

# Bite force and encephalization in the Canidae (Mammalia: Carnivora)

E. M. Damasceno<sup>1,3</sup>, E. Hingst-Zaher<sup>2</sup> & D. Astúa<sup>1</sup>

<sup>1</sup> Department of Zoology, Universidade Federal de Pernambuco, Recife, Brazil

<sup>2</sup> Museu Biológico, Instituto Butantan, São Paulo, Brazil

<sup>3</sup> Faculty of Life Sciences, University of Manchester, Manchester, UK

## Keywords

brain volume; sociality; skull adaptations; independent contrasts; hypercarnivory.

## Correspondence

Diego Astúa, Av. Prof. Moraes Rego s/n, Dept. Zoologia – Centro de Ciências Biológicas, Cidade Universitária, Recife-PE 50670-420, Brazil  
Email: diegoastua@ufpe.br

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## Abstract

The ways in which the taxonomic differences in morphology, behavior or life history relate to each other have been used regularly to test ideas about the selective forces involved in their evolution. Canid species vary significantly in diet, hunting techniques, sociality and cranial morphology. The main goal of this study is to test and explore the possible correlation between bite force and brain volume in canids. For that, we calculated the bite force based on the beam theory, and the brain volume based on three cranial measurements. The species with biggest values of bite force quotient (BFQ) were *Speothos venaticus* (162.25), *Cuon alpinus* (129.24) and *Lycaon pictus* (124.41) due to several adaptations acquired along with hypercarnivory. Species with the highest values of brain volume quotient (BVQ) were *S. venaticus*, *Cu. alpinus* and *L. pictus* with, respectively, 141.35, 139.01 and 131.61, possibly due to the same adaptations that resulted in their bigger BFQ. The highest values of bite force belonged to *Canis lupus* (830.51 Pa), *L. pictus* (719.03 Pa) and *Ca. rufus* (530.52 Pa) and the smallest values belong to *Urocyon littoralis* (98.14 Pa), *Vulpes macrotis* (92.53 Pa) and *V. zerda* (72.6 Pa). *Ca. lupus*, *L. pictus* and *Chrysocyon brachyurus* possess the largest brain volumes with respectively 159.29, 146.94 and 120.84 mm<sup>3</sup> and the smallest values belong to *Nyctereutes procyonoides* (28.2 mm<sup>3</sup>), *V. rueppelli* (27.86 mm<sup>3</sup>) and *V. zerda* (20.65 mm<sup>3</sup>). The independent contrasts correlation showed that there is no correlation between BVQ and BFQ ( $r = 0.14/P = 0.46$ ), as well as no correlation between BFQ and BF ( $r = 0.22/P = 0.26$ ), which indicates the efficiency of the size correction. Bite force and brain volume estimates are much higher in the group hunting hypercarnivores (*Lycaon*, *Cuon* and *Speothos*) and only these showed correlation between BFQ and BVQ. Our results indicate that cranial adaptations for hypercarnivory also influence braincase size.

## Introduction

In mammals, bite strength is directly related to diet and feeding behavior (Huber *et al.*, 2005; Santana & Dumont, 2009), and especially so in carnivores, in which the skull and mandible must resist the external forces generated by their prey attempting to escape the attack (Thomason, 1991) and thereafter, subduction and dismemberment of the kill (Therrien, 2005; Carbone, Teacher & Rowcliffe, 2007; Christiansen, 2007). Bite force has been widely studied due to its capacity to predict feeding habits and hunting behavior. For instance, studying bite force in mammals allowed the modeling of predatory behavior in fossil taxa (Wroe, McHenry & Thomason, 2005), analyzing the predatory behavior on the extant canids (Slater & Van Valkenburgh, 2009), and testing the correlation between behavior and bite force in bats (Santana & Dumont, 2009). Bite forces have

already been calculated for several orders of mammals (Thomason, 1991; Christiansen & Wroe, 2007; Ross *et al.*, 2007; Freeman & Lemen, 2008), several ursids (Christiansen, 2007; Sachetti, Cárdenas & Camacaro, 2009; Oldfield *et al.*, 2012), saber-toothed predators (Therrien, 2005), felids (Sakamoto, Lloyd & Benton, 2010) and domestic dogs (Ellis *et al.*, 2008), but not yet for all members of the Canidae family.

