



CHICAGO JOURNALS



Diet, Morphology, and Interspecific Killing in Carnivora

Author(s): Emiliano Donadio and Steven W. Buskirk

Reviewed work(s):

Source: *The American Naturalist*, Vol. 167, No. 4 (Apr., 2006), pp. 524-536

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/3844707>

Accessed: 21/02/2012 05:46

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at

<http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Diet, Morphology, and Interspecific Killing in Carnivora

Emiliano Donadio* and Steven W. Buskirk†

Department of Zoology and Physiology, University of Wyoming,
Laramie, Wyoming 82071

*Submitted June 7, 2005; Accepted December 20, 2005;
Electronically published March 7, 2006*

ABSTRACT: Interspecific killing is a key determinant of the abundances and distributions of carnivores, their prey, and nonprey community members. Similarity of body size has been proposed to lead competitors to seek similar prey, which increases the likelihood of interference encounters, including lethal ones. We explored the influence of body size, diet, predatory habits, and taxonomic relatedness on interspecific killing. The frequency of attacks depends on differences in body size: at small and large differences, attacks are less likely to occur; at intermediate differences, killing interactions are frequent and related to diet overlap. Further, the importance of interspecific killing as a mortality factor in the victim population increases with an increase in body size differences between killers and victims. Carnivores highly adapted to kill vertebrate prey are more prone to killing interactions, usually with animals of similar predatory habits. Family-level taxonomy influences killing interactions; carnivores tend to interact more with species in the same family than with species in different families. We conclude that although resource exploitation (diet), predatory habits, and taxonomy are influential in predisposing carnivores to attack each other, relative body size of the participants is overwhelmingly important. We discuss the implications of interspecific killing for body size and the dynamics of geographic ranges.

Keywords: carnivores, interspecific killing, diet, morphology.

Carnivores exhibit morphologies and behaviors (McDonald 2002) and occupy geographic ranges (Tannerfeldt et al. 2002) that reflect interference competition in its various forms. The most extreme form of interference competition between species, killing, is increasingly recognized as an important factor structuring communities. Such killing has been credited with limiting the abundance and distributions of some carnivores (Laurenson 1995; Lind-

ström et al. 1995) and affecting the densities of taxa two to three trophic levels distant from the killing carnivore (Palomares et al. 1995; Crooks and Soulé 1999).

Among carnivores, body size is a key correlate of life-history traits, including reproduction (Gittleman 1986), size of prey (Rosenzweig 1966), size of home range (Gittleman and Harvey 1982), population density (Carbone and Gittleman 2002), and metabolic rate (McNab 1989). In addition, body size influences the outcomes of interference interactions, with large-bodied carnivores able to exclude small ones from habitat patches or prey carcasses. These highly asymmetrical interactions mediated by body size are common (Palomares and Delibes 1994; Kamler et al. 2003) and include killing, with the smaller animal almost invariably the loser (Palomares and Caro 1999).

When should a carnivore kill a sympatric carnivore of another species? Competition theory suggests that it should do so when benefits outweigh costs. Benefits could include the freeing of resources that otherwise would be used by the competitor that is killed (Case and Gilpin 1974). Competition for food has been suggested as a key factor precipitating interspecific killing (Polis et al. 1989; Palomares and Caro 1999); extensive dietary overlap among large African carnivores is correlated with high levels of interspecific aggression (Schaller 1972; Mills and Biggs 1993). Similarly, most agonistic encounters between carnivore species in seasonal environments occur when food is scarce (Palomares and Caro 1999). Thus, diet overlap seems to be a factor likely to motivate interspecific killing.

If this hypothesis is true, interspecific killing should also be influenced by predatory habits, which we define here as the degree to which a carnivore kills and consumes vertebrate prey. High diet overlap should facilitate killing encounters because species searching for similar prey should occupy similar habitats, thereby increasing encounter rates (Polis et al. 1989; Buskirk 1999). Although appealing, this explanation fails to consider covariation among body size, diet overlap, and the outcomes of interspecific killing. Carnivore species with similar body sizes are expected to use the same prey base because similarly sized predators tend to eat similarly sized prey (Rosenzweig 1966). Therefore, the diet overlap hypothesis predicts the

* E-mail: emiliano@uwyo.edu.

† E-mail: marten@uwyo.edu.

most frequent killing interactions between the most similarly sized carnivores. Anecdotal data, however, contradict this prediction. Carnivores seem to be more prone to interact when body sizes of potential competitors differ by a factor of two (Palomares and Caro 1999) to four (Buskirk 1999).

Tooth morphology strongly reflects diet, but it should also differentially predispose species to participate in killing events. More predaceous carnivores, whose diet is mainly meat, tend to have massive canines and a first lower molar (m_1) with a long blade in relation to its total length (Van Valkenburgh 1989). In agonistic interactions with other species, these adaptations for prey capture should confer an advantage to species that have them (Case and Gilpin 1974). Therefore, species with dentition more adapted to killing and consuming vertebrate prey should participate more in interspecific fights because they have the weaponry to succeed in them. Conversely, less predaceous carnivores lacking these dental adaptations should avoid fights.

Carnivore species within a family typically exhibit high similarity in their trophic apparatus and greater similarity in size to each other than to species from other families (Gittleman 1985; Van Valkenburgh 1989). As a consequence, niches should overlap more within than among families. For example, the Felidae are generally larger bodied and more predaceous than the smaller, more omnivorous Procyonidae. Even within a geographic region, the pattern is apparent. In Africa, body size, tooth morphology, and killing technique are more similar within the assemblages of large sympatric felids (e.g., cheetah *Acinonyx jubatus*, lion *Panthera leo*, and leopard *Panthera pardus*) and wild canids (e.g., side-striped jackal *Canis adustus*, golden jackal *Canis aureus*, black-backed jackal *Canis mesomelas*, and wild dog *Lycaon pictus*) than between assemblages. Thus, taxonomic relatedness covaries with the morphological factors that should influence the frequency of interspecific killing, which we considered in our analysis.

