mass of Pleistocene canids from cranial and dental measurements. Specifically, they cite their inability to reproduce the equation published by Palmqvist *et al.* (1999, p. 78) or calculate the values adjusted for the regression coefficients with the same metric data. The discrepancy arises because the mean estimates of body mass used by Palmqvist *et al.* (1999) for extant canids were not those reproduced in their table 1, but slightly different ones which included corrections for averaging the mass of both sexes for each species. The correct values are presented here (Table 1). There are slight differences between the regression coefficients provided by Palmqvist *et al.* (1999) and those supplied by Kaufman & Smith (2002); even so, the estimates of body mass obtained for Pleistocene canids with both sets of equations are remarkably similar.

A more important issue outlined by Kaufman & Smith (2002) is that the ratio of samples (N) to predictor variables (P) used in the multiple regression equation of Palmqvist *et al.* (1999) is low (10:7) and should have been limited to at least 10:1 (Darlington 1990). Partly to avoid this problem, Kaufman & Smith (2002) provide a regression equation that combines only two dental measurements, the mesiodistal length of the upper canine and the buccolingual breadth of the lower fourth premolar. This equation, however, is virtually identical to the one obtained by Prevosti & Palmqvist (2001, p. 379) using a stepwise procedure for selection of variables to be included within the regression function; unfortunately, the latter article was not available for Kaufman & Smith (2002).

Kaufman & Smith (2002) recall that ‘decisions need to be made in analyses of this kind (i.e. the estimation of body mass for extinct taxa) that require expertise in the biology and ecology of the animals under consideration’, but state that they ‘are both primatologists, and do not feel qualified to seriously evaluate Carnivora’. They select the best predictor for body mass from metric data in Palmqvist *et al.* (1999), the mesiodistal length of the upper canine. The body masses predicted with their equation for *Canis (Xenocyon) falconeri* and *Canis etruscus* are, respectively, 31.9 and 7.8 kg. However, they find reason to question these values (but a wrong reason, as explained below), because according to the data in table 1 of Palmqvist *et al.* (1999) the length and width of the canines of *C. falconeri* are greater than twice the corresponding values for *C. etruscus*, while for every other tooth measurement the difference between both species is much smaller. Because of this difference, and given that the canine teeth are sexually dimorphic in some carnivores (e.g. big cats and bears; see Van Valkenburgh & Ruff 1987), they suggest the possibility that the mean values for canine dimensions provided by Palmqvist *et al.* (1999) for each Pleistocene species ‘happen by chance to represent mostly male size for the larger species and mostly female size for the smaller species. If this is the case, then body masses determined from canines would magnify true species differences’.

The latter suggestion, however, is incorrect. It is true that the great apes show a high level of sexual dimorphism in the size of the upper canines, which correlates well with differences in body mass between both sexes, reflecting the level of competence among males (see Plavcan & van Schaik 1997). However, the estimates of

dimorphism provided for canids in Table 1 show that the canines of these carnivores are not as dimorphic as those in primates. The dimorphism in body mass for each canid species, calculated dividing the logarithm of the mean mass for males by the corresponding log-value for females (i.e. the procedure described by Plavcan & van Schaik 1997), ranges between 0.65 and 1.18. The dimorphism for upper canine length has a narrower range, fluctuating between 0.92 and 1.16. The latter range is similar to those for other tooth measurements, such as the length of the upper and lower carnassial teeth (Table 1).

The comparative study of tooth measurements in modern canids by Palmqvist *et al.* (1999) revealed a close relationship between craniodental morphology and feeding behaviour in hypercarnivores (i.e. those species that hunt large prey in packs, with diets consisting of >70% vertebrate meat) and carnivores/omnivores (i.e. those canids of solitary habits, in which meat represents <70% of diet, with fruits and insects making up the balance). Using principal components and discriminant function analysis, Palmqvist *et al.* (1999; Fig. 1) found that the upper canines were disproportionately larger in *C. falconeri* than in *C. etruscus*, because the former species had a diet based exclusively on flesh (i.e. similar to that of modern Eurasian and North American gray wolf (*Canis lupus*), Indian dhole (*Cuon alpinus*), African painted dog (*Lycaon pictus*) and South American bush dog (*Speothos venaticus*)), while the latter had a more omnivorous diet (i.e. as in African jackals (*Canis adustus*, *C. aureus* and *C. mesomelas*) and North American coyote (*C. latrans*)). This subsequently is also supported by biogeochemical analyses of carbon- and nitrogen-isotope ratios from bone collagen and trace-element ratios of bone hydroxylapatite, used for determining the dietary niches of fossil mammals from Venta Micena (Gröcke *et al.* 2002; Palmqvist *et al.* in prep.). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of canids suggest an open environment for both species and record their trophic level, indicating a diet based exclusively on flesh for *C. falconeri*, similar to that of contemporary sabre-tooth felids, and a more omnivorous feeding behaviour for *C. etruscus*.

