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Research Article

Bite force sexual dimorphism in Canidae (Mammalia: Carnivora): relations between diet, sociality and bite force intersexual differences

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Abstract

Bite force is a key trait for understanding aspects of vertebrate ecology and evolution, as it relates directly to different evolutionary pressures, like diet and behaviour. Sexual dimorphism in bite force (SDBF) is an underexplored condition that may shed light on niche divergence between sexes and the effects of sexual selection in species. Here we evaluated differences in modelled bite forces between sexes within Canidae (33 species and two subspecies) and assessed their possible correlations with diet, sociality, hunting strategies, and size dimorphism. We calculated SDBF and bite force quotients through indexes and compared them among different diets, hunting strategies, and sociality groups. Furthermore, we correlated the indexes and size sexual dimorphism using phylogenetic independent contrasts. Only two species showed significant SDBF: the Cape fox (*Vulpes chama*) and the Ethiopian wolf (*Canis simensis*). We found no significant differences in bite force dimorphism intensity between sociality levels, dietary levels, or hunting strategies. We found a relationship between bite force sexual dimorphism and size sexual dimorphism, and a correlation between bite force and the bite force quotient dimorphism. However, we found no association between sexual dimorphism in bite force quotient and sexual size dimorphism. Our findings show that Canidae do not have bite force dimorphism, possibly due to the widespread social monogamy in the family, when compared to other Carnivora. This implies possible restrictions that constraint the range of bite strength in adults, especially in females.

Introduction

Bite force (BF) is considered to be the link between masticatory apparatus, feeding ecology, and foraging behaviour in most groups, and as such is often analysed under different viewpoints in a range of biological questions (Damasceno et al., 2013; Therrien, 2005; Thomason, 1991). In the mammalian order Carnivora, BF is strongly influenced by diet, with dietary groups distinguished by the proportion of vertebrate meat in their diets and the morphological apparatus linked to those habits (Van Valkenburgh and Koepfli, 1993; Van Valkenburgh, 1988b). For instance, species with a highly carnivorous diet (>70% meat, or hypercarnivorous) show morphological specializations such as broader snouts and bigger blade size on carnassial teeth. Those that are more opportunistic and with lower proportions of meat in their diets (<50% meat or hypocarnivorous) present a larger proportion of grinding area on their cheek teeth and narrower snouts (Damasceno et al., 2013; Van Valkenburgh and Koepfli, 1993; Van Valkenburgh, 1988b). In the Canidae family, bite force is strongly related to behaviour: species that are more social and form true packs (Fox, 1975) exhibit stronger bite forces for their size (Damasceno et al., 2013). Although relationships between bite force and dietary or sociality levels have been elucidated, an appraisal of the role of sexual dimorphism in these relationships is still lacking.

One of the characters that can be sexually dimorphic in any species is bite force. Sexual dimorphism in bite force (SDBF) is well studied in lizards (Order Squamata) (Herrel et al., 2010, 2007; Lappin et al., 2006; Herrel et al., 2002, 1995), but with relatively less attention in mammals, except in members of Musteloidea superfamily, and lemurs (Law and Mehta, 2018; Campbell and Santana, 2017; Thomas et al., 2015). In Canidae, the effect was assessed in the red fox (*Vulpes vulpes*) only, in which no significant SDBF was found (Forbes-Harper et al., 2017). As bite force *per se* correlates with body size (Wroe et al., 2005), differences in body size between males and females may affect bite force dimorphism as well. Sociality may also influence SDBF, as it strongly affects differences in body size between males and females (Law, 2019; Frayer and Wolpoff, 1985; Ralls, 1977).

Canids show different group organization strategies, from solitary individuals, which live alone almost their entire life, to social types, which at some moment of their life form a cohesive group labelled as “true packs” (Fox, 1975). In more social canids, fights for hierarchy within groups and packs are frequent (Moehlman, 1989), making bite force an important feature. Damasceno et al. (2013) studied the relation between bite force, diet, sociality, and braincase size in canids, demonstrating that hypercarnivorous species with social behaviour had both stronger bite forces and bigger braincases, but the role of sociality and diet on bite force sexual dimorphism is still under-explored. Yet, based on the findings of Damasceno et al. (2013), it is possible that most hy-

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percarnivorous and social hunters show more intense dimorphism in bite force.

