

LETTER

Species co-existence and character divergence across carnivores

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Abstract

Co-occurring species might be morphologically similar because they are adapted to the same environment, or morphologically dissimilar to minimize competition. We use sister species comparisons to evaluate the relationship between morphological disparity and regional patterns of co-occurrence across carnivores. Up to 63% of the variation in range overlap can be explained by morphological divergence in dentition. Species that differ more in carnassial tooth length overlap more in their geographical range. Carnassials are the primary teeth associated with food processing, and hence difference in carnassial size may be a good indicator of difference in resource use. We suggest this pattern is consistent with competition in sympatry driving ecological character displacement, or competitive exclusion among ecologically similar species. Our study uses newly available data on global distributions, morphology and phylogeny, and is the first to demonstrate a close relationship between morphological disparity and co-occurrence at a regional scale encompassing multiple communities.

Keywords

Carnivores, character displacement, co-existence, competition, dentition, ecological species sorting, phylogeny.

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INTRODUCTION

One of the main goals of ecology is to explain patterns of co-occurrence among species in relation to their morphological and ecological characteristics. In general, there are three possibilities. First, co-occurring organisms might tend to have similar ecomorphology, because they are adapted to the same physical environment (Grant 1972). Second, co-occurring organisms might tend to have different ecomorphology and niche preferences, thereby reducing competitive interactions and permitting co-existence (Brown & Wilson 1956; Hutchinson 1959). The latter situation could arise either as a result of selection for ecological character divergence between sympatric populations (Brown & Wilson 1956) or because only species with divergent niche preferences are able to colonize overlapping areas, i.e. species sorting (Grant 1972). Finally, species differences and patterns of co-occurrence might be unrelated to one another, for example, if random patterns of dispersal determine which

species co-exist in an area and if measured species differences are not the target of strong selection by the environment or competition (Hubbell 2001).

Here, we present the first global analysis of co-occurrence and character divergence for the mammalian order Carnivora, spanning multiple communities and diverse carnivore groups. The role of interspecific interactions and, in particular, competition in structuring communities is controversial (Lewin 1983; Losos 2000; Schluter 2000a; Hubbell 2001). Nonetheless, there is increasing evidence that co-occurring guilds of species frequently demonstrate greater morphological disparity than predicted from null expectations (Dayan & Simberloff 2005). However, most studies have been at fine geographical scales and of limited taxonomic scope; an important question is whether similar processes structure species distributions and trait differences on a broader scale, for example, patterns of regional co-occurrence. To date, a lack of suitable data on species attributes and distributions has prevented large-scale studies.

We take advantage of newly compiled global data sets to explore patterns of regional co-occurrence and morphological divergence among carnivore species. Carnivores have been the focus of a number of studies into niche partitioning, demonstrating morphological disparity in local guilds (e.g. Simms 1979; Dayan *et al.* 1989, 1990; Dayan & Simberloff 1994; Van Valkenburgh & Wayne 1994; Palomares & Caro 1999; Van Valkenburgh 1999; Loveridge & Macdonald 2002, 2003), but until recently comprehensive global-scale data have been lacking. Here, we use phylogenetically independent contrasts among carnivore sister species to test whether morphological divergence can predict levels of regional range overlap. Phylogenetic approaches allow assessment of ecological diversity within an evolutionary framework, and provide a simple null model for exploring the relationship between co-existence and evolutionary divergence (Letcher *et al.* 1994; Barraclough *et al.* 1998; Webb *et al.* 2002). By measuring phylogenetic branch lengths, and hence the evolutionary distance between species, it is possible to control for the effects of divergence time on amounts of morphological divergence and levels of range overlap (Letcher *et al.* 1994; Barraclough *et al.* 1998, 1999; Barraclough & Vogler 2000).