In the Carnivora, bite force is of major relevance because of the difficulty imposed by the flesh-eating diet in capturing and killing the prey. Estimates on carnivore bite force have been used in ecological and paleontological studies involving diet (Christiansen & Wroe, 2007), skull allometry (Christiansen & Adolfsen, 2005; Bourke *et al.*, 2008), phylogenetic variation in felids (Sakamoto *et al.*, 2010) and development in juveniles of spotted hyena, *Crocuta crocuta* (Binder & Van Valkenburgh, 2000).

Other morphological aspects are critical to the survival and adaptation of mammals. One of these is brain volume (Sol *et al.*, 2004, 2008), for its association to intelligence and cognition which are essential for living and hunting in group. Brain volume is a morphological characteristic largely studied in primates, but scarcely studied in carnivorans. Brain size and volume are known to be associated with sociality (Pérez-Barbería, Shultz & Dunbar, 2007; Shultz & Dunbar, 2010) and cognitive skills (Sol *et al.*, 2004; Deaner *et al.*, 2007; González-Lagos, Sol & Reader, 2010) in primates. Likewise, relations between brain size, diet and mating have been explored in the Order Carnivora (Gittleman, 1989), as well as correlations between encephalization and sociality (Finarelli & Flynn, 2009). Also, in felids, the relationships between bite forces, skull shape and brain size were tested (Christiansen, 2008). So far, this relation has been tested only for extinct canids (Finarelli, 2008).

Canids are particularly interesting for the study of bite force and encephalization. Their diets and hunting methods vary widely, ranging from species that feeds solitarily on insects, like the bat-eared dog, *Otocyon megalotis* (Clark, 2005), to hypercarnivore species that hunt in packs, such as the African hunting dog, *Lycaon pictus* (Malcom, 1999). Hunting techniques are intimately linked with the sociality level in canids, as species that hunt cooperatively are also described as the most social, and according to the ‘social brain’ hypothesis, the most social species are also the species with the largest brains (Dunbar, 1998). Moreover, there is a strong correspondence between morphology and diet among canids (Van Valkenburg & Koepfli, 1993); hypercarnivore species have relatively deep jaws to withstand the loads imposed by killing and feeding on large prey, larger canines and incisors, and molar adaptations to shear in detriment of grinding.

Comparisons of skull allometries in carnivore marsupials and members of the Order Carnivora showed that smaller brains allow more room for primary jaw adductors and vice versa (Wroe & Milne, 2007). That observation led to the hypothesis that eutherian carnivores sacrificed a stronger bite (when compared to marsupial carnivores) for a larger brain. Because canids present such wide variation in diet and social behavior, the main goal of this work was to find out whether this hypothesis holds in a lower taxonomic level, within the Canidae family. Therefore, we tested if species of wild dogs with bigger braincases also had the weakest bites.

## Methods

### Examined material

In order to estimate bite force, we took measurements from skull images of 32 species of Canidae (Supporting Information Table S1), representing over 90% of living groups. Every genus of the subfamily Caninae and almost all species of each genus were sampled (Tedford, Taylor & Wang, 1995). We digitally photographed the skulls from three views: for the dorsal and ventral view images, we aligned the palate with the auditory bullae parallel to the camera and on the lateral view

aligning the midsagittal plane parallel to the camera. Every picture had a ruler as a scale. Then, we digitized landmarks on the images and used them to measure the distances and the areas necessary for posterior calculations using TpsDig 2 software (Rohlf, 2006).