In addition to sociality, another potential main driver of overall sexual dimorphism (and therefore of SDBF) is the mating or breeding system of a species (Van Valkenburgh and Sacco, 2002; Gittleman and Valkenburgh, 1997). According to the sexual selection theory, polygamy often results in more pronounced sexual differences in traits than monogamy, as intrasexual competition for mates is more intense in the former (Andersson, 1994; Frayer and Wolpoff, 1985; Ralls, 1977). Canidae are less sexually dimorphic than other Carnivora families, as canids are mostly monogamous (Macdonald et al., 2019), forming monogamous pairs more often and, as a consequence, intrasexual fights for access to the opposite sex are rare (Van Valkenburgh and Sacco, 2002; Gittleman and Valkenburgh, 1997).

Here, we investigate the existence of sexual dimorphism in bite force in Canidae and the main drivers related to it. We expect the most social, hypercarnivorous, and social hunters to exhibit more intense SDBF. As the group is almost entirely monogamous, the effects of diet and behaviour may be more easily detectable than polygamous species. Moreover, we investigate the interference of size sexual dimorphism and how it is related to sex differences in bite force.

Methods

Data origin and BF

To test the existence and pattern of bite force sexual dimorphism, we used data from Damasceno et al. (2013). From that dataset, we assembled 551 specimens of both sexes, covering all Canidae genera, 33 species, and two subspecies. All data were originally estimated from digital photos of dry skulls. Because BF values calculated through dry skulls usually underestimate bite forces measured *in vivo*, the values obtained were adjusted by Thomason's (1991) correction method. For further details on methods, calculations and design refer to Damasceno et al. (2013).

Bite force quotient

Bite force values calculated from individuals are highly correlated with body size (Sakamoto et al., 2010; Wroe et al., 2005; Van Der Meij and Bout, 2004). To evaluate their morpho-functional aspects unrelated to size, we need to calculate an additional index controlling for the body size bias. The bite force quotient (BFQ) values consist of the proportion between size corrected bite force values and bite force estimates based on skull length — for further details see Sakamoto et al. (2010) and Damasceno et al. (2013). The BFQ cannot be treated as a force (Pa), as it is only a proportion where body size interference is absent (Sakamoto et al., 2010).

Data analysis

To test the presence of significant bite force sexual dimorphism we performed t-tests between males and females of each species for BF and BFQ values. As many samples showed non-normality, we chose to use additional Welch t-tests and Wilcoxon test (Zimmerman and Zumbo, 1993). The analyses were performed in R (R Core Team, 2016).

Index creation, ANOVA and correlation analysis

To measure and compare levels of SDBF from each species, we estimated a Bite Force Sexual Dimorphism Index (BFI), which consists of the following ratio:

$$BFI = \frac{\text{Average males Bite Force}}{\text{Average females Bite Force}} \quad (1)$$

We chose this kind of index to measure the intensities of sexual dimorphism because even though they are sex-biased or an asymmetrical configuration, the values obtained can be intuitively read (Lovich and Gibbons, 1992). Additionally, to suppress the absence of a symmetrical measure, and to obtain a value in which there was no sex-directed bias we used Log N transformed indexes for each species (Lovich and Gibbons, 1992).

Similarly, to measure bite force sexual dimorphism without size interference, we used the Bite Force Quotient Sexual Dimorphism Index (BFQI) as described below and with the same transformations of BFI ($\log N$).

$$BFQI = \frac{\text{Average males quotient}}{\text{Average females quotient}} \quad (2)$$

Additionally, for an estimate of size per specimen, we used skull length values measured from each skull photograph from the dorsal view using tpsDig2 software (Rohlf, 2006). Skull length is commonly used as a proxy for body size (Van Valkenburgh, 1990) and was used to estimate size sexual dimorphism in our samples.

We conducted Analyses of Variance using BFI and BFQI according to species levels of sociality (solitary, facultative social, social; as described by Fox 1975) and dietary/dentition classification based on Van Valkenburgh (1988b,a) which were: i) Hypercarnivorous diet, where vertebrate meat comprises >70% of their diet; ii) Mesocarnivorous diet, proportion 50–70% of vertebrate meat at their diets; and iii) Hypocarnivorous diet <50% of meat in their diet. By doing that, we aimed to evaluate if bite force sexual dimorphism estimates differ among the three sociality levels and between diet categories.