The Carnivora provide an ideal subject for such studies because of the wealth of data linking easily measured aspects of morphology to resource use and niche partitioning. We consider two key traits believed to reflect ecological niche: body mass, as a surrogate for body size, and dentition. Body size is frequently cited as one of the most fundamental characteristics of an organism (Peters 1983; Damuth & MacFadden 1990; Brown & West 2000), and has been shown to be an important predictor of competitive ability among carnivore species; particularly when competition is direct (e.g. Loveridge & Macdonald 2002; Donadio & Buskirk 2006). However, dental morphology is likely to be more indicative of diet. Carnivore dentition can be functionally subdivided into grasping incisors, penetrating canines and food-processing cheek teeth. Here, we focus on canines, used by carnivores for securing and killing prey (Biknevicius & Van Valkenburgh 1996), and on the carnassials, which are either bladelike for slicing meat (e.g. in felids), or blunt-cusped for cracking bones (e.g. in hyenas) or masticating plant matter (e.g. in ursids; Ewer 1973), or a combination of both (e.g. in Canids, *Viverra*). Character divergence in canines has been previously documented within local guilds of mustelids, herpestids and felids (Dayan *et al.* 1989, 1990; Dayan & Simberloff 1994), and divergence in carnassials within canids (Dayan *et al.* 1992; Van Valkenburgh & Wayne 1994). If morphological partitioning is important for regional patterns of co-occurrence, we predict that it would also be the most apparent in traits closely tied to the resource base.

MATERIAL AND METHODS

Phylogenetic contrasts

All carnivore sister species pairs (pairs of species that are each others closest extant relatives) were identified from the phylogenetic tree of Bininda-Emonds *et al.* (1999). This estimate of phylogeny is the only tree with complete species level sampling for Carnivora. Marine taxa (with the exception of the polar bear, *Ursus maritimus*, with a distribution extending across the sea-ice surface) and domestic cats and dogs were excluded, leaving 50 species pairs (Table S1 in Supplementary Material). As the reconstruction of ancestral ranges is problematic (Losos & Glor 2003), we used only contrasts between sister species and did not attempt to infer the geographical distribution of ancestral taxa or perform contrast across nodes deeper in the phylogenetic tree. Pairwise divergence times were estimated from molecular sequence data using maximum likelihood branch lengths and multiple fossil calibrations (see Cardillo *et al.* 2005).

Body mass data were obtained from the database on mammalian life history (K. E. Jones and co-workers, unpublished data), and represent median species values derived from multiple sources. We used data on three dental measures: maximum upper canine diameter, length of the lower carnassial (M_1) and length of the upper carnassial (pm^4). Median species values were obtained from over 19 000 individual measurements of museum specimens (Meiri *et al.* 2005). Character divergence was quantified by performing contrasts in the logarithm of the trait values between sister pairs. For each sister pair, A and B, we calculated:

$$\text{Log}(X_A) - \text{Log}(X_B),$$

where X was the trait value and $X_A > X_B$.

Geographical overlap

Species distributions were derived from digital range maps (Grenyer *et al.* 2006). Distributions reflect current extent of occurrence, but for the black-footed ferret (*Mustela nigripes*) we used an estimate of the historical range, as this species went extinct in the wild during the 1900s. We calculated geographical range overlap based on the relative area of common occurrence (Barraclough *et al.* 1998; Barraclough & Vogler 2000) as: area of overlap/range size of the species with the larger range.

We used this measure because, when high, it is likely that specimen measurements will be from individuals sampled in the zones of overlap; however, other measures of overlap led to similar conclusions (see Tables S2 and S3). Because our measures of overlap are bounded between 0 and 1, they were arcsine-transformed prior to analyses.

Statistical analysis

First, we constructed a series of univariate regression models to explore how range overlap varied with divergence time, contrasts in morphological traits and geographic range size (mean range size of the species within each sister pair). Second, we included time, morphological traits and range size in a single model with range overlap as the response, and then removed non-significant terms in a stepwise manner by backward elimination, to produce minimum adequate models (Crawley 2002). Model sensitivity was assessed by removing points of high leverage and repeating the simplification procedure starting from the maximum model (Crawley 2002). We also examined whether the relationships between divergence and overlap demonstrated clade differences by including taxonomic family in the minimum adequate models derived above, and contrasted the goodness-of-fit of the models with and without allowing model parameters to vary by family. All analyses were performed in the statistical package R (R: a programming environment for data analysis and graphics, version 2.2.0; <http://www.r-project.org/>).