### Bite force

We calculated bite force estimates based on the beam theory (Thomason, 1991) which uses the estimated cross-sectional areas of the following muscles: *m. masseter/m. pterygoideus* and *m. temporalis* (T), as well as the distances between the centroids of these areas and of the temporomandibular joint (TMJ) and the distance from TMJ and the bite force output (in this case, the canines), which corresponds to the moment’s arm or lever (*c*). All distances and areas are presented in Fig. 1.

The muscles areas (M and T) are multiplied by 300 Kpa (0.3 N mm<sup>-2</sup>), the estimated force applied by mammalian muscle (Weijjs & Hillen, 1985), and by the distances between its centroids and TMJ (*dm* and *dt*). Afterwards, they were added together and multiplied by two to equal both sides of the skull. This total value, divided by the moment’s arm (*c*) equals the ‘absolute’ bite force (*F*).

$$F = \frac{2 \times (dm \times \{M \times 300 \text{ KPa}\} + dt \times \{T \times 300 \text{ KPa}\})}{c}$$

Bite forces calculated through dry skulls usually underestimate bite forces measured *in vivo*, so Thomason’s (1991) correction method must be applied. Even though this method was heavily criticized by numerous authors (Christiansen & Adolfssen, 2005; Wroe & Milne, 2007) for not fitting to bigger species, Thomason’s correction method was recently tested in predators whose body weight resembles canids and was proved to be efficient (Sakamoto *et al.*, 2010). The correction method consists on the formula:

$$F_{corr} = 10^{(0.859 \times \log F + 0.559)}$$

Due to the great influence of body size on bite force (van der Meij & Bout, 2004; Christiansen & Adolfssen, 2005; Wroe *et al.*, 2005), and because canids vary greatly in size, a size correction is also necessary. We used skull length (measured directly on each photograph used for bite force calculations) as body size estimators, as actual body weight information was not available for all specimens. Skull length represent the best skeletal predictors for mass in canids (Van Valkenburg, 1990). We regressed (using simple linear regression) the logarithm of corrected bite force on the logarithm of each specimen skull length (Fig. 1). This analysis generated a function used to calculate bite force based on skull length ( $F_L$ ):

$$F_L = 10^{(1.95 \times \log L - 1.12)}$$

This step needs to be done with the actual data, as the result of the regression needs to be expressed in terms of the original variables, to be used in subsequent steps.

Additionally, Sakamoto *et al.* (2010) argued that the actual individual data (and not species means) need to be used in this step. However, in order to rule out any effect due to non-independence of data because of common ancestry, we repeated this same regression using species mean, with and without the use of a phylogenetic comparative method. Here, we used phylogenetic independent contrasts (PICs) (Harvey & Pagel, 1991). Calculations of PICs and diagnostic procedures were performed with the PDAP:PDTree module (Midford, Garland Jr & Maddison 2005) of Mesquite (Maddison & Maddison, 2007), using the phylogenetic hypothesis of Perini, Russo & Schrago (2010) (but see below, correlation analyses, for further details on phylogeny choice). Results from these two regressions were similar (Bite force and skull length with contrasts,  $r = 0.88/P < 0.001$  and without contrasts  $r = 0.96/P = 0.001$ ; brain volume and skull length with contrasts,  $r = 0.89/P < 0.001$  and without contrasts  $r = 0.96/P = 0.002$ ), indicating no major effect of the phylogenetic relationships between species in this relation, thus enabling us to use the results from the regression using individuals in the subsequent step.

Next, we calculated bite force quotient (BFQ). It is the proportion between corrected bite force and skull length based bite force (Sakamoto *et al.*, 2010).

$$BFQ = \frac{F_{corr}}{F_L}$$

The quotient is not a force value (Pa), it is a proportion where body size influence is absent (Sakamoto *et al.*, 2010).