To evaluate if a possible bite force sexual dimorphism is affected by the species size or size sexual dimorphism, we performed correlation tests between size estimates and BFI and BFQI. We used skull lengths as size estimates and generated a skull length sexual dimorphism index (SLI) similar to BFI and BFQI. All values used in correlation tests were log-transformed.

To test for correlations among multiple taxa, we must assure that there is no possible phylogenetic interference in the analysis. In other words, the results may show a correlation that is brought about by the species' phylogenetic proximity and not by adaptive or sexual selection, inflicting type I error (Garland et al., 1992; Harvey and Pagel, 1991; Felsenstein, 1985). To avoid this "phylogenetic noise" from affecting the analysis, we used Felsenstein's Phylogenetic Independent Contrasts (PICs) (Garland et al., 1992; Harvey and Pagel, 1991; Felsenstein, 1985). Calculation of PICs and diagnosis procedures were performed using the PDAP:PDtree module (Midford et al., 2008) on Mesquite (Maddison and Maddison, 2019). We used three different phylogenetic hypotheses for Canidae that had most of our taxa and branch length information: Perini et al. (2010), Zrzavý et al. (2018), and Lamarca and Schrago (2020). The tree from Lamarca and Schrago (2020) passed all the PDAP diagnostic tests. For the remaining two, because of significant correlations between contrasts and the square root sum of the corrected branch lengths, branch lengths were initially transformed using Grafen's Rho transformation (Grafen, 1989) according to independent contrast methods. The phylogenetic hypothesis of Zrzavý et al. (2018) was successfully standardized, and because of the tree polytomies, we reduced degrees of freedom (following Garland and Diaz-Uriarte, 1999). However, as there was still a correlation between contrasts and branch lengths for the hypothesis of Perini et al. (2010), we changed the standardization method to stratigraphic tools (Marjanovic and Laurin, 2007; Josse et al., 2006). The minimum terminal branch value was assigned to 3.0 (for both trees) and the internal branch minimum value was set to 0.5 and 1.0, as previous diagnosis tests showed negative correlations between the contrasts and the square root sum of corrected branch lengths (Laurin, 2011; Laurin et al., 2009; Marjanovic and Laurin, 2007). By doing this, we properly performed standardization of the contrasts for this tree, and the variables passed diagnostic tests.

Results

Sexual Dimorphism in Bite Force and Bite Force quotient

Among all 32 taxa that could be tested (Tab. 1), only two species showed significant sexual dimorphism in bite forces: the Cape fox (*Vulpes chama*; $p=0.0085$) and the Ethiopian wolf (*Canis simensis*; $p=0.0178$). The bite force of Cape fox males was 25% stronger than that of females on average, and males Ethiopian wolves had bite forces 22% stronger than females. It is worth remembering that absolute bite

Table 1 – Canidae taxa analysed with bite force dimorphism indexes (BFI), size-corrected bite force dimorphism or quotient sexual dimorphism (BFQI), skull length sexual dimorphism index (SLI) and the sample size of males and females for each taxon.