To examine the robustness of the results to assumptions regarding the underlying process of evolution, we repeated the regression models controlling for divergence time by dividing overlap by the square root of the sum of the branch lengths connecting the species pairs. This transformation, assumes a Brownian motion model of state change (Felsenstein 1985), and removed the underlying trend between overlap and time ($P = 0.57$, $r^2 < 0.01$ for the regression of transformed overlap against divergence time). Finally, we excluded fully allopatric pairs, and considered only overlapping (sympatric) sister pairs, where potential for competition is greatest.

RESULTS

We found that tooth size was the strongest predictor of range overlap, with carnassial length performing marginally better than canine diameter (Table 1). Sister species that differ the most in carnassial length have the greatest geographical overlap (Fig. 1). Although body mass was also a significant predictor, it explained only half of the variation in overlap as the best tooth measures ($r^2 = 0.23$ and $r^2 = 0.45$ for the regression models with body mass and upper carnassials, respectively; Table 1). Simplification from a maximum model including canine diameter, carnassial length, mass, area and divergence time among the starting variables, retained pm^4 as the sole significant predictor of overlap (Fig. 1). Excluding points of high leverage and repeating model simplification again retained only pm^4 as a significant predictor variable. When we controlled for divergence time by dividing overlap by the square root of

Table 1 Results of the univariate regression models of range overlap against divergence time, contrasts in ecological traits and range size

Explanatory variable	t	r^2	P -value
Time	3.10	0.17	< 0.01
M_1	5.78	0.41	< 0.01
pm^4 *	6.24	0.45	< 0.01
Canine	5.45	0.38	< 0.01
Range size	1.21	0.03	0.23
Body mass	3.76	0.23	< 0.01

Values indicate the strength and significance of the alternative explanatory variables in the regression models with range overlap as the response variable. Divergence time represents time to the most recent common ancestor (time) in millions of years. All trait variables represent log-transformed sister species contrasts; number of sister pairs (n) = 50.

*This model is the minimum adequate model in the multivariate analysis.

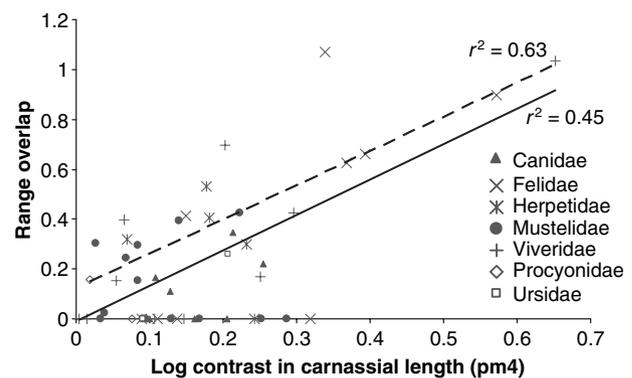


Figure 1 Scatter plot of range overlap against divergence in upper carnassial length. Range overlap scores are arcsine-transformed (see Material and methods). Fitted lines represent the fit of the regression model for all sister pairs (solid line) and for sympatric sister pairs only (dashed line). The regression models were robust to the exclusion of points of high leverage and to the removal of felids, which are overrepresented among the contrasts with both high range overlap and large differences in carnassials (see text for details).

the sum of the branch lengths connecting the species pairs, pm^4 remained the sole explanatory variable in the minimum adequate model ($P < 0.01$, $r^2 = 0.26$). Models using alternative measures of range overlap were broadly congruent, carnassial length remained a highly significant predictor of range overlap, although range size and divergence time were retained as additional explanatory variable in the minimum adequate models (Tables S2 and S3).