Although the ecomorphological study of Palmqvist *et al.* (1999) revealed that the upper canines of hypercarnivorous canids are comparatively larger than those in omnivores, for other variables (e.g. the size of the talonid basin in the lower carnassial or jaw length) such a trend is reversed. There are two morphometric indexes, the buccolingual breadth of upper canine teeth and jaw depth measured at the level of the second molar, divided by mandible length in both cases, that illustrate the differences between both feeding groups: Fig. 1 shows that hypercarnivorous canids have larger canines and more stoutly built mandibles than omnivorous species, with the only exception of the South American red fox (*Dusicyon culpaesus*), in which the canines are disproportionately wide. For this reason, the regression equation adjusted by Kaufman & Smith (2002), based exclusively on upper canine length, is inadequate, providing non-randomly distributed deviations between observed and predicted values of mass for living canids, and thus biased estimates for fossil species.

Using metric data in Table 1, a regression analysis was performed in a large data set of canid species ($N=28$) that includes representatives of 14 genera of the three extant canid subfamilies

Table 1. Mean values of body mass (*BM*, in kg; * values for Pleistocene canids estimated in this article using eq. 1.1) and six craniodental measurements (in mm) for several species of modern canids ($n = 28$), calculated from unpublished metric data provided by B. Van Valkenburgh. Metric data include mesiodistal length and buccolingual breadth of upper canine (LC^1 , BC^1), length and breadth of upper carnassial (LP_4 , BP_4 , excluded the protocone), length and breadth of lower carnassial (LM_1 , BM_1), mandible length (L_{mand}) and jaw depth measured at second molar (JD_{M2}). Estimates of sexual dimorphism in each species for BM , LC^1 , LP_4 , and LM_1 were obtained dividing the logarithm of the mean for males by the corresponding value for females. FB = feeding behaviour (HC : hypercarnivore, >70% flesh in diet; CO : carnivore/omnivore, <70% flesh in diet; a : inferred for Pleistocene canids by Palmqvist *et al.* (1999), and from data in Fig. 1). S = sex (m : mean for males; f : mean for females).