Species/subspecies	N ♂/♀	BFI	BFQI	SLI
<i>Atelocynus microtis</i> (Sclater, 1982)	10/4	1.1553	0.8313	1.0763
<i>Canis adustus</i> Sundevall, 1847	6/10	1.0941	1.0373	1.0017
<i>Canis anthus</i> F. Cuvier, 1820	4/7	1.0832	1.1142	1.0170
<i>Canis aureus</i> Linnaeus, 1758	1/1	1.2551	0.9936	1.0117
<i>Canis latrans</i> Say, 1823	13/8	1.0278	1.0059	0.9694
<i>Canis lupus</i> Linnaeus, 1758	9/10	1.0721	0.9257	1.0394
<i>Canis lupus dingo</i> Meyer, 1793	11/5	1.2225	1.0478	1.1426
<i>Canis lupus hallstromi</i> Troughton, 1957	3/3	0.9963	1.2138	1.0564
<i>Canis mesomelas</i> Schreber, 1775	8/11	1.2100	1.1028	1.0716
<i>Canis rufus</i> Audubon and Bachman, 1851	1/1	1.0911	1.4671	1.0034
<i>Canis simensis</i> Rüppell, 1835	4/2	1.2244	0.9119	1.0629
<i>Cerdocyon thous</i> (Linnaeus, 1766)	15/6	0.9992	1.0157	0.9836
<i>Chrysocyon brachyurus</i> (Illiger, 1815)	5/6	1.2585	1.1659	0.9900
<i>Cuon alpinus</i> (Pallas, 1811)	10/8	1.2260	1.0064	1.0309
<i>Lycalopex culpaeus</i> (Molina, 1782)	15/11	1.2159	1.0771	1.0555
<i>Lycalopex fulvipes</i> (Martin, 1837)	1/1	1.2444	1.0998	1.1435
<i>Lycalopex griseus</i> (Gray, 1837)	7/9	1.0984	1.0834	1.0172
<i>Lycalopex gymnocercus</i> (G. Fischer, 1814)	14/11	1.1115	1.0885	1.0299
<i>Lycalopex sechurae</i> (Thomas, 1900)	15/11	1.1142	0.9967	1.0319
<i>Lycalopex vetulus</i> (Lund, 1842)	5/6	1.0513	1.0079	0.9715
<i>Lycaon pictus</i> (Temminck, 1820)	14/7	1.0365	0.9906	1.0086
<i>Nyctereutes procyonoides</i> (Gray, 1834)	10/11	1.0481	1.0115	1.0055
<i>Otocyon megalotis</i> (Desmarest, 1822)	8/9	0.9610	0.8486	0.9782
<i>Speothos venaticus</i> (Lund, 1842)	11/5	1.2366	1.0365	1.0814
<i>Urocyon cinereoargenteus</i> (Schreber, 1775)	12/14	1.0661	1.2040	1.0315
<i>Urocyon littoralis</i> (Baird, 1858)	13/12	1.0364	1.0097	1.0506
<i>Vulpes bengalensis</i> (Shaw, 1800)	2/3	0.9614	0.9235	1.1197
<i>Vulpes chama</i> (A. Smith, 1833)	6/8	1.2528	1.1120	1.0843
<i>Vulpes lagopus</i> (Linnaeus, 1758)	10/5	1.0517	1.0455	1.0435
<i>Vulpes macrotis</i> Merriam, 1888	9/10	1.1080	0.9890	1.0199
<i>Vulpes pallida</i> (Cretzschmar, 1827)	8/4	1.1281	0.9110	1.0355
<i>Vulpes rueppellii</i> (Schinz, 1825)	14/6	1.1108	1.1093	1.0720
<i>Vulpes velox</i> (Say, 1823)	6/3	1.0966	1.0182	1.0869
<i>Vulpes vulpes</i> (Linnaeus, 1758)	13/9	1.0593	0.9771	1.0520
<i>Vulpes zerda</i> (Zimmermann, 1780)	9/12	0.9794	0.8718	0.9950

force was used, meaning the results are not corrected by size differences. None of the species showed significant differences in bite force quotient values (size-corrected) between males and females. Raw bite forces and bite force quotients for all specimens used in this study are available as Supplemental Material.

Size sexual dimorphism

Three species showed significant size sexual dimorphism (represented by skull length). Males from species *Vulpes chama* and *Vulpes rueppellii* showed bigger skull lengths than females, and females from *Vulpes pallida* showed on average, slightly bigger skull lengths than males (Tab. 2).

Table 2 – Significant results of Student's t-test of size sexual dimorphism in Canidae using skull lengths as estimates of size, the sample sizes (N) of males and females, and the obtained p-value. SLI: skull length index, a proxy for body size.

Species	N ♂/♀	p	SLI	Average skull length difference	larger sex
<i>Vulpes chama</i>	06/08	<0.01	1.0199	2 %	♀
<i>Vulpes rueppellii</i>	14/06	0.01	1.0721	5 %	♀
<i>Vulpes pallida</i>	08/04	0.04	0.9950	0.05%	♂

Indexes results

The species with highest BFI values were species with an absence of sexual dimorphism in bite force except for Cape foxes: the four highest values of BFI were from the Maned wolf (*C. brachyurus*; 1.258), the Golden jackal (*C. aureus*; 1.255), the Cape fox (*V. chama*; 1.252), and the Darwin fox (*L. fulvipes*; 1.244). The null levels of BFI (values close to one, considered very monomorphic) were occupied by the Coyote (*C. latrans*, 1.02), the New Guinea singing dog (*C. lupus hallstromi*, 0.99), and by the Crab-eating fox (*C. thous*, 0.99) (Tab.1, see also Fig.1). The considered “negative values” where females had a stronger bite than males were from species such as *Urocyon littoralis* (0.96), *Otocyon megalotis* (0.96), and *Vulpes bengalensis* (0.96; this species had a very small sample size: two males / three females).