When we consider only overlapping species pairs, explanatory power increased for all of the regression models, with the exception of range size (Table 2). Pm^4

Table 2 Results of the univariate regression models of range overlap against divergence time, contrasts in ecological traits and range size for sympatric sister species only

Explanatory variable	<i>t</i>	<i>r</i> ²	<i>P</i> -value
Time	4.02	0.37	< 0.01
<i>M</i> ₁	6.12	0.58	< 0.01
pm ⁴	6.82	0.63	< 0.01
Canine	5.61	0.54	< 0.01
Range size	-0.78	0.02	0.44
Body mass	4.21	0.40	< 0.01

Model parameters as for Table 1, *n* = 29.

was again found to be the best predictor, and alone explained 63% of the variation in range overlap (Fig. 1), body mass was retained as an additional explanatory variable in the minimum adequate model, although support for its inclusion was marginal (*P* = 0.04, partial *r*² = 0.06). There was no significant difference among families in either slope or intercept for the regression models of tooth size against overlap. When family was included as an interaction term in the minimum adequate model identified above, there was a slight decrease in explanatory power after adjusting for the increased number of explanatory terms in the model (adjusted *r*² = 0.55 and 0.67 with and without allowing model parameters to vary among families, respectively), and its retention was not justified when models were contrasted using ANOVA (d.f. = 14, *P* = 0.88). Small sample size prohibited significance testing separately within each family; however, there was a positive trend between morphological divergence and overlap for the majority of families; the two exceptions were Herpestidae (mongooses: five contrasts) and Procyonidae (raccoons: two contrasts).

The significant relationship between carnassial length and overlap is not a product of few contrasts in a single clade, but rather a more general feature of the Carnivora. Nonetheless, we observed that the relationship appeared most pronounced within felids. To explore the importance of the felid clade on our overall results, we repeated the regression for only non-felid sister pairs, the model was still highly significant, although explanatory power was reduced (*n* = 24, *P* < 0.01, *r*² = 0.56; sympatric sisters only). Additionally, removing the sister species contrast between the Malagasy civet (*Fossa fossana*) and falanouc (*Eupleres goudoti*), identified as being of high leverage, further reduced explanatory power, but the significant relationship between carnassials and overlap remained (*n* = 23, *P* < 0.05, *r*² = 0.21).

DISCUSSION

Geographical range overlap is greatest among sister species of carnivores that differ in morphological traits, most

notably carnassial teeth. One possible explanation is that post-speciation range movement and morphological divergence has led to greater overlap by chance. However, tooth size remained the best predictor of species overlap even when divergence time was corrected for. We conclude that there is morphological partitioning, particularly in dentition, between regionally co-occurring carnivore species.

While both canines and carnassials are known to correlate with prey size (Dayan *et al.* 1989, 1992; Dayan & Simberloff 1998), canines may also be under strong sexual selection (Gittleman & Van Valkenburgh 1997) and display greater intraspecific variability than carnassials (Meiri *et al.* 2005). Direct sexual selection on carnassial length is unlikely (Gittleman & Van Valkenburgh 1997). That we find carnassial length to be the better predictor of geographical range overlap than either body size or canines suggests that interspecific competition for food is a critical factor determining species co-existence in carnivores. It remains possible that carnassial length is a better indicator of species size differences than body mass, as mass may demonstrate greater intraspecific variation (Ralls & Harvey 1985). However, a significant relationship with body size and range overlap would still be important, and would not alter our main conclusion, that morphological disparity is a key feature of co-occurring carnivore species at large spatial scales.

While carnivore taxonomy has remained relatively stable in comparison with some other mammal clades, for example, primates (Isaac *et al.* 2004), in a few cases sister species used in our analyses have undergone taxonomic revision. Future taxonomic changes are also likely because of the controversy over species concepts. We used the 1993 taxonomy of Wilson and Reeder in our study, because it corresponds to the available phylogenetic and geographical range data. Most recent taxonomic changes in mammals represent splits, frequently by the elevation of geographically distinct subspecies to the level of species (Isaac *et al.* 2004). Consequently, new sister pairs will tend to be morphologically similar, to have previously been recognized as a single species, with non-overlapping ranges. Low range overlap among morphologically similar sister species would strengthen our general conclusions.