To examine whether body size, diet, predatory habits, and taxonomy of potential competitors were related to interspecific killing among Carnivora, we developed the following predictions. First, the occurrence of lethal interactions should depend on relative body sizes of potential participants. Large differences in body size should reduce interspecific killing because large niche differences should reduce the benefits of killing to any potential attacker. Small differences in body size should reduce the occurrence of interspecific killing as well because attacking another species of similar body size carries high risks associated with the uncertain outcome. Intermediate differences in body size, however, should predispose species pairs to participate in interspecific killing; the larger carnivore should be more prone to initiate an agonistic en-

counter when it perceives the opponent as large enough to be a competitor, yet small enough to be defeated with low risk. Second, at intermediate body size differences, presumably associated with frequent interspecific killing, diet niche overlap between species should be high, justifying the costs associated with attacking another species of carnivore. Third, predatory habits should influence the predisposition of carnivore species to engage in killing. More predaceous species with dentition specialized for killing prey should participate in interspecific killing events more often than less predaceous species, which we expect to avoid such interactions. Similarly, interactions should be more common between more predaceous species than between less predaceous ones. Finally, interspecific killing should more frequently involve closely related (i.e., same family) than distantly related species because of the morphological similarities and common ecological needs of same-family assemblages.

Here, we review theory and empirical data dealing with a particular type of interference competition, killing within Carnivora, and examine the potential relationships between this interaction and a set of ecological and morphological predictors. We first investigate how body size differences between interacting species influence the frequency of interspecific killing. We then explore how diet overlap, predatory habits, and taxonomy at the family level relate to interspecific killing. Finally, we discuss the potential implications and importance of interspecific killing within a general framework of competition, evolution, and community structure.

Methodology

Body Size and the Potential for Interspecific Killing

We used two approaches to explore the role of body size in interspecific killing. First, we reanalyzed data reviewed by Palomares and Caro (1999), plus additional data, to examine the relationship between the frequency of interspecific killing and difference in body size. From the 97 species pairs Palomares and Caro (1999) reported as having participated in interspecific killing, we discarded those involving domestic species ($n = 7$) and those involving otter species and the aardwolf (*Proteles cristatus*; $n = 5$) because of their specialized diets, habitats, and dentition. Because our raw data were differences in body size between competitors, we reduced species pairs involved in reciprocal killing (e.g., lions were reported to kill spotted hyenas *Crocuta crocuta* and vice versa) to a single unit of analysis to avoid potential pseudoreplication. Also, we added to our analysis 12 new species pairs (table 1) not reported by Palomares and Caro (1999), for a total of 92 species pairs involving 59 different species of carnivores. We cal-

Table 1: Instances of interspecific killing among mammalian carnivores not reported in Palomares and Caro (1999) and included in this analysis

Killed species	Killer species	Continent	Source
<i>Canis aureus</i> (golden jackal)	<i>Panthera tigris</i> (tiger)	Asia	Schaller 1967
<i>C. aureus</i>	<i>Panthera pardus</i> (leopard)	Asia	Schaller 1967
<i>Conepatus humboldtii</i> (hog-nosed skunk)	<i>Puma concolor</i> (puma)	South America	Johnson and Franklin 1994
<i>Gulo gulo</i> (wolverine)	<i>P. concolor</i>	North America	Krebs et al. 2004
<i>Leopardus pardalis</i> (ocelot)	<i>P. concolor</i>	Central America	Núñez 1999
<i>Leptailurus serval</i> (serval)	<i>P. pardus</i>	Africa	Schaller 1972
<i>Martes americana</i> (American marten)	<i>Lynx rufus</i> (bobcat)	North America	Bull and Heater 2001
<i>M. americana</i>	<i>Canis latrans</i> (coyote)	North America	Bull and Heater 2001
<i>Pseudalopex culpaeus</i> (culpeo fox)	<i>P. concolor</i>	South America	Novaro 1997b
<i>Pseudalopex griseus</i> (chilla fox)	<i>P. concolor</i>	South America	Yañez et al. 1986
<i>Urocyon cinereoargenteus</i> (gray fox)	<i>C. latrans</i>	North America	Fedriani et al. 2000
<i>U. cinereoargenteus</i>	<i>L. rufus</i>	North America	Fedriani et al. 2000
<i>U. cinereoargenteus</i>	<i>P. concolor</i>	North America	Logan and Sweanor 2001

culated the body size difference for each species pair as $\text{BSD} = (Mb_1 - Mb_2)/Mb_1$, where Mb_1 is the mass of the larger species and Mb_2 the mass of the smaller one. This measure was arcsine square root (arcsine $\sqrt{\text{BSD}}$) transformed, and nine size intervals were constructed. We compared the distribution of arcsine $\sqrt{\text{BSD}}$ for species pairs involved in interspecific killing to its expected values obtained from data on geographic range overlap (see "Geographic Range Overlap Analysis"). To account for the effects of taxonomy, we compared the observed distribution of interspecific killing between same- and different-family species pairs with their expected distributions, also derived from the geographic range overlap analysis.

Next, we examined the intensity of interspecific killing, expressed as the proportion of mortality in the victim population caused by the killer population, and its relationship to the arcsine $\sqrt{\text{BSD}}$ of the species pair. We did so by collecting from the literature data on adult and sub-adult known-cause mortality of carnivore species. Over 90% of the data we used reported known deaths from a radio-tracked sample of the population. The remaining 10% reported data on intensively observed populations of large African carnivores. Therefore, our estimations of intensity of interspecific killing are likely to represent its importance in the wild. Despite this, some values might be underestimated because of the impossibility of identifying the cause of death for some individuals. In this analysis, we accounted for the effects of taxonomy by incorporating it as a dummy variable (see "Statistical Analysis"). Intensity of interspecific killing was evaluated for 35 species pairs, of which 11 were same-family species pairs and 24 were different-family species pairs.