Species	FB	S	N	BM	LC ¹	BC ¹	LP ⁴	BP ⁴	LM ₁	BM ₁	L _{mand}	JD _{M2}	BM dim	LC ¹ dim	LP ⁴ dim	LM ₁ dim	
<i>Alopex lagopus</i>	CO	m	5	3.8	6.2	4.0	12.1	4.9	13.5	5.0	91.6	13.8	1.18	1.02	1.03	1.03	
		f	5	3.1	6.1	3.8	11.3	4.7	12.6	4.9	86.7	12.2					
<i>Canis adustus</i>	CO	m	5	9.4	7.5	4.6	14.8	5.1	16.3	6.6	114.2	15.3	1.06	1.04	1.02	1.01	
		f	5	8.3	6.9	4.3	14.1	5.1	16.0	6.6	113.1	14.9					
<i>Canis aureus</i>	CO	m	3	12.0	7.4	4.2	15.5	5.8	17.3	6.5	108.9	15.3	1.08	1.01	1.01	1.01	
		f	5	10.0	7.3	4.2	15.2	5.6	17.0	6.3	102.8	14.3					
<i>Canis latrans</i>	CO	m	5	14.5	9.0	5.7	18.8	6.9	21.4	7.6	133.8	19.5	1.09	1.01	1.00	1.01	
		f	5	11.5	8.8	5.1	19.0	6.9	21.0	7.5	128.1	18.5					
<i>Canis lupus</i>	HC	m	5	45.0	14.0	8.5	24.4	10.0	28.7	11.1	176.2	29.8	1.03	1.05	1.02	1.02	
		f	5	41.0	12.3	8.2	23.2	9.3	26.5	10.8	169.2	29.1					
<i>Canis mesomelas</i>	CO	m	4	8.2	7.6	4.6	17.1	5.9	18.2	7.1	110.6	15.9	1.07	1.02	1.11	1.01	
		f	3	7.1	7.4	4.3	15.8	5.5	17.5	6.7	105.2	14.8					
<i>Canis simensis</i>	CO	m	2	16.5	9.0	5.9	15.9	6.1	18.5	6.2	141.1	18.2	1.11	1.03	1.02	1.02	
		f	4	12.5	8.5	5.4	15.2	5.7	17.6	6.2	137.5	16.7					
<i>Cuon alpinus</i>	HC	m	5	17.5	9.1	5.4	19.6	6.8	20.8	8.1	134.3	24.2	1.17	1.01	1.00	1.00	
		f	5	11.5	8.9	5.4	19.7	6.6	20.5	7.8	129.5	22.3					
<i>Cerdocyon thous</i>	CO	m	3	7.0	6.5	4.2	12.0	4.9	14.4	5.4	104.0	16.3	1.05	1.05	1.00	1.01	
		f	3	6.4	5.9	3.6	12.1	4.7	14.1	5.8	107.2	16.5					
<i>Dusicyon culpaeus</i>	CO	m	3	13.0	8.6	5.5	15.4	6.2	16.5	6.4	125.5	17.1	1.05	1.00	1.00	1.01	
		f	3	11.5	8.5	5.1	15.4	5.6	15.9	6.2	123.9	15.7					
<i>Dusicyon gymnocercus</i>	CO	m	2	5.5	6.0	3.7	13.2	4.7	14.5	6.0	107.3	13.7	1.06	0.97	1.04	1.02	
		f	3	5.0	6.4	3.7	12.0	4.4	13.6	5.3	100.5	13.1					
<i>Dusicyon griseus</i>	CO	m	5	4.6	5.7	3.5	12.3	4.4	13.8	5.3	92.7	12.2	1.06	1.07	1.01	1.01	
		f	5	4.2	5.1	3.0	11.9	4.1	13.3	5.2	90.5	11.8					
<i>Dusicyon vetulus</i>	CO	m	4	3.5	4.7	3.1	7.9	3.5	9.4	3.7	80.4	10.8	1.08	1.07	1.00	0.98	
		f	2	3.2	4.2	3.3	7.9	3.1	9.8	4.1	80.0	10.4					
<i>Fennecus zerda</i>	CO	m	3	1.3	2.4	1.3	6.9	1.9	7.6	2.7	55.8	6.4	0.65	0.92	0.98	0.98	
		f	4	1.5	2.6	1.3	7.2	1.8	7.9	2.8	55.8	6.9					