Our interpretation assumes geographical overlap is a surrogate of potential for competition. Direct interspecific interactions may be low even where overlap is great, as species may occupy different microhabitats (Bowers & Brown 1982) or have different activity cycles (Kronfeld-Schor & Dayan 2003) and dietary preferences. Further, character divergence might be most apparent in zones of overlap (Brown & Wilson 1956), and hence hard to detect using species' averages. Critically, such fine scale niche partitioning would most likely confound attempts to detect a relationship using phylogenetic contrasts between sister

species, hence our analyses are conservative. Another possibility is that contemporary range overlap is a poor indicator of historical overlap; however, once again this would most likely confound attempts to detect a relationship between overlap and divergence, especially where competition in sympatry was important in driving character displacement. Finally, it may be possible that the relationship between range overlap and morphological divergence is a product of both co-varying with a third, independent variable, such as diversity of prey types (Van Valkenburgh & Janis 1993). While there is some evidence for an association between carnivore species richness and prey species richness (Gittleman & Gompner 2005), we can think of no reason why we should expect low geographical overlap between sister species in regions of low prey diversity unless competition were still important.

The relationship between range overlap and trait divergence does not differ significantly between carnivore families. However, four of the five species contrasts demonstrating the greatest divergence in carnassials along with high range overlap, are felids (cats). Cats are the most carnivorous clade within Carnivora, and hence may have the highest dietary overlap among the sister species pairs. This may be important for two reasons. First, they are likely to use their food processing teeth in similar ways (Ewer 1973); consequently variation in carnassial length is most likely to reflect variation in prey size, rather than dietary shifts to new food groups. Second, competition is likely to be strong and in some cases may take the form of direct interference or intraguild predation (Polis *et al.* 1989). Intraguild predation within hypercarnivores (estimated dietary intake > 70% meat) has been well documented, and may be particularly common within Felidae (Palomares & Caro 1999; Donadio & Buskirk 2006). Nonetheless, a significant relationship remains when we restrict the analysis to non-cats and exclude further points of high leverage. The correlation between trait divergence and range overlap is therefore a general attribute across carnivores, and neither a product of a few influential points, nor driven by a single clade.

There are two broad explanations for our finding of a relationship between range overlap and trait divergence (Brown & Wilson 1956). First, ecological character displacement, in which morphological differences arise as a product of adaptive divergence between sympatric predators in response to competition for prey and second, ecological species sorting, in which range overlap is inhibited among similar species competing for the same resource base. In the former case, competition drives divergence in sympatry, in the latter case, species diverge in allopatry, and competition is only important later, when species come into secondary contact. Determining the direction of causation from observational data is at best

complicated (Diamond 1986; Schluter & McPhail 1992; Schluter 2000a,b). However, if species sorting predominates, we might predict large differences in traits between allopatric sisters to be just as likely as small differences. In contrast, ecological character displacement may lead to larger differences and faster rates of divergence in morphology among sympatric sisters than for allopatric sisters, due to the additional effect of competition driving trait divergence (Schluter 2000a,b).

While our analysis was not designed to differentiate between ecological character displacement and ecological species sorting, we note that morphological contrasts between sisters with small overlap do not span the range of values encompassed by sisters with large geographic overlap (Fig. 1). The five largest contrasts are all for sister species with high overlap. Further, the positive relationship between divergence time and morphological divergence (Table 1) is driven entirely by contrasts among sympatric species (Table 2); there is no significant correlation between morphology and time among allopatric contrasts ($P = 0.82$, $r^2 < 0.01$). This pattern is consistent with the process of ecological character displacement in sympatry as described above. However, it is possible that both processes are important; ecological sorting may be occurring at low levels of overlap following the divergence of traits largely in allopatry, whilst character displacement may drive the relationship as overlap increases (Rice & Pfennig 2006).

In conclusion, we show that morphological disparity is important for co-occurrence of carnivores at regional scales. This was most apparent in traits closely tied to resource use and among species occupying similar ecological niches. Although we would expect interspecific competition to reflect community-wide dynamics, we detected a signal comparing only sister species; such species pairs are likely to be relatively similar in ecology because of recent shared ancestry, and hence provide a powerful means for detecting the effects of competition.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Sister species pairs, divergence times, range size, geographical overlap and respective trait values.

Table S2 Results of the univariate regression models using alternative measures of range overlap.

Table S3 Results of the multivariate regression models using alternative measures of range overlap

This material is available as part of the online article from: <http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2006.01005.x>

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