Diet Overlap

Resource overlap is commonly used to assess the potential for competition (Schoener 1983); therefore, we tested

whether published data on diet overlap among sympatric carnivores supported a dietary explanation for the frequency of interspecific killing. Diet overlap indexes were estimated for all possible species pairs in each reviewed study; we did not attempt to estimate overlap indexes across studies because of ecological differences between study sites. Some studies reported diets for the same pair of species in more than one site. In these cases, we considered the same pair from different sites as separate samples; by doing so, we took into account the variability of trophic relationships of pairs of species co-occurring in different sites and exposed to dissimilar prey bases.

To calculate diet overlap, we used the number of times a prey item occurred as a percentage of the total number of prey items in all samples. When data were presented as the percentage of occurrence per sample, we estimated the minimum number of consumed individuals in each prey category by using the formula $P_i n/100$, where P_i is the percentage of the i prey category and n is the number of scats or stomachs analyzed.

For each pair, we calculated the Schoener percent overlap index (Renkonen 1938; Schoener 1970):

$$P_{jk} = 100 \sum_{i=1}^n \min(p_{ij}, p_{ik}),$$

where P_{jk} is the percentage overlap between species j and k , p_{ij} and p_{ik} are the proportions of resource i out of the total resources used by species j and k , and n is the total number of resource states (i.e., prey categories). This index, widely used in ecological and evolutionary analyses, measures resource overlap (percent) between two species and ranges from 0% (no overlap) to 100% (complete overlap; Krebs 1989). An acknowledged shortcoming of comparing niche overlaps obtained from different studies is that food habits were generally quantified on the basis of

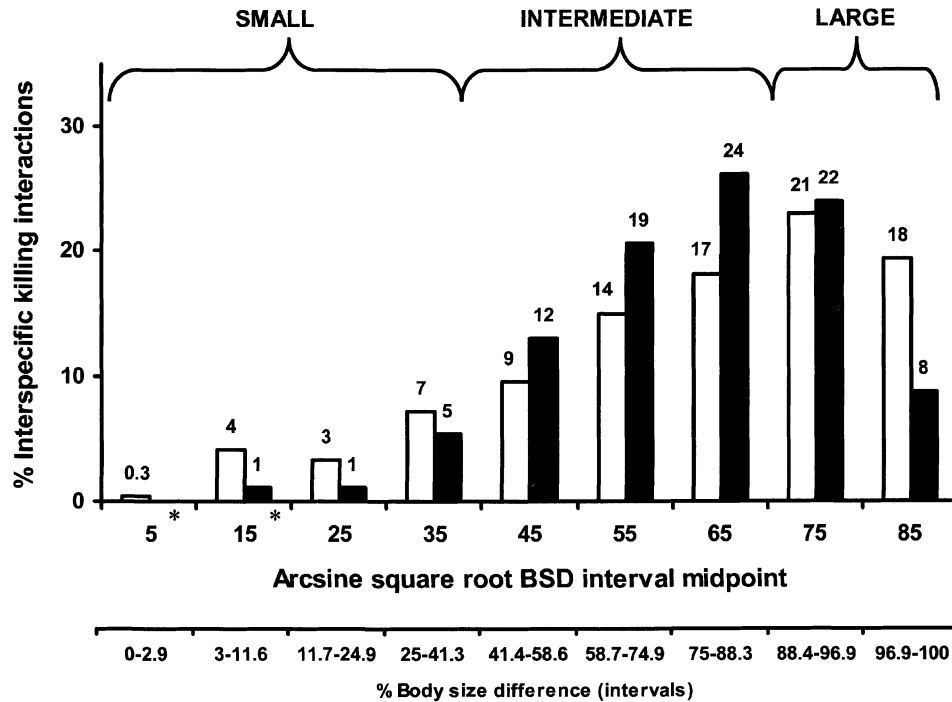


Figure 1: Expected (*open bars*) and observed (*filled bars*) frequency distributions of killing interactions within the Carnivora as a function of the arcsine-transformed square root body size difference (arcsine $\sqrt{\text{BSD}}$) for each species pair. Expected and observed distributions differed at $\alpha = 0.05$. The observed frequency of lethal interactions tended to be less than or similar to the expected frequency when body size differences of competing species were either very small or very large; conversely, at intermediate body size differences, interactions tended to be more frequent than expected. The categories are as follows: small = small difference in body size, low frequency of killing; intermediate = intermediate difference in body size, high frequency of killing; large = large difference in body size, low frequency of killing. The secondary X-axis represents percentage differences in body size of the opponents, obtained from back-transforming the arcsine $\sqrt{\text{BSD}}$ values. Sample sizes are displayed above bars; asterisks represent intervals that were aggregated for statistical analysis.

unequal sample sizes, different seasons, and different levels of prey identification. A low taxonomic resolution of prey identification—for example, to order—usually overestimates niche overlap (Greene and Jaksic 1983). However, 77% of the species pairs analyzed had prey described to genus or species, making such bias unlikely. Direct observations, kills, scats, and stomach analyses were the sample units used in the studies we reviewed; only those studies where each carnivore species was represented by a sample size ≥ 15 were considered. A total of 243 indexes were estimated.

We placed diet overlap indexes into three categories based on the relationship between body size difference (arcsine $\sqrt{\text{BSD}}$) and the expected and observed frequencies of interspecific killing. Two categories included indexes for species pairs with arcsine $\sqrt{\text{BSD}} = 0-40$ (“small”: small difference in body size, low frequency of killing; i.e., expected frequencies of killing were similar to or greater than the observed) and pairs with arcsine $\sqrt{\text{BSD}} = 70-90$ (“large”: large difference in body size, low frequency of

killing). The third category (“intermediate”) included indexes for species pairs with intermediate differences in body size (arcsine $\sqrt{\text{BSD}} = 40-70$), associated with high frequency of interspecific killing (i.e., expected frequencies of killing were notably lower than the observed; fig. 1).