### Brain volume

We estimated brain volume following Finarelli (2006), using the natural logarithm of three external skull measurements:

height (H), length (L) and width (W) (Fig. 1). Finarelli's method is appropriate because the measures used neurocranium external dimensions along three orthogonal axes. They correspond approximately to measures previously used to estimate cranial volume in primates (e.g. Martin, 1990; Elton *et al.*, 2001) and are consistent with three cranial measures used by Young (1959) to define intracranial dimensions (Finarelli, 2006).

$$\ln_{(brainvol.)} = -6,23 + 1,06.\ln(H) + 0,28.\ln(L) + 1,27.\ln(W)$$

After calculating brain volume, we performed a simple linear regression between the log of brain volume and log of skull length, which generated the following function.

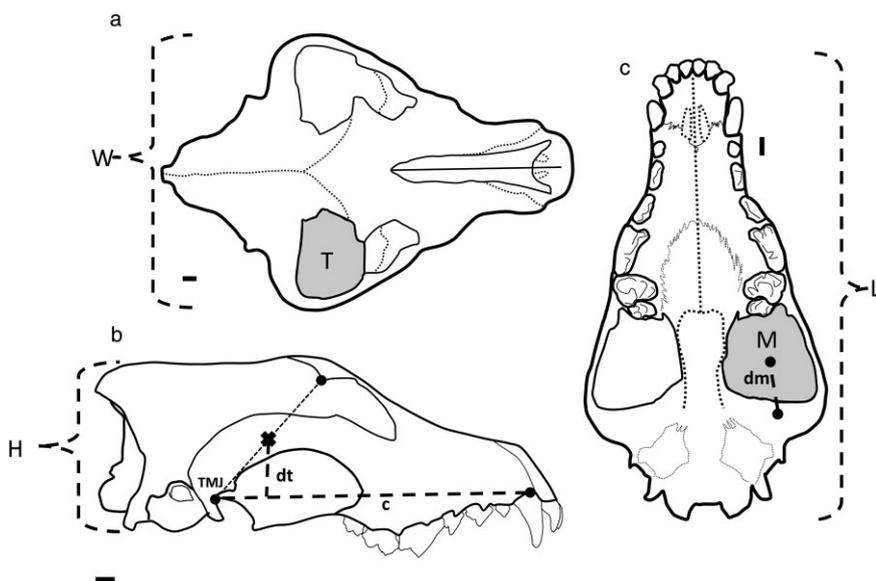
$$\text{Log}_{(brainvol.)} = 1,7501.\log_{(length)} - 2,0889$$

After obtaining the brain volume estimated through skull length, we generated a size influenced value. In order to remove this influence we calculated the proportion between 'absolute' brain volume (estimated through the three skull measurements) and the volume based on skull length ( $bv_{length}$ ). This proportion is called brain volume quotient (BVQ) which is calculated through the formula:

$$BVQ = \frac{brainvol.}{bv_{length}}$$

### Correlation analyses

We tested the correlation between the 'absolute' and quotient values of bite forces and brain volumes. Again, to account for non-independence of data due to common ancestry, we used PICs (Harvey & Pagel, 1991). As above, calculations of PICs



**Figure 1** Diagrams showing the areas and distances used to calculate bite forces and brain volume. Variables for bite force estimates: M, cross-sectional areas of *musculus masseter*; T, cross-sectional areas of *musculus temporalis* muscles; dm, distance between the centroid of M and temporomandibular joint (TMJ); dt, distance between the centroid of T and TMJ; c, distance between bite point (canine) and TMJ. Variables for brain volume estimates: H, skull height; L, skull length; W, skull width.

and diagnostic procedures were performed with the PDAP:PDTree module (Midford *et al.*, 2005) of Mesquite (Maddison & Maddison, 2007). We used here three phylogenetic hypotheses: Lindblad-Toh *et al.* (2005), Prevosti (2009) and Perini *et al.* (2010). Branch lengths, however, were only available in the latter, and these went through Grafen's transformation method, with rho ( $\rho$ ) value of 0.5 to decrease the chances of type I error and suit the variables according to independent contrasts method (Grafen, 1989; Díaz-Uriarte & Garland Jr 1996). For the two others, we used branch lengths of one, and these two we mainly included for comparison purposes on the effect of phylogeny topology and taxon sampling on our conclusions. In all cases, all variables passed the diagnostics, i.e. showed no correlation between absolute contrasts and their standard deviations after being log-transformed and after Grafen's transformation method.

