

Variability and correlations in carnivore crania and dentition

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Summary

1. We analysed patterns of variability and correlations in skulls and teeth of a wide (>100 species; >17 000 specimens) sample of terrestrial carnivores.
2. Within species, larger craniodental components vary less than do smaller ones.
3. The higher variability of canines in comparison with lower carnassials probably reflects the low complexity of the former.
4. Among species, however, trait variation is not size-related, suggesting that the higher intraspecific variability of small traits is not an artefact of measurement error.
5. Correlations between the carnassial teeth are higher in carnivores feeding mainly on vertebrates than in those that eat mostly invertebrates or fruit, suggesting that the degree of functional integration between these teeth is under differing selective pressures.
6. Correlations between the carnassials probably have a phylogenetic basis as well, with caniform carnivores having higher correlation coefficients than feliform ones.

Key-words: Canines, carnassials, coefficient of variation, diet, skulls

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Introduction

Terrestrial members of the Carnivora usually share a unique dental pattern: long, sharp, robust canines (Biknevicius & Van Valkenburgh 1996; Gittleman & Van Valkenburgh 1997) and a pair of scissor-like carnassials, the last upper pre-molar (PM⁴) and the first lower molar (M₁), adapted for cutting flesh (Ewer 1973).

Carnivores are extremely diverse in size, diet, social behaviour, locomotion and activity patterns (Gittleman 1985; Macdonald 1992; Kruuk 2002). This variability is reflected in the size and shape of carnivore skulls and teeth. Felids stand at one end of a continuum, with uniformly short skulls for their masses (Radinsky 1981; Holliday & Stepan 2004), enabling them to exert larger forces when delivering a killing bite with the canines (Van Valkenburgh & Ruff 1987). Other carnivores (e.g. *Eupleres goudotii*, *Hemigalus derbyanus*, see Wilson & Reeder 1993 for authorities) have more elongated skulls. Likewise, felid lower carnassials are always shaped for meat-slicing throughout their length, with a relative blade length of 1 (Van Valkenburgh 1989; Holliday & Stepan 2004). The great diversity of feeding habits of viverrids and mustelids on the other hand is manifested in high dental diversity (Popowicz 2003), often with a well-developed talonid basin in more omnivorous species. The carnassials of some

carnivores (e.g. bears) are so modified that they are hardly recognizable as carnassials at all (Butler 1946).

This great morphological diversity results from the action of selective forces and developmental pathways (Pengilly 1984; Jernvall, Keranen & Thesleff 2000; Szuma 2000; Dayan, Wool & Simberloff 2002). These are likely to vary with diet and with phylogeny. Therefore, variation within carnivore dentitions is likely to differ between different teeth, between taxa and according to diet. Patterns of variation within the dentition of only a few carnivore species have been studied in detail. Canids in particular have received considerable attention, especially Red Foxes (*Vulpes vulpes*, Gingerich & Winkler 1979; Pengilly 1984; Ansong 1994; Szuma 2000), as well as Grey Foxes (*Urocyon cinereoargenteus*, Polly 1998) and wolves (*Canis lupus*, Dayan *et al.* 2002). Kurten (1966) described variation in the dentition of two species of bears: the extinct *Tremarctos floridanus* and the extant *T. ornatus*. Patterns of variability in the skulls and dentition of six species of mustelids – *Meles meles* (Lüps & Roper 1988), *Martes americana* (Polly 1998), *M. martes* and *M. foina* (Wolsan, Ruprecht & Buchalczyk 1985), *Mustela erminea* and *M. frenata* (Dayan *et al.* 2002) – have also been studied. Dayan *et al.* (2002) also examined one felid – the wildcat (*Felis silvestris*), the only member of the diverse suborder Feliformia in which these aspects were studied.

These works present a fairly uniform picture: within species, carnassials have low variability, whereas canines are highly variable in size (see also Gingerich

& Schoeninger 1979; Yinyun 1982). The carnassials (especially M_1) are perceived as good traits on which to base taxonomic conclusions, following Simpson, Roe & Lewontin's (1960) assertion that for a character to be a reliable taxonomic tool it must have relatively low intraspecific variability. The length of the first lower molar of mammals in general has become a standard measure of size in much paleontological research (e.g. Gould 1975; Creighton 1980; Klein 1986; Alroy 2003).