Predatory Habits and Tooth Morphology

To analyze the relationship between tooth morphology and interspecific killing, we estimated the relative blade length (RBL; Van Valkenburgh 1989) for each of the 59 species involved in interspecific killing events. RBL is the ratio of anteroposterior length of the blade of m_1 to total length of m_1 . This ratio is a strong correlate of diet and predatory habits and allowed us to disaggregate carnivore species into those with $\text{RBL} > 0.65$ (meat-dominated diets, more predaceous) and those with $\text{RBL} \leq 0.65$ (more omnivorous, less predaceous; Van Valkenburgh 1989). We obtained data on RBL from Van Valkenburgh (1989) and specimens we measured at the University of Wyoming Zoology Museum

and the National Museum of Natural History, Washington, DC. For each species, one adult male and one adult female were measured, and their ratios were averaged.

We evaluated whether predatory habits predisposed carnivores to participate in killing events by comparing them to two expected distributions: first, the observed frequency of interactions for each predatory category, and second, the observed frequency of interactions for species pairs when both members belonged to the same category. For more predaceous carnivores, we evaluated the influence of taxonomy by comparing the observed and expected frequency of interactions for species pairs in which members belonged to either the same or different families. All expected distributions were obtained from the geographic range overlap analysis.

Geographic Range Overlap Analysis

Sympatry is required for competition; therefore, for all carnivore species pairs, we determined whether sympatry occurred by overlaying maps of geographic ranges (Caro and Stoner 2003) of the 59 carnivore species reported to be involved in interspecific killing. We considered two species to have overlapping ranges if the overlapping area of their ranges represented >10% of the range of the species with the smaller range. For each species pair with overlapping ranges, we calculated the arcsine $\sqrt{\text{BSD}}$. All the arcsine $\sqrt{\text{BSD}}$ values were classified into nine size intervals, and the expected proportion of values in each interval was estimated by dividing the number of values in a given size interval by the total number of values obtained from overlaying range maps. We estimated the expected frequency of observations for each size interval (E_i) as $E_i = F_i O_i$, where F_i was the expected proportion of arcsine $\sqrt{\text{BSD}}$ values for the i th size interval and O_i was the total number of observed interacting species pairs. A similar approach was used to compute the expected frequencies when controlling for taxonomy at the family level. For same-family species pairs, sympatry was assessed by overlaying the geographic range map of a focal species with the maps of all the remaining species from the same family. The opposite procedure was used to evaluate sympatry for different-family species pairs. In this case, we compared the range map of a focal species with the maps of all remaining species from different families.

To estimate the expected frequencies of interactions for less and more predaceous carnivores, we compared range maps of each less predaceous species to the maps of all the remaining species regardless of their predatory habits. The potential for a killing interaction for a given pair was scored as positive if the species' geographic ranges overlapped. The expected proportion of interaction for each predatory category was estimated as the number of positive

scores in each category divided by the sum of the positive scores in both categories. We estimated the expected frequency of observations for each predatory category by multiplying the expected proportion by the total number of observed interacting species pairs. We used the same approach to explore the potential for interspecific killing within predatory categories (i.e., geographic ranges were compared separately for species of each category) and to evaluate the effect of taxonomy at the family level for more predaceous carnivores (i.e., geographic ranges between same-family species were compared separately from those between different-family species).

We recognize that geographic range overlap is a crude measure of the potential for interspecific competition since sympatric species may occupy different habitats, but estimating habitat overlap was difficult because of the lack of information on some carnivore species from South America and Asia that have been barely studied. As a consequence, and in order to avoid false accuracy in our analysis, we did not try to estimate the degree of habitat overlap.

Geographic ranges were taken from Corbet (1978), Eisenberg (1989), Corbet and Hill (1992), Reid (1997), Stuart and Stuart (1997), Eisenberg and Redford (1999), Feldhamer et al. (2003), and Macdonald and Barret (2004) and supplemented with data from Hall (1981), Nowell and Jackson (1996), and Parera (2002). Body masses were averaged across sexes and, when information was available, across populations for each species. Body masses were taken principally from Silva and Downing (1995) and supplemented with data from Pocock (1951), Youngman (1990), Redford and Eisenberg (1992), Nowell and Jackson (1996), Emmons and Feer (1997), Novaro (1997a), Nowak (1999), and Ray and Sunquist (2001). Nomenclature follows Wilson and Reeder (1993), except for the African wildcat *Felis lybica* (Meester et al. 1986), San Joaquin kit fox *Vulpes macrotis* (Thornton and Creel 1975), and western spotted skunk *Spilogale gracilis* (Dragoo et al. 1993), which were considered valid species. Raw data on the extent of mortality from interspecific killing, body weights, diet overlap indices, and RBL ratios are available from the authors upon request.

Statistical Analysis

We used a G-test of goodness of fit to compare the expected and observed distributions of killing events as a function of both arcsine $\sqrt{\text{BSD}}$ and predatory categories. We used the Yates correction for continuity for those cases where $df = 1$ (Zar 1998).