The highest BFQI obtained belonged to the New Guinea singing dog (*Canis lupus hallstromi*, 1.21), the Gray Fox (*Urocyon cinereoargenteus*, 1.20) and the Maned wolf (*Chrysocyon brachyurus*, 1.16) (Table 1). Null values were observed in *Urocyon littoralis*, *Lycalopex vetulus*, *Cuon alpinus*, and *Canis latrans*, all species showed values very close to one (1.0059 – 1.0097). The species in which females had stronger BFQI were the Short-eared-fox (*Atelocynus microtis*, 0.83), the Bat-eared-fox (*Otocyon megalotis*, 0.84), the Fennec fox (*Vulpes zerda*, 0.87), and the Pale fox (*V. pallida*, 0.91).

The highest SLI values (skull length dimorphism index, a proxy for size) were obtained by Darwin's fox (*Lycalopex fulvipes*; 1.14) followed by the Dingo (*Canis lupus dingo*; 1.14) and by the Bengal fox (*Vulpes bengalensis*; 1.08) closely followed by the Cape fox (*Vulpes velox*; 1.08). The species that showed monomorphic values were the

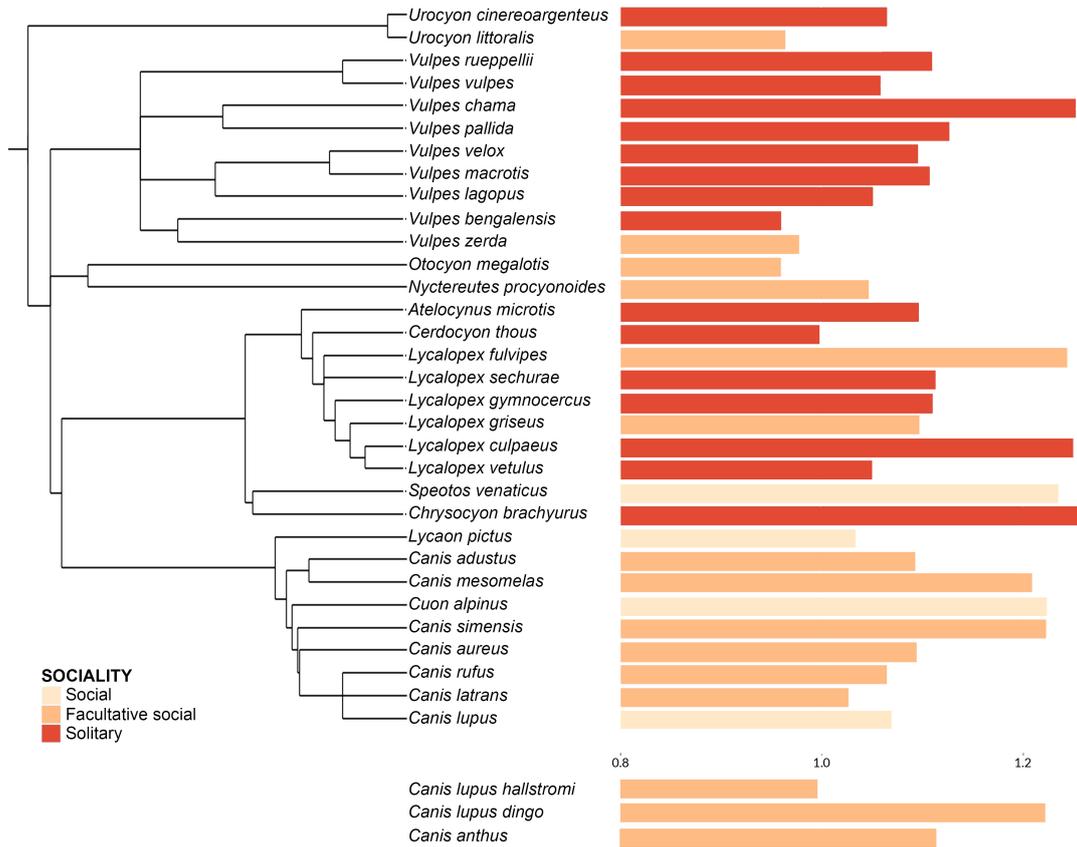


Figure 1 – Phylogeny of Canidae (Zrzavý et al., 2018) with indexes of bite force sexual dimorphism (BFI). *Canis lupus hallstromi*, *Canis lupus dingo*, and *Canis anthus* were not represented in the phylogeny and their values are presented at the bottom for comparison.

Raccoon dog (*Nyctereutes procyonoides*; 1.00), African wild dog (*Lycaon pictus*; 1.00), and the Side-striped Jackal (*Canis adustus*; 1.00). The SLI values which had bigger females were the Coyote (*Canis latrans*; 0.96), the Hoary fox (*Lycalopex vetulus*; 0.97), and the Crab-eating fox (*Cerdocyon thous*; 0.98).

ANOVA

The ANOVA tests showed no significant difference in BFI, BFQI, and SLI between the three groups of sociality level (solitary, facultative social, social; see Fig.1) and the three categories of diet (hypercarnivorous, mesocarnivorous, hypocarnivorous). This shows that the differences in bite forces, quotients of bite force, and size among males and females are affected neither by sociality nor by categories of dentition/diet.

Correlation analyses

BFI and BFQI values were significantly correlated when we used contrasts based on the hypotheses by Zrzavý et al. (2018) and Lamarca and Schrago (2020), but not when we used the hypothesis of Perini et al. (2010). However, significant correlations showed a good fit only for Lamarca and Schrago (2020) (Tab. 3).