Carnivore skulls and teeth often show negative correlation between trait variability (expressed as the coefficient of variation, CV) and trait size (Wolsan *et al.* 1985). Pengilly (1984) attributed this relationship to the greater morphological complexity of large teeth and claimed developmental factors are important in generating morphological variability (see also Szuma 2000; Dayan *et al.* 2002). Polly (1998) explained this pattern as stemming from the greater influence of measurement error at small sizes (but see Dayan *et al.* 2002).

Mammalian mastication takes place between opposing teeth on the upper and lower jaws, necessitating a high degree of integration between them. It is therefore unsurprising that, within species, where tooth function and shape are relatively constant, opposing teeth are usually highly correlated in size. However, the strongest relationship occurs not between the carnassials but between the canines (Kurten 1953), the central premolars (Kurten 1953; Gingerich & Winkler 1979; Pengilly 1984; Szuma 2000), or the first molars (Kurten 1953). A different pattern was predicted if carnassial shearing action drove the correlation pattern, because the carnassials show the highest level of functional integration (Szuma 2000), while the premolars do not even occlude. All these patterns have been described only for arctoid carnivores (usually *Vulpes vulpes*).

We sought patterns of variation and correlation in many carnivore species, including many species of the highly diverse (Popowics 2003) Feliformia. We use interspecific comparisons of intraspecific patterns to test existing hypotheses regarding tooth variability and correlations. Specifically we ask:

1. Does the pattern of increasing CV with decreased trait size within species prevail in carnivores?
2. Are CVs of the same measurement in small carnivore species greater than those in larger ones, indicating that measurement error is a major factor?
3. Should the higher variability of canines as compared with carnassials be attributed to their relative size or to their low tooth complexity?
4. Is the correlation between the lengths of the upper and lower carnassials a function of diet or phylogeny?

Materials and methods

We measured carnivore skulls in natural history collections (see Acknowledgements); Meiri, Dayan and Simberloff are responsible for c. 75%, 19% and 6% of

all measurements, respectively. Measurements were taken with digital callipers to 0.01-mm precision or vernier callipers to 0.02-mm precision (for measurements exceeding 300 mm). We used only adult specimens (those in which there is complete suture closure) when measuring cranial components. We used specimens with fully erupted permanent dentition for dental measurements, even if they were not identified as adults by the criterion for skulls outlined above. We did not measure worn teeth or use captive animals. We took seven measurements: length of the lower (M_1), and upper (PM^4) carnassials, maximum diameter of the upper canine ($C^{\text{sup}}L$, following B. Kurten, personal communication to T. Dayan), greatest breadth of the braincase (Br, Von den Driesch 1976), the breadth of the skull at the widest part of the zygomatic arches (Zyg), skull height (Ht, height of the occipital triangle, Von den Driesch 1976) and condylo-basal length (CBL). Because sexual size dimorphism is ubiquitous in carnivores, we treated the sexes as different morphospecies to avoid inflating variability indices (Yinyun 1982; Polly 1998). Our minimum sample size for a given measurement in a given species is 10 specimens, the average ranging from 57 (Zyg) to 103 (PM^4). Carnivores sampled belong to 98 species (182 morphospecies) in all eight terrestrial carnivore families. We followed the taxonomy of Nowak (1999).

To check whether CV increases with decreasing variable size we correlated variable size and CV for each morphospecies with $n = 10$ specimens in at least four measurements. To test further the influence of size on the level of variability, we correlated CV with variable size for each of the seven morphological indices we measured, among all the morphospecies.

We compared the relationship between intraspecific CVs of teeth to that between their average relative sizes. The relative sizes of the different teeth vary between species, so if absolute size were a major factor influencing variability, we would expect relatively small teeth to have higher CVs. To examine whether this is so, we used only specimens in which both relevant teeth were measured (minimum 20 specimens per morphospecies) and computed morphospecies-specific CVs. We selected the morphospecies for which the canine/carnassial size ratio was smallest and those for which it was largest (separately for $C^{\text{sup}}L/M_1$ and $C^{\text{sup}}L/PM^4$). We then compared the ratio of CVs of these two teeth in both groups.