We used a multiple linear regression analysis to explore the relationship between the response variable, intensity of interspecific killing, and the predictor variables, arcsine

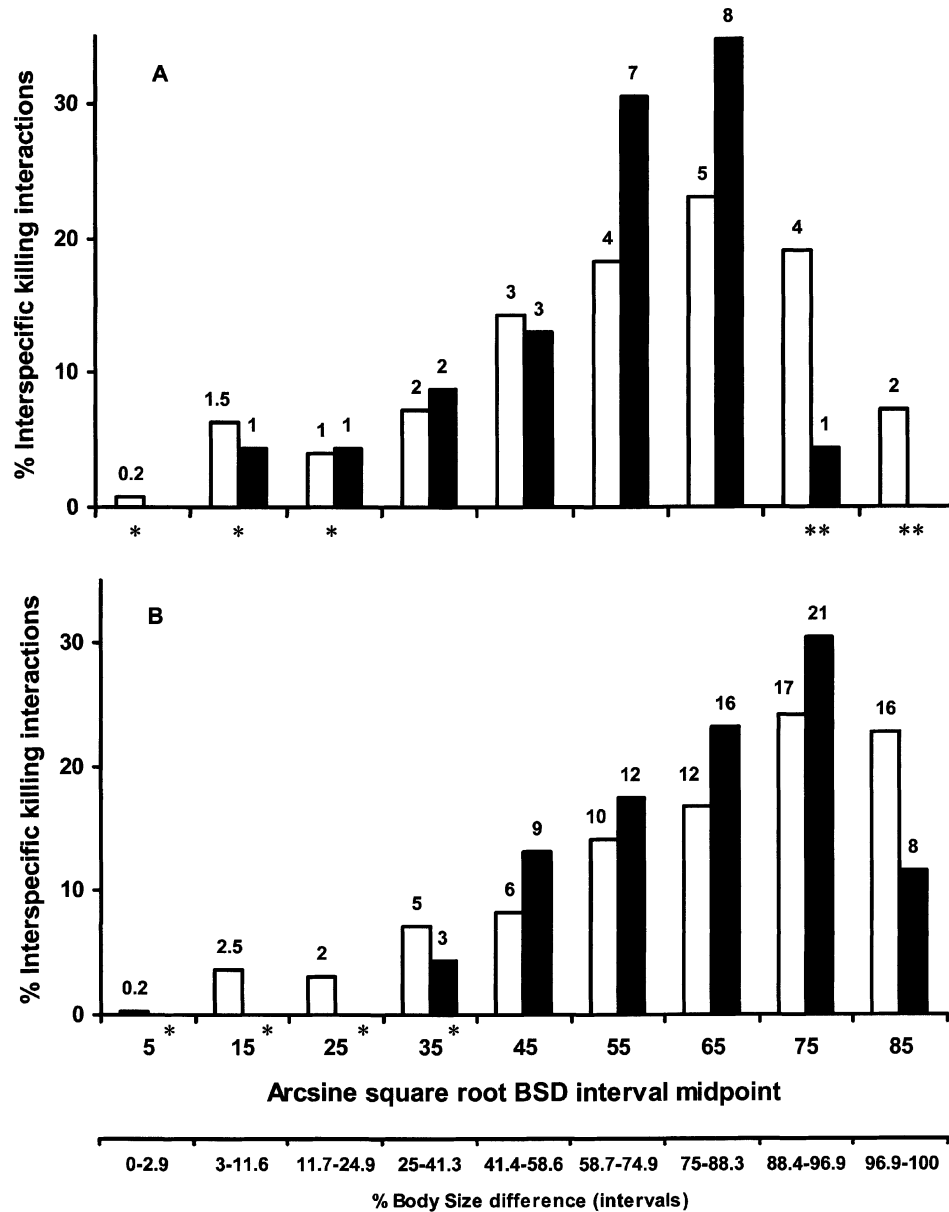


Figure 2: Expected (*open bars*) and observed (*filled bars*) frequency distributions of killing interactions within the Carnivora, controlling for taxonomy at the family level, as a function of the arcsine-transformed square root body size ratio ($\arcsine \sqrt{\text{BSD}}$) for each species pair. *A*, For same-family species pairs, the observed frequency of lethal interactions tended to be higher than expected at a narrow interval of intermediate body size differences, while the frequency was similar to and lower than expected at small and large body size differences, respectively; however, the observed and expected distributions did not differ at $\alpha = 0.05$. *B*, For different-family species pairs, the observed frequency of lethal interactions peaked at a wider interval of intermediate body size differences, while the frequency tended to be lower than expected at both small and large BSDs; the observed and expected distributions were significantly different at $\alpha = 0.05$. For both graphs, the secondary X-axis represents percentage differences in body size of the opponents, obtained from back-transforming the $\arcsine \sqrt{\text{BSD}}$ values. Sample sizes are displayed above bars; asterisks and double asterisks represent intervals that were aggregated for statistical analysis.

$\sqrt{\text{BSD}}$ and taxonomy at the family level. Only mortality data within the limits of $\arcsine \sqrt{\text{BSD}}$ where the response variable was expected to increase were incorporated in the model (i.e., data for species pairs whose $\arcsine \sqrt{\text{BSD}}$ fell

between 0 and 70). To conduct this analysis, we defined the following full model:

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_1 X_2 + \varepsilon,$$

where Y is the arcsine square root–transformed proportion of mortality due to interspecific killing, X_1 is the arcsine $\sqrt{\text{BSD}}$ for a given pair of interacting species, X_2 is a categorical variable coded as 1 if both species of the pair belong to one family or 0 if they belong to different families, X_1X_2 is the interaction term, and ε is the random-error term. To analyze the effect of taxonomy on the intensity of interspecific killing at the family level, we compared the full model with a set of reduced models lacking the taxonomic term, the interaction term, or both. The Akaike Information Criterion (corrected; AIC_c) was employed to select the best model (Anderson et al. 2000).

We used the Spearman rank-order correlation coefficient (r_s) to evaluate the relationship between body size differences for same- and different-family species pairs and diet overlap. We used a two-way ANOVA to determine whether diet overlap varied between same- and different-family species pairs and among arcsine $\sqrt{\text{BSD}}$ –frequency of killing categories. Following significant results of the ANOVA test, we conducted all possible pairwise t -test comparisons among categories. Statistical significance for all tests was inferred at $\alpha = 0.05$. For post hoc pairwise comparisons, we controlled for Type I errors by using the Bonferroni procedure; the new α level was estimated as $\alpha = 0.05/k$, where k represented the number of post hoc statistical comparisons. All statistical analyses were performed using the program SPSS 10.0 for Windows (SPSS 1999).