## Results

### Bite force and brain volume estimates

Results of bite force calculations and brain volume estimates are presented in Table 1.

### Correlation analyses

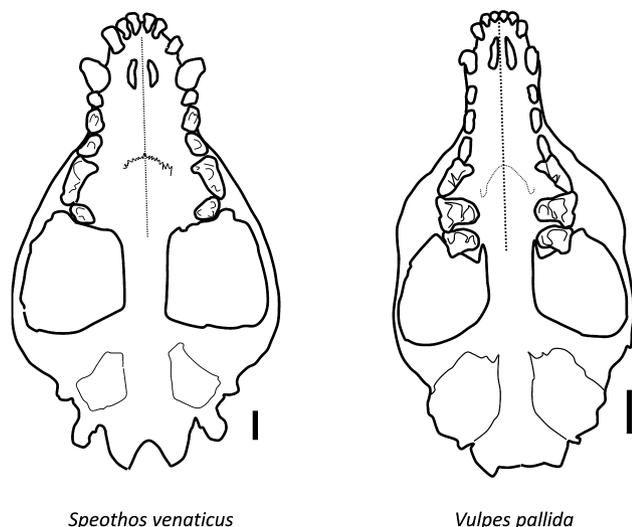
We found a strong and significant correlation between bite force and brain volume in all phylogenies. However, BFQ and BVQ are uncorrelated when using the topology and branch lengths (Perini *et al.*, 2010), yet they are weakly correlated when using the phylogenies from Lindblad-Toh *et al.* (2005) and Prevosti (2009) (Table 2).

**Table 1** Taxa analyzed with bite force quotient (BFQ) values, corrected bite force, brain volume quotient (BVQ), corrected brain volume and the sample size ( $n$ ) for every species. See text for details