Finally, we tested whether the magnitude of the correlation between the carnassial teeth varies with dietary preferences. Carnivores were assigned to dietary categories according to the food type most often eaten: terrestrial vertebrates, terrestrial invertebrates, fishes, crabs and fruits. Data on diets were taken from the literature, with preference given to reviews and to works giving quantitative data (a list of the references on dietary preferences is available from the corresponding author). Using the product-moment correlation coefficient between the carnassial pair as the dependent

variable, we tested the effects of dietary category and familial affinity using a two-way ANOVA. In this analysis we analysed both sexes together for each species, because interspecific differences in diet probably greatly exceed intersexual ones, and treating the sexes separately here may unnecessarily inflate the number of degrees of freedom.

Results

The different morphological variables differ in their CVs (Fig. 1; average sizes, sample sizes, and coefficients of variation for the different morphological characters in different morphospecies are available from the corresponding author). Within species, CV tends to increase with decreasing trait size: 160 of 169 Spearman-rank correlations with $n \geq 4$ traits were negative; the mean r was -0.63 . Sixty-one correlations (all negative) are significant. Across species, correlation of the mean of each character and its CV reveals a more complex picture (Table 1). Interestingly, although the correlation coefficients are not always significant, they are always positive for cranial traits but negative for dental ones. The probability that all the cranial correlations will be ranked above all dental ones (or vice versa) by

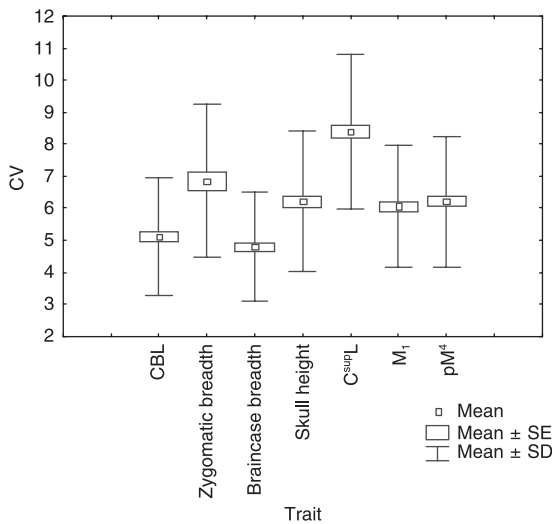


Fig. 1. Measures of central tendency of coefficients of variation in different craniodental characters of carnivore morphospecies. Sample sizes are the same as in Table 1.

Table 1. Interspecific correlations between character size and CV

Trait	n	Mean size (mm)	Standard deviation	r	P
PM ⁴	178	11.1	6.0	-0.28	0.0001
M ₁	172	11.3	5.2	-0.12	0.124
C ^{sup} L	173	6.3	4.2	-0.09	0.257
CBL	170	110.8	53.5	0.13	0.08
Br	171	43.6	18.3	0.16	0.037
Zyg	64	67.7	45.7	0.19	0.123
Ht	163	30.6	15.2	0.33	0.00002

chance is 0.016 (binomial probability for a 3:4 partition distinction of seven traits). The amount of variation explained is always low (up to 11%, for height).

Canines are more variable than both the lower (paired t -test, $n = 165$ morphospecies, $t = 17.82$, $P < 0.0001$) and upper carnassials ($n = 170$, $t = 11.12$, $P < 0.0001$). There is no consistent difference between the CVs of the two carnassials ($n = 169$, $t = 0.74$, $P = 0.46$). Table 2 shows the average of the 20 most extreme size ratios of different tooth pairs, the average ratio of CVs of these teeth in those 20 morphospecies, and the outcome of a Mann-Whitney U -test of the differences in CV between these pairs. Canines are more variable than lower carnassials regardless of relative size, but relatively large canines are not much more variable than relatively small upper carnassials. We obtain similar results for the 15 (rather than 20) morphospecies for which size ratio is highest and lowest (M₁, $U = 107$, $P = 0.82$; PM⁴, $U = 57$, $P = 0.021$). Relatively large carnassials tend to be less variable regardless of whether they are upper or lower ones (Table 2).