Results

Body Size and the Potential for Interspecific Killing

The observed distribution of interspecific killing events as a function of body size differences differed significantly from the expected distribution ($G = 18.2$, $\text{df} = 7$, $P = .01$). Overall, species pairs with intermediate differences in body size tended to participate more than expected in killing events, while species pairs with small and large

differences in body size tended to do so less than expected (fig. 1).

When taxonomy was taken into account, observed and expected killing events as a function of body size difference did not differ significantly for same-family species pairs ($G = 9.1$, $\text{df} = 5$, $P = .1$; fig. 2A); conversely, expected and observed killing events significantly differed for different-family species pairs ($G = 14.3$, $\text{df} = 5$, $P = .01$; fig. 2B). The observed distributions of interspecific killing events differed for same- and different-family pairs ($G = 47.7$, $\text{df} = 4$, $P < .001$; filled bars in fig. 2). Most notably, same-family species pairs interacted within a range of smaller differences in body size, whereas different-family species pairs interacted within a range of larger differences in body size.

There was a positive linear relationship between the intensity of interspecific killing and arcsine $\sqrt{\text{BSD}}$, but this relationship was influenced by taxonomy. AIC_c values showed that the model including differences in body size and the interaction term was superior to alternative models (table 2). Clearly, taxonomy strongly influenced the slope of this relationship; as body size differences between competing species increased, the intensity of interspecific killing increased more sharply for same-family than for different-family species pairs (fig. 3). For all models, variances were homoscedastic and residuals were normally distributed.

Diet Overlap

Diet overlap was negatively correlated with body size difference (same-family species pairs, $r_s = -0.51$, $P < .001$, $n = 97$; different-family species pairs, $r_s = -0.38$, $P < .001$, $n = 146$; fig. 4). Mean diet overlap differed among body size difference–frequency of killing categories (table 3). The “small” and “intermediate” categories had a larger mean diet overlap than the “large” category ($P < .001$); mean diet overlap did not differ between the small and intermediate categories ($P = .53$). Mean diet overlap was

Table 2: Multiple and single linear regression models developed to explore the relationship between intensity of interspecific killing and differences in body size and phylogenetic relationships of interacting species

Model	Regression equation	AIC_c	Δ_i	w_i	Adjusted R^2	F	df
1	$Y = -.96 + .53X_1 + .21X_1X_2$	185.6	.0	.46	.311	8.7	2, 32
2	$Y = -4.14 + .58X_1 + 11.95X_2$	186.5	.8	.30	.294	8.1	2, 32
3	$Y = 4.02 + .44X_1 - 22.1X_2 + .58X_1X_2$	187.6	2.0	.17	.301	5.9	3, 31
4	$Y = -7.36 + .71X_1$	189.6	4.0	.06	.198	9.4	1, 33

Note: Intensity of interspecific killing was the dependent variable; $n = 35$. For each model, the Akaike Information Criterion (corrected; AIC_c), Δ_i , Akaike weight (w_i), adjusted R^2 , F , and df values are presented. All models had a slope significantly different from 0 ($P < .005$). Y = arcsine-transformed square root proportion of mortality due to interspecific killing in the victim population; X_1 = arcsine square root body size ratio for a given pair of interacting species; X_2 = taxonomic term (0 if species belong to different families, 1 if species belong to the same family).