The regressions made with Zrzavý et al. (2018) and Perini et al. (2010) phylogenetic trees showed correlations between BFI and skull length dimorphism index (SLI), showing that 27–30% of bite force sexual dimorphism variation is explained by size dimorphism ($R^2=0.30$). This result was expected since BFI retains size effects in its values. Regressions using all three phylogenetic hypotheses showed that the quotient of bite force sexual dimorphism (BFQI) is uncorrelated with skull length sexual dimorphism (SLI), meaning no significant relation to size dimorphism and the bite force quotient dimorphism (Tab. 3).

Discussion

Overall, SDBF was not detected in Canidae with two exceptions (*Canis simensis* and *Vulpes chama*) that display significant SBDF with effects of size sexual dimorphism. For the whole group, we found a relationship between SDBF and SSD, already expected due to the relationship between size and bite force (Wroe et al., 2005), but little evidence of a relationship between bite force quotient dimorphism (BFQ) and size (SLI). We also found no differences in bite force dimorphism values (BFI) between groups by sociality levels, hunting strategies, and dietary levels showing it has no influence at SDBF in Canidae. Our findings show that Canidae has no expressive sexual dimorphism in bite force, which could be explained by the social monogamy, very frequent in the group, suggesting that the selective pressures related to monogamy are stronger than those related to diet and social behaviour.

Sexual dimorphism in bite force

The only two species that showed significant SDBF were *Vulpes chama* and *Canis simensis*. These species have little in common, as they do not share diet or sociality categories, nor hunting strategy. The Cape

Table 3 – Results of the correlations analyses (values of R^2 and significance (p)) between Phylogenetic Independent Contrasts for bite force sexual dimorphism index (BFI), bite force quotient sexual dimorphism index (BFQI) and skull length sexual dimorphism index (SLI). The regressions were performed using different phylogenetic trees: (A) (Perini et al., 2010), (B) (Zrzavý et al., 2018), and (C) (Lamarca and Schrago, 2020) .