Correlation coefficients between the sizes of the upper and lower carnassials of 17 542 carnivore specimens representing 111 species and the dietary preferences of these species are available from the corresponding author. There is no interspecific correlation between the mean size of the carnassials ($[M_1 + PM^4]/2$) and the intraspecific correlation between them ($n = 111$, Spearman $r = 0.15$, $P = 0.11$).

A two-way analysis of variance reveals that food habits significantly affect the intensity of the correlation between the carnassials (Fig. 2; $F_{4,99} = 5.01$, $P = 0.001$), whereas the effect of family is marginally non-significant ($F_{7,99} = 1.93$, $P = 0.07$). A *post-hoc* Tukey test reveals significant differences between the correlations of species that eat land vertebrates and frugivorous species ($P = 0.034$) and between eaters of vertebrates

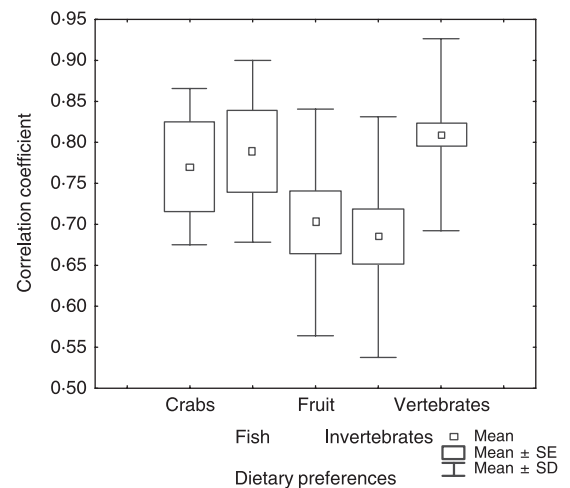


Fig. 2. Means and standard errors of the correlation coefficients between the upper and lower carnassials in carnivore species with different dietary preferences. Sample sizes are: 3, 5, 13, 19 and 71 species for crabs, fishes, fruits, terrestrial invertebrates, and terrestrial vertebrates, respectively.

Table 2. Twenty most extreme tooth size ratios and their CV ratios

	$C^{\text{sup}}L/M_1$	$C^{\text{sup}}L/PM^4$	PM^4/M_1
Average of 20 smallest size ratios	39%	42%	68%
Average of 20 largest size ratios	86%	101%	135%
Average CV ratio of 20 smallest size ratios	149%	147%	113%
Average CV ratio of 20 largest size ratios	151%	121%	93%
Mann–Whitney U	197	113	102
Probability	0.94	0.019	0.008

and invertebrates ($P = 0.001$). No other differences are significant.

Treating carnivores feeding mainly on vertebrate prey separately, we find a significant difference between members of different families ($F_{6,64} = 2.74$, $P = 0.02$). Caniforms have relatively high correlation coefficients (procyonids: $n = 1$, $r = 0.864$; mustelids: $n = 20$, $r = 0.860$; canids $n = 13$, $r = 0.845$). Feliform carnivores have lower correlation coefficients (viverrids $n = 4$, $r = 0.81$; felids: $n = 22$, $r = 0.784$; herpestids: $n = 10$, $r = 0.731$; hyaenids: $n = 1$, $r = 0.59$). A nested ANOVA with families within suborders reveals that the difference between feliforms and caniforms is significant ($F = 6.45$, $P = 0.014$), but no significant differences occur within each suborder ($F = 1.01$, $P = 0.42$).