Species/subspecies	Bite force	BFQ	Brain volume	BVQ	$n$
<i>Alopex lagopus</i> (Linnaeus, 1758)	140.61	88.41	40.04	101.31	37
<i>Atelocynus microtis</i> (Sclater, 1882)	312.12	106.66	70.55	101.81	21
<i>Canis adustus</i> (Sundevall, 1847)	248.69	86.71	62.57	94.71	30
<i>Ca. aureus</i> (Linnaeus, 1758)	254.69	93.82	64.01	101.58	30
<i>Ca. simensis</i> (Ruppel, 1835)	413.39	83.96	88.10	85.57	8
<i>Ca. familiaris dingo</i> (Meyer, 1793)	494.48	113.28	92.24	102.23	33
<i>Ca. familiaris hallstromi</i> (Troughton, 1957)	298.52	108.50	66.33	113.38	6
<i>Ca. latrans</i> (Say, 1823)	397.10	94.02	90.54	100.19	30
<i>Ca. lupus</i> (Linnaeus, 1758)	830.51	106.14	159.29	107.18	30
<i>Ca. mesomelas</i> (Schreber, 1775)	243.41	97.64	58.06	98.55	30
<i>Ca. rufus</i> (Audubon e Bachman, 1851)	530.52	99.17	102.98	92.96	6
<i>Chrysocyon brachyurus</i> (Illiger, 1815)	525.54	98.86	120.84	104.10	22
<i>Cuon alpinus</i> (Pallas, 1811)	497.74	129.24	110.88	139.01	20
<i>Cerdocyon thous</i> (Hamilton Smith, 1839)	184.16	99.1	48.82	96.72	32
<i>Lycalopex fulvipes</i> (Martin, 1837)	182.93	112.21	34.41	91.92	2
<i>L. vetulus</i> (Lund, 1842)	125.14	104.23	37.77	104.26	18
<i>L. culpaeus</i> (Molina, 1782)	281.57	99.25	63.30	93.34	31
<i>L. griseus</i> (Gray, 1837)	154.29	88.07	41.76	100.01	30
<i>L. gymnocercus</i> (Fischer, 1814)	190.32	89.88	47.66	86.65	30
<i>L. sechurae</i> (Thomas, 1900)	168.33	106.95	34.66	89.06	30
<i>L. pictus</i> (Temminck, 1820)	719.03	124.41	146.94	131.61	30
<i>Nyctereutes procyonoides</i> (Gray, 1834)	147.29	109.01	28.20	81.74	30
<i>Otocyon megalotis</i> (Desmarest, 1822)	111.64	87.25	32.24	91.65	30
<i>Speothos venaticus</i> (Lund, 1842)	287.88	162.25	65.48	141.35	21
<i>Urocyon cinereoargenteus</i> (Schreber, 1775)	136.97	100.64	36.58	102.76	39
<i>U. littoralis</i> (Baird, 1858)	98.14	95.63	30.96	115.74	30
<i>Vulpes zerda</i> (Zimmerman, 1780)	72.60	97.10	20.65	101.84	30
<i>V. bengalensis</i> (Shaw, 1800)	139.85	114.13	33.51	104.17	10
<i>V. chama</i> (Smith, 1833)	136.21	91.49	47.75	130.83	19
<i>V. macrotis</i> (Merriam, 1888)	92.53	86.40	30.76	107.25	21
<i>V. pallida</i> (Cretzschmar, 1827)	103.31	96.96	30.72	112.32	19
<i>V. rueppelli</i> (Schinz, 1825)	114.39	91.35	27.86	83.60	30
<i>V. velox</i> (Say, 1823)	134.36	96.50	34.60	101.10	14
<i>V. vulpes</i> (Linnaeus, 1758)	224.27	91.46	52.74	97.69	32

**Table 2** Values for Pearson's correlation coefficient ( $r$ ) and significance ( $P$ ) for the correlation analyses between bite force quotient (BFQ), brain volume quotient (BVQ), bite force (Bf) and brain volume (Bvol) for all the phylogenies used

$r$ ( $p$ )	Lindblad-Toh <i>et al.</i> (2005)	Prevosti (2009)	Perini <i>et al.</i> (2010)
BFQ $\times$ Bf	-0.03 (0.85)	-0.044 (0.83)	0.22 (0.26)
BVQ $\times$ Bvol	0.22 (0.24)	0.055 (0.78)	0.26 (0.18)
BFQ $\times$ BVQ	0.57 (0.001)	0.65 (<0.001)	0.14 (0.46)
Bf $\times$ Bvol	0.90 (<0.001)	0.83 (<0.001)	0.98 (<0.001)

**Figure 2** Ventral view of the skulls of *Speothos venaticus* and *Vulpes pallida*, representing hypercarnivores and hypocarnivores, respectively.

## Discussion

Bite force and brain volume estimates are much higher in the group hunting hypercarnivores (*Lycaon*, *Cuon* and *Speothos*) and only these species showed correlation between BFQ and BVQ. The bite force quotient values seem to be related with skull morphology, as well as BVQ results that also point at a tighter association with skull morphology than with ecological characteristics. The 'absolute' values, on the other hand, showed the expected pattern, with the highest values for the biggest species and the lowest values for the smallest species, just as presented in Christiansen & Adolfssen (2005).

### Bite force quotient

The species with the highest values of BFQ are the three hypercarnivore canids (*Speothos venaticus*, *Cuon alpinus*, *L. pictus*). When compared to all other canids, hypercarnivores have relatively wider snouts (Fig. 2), more mechanical advantages on the jaw adductors, deeper jaws (Fig. 3), larger anterior teeth (incisive and canine), reduced crushing post-carnassial molars, elongated blades (trigonid) on the inferior m1 (Gittleman, 1989; Van Valkenburgh, Wang & Damuth, 2004). In the bush dog, African wild dog and the dhole, the m1 talonid has also become a blade or trenchant heel, which increases the cutting ability.