Indexes	p			R^2		
	A	B	C	A	B	C
BFI × BFQI	0.51	0.095	0.003	0.02	0.10	0.83
BFI × SLI	0.00	0.004	0.340	0.51	0.30	0.06
BFQI × SLI	0.30	0.910	0.080	0.04	—	0.28

fox is considered solitary, as it only forms pairs for breeding seasons, it hunts solitarily and has a hypocarnivorous diet-morphology, i.e. less than 50% of vertebrate meat in its diet composition, that also includes plants and non-vertebrate material (Sillero-Zubiri and Marino, 2004; Van Valkenburgh, 1988b). The Ethiopian wolf is regarded as facultative social, i.e. there is a sporadic formation of groups beyond the breeding pair (Fox, 1975), it occasionally forms small hunting packs (facultative hunter), and most of its diet is vertebrate flesh, showing a mesocarnivorous morphology (Sillero-Zubiri and Marino, 2004; Van Valkenburgh, 1988b). The absence of bite force sexual dimorphism in more social and hypercarnivorous species diverges from what we originally expected (canid species with more pronounced sexual dimorphism in bite force would show high levels of sociality, being social hunters with a hypercarnivorous diet).

In the case of *C. simensis*, it cannot be ruled out that its small sample (only 4 males and 2 females were obtained for this study) might have affected the obtained results. Other species, such as *C. rufus*, *C. aureus*, and *C. lupus hallstromii* had similarly small samples (1♂/1♀, 1♂/1♀, and 3♂/3♀, respectively), and we could not test for SDBF in the former two. In fact, a more conservative analysis, such as a t-Welch test, would result in a non-significant *p*-value for *C. simensis*. However, this species is endangered, possibly the most threatened canid species nowadays (Marino and Sillero-Zubiri, 2011). *Canis rufus* is critically endangered and *C. lupus hallstromii* is a subspecies rarely recorded in the wild (McIntyre et al., 2020; Phillips, 2018). Therefore, larger samples of skulls with properly identified sex for all these taxa are unlikely to be obtained soon, and as such, the actual effect of sample size on this result will remain open for now.

SDBF and sexual size dimorphism

Canis simensis is sexually dimorphic in body size, with males being 22% bigger than females (Sillero-Zubiri and Marino, 2004). Yet, we found no significant differences between bite force quotient (BFQ) between males and females, thus strengthening the hypothesis of size dependence attached to the bite force sexual dimorphism. The Cape fox presented significant sexual dimorphism in bite force, with males displaying, on average, bites 25% stronger than females, with no significant sexual dimorphism of bite force quotient values, which express probable size interference in the SDBF described. Possible drivers for the bite force sexual dimorphism found in *V. chama* and *C. simensis* are unknown at the moment, while consistent behavioural, life history, and ecological information on these taxa are still limited (Kamler and Macdonald, 2014; Marino and Sillero-Zubiri, 2011).

Most correlation tests - except the regression using the Lamarca and Schrago (2020) phylogenetic tree - between the Index of bite force sexual dimorphism (BFI) and estimated size dimorphism (SLI) resulted in significant correlation with a moderate fit (27–30%) between size and bite force sexual dimorphism. In the case of Cape fox (*Vulpes chama*), which exhibited bite force sexual dimorphism and size dimorphism (skull length), but no BFQ (bite force without size effect) sexual dimorphism, this reinforces a substantial influence of size dimorphism on bite force dimorphism. It is worth pointing out that the detected effect of size dimorphism in bite force dimorphism in the Cape Fox is relatively small, with 2% differences between males and females, in contrast with 25% effect of bite force sexual dimorphism which suggests a small effect of size in bite force dimorphism. We also found size sexual dimorphism (skull length) in Ruppell's foxes (*Vulpes rueppellii*) and Pale foxes (*Vulpes pallida*) consistent with Bidau and Martinez (Bidau and Martinez, 2016). For the remaining Canidae species, possible differences among male and female bite forces are still strongly dependent on size differences.

SDBF, diet, and sociality

The fact that solitary, facultative social and social groups showed homogeneity indicates that SDBF is not affected or structured by the sociality of the groups. A similar conclusion can be reached for the three dietary levels (hyper, meso, and hypocarnivorous). We originally expected the species that are more social and more prone to consume

meat to show higher levels of sexual dimorphism in bite force, similar to what was found on overall bite forces (Damasceno et al., 2013), as inherent group competition among individuals of the same sex would increase chances to develop SSD and SDBF.