Discussion

Variability provides the raw material for evolution to work on. Cranial and dental variability can allow different individuals to exploit different resources. In carnivores this is especially true for the most variable trait we measured, the canines. The canines are usually the teeth carnivores use to kill their prey, and canine size is thought to be influenced by the size of prey usually encountered (e.g. Dayan *et al.* 1989, 1990). Great variability in canine size within a population can enable different individuals to specialize in different prey. Such variability can take the shape of continuous variation or of enhanced sexual size dimorphism (Van Valen 1965; Rothstein 1973; Meiri *et al.* 2005b). Because we analysed the sexes separately our data seem to be pointing towards the first possibility (while remaining silent regarding the second).

Dayan *et al.* (1989, 1990) pointed out that canine size is tightly regulated by interspecific competition. It appears that tooth size within a population is affected by both smaller and larger competitors. We would therefore expect canine size to be relatively invariant, whereas, in fact, we find it has the highest variability of all measurements. Geographical differences in community composition, with regards to both resource base and the presence or absence of ecological competitors, may explain some of the variation in canine size. If ecological fine-tuning of this highly important trait is operating at the local scale we can envisage high geographical variability in canine diameters while other

traits, presumably under less severe selective pressures, will stay relatively constant. One should note, however, that high variability in canines relative to other craniodental traits was also found within populations residing in restricted geographical areas (e.g. Dayan *et al.* 2002).

Within species, canines almost always vary more than carnassials. This higher variability is probably a combined function of size (relative to the upper carnassial) and low complexity (making them more variable than the lower carnassial regardless of size). Variability can be either an inherent attribute of a tooth (resulting from developmental pathways and their interplay with stabilizing selection) or an artefact of the statistic used (same measurement error and smaller size lead to higher CV, Polly 1998). Canines are smaller and less complex than carnassials, so their higher CVs can be a consequence of both inherent and artefactual causes. Our results suggest that size differences are responsible for patterns of variability of canines *vs* upper carnassial and upper *vs* lower carnassials, but that the higher complexity of lower carnassials make them inherently less variable than the canines.

We believe that measurement error has only a limited effect on the coefficients of variation, as shown by the fact that, between species, mean CVs do not as a rule increase with decreasing mean size.

A few words of caution are warranted regarding the interpretation of our results. First, our data are probably highly affected by geographic variation (which can affect size and also dietary preferences, e.g. Hilderbrand *et al.* 1999; Goszczynski, Jedrzejewska & Jedrzejewski 2000; Clavero, Prenda & Delibes 2003) and by temporal variation (e.g. Yom-Tov 2003; Yom-Tov, Yom-Tov & Baagøe 2003). The specimens we measured sometimes span extremely wide geographical ranges, often with major influences on the variables we measured (Meiri, Dayan & Simberloff 2004a,b; Meiri, Simberloff & Dayan 2005a). Differences in measurement techniques between us may also inflate CVs (Yezerinac, Loughheed & Handford 1992; Palmeirim 1998), although both Simberloff and Meiri received their training from Dayan, and there was no apparent bias in the allocation of specimens to be measured.

Furthermore, some measurements seem inherently variable – in the Mephitinae and Lutrinae, for example, bony ‘skirts’ sometimes (but not always) develop at the sides of the skull, especially in large individuals (S. Meiri, personal observation), adding variability to the breadth measurements. Sagittal crests also differ greatly in size even between similar-sized specimens within a morphospecies, and zygomatic breadth was found to increase with age well into adulthood (Ansoerg 1994). In canines the exact position of the enamel/dentine junction is not always easy to locate, and crowded dentition combined with tooth curvature often make M_1L a difficult measurement to take. Dayan *et al.* (2002) noted that measurement variability results from the particular structure of a morphological trait, the clear-cut landmarks for measurement, its proximity

to other characters (such as other teeth), the ease with which callipers can be placed, etc., a conclusion we can only reiterate. However, these problems probably do not bias our analyses in any consistent way. Geographical variation in size is manifest in both the smallest and the largest carnivores (Meiri *et al.* 2004a,b), and we believe other sources of variance are unlikely to affect our results systematically with respect to size, diet or phylogenetic affinity.