Several of these characters can increase hunting efficiency, and are also useful for knocking down prey, resisting bending forces and cutting flesh. But one main feature that considerably increases bite force is tooth row reduction, through the loss of post-carnassial molars (Van Valkenburgh, 2007). This is found in other hypercarnivore groups, such as cats and mustelids (Radinsky, 1981). In general, canids have two upper and three lower molars, but bush dogs have in most cases only one upper (91.5%) and two lower molars (Beisiegel & Zuecher, 2005), dholes only have two upper and two bottom molars (Cohen, 1978) and African wild dogs have two upper and three bottom molars.

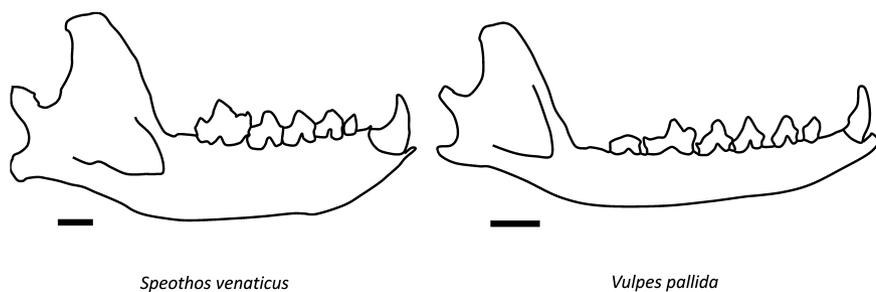
Even though wolves have a hypercarnivore diet and hunt preys that are heavier than themselves (Hammer, Harper & Ryan, 2001; Van Valkenburgh, 2007), they do not present a BFQ value similar to the other hypercarnivore species. A possible reason for this is that wolves do not present morphological adaptations as marked as in the other hypercarnivorous hunters.

The species with the lowest BFQ values are side-striped jackals (*Canis adustus*), kit foxes (*Vulpes macrotis*), Ethiopian wolves (*C. simensis*) and bat-eared foxes (*O. megalotis*). Even though these species are not related phylogenetically nor resemble each other in external morphology, they all live in desert-like environments. For that reason, they all are opportunistic feeders, feeding on anything that is most abundant, small rodents, reptiles, ground-nesting birds (McGrew, 1979; Sillero-Zubiri & Gottelli, 1994). The only exception is the bat-eared fox that is mainly insectivorous, feeding on termites, beetles, crickets and grasshoppers (Clark, 2005), presenting a slender, delicate skull with 4–5 molars, basically, the opposite skull morphology from hypercarnivores.

### Brain volume quotient

Species with the highest BVQ values were the hypercarnivores bush dog, the dhole and the African wild dog (Table 1). The social brain hypothesis (Dunbar, 1998) states that species that present social behavior have bigger brains. Nevertheless, the grey wolf (a highly social species) had its BVQ values ranked only in 10th position, not only lower than the other social species, but below four species of non-social foxes. Based on these results, we can speculate that *Speothos*, *Cuon* and *Lycaon* have the highest values of BVQ because they are hypercarnivorous species.

These results suggest that the BVQ is not linked exclusively to sociality in the pack-hunting species, but is mainly related to skull shape, in *Speothos*, *Cuon* and *Lycaon* as they have



**Figure 3** Lateral view of the mandibles of *Speothos venaticus* and *Vulpes pallida*, representing hypercarnivores and hypocarnivores, respectively.

similar skull morphologies. This indicates that adaptive convergences that increased bite force also increased brain volume. For example, a wider occipital bone results in larger braincase and also stronger neck muscles, thus giving considerable resistance to lateral loadings such as a struggling prey (Radinsky, 1981).