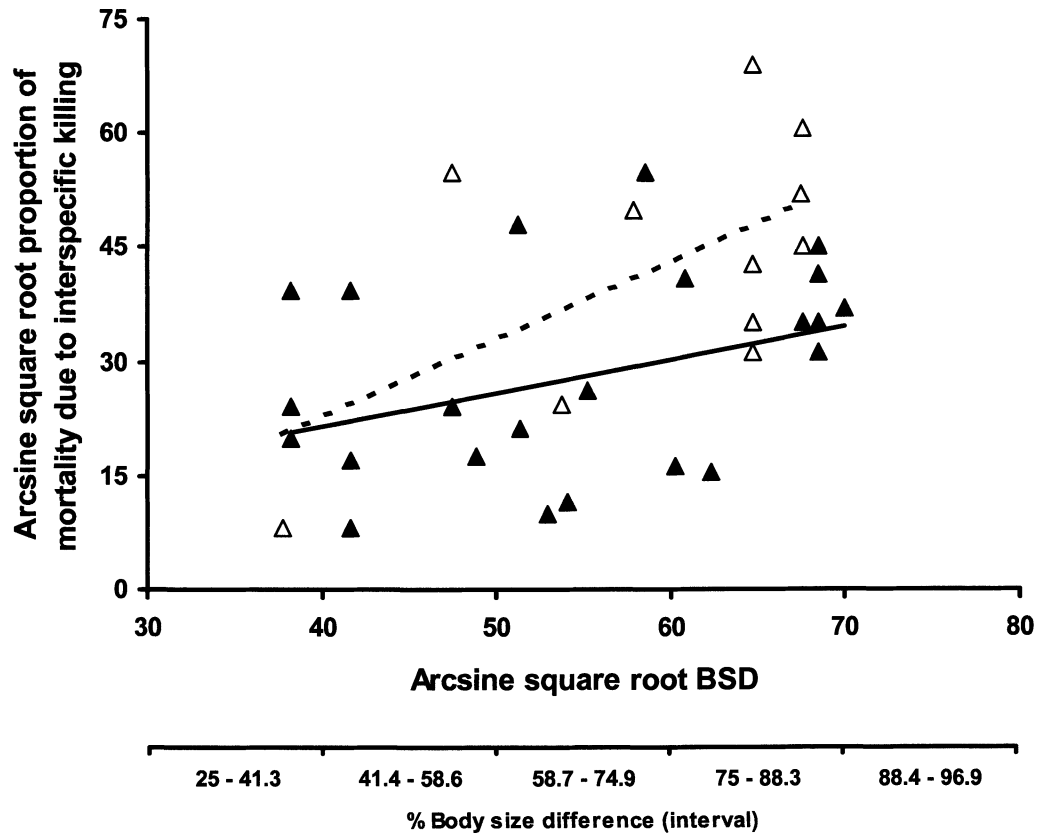


Figure 3: Effect of taxonomy on the relationship between intensity of interspecific killing and body size differences of interacting species pairs. As body size differences increase, the intensity of interspecific killing increases more sharply for same-family species pairs (*dashed line*) than for different-family species pairs (*solid line*). Open triangles represent same-family species pairs; filled triangles represent different-family species pairs. The secondary X-axis represents percentage differences in body size of the opponents, obtained from back-transforming the arcsine $\sqrt{\text{BSD}}$ values.

not significantly different between same- and different-family species pairs (table 3).

Predatory Habits and Tooth Morphology

The frequency distribution of interspecific killing as a function of predatory category differed significantly from expected values. More predaceous carnivores participated in interspecific killings more than expected, and less predaceous carnivores participated less than expected ($G_c = 15.5$, $df = 1$, $P < .001$; fig. 5A). Further, more predaceous carnivores interacted with species in the same category more than expected, whereas less predaceous carnivores showed the opposite trend ($G_c = 16.5$, $df = 1$, $P < .001$; fig. 5B). Finally, killing interactions involving only more predaceous carnivores were independent of taxonomy at the family level ($G_c = 1.9$, $df = 1$, $P = .17$; fig. 5C).

Discussion

Interspecific killing events between mammalian carnivores are not random; they are more likely to occur between species with high dietary overlap and when body size differences of potential competitors fall within a specific range. Further, species with teeth adapted to kill and consume vertebrate prey are more likely to be involved in agonistic encounters. Because body size, diet, and dentition are generally similar within families, interspecific killing is not independent of taxonomy at the family level, although results on diet and dentition were equivocal.

Body Size, Interspecific Killing, and Diet Overlap

Both frequency and intensity of killing increased steadily and reached maxima when the larger species was 2–5.4 times the mass of the victim (figs. 1, 3). We hypothesize that when the ratio of body sizes is <2 , the likelihood of the killer being injured or killed is prohibitive (but see

Table 3: Mean diet overlap for sympatric carnivore species pairs as a function of taxonomic relatedness at the family level and body size difference–frequency of killing category

	Category			Marginal means
	Small	Intermediate	Large	
Within families	53.3 $\pm$ 3.8 (n = 30)	43.2 $\pm$ 3.1 (n = 54)	26.9 $\pm$ 6.3 (n = 13)	44.2 $\pm$ 2.4 ^A
Between families	49.4 $\pm$ 4.2 (n = 27)	48.7 $\pm$ 2.5 (n = 89)	20.5 $\pm$ 4.2 (n = 30)	43.0 $\pm$ 2.1 ^A
Marginal means	51.5 $\pm$ 2.8 ^B	46.6 $\pm$ 2.0 ^B	22.4 $\pm$ 3.5 ^C	

Note: Values are percentages $\pm$ 1 SE. Small = small difference in body size, low frequency of killing; intermediate = intermediate difference in body size, high frequency of killing; large = large difference in body size, low frequency of killing. $F_{\text{taxonomy}} = 0.2$; $df = 1, 237$; $P = .65$. $F_{\text{category}} = 17.8$; $df = 2, 237$; $P < .001$. $F_{\text{interaction}} = 1.4$; $df = 2, 237$; $P = .243$. Means with different superscripts differed at $\alpha' = .016$.

discussion of the influence of taxonomy below). Likewise, at ratios >5.4 , the benefit to the larger animal of killing the smaller competitor is small because of reduced niche overlap.

Our analyses partially support the view that carnivores tend to direct their attacks toward their closest dietary competitors (Polis et al. 1989). High dietary overlap was associated with frequent killing events, and killing interactions decreased abruptly when diet overlap was reduced. However, attacks were avoided when body sizes were too similar, even between competitors using similar food resources. We draw two main conclusions from these results. First, interspecific killing can result from overlap in the resources that competitors use; reports of fights over carcasses that result in death are common in the literature (e.g., Schaller 1972; Koehler and Hornocker 1991). Second, the occurrence of interference interactions as a consequence of niche overlap appears to be strongly mediated by body size differences between the contenders. Similar diets may lead competitors to similar habitats and increase the rate of interspecific strife, but relative body size of the opponents is the primary determinant of the occurrence of killing interactions.

Two other hypotheses besides resource overlap have been proposed to explain interspecific killing in carnivores. First, the killer may actively hunt and consume victims to obtain nutritional benefits (Palomares and Caro 1999). Available data, however, offer little support for this idea. Eaton (1979) reviewed the context under which 124 different interspecific strife events took place between carnivore species in Africa; only 22.5% of these observations were related to predation events. Sunde et al. (1999) compared the degree to which Eurasian lynxes (*Lynx lynx*) consumed foxes (*Vulpes vulpes*) and typical prey species (hares *Lepus timidus* and roe deer *Capreolus capreolus*). Their results showed that the proportion of fox carcasses left uneaten was significantly larger than that for the typical herbivorous prey, suggesting that lynxes killed foxes for some reason other than to ingest them. The second alternative argues that killing other carnivores reduces predation risk to the killer or its progeny through the removal

of a potentially reciprocal aggressor (Eaton 1979). Clearly, this behavior would be advantageous only if mutual killing existed; however, out of 89 pairs of species reported as being involved in lethal interactions, only five were found to participate in mutual killing (Palomares and Caro 1999). Although these two alternative hypotheses might partially explain killing behaviors under some circumstances, they appear inferior to the resource overlap hypothesis in explaining killing interactions.