Within species, CV is usually a negative function of trait size. CBL and BR are the least variable, canines the most variable. There is no clear-cut within-species distinction between the variability of teeth and cranial components. Because variability patterns of the same traits show no uniform relationship with respect to absolute size among species, even for the smallest trait (the canines), we think measurement error is not the source of the intraspecific phenomenon. Polly (1998) felt that the high variability of small traits is artefactual, because the effect of measurement error is greater the smaller the size is (Lande 1977). The morphological complexity of a given tooth is probably the same regardless of carnivore size. Therefore the inverse relationship between relative tooth size and relative tooth CV, which we show in the lower *vs* upper carnassials, and in the canines *vs* the upper carnassials, probably means size does affect variability indices. This result may well stem from measurement error. However, the fact that M_1 is less variable than $C^{sup}L$ regardless of relative size, and the fact that, for a given trait, there is no negative interspecific correlation of size and variability, even in the canines, certainly means measurement error cannot be responsible for the whole pattern. For some cranial traits (Ht, Br) CV is actually higher the larger the absolute size is.

A complex picture emerges when relative sizes and variabilities of different teeth are compared. The lower carnassial is less variable than the canine, regardless of the relative size of these two teeth. Canines are usually smaller than upper carnassials and are also more variable. However relatively large canines (those with a high canine/PM⁴ ratio) have CVs similar to those of the upper carnassials of the same species. This result does not agree with Pengilly's (1984; see also Dayan *et al.* 2002) prediction that the greater complexity, rather than the size, of the cheek teeth compared with that of canines is responsible for the relatively low variability in the former.

In Red Foxes, at least, there is substantial evidence that the highest correlations within the postcanine teeth are between premolars (Kurten 1953; Gingerich & Winkler 1979; Pengilly 1984; Szuma 2000) and not between the carnassials. The premolars do not occlude, whereas the carnassials have the greatest occlusal complexity. Therefore Pengilly (1984) and Szuma (2000) deduced that developmental factors rather than selective pressures determine patterns of functional integration. We did not measure premolars other than PM⁴ and therefore cannot comment on the generality

of this pattern. However, if a more precise match between the carnassials is required in carnivores specializing in vertebrate prey than in those feeding mostly on invertebrates or fruits, our results support a functional, selective explanation for the degree of correlation between the carnassials. It would be interesting to compare patterns of correlation between carnassials to patterns of correlation between premolars in carnivores that specialize in taking vertebrate prey to a greater degree than does *Vulpes vulpes*.

The occluding parts of the lower carnassials are the trigonids that form the blades. It might be that in carnivores it is the trigonid that must be under strong stabilizing selection, whereas more posterior parts (the talonid basin) are more variable. We did not measure the different carnassial parts and cannot equate RBL (see Van Valkenburgh 1989) with the degree of correlation between the carnassials. However, that felids and herpestids, characterized by relatively long carnassial blades, do not have higher correlations than do canids and mustelids makes us suspect the observed pattern is indeed related to diet and is not an artefact of less carnivorous species having lower RBL values. It would be interesting to compare the correlation between the 'carnassials' of the highly carnivorous Polar Bear (*Ursus maritimus*) with those of other arctoid, and also aeluroid, carnivores.

Carnivores show relatively regular patterns of variability in their dentitions and crania. Canines are usually highly variable, and CVs of characters within a species tend to decrease with increasing size. Our findings suggest that this pattern is a real biological phenomenon rather than an artefact of measurement error combined with the use of an inappropriate statistic (cf. Polly 1998). The low relative variability of lower carnassials compared with that of similar-sized canines, and the similar variability of similar-sized upper carnassials and canines, imply that at least some of the variation and covariation of carnivore teeth and crania might be determined by developmental constraints. The higher correlations in the dentition of caniform carnivores suggest phylogenetic constraints.

However, the clear effect of diet at the family level means that selective forces related at least in part to the function of various parts of the skull and dentition also exert important influence on these traits.

In relation to the questions we raise we conclude that intraspecifically CV of different traits is inversely correlated with size, but CV of the same trait is size-independent at the interspecific level. Measurement error has only a small influence on variability indices, while tooth complexity has at least some influence. The correlation between the carnassials depends on both phylogenetic affinity and diet.

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