<i>Chrysocyon brachiurus</i>	CO	m	2	23.0	11.4	7.6	18.4	6.6	24.3	10.0	168.9	24.3	1.05	1.03	1.01	1.04	
		f	2	20.0	10.5	6.1	17.8	6.4	21.5	8.5	167.6	21.9					
<i>Lycaon pictus</i>	HC	m	3	25.0	11.3	7.3	20.6	7.6	24.5	9.2	144.6	25.5	1.00	1.02	1.00	1.01	
		f	4	25.0	10.8	7.1	20.3	7.3	23.5	8.6	144.6	25.5					
<i>Lycalopex sechurae</i>	CO	m	3	5.0	4.8	3.1	9.9	3.6	11.9	4.8	91.6	12.2	1.16	1.03	1.02	1.03	
		f	2	4.0	4.6	2.8	9.5	3.2	11.0	4.3	83.8	10.4					
<i>Nyctereutes procyonoides</i>	CO	m	3	7.5	5.0	3.0	9.6	3.5	11.6	4.3	80.0	12.4	1.00	1.04	1.02	1.02	
		f	3	7.5	4.7	2.7	9.1	3.4	11.0	4.2	75.8	12.7					
<i>Otocyon megalotis</i>	CO	m	5	4.0	4.7	3.0	5.1	2.6	5.9	3.4	78.2	10.3	0.95	1.13	0.98	0.99	
		f	4	4.3	3.9	2.4	5.3	2.7	6.0	3.3	77.8	10.5					
<i>Speothos venaticus</i>	HC	m	3	9.0	6.4	4.3	12.2	4.5	13.6	5.4	96.4	17.1	1.00	0.97	0.99	1.01	
		f	4	10.0	6.8	4.6	12.6	4.6	13.2	5.2	92.9	18.9					
<i>Urocyon cinereoargenteus</i>	CO	m	5	5.4	4.8	3.1	9.4	3.6	11.3	3.9	83.5	10.3	1.05	1.10	1.03	1.01	
		f	5	5.0	4.2	2.8	8.8	3.6	11.1	3.9	80.1	10.3					
<i>Urocyon littoralis</i>	CO	m	5	2.0	4.4	2.8	7.9	3.4	7.7	3.9	71.0	9.4	1.00	1.06	1.00	0.92	
		f	5	2.0	4.0	2.7	7.9	3.4	9.3	3.8	69.4	9.3					
<i>Vulpes bengalensis</i>	CO	m	5	2.5	4.5	2.2	8.9	2.6	10.8	3.7	82.2	9.6	1.00	1.16	1.06	1.03	
		f	2	2.5	3.7	2.0	7.8	2.5	10.0	3.6	76.1	8.2					
<i>Vulpes chama</i>	CO	m	5	2.6	3.8	2.5	9.3	3.3	11.1	4.4	81.6	9.6	1.00	1.01	1.01	1.00	
		f	5	2.6	3.5	2.2	9.1	2.9	11.0	3.9	77.3	8.6					
<i>Vulpes macrotis</i>	CO	m	5	2.4	4.6	2.8	9.2	3.4	11.0	3.8	79.0	9.6	1.00	1.02	1.00	0.99	
		f	5	2.4	4.4	2.7	9.3	3.5	11.3	3.9	78.9	9.5					
<i>Vulpes pallida</i>	CO	m	6	2.2	3.4	1.9	8.0	2.3	9.2	3.3	72.4	8.1	0.83	1.04	1.01	1.02	
		f	1	2.6	3.3	1.9	7.8	2.4	8.9	3.4	69.1	8.3					
<i>Vulpes ruepelli</i>	CO	m	5	2.4	4.0	2.4	9.6	2.9	11.1	3.7	77.5	10.1	1.00	1.06	0.99	1.00	
		f	5	2.4	3.7	2.0	9.9	2.9	11.2	3.7	74.9	9.0					
<i>Vulpes vulpes</i>	CO	m	5	6.7	7.2	4.8	14.4	5.6	16.4	5.9	110.1	14.9	1.13	1.03	1.02	1.02	
		f	5	5.4	6.8	4.4	13.5	5.2	15.7	5.6	100.7	14.0					
<i>Canis falconeri</i>	HC ^a	–	2/7	29.7*	13.1	8.2	22.2	8.5	26.1	11.7	164.9	32.6	–	–	–	–	
<i>Canis etruscus</i>	CO ^a	–	1/3	10.8*	6.5	4.0	17.8	6.8	22.8	9.0	134.8	20.8	–	–	–	–	