The homogeneity of SDBF found among all levels of sociality suggests equal competition between sexes of social species (*Canis lupus*, *Cuon alpinus*, *Lycan pictus*, and *Speothos venaticus*). Canid social groups follow a hierarchical organization with a main dominant pair, leading to common intra-sexual clashes for dominance within-group and with extrinsic individuals (Moehlman, 1989; Fox, 1975). Therefore, the monomorphism found in BF in social groups may be associated with intra-sexual competition balanced between sexes rather than lack of competition (Fernandez-Duque and Huck, 2013). Likewise, the homogeneity among different levels of carnivory implies the absence of possible feeding partition between males and females within groups. In other words, from species exhibiting more durophagous (related to hypercarnivory) diet to a more omnivorous, less specialized species (hypocarnivory) there is no sign of feeding partition that would be reflected in SDBF. Finally, the absence of SDBF among different hunting strategies suggests that bite force is similar for males and females regardless of species hunting in packs or foraging alone, which indicates a strong conservation in feeding behaviour in Canidae. A similar result was found for types of diet, where no difference of bite dimorphism was found among hyper, meso, and hypocarnivorous groups. However, for carnivorans in general, there is an overall trend for most solitary species to exhibit more prominent sexual dimorphism (Law, 2019). Probably, the main reason for the members of the Canidae family to answer differently from the rest of the order is related to its prevalence of social monogamy, which could help restraint the development of sexual dimorphism (Macdonald et al., 2019; Van Valkenburgh and Sacco, 2002).

SDBF and breeding systems

For the vast majority of the group, the best possible explanation for the absence of SDBF is the fact that social monogamy is the main breeding system in Canidae, which possibly results in higher extents of monomorphism in the group than originally expected (Kamler and Macdonald, 2014; Cameron et al., 2011). While monogamous species tend to have equal selective pressures between the sexes, polygamous or polyandrous species are more likely to have intense selective pressures in one of the sexes (Cassini, 2020; Emlen and Oring, 1977). This effect may select monogamous populations to be more monomorphic (Isaac, 2005; Gittleman and Valkenburgh, 1997).

Canids are described as almost entirely social monogamous (Kleiman, 2011; Gittleman and Valkenburgh, 1997) while different types of mating systems prevail in the rest of the order Carnivora (Gittleman and Valkenburgh, 1997). Macdonald et al. (2019) considered social monogamy and parental care to be the common rule, but variations such as polygamy (at both sexes), plural breeding, communal breeding, and cooperative breeding may also occur. However, all species show a central breeding pair. Our work supports the idea of a strong role for sexual selection in delimiting divergent or similar traits between males and females. Monogamy may play an important role in structuring the monomorphism between bite forces of males and females, overruling possible effects of diet and sociality.

Ecomorphological and sexual selection implications

Our results show that canids have almost no bite force differences between males and females, which could be reflecting a lack of feeding niche divergence between sexes in the entire family. Thus, we should expect a consistent food composition overlap and low variation in resource-use between sexes (Law and Mehta, 2018; Campbell and Santana, 2017). However, Forbes-Harper et al. (2017) found feeding differences between sexes and age in red foxes introduced in Australia (juveniles and males feed more on sheep carrion than females which thrive more on rodents and invertebrates) and no differences in bite force. This may suggest that for feeding partition to occur, it does not necessarily need divergence in levels of bite force, but only a minimum

force that is strong enough to maintain access to a variety of foods. It is also possible that this strong monomorphism in the group, consequence of socially monogamous breeding systems, may constrict possible differences in feeding apparatus, limiting food partition between sexes in most Canidae.

An alternate possibility is that the feeding constraints in canids would be selecting females for stronger bite forces despite being smaller in size. Size sexual dimorphism has been described in some Canidae species: red foxes (Nowak, 1999) males have heavier bodies, Culpeo fox males have skulls 5% bigger than those of females (Travaini et al., 2000) and Ethiopian wolf males are 20% bigger than females (Sillero-Zubiri and Gottelli, 1994). Therefore, females possibly developed stronger bite forces for their size so as not to lose access to resources that are bite force demanding, such as large prey or carrion (Christiansen and Wroe, 2007).

Our work reinforces the strong role of sexual selection theory in delimiting divergent or similar traits between males and females. In this case, the selective pressure of monogamy is probably stronger than the force exerted by diet types, niche divergence, and social systems, and reinforces the role of sexual selection in evolution which, in this case, is capable of constraining entire clades such as the Canidae family. ☞

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Supplemental material 1 Raw Bite Force, Bite Force Quotient and Skull Length data