Predatory Habits and Interspecific Killing

Predatory habits influenced the occurrence of lethal encounters. More predaceous carnivores were involved as killers and victims in 88% and 53%, respectively, of the 92 interacting species pairs analyzed. Further, killing events between more predaceous species were more frequent than expected from their overlapping ranges. These results are consistent with data reported by Palomares and Caro (1999); six out of the seven most common killer species they reported were identified as more predaceous by our analysis. Clearly, dental adaptations for killing prey predisposed carnivores to interspecific strife. This fact supports the prediction that species that had evolved weapons for reasons other than competition (i.e., to kill prey) favored an interference strategy in competitive interactions; the advantages conferred by these preadaptations to interspecific killing influence the risk-benefit ratio to the killer because species with morphological and behavioral traits evolved for killing prey should be able to inflict lethal damage on their competitors in a relatively safe and efficient way (Case and Gilpin 1974; Polis 1988).

Taxonomy and Its Relationship to Interspecific Killing and Diet Overlap

Taxonomy at the family level influenced the frequency and intensity of lethal encounters, but the strength of this relationship depended on the trait analyzed, with body size differences being more important than predatory habits. Body size differences were smaller for same-family species

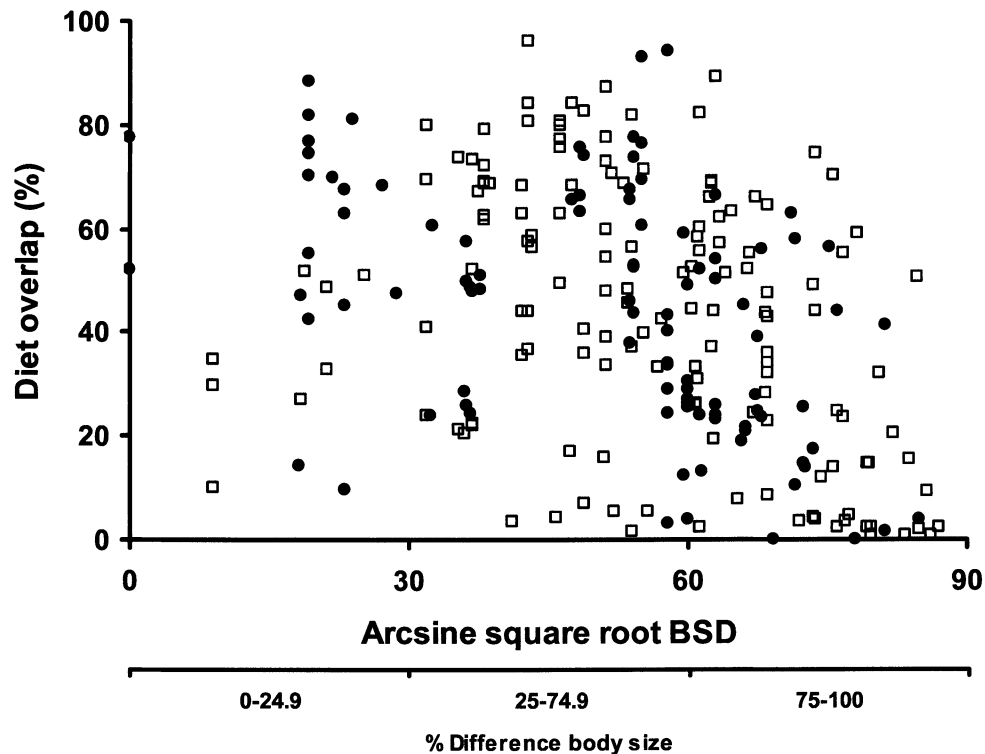


Figure 4: Scatter plot of diet overlap percentages and body size differences for carnivore species pairs. Circles represent same-family species pairs; squares represent different-family species pairs. For both groups, diet overlap is negatively related to body size difference.

pairs involved in interspecific killing than for species from different families involved in such killing, a hypothesized consequence of confamilials being more similar in body size (Gittleman 1985). For same-family species pairs, the relationship between observed and expected frequencies of interactions was as predicted at intermediate and large differences in body size. However, the overall pattern did not reach statistical significance because, contrary to our predictions, same-family pairs did not interact less than expected at small differences in body size. This suggests that for closely related species it is more difficult to avoid risky confrontations. In addition, at a given difference in body size, interspecific killing was more intense for same-family than for different-family species pairs (fig. 3). These trends are probably a consequence of closely related species being more constrained by similar ecological needs. Our results are the first support for a link between taxonomy and the strength of competition in the order Carnivora, at least as related to killing interactions.

Interference competition was more intense between same-family species pairs (fig. 3), but this was not the case for exploitative competition as measured by diet overlap (table 3; fig. 4). This finding is puzzling, inasmuch as we expected higher diet overlap for same-family species pairs;

it might relate to more complex interactions involving both mechanisms of competition. Interference interactions with the larger competitor displacing the smaller one to less productive microhabitats have been reported for closely related carnivores, particularly canids (Johnson et al. 1996). Microhabitat partitioning exposes the smaller species to a different availability of shared prey, probably resulting in a decrease in diet overlap (Johnson and Franklin 1994). Future studies should evaluate not only the diets of competing species but also prey availability within the microhabitats that competitors occupy; this would prove useful in deepening our understanding of how diet overlap varies as a function of taxonomic relationships.

Interspecific Killing, Character Displacement, and Community Structure

The idea that competition leads to character divergence dominates published research on coexistence between mammalian carnivores (Dayan et al. 1989, 1992; Jones 1997). Although character divergence appears to be a likely response when only exploitative competition occurs, our data suggest that in the face of lethal interference competition, increasing body size of the smaller member of a