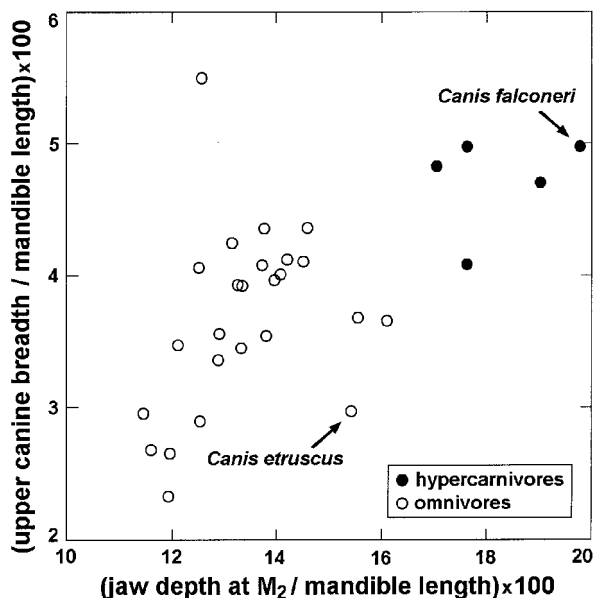


Fig. 1. Relationship among modern canids between two craniodental indexes, upper canine buccolingual breadth and jaw depth below the second molar, divided by mandible length (means for species calculated from data in Table 1). The values for Pleistocene canids, *C. falconeri* and *C. etruscus*, are also shown. Dotted circles = hypercarnivorous species, open circles = omnivorous species.

(Caninae, Simocyoninae and Otocyoninae), thus allowing an ecomorphological, 'taxon-free' approach. Values of body mass and tooth measurements were averaged for both sexes in each living species. The statistical package SPSS v.10.0 (Norusis 2000) was used for the adjustment, and the selection of predictor variables was performed with a stepwise method. The equation obtained in the analysis is:

$$\log \text{ body mass} = 1.031 (\log C^1 \text{ length}) + 1.420 (\log \text{ mandible length}) - 6.509 \quad (1.1)$$

In \log_e units, this equation has a $N:P$ ratio of 14 and a standard error of estimate (SEE) of only 0.266, with $r = 0.953$, $r^2_{\text{adjusted}} = 0.902$, and $F_{25,2} = 124.776$ ($p < 0.0001$). It predicts 29.7 kg of body mass for *C. falconeri* (with a $p < 0.05$ confidence interval comprised between 16.4 kg and 53.8 kg) and 10.8 kg for *C. etruscus* ($p < 0.05$ interval: 5.4–21.6 kg). These values are similar to those obtained by Palmqvist *et al.* (1999) using an equation adjusted with a smaller data set ($n = 10$). In addition, the values obtained using the sets of equations provided by independent analyses for males and females of each species (equations not reported here) give similar values for *C. falconeri* (30.9 kg with the adjustment for males and 26.8 kg with that for females) and *C. etruscus* (9.9 kg and 10.2 kg, respectively). These values agree well with the range of sexual dimorphism in body mass shown by modern canid species (Table 1), thus indicating that the estimates of mass derived from both craniodental measurements are not biased by the sex of the fossil specimens.

However, the equation reported above will be of limited use, because complete mandibles are not available for many fossil species. An alternative equation in which tooth measurements exclusively are used is:

$$\log \text{ body mass} = 2.846 (\log C^1 \text{ length}) - 0.903 (\log P^4 \text{ breadth}) - 1.925. \quad (1.2)$$

Also in \log_e units, this equation has a SSE of 0.274, with

$r = 0.950$, $r^2_{\text{adjusted}} = 0.895$ and $F_{25,2} = 116.277$ ($p < 0.0001$). It predicts 36.7 kg of body mass for *C. falconeri* ($p < 0.05$ interval: 18.5–72.8 kg) and only 6.2 kg for *C. etruscus* ($p < 0.05$ interval: 3.3–11.7 kg). Given the relative weight of both dental measurements in this function, estimated from their partial regression coefficients, canine length contributes more to the prediction of body mass than upper carnassial breadth. This is probably the reason why the value of mass predicted for *C. falconeri* seems to overestimate its actual body size, while the corresponding one for *C. etruscus* is lower than the one expected from other tooth measurements.

We agree with Kaufman & Smith (2002) that the estimation of body mass for fossil species is a 'very difficult task' and 'lies both in careful and creative statistical methodology', on the one hand, 'and in good biological judgement regarding the functional relationship between body size and the traits used to estimate it', on the other. In keeping with the later statement, Palmqvist *et al.* (1999) afforded a comprehensive multidimensional study of the relationship between craniodental morphology, diet and hunting behaviour in modern canids, in order to estimate the functional significance and covariation among the various tooth measurements used for reconstructing the palaeobiology of Pleistocene taxa. Kaufman & Smith (2002) did not take these aspects into consideration in their criticism, focusing instead on statistical issues, and made suggestions based on inadequate assumptions about the level of sexual dimorphism in living canids.

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