### Correlation analyses

The correlation analyses between BVQ and BFQ yielded different results between the phylogeny of Perini *et al.* (2010), with branch lengths, and those of Prevosti (2009) and Lindblad-Toh *et al.* (2005), both with branch lengths arbitrarily assigned to one. While the former indicated no correlation between the studied variables, the latter two showed a significant, albeit weak ( $r^2$  ranging from 0.32 to 0.42) correlation (Table 2). Proper branch lengths, either as evolutionary rates or as divergence times, are essential for an appropriate use of phylogenetic comparative analysis. Phylogenies without branch lengths tend to increase type I error rates (rejection of a true null hypothesis) (Purvis & Rambaut, 1995; Díaz-Uriarte & Garland Jr 1996). They are therefore less reliable, and as a consequence, we will only consider the results that used the phylogeny of Perini *et al.* (2010), and will only discuss these further on.

A weak correlation was found between the quotients and its respective absolute values, indicating that a significant correction was achieved by the quotients. Body size influence was observed due to strong correlation between bite force and brain volume and absence of correlation between their quotients (Table 2).

There was no correlation between BFQ and BVQ, even though the three highest values of BFQ are also the highest values of BVQ. This shows that in spite of being linked to morphology, both variables are independent in the Canidae family. The morphological difference and therefore differences in both force and brain volume are much more conspicuous among *Lycaon+Cuon+Speothos* group and the other canids than among the family itself. Hence, BFQ and BVQ calculus was efficient in pointing out and differentiating pack-hunting hypercarnivores, but it did not set apart among the remaining species, the most carnivores from the least carnivores nor the solitary from the social species. In other words, bite force and brain volume correlate only among the hypercarnivores. These results agree with analysis in insectivores

and primates that show correlation between dietary specialization with increase in encephalization (Bauchot and Stephan 1966, 1969 *apud* Gittleman 1986). Other studies involving active consumption rates (ACR) found a positive correlation between ACR and sociality (Wilmers & Stahler, 2002). In situations where fast ingestion is favored, for example, between cubs from the same litter or adults feeding communally from the same kill, selection shall favor those with sharper teeth and strongest bite (Van Valkenburgh 1991; Van Valkenburgh, 2007).

When eutherian and metatherian carnivores were compared, brain volume and bite force were negatively correlated (Wroe & Milne, 2007). In canids, however, species with bigger brains also have stronger bites. This could mean that a large braincase also gives room for large and longer *m. temporalis*, that is the most important mandibular adductor in the carnivoran skull. In marsupials and placental mammals, in order to achieve stronger bites, species must sacrifice brain volume to increase muscles involved in biting. When compared throughout the Canidae, hypercarnivore canids possess stronger bite forces than all other meso and hypocarnivore species. But when compared with hypercarnivores of other families (such Felidae, Mustelidae and Dasyuridae), hypercarnivore canids cannot achieve equivalent bite forces (Wroe *et al.*, 2005). This could possibly be because bigger brain volume in canids could not allow such an extreme change in skull morphology, as it has been suggested that canids need this bigger brain for cognitive development, in order to master complex social behaviors (Dunbar, 1998).

### Conclusion

Bite force and brain volume are related to body size and should therefore be corrected for size in any subsequent analysis. BFQ is related to skull morphology, as hypercarnivore species have the highest quotient values and the hipo and mesocarnivores have the lowest ones. Apparently, the BVQ is also related to skull morphology but has no relation with sociality level of species. BFQ and BVQ are related only in its extremes: species with the highest BFQ are also the ones with highest BVQ are all hypercarnivores, with craniodental adaptations such as larger snouts and deeper jaws, which indicates a relation between diet specialization and cranial morphology including an increase in brain volume.

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## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Table S1** List of taxa used, their mean bite force quotient, brain volume quotient, their classifications pertaining to diet and sociality and the source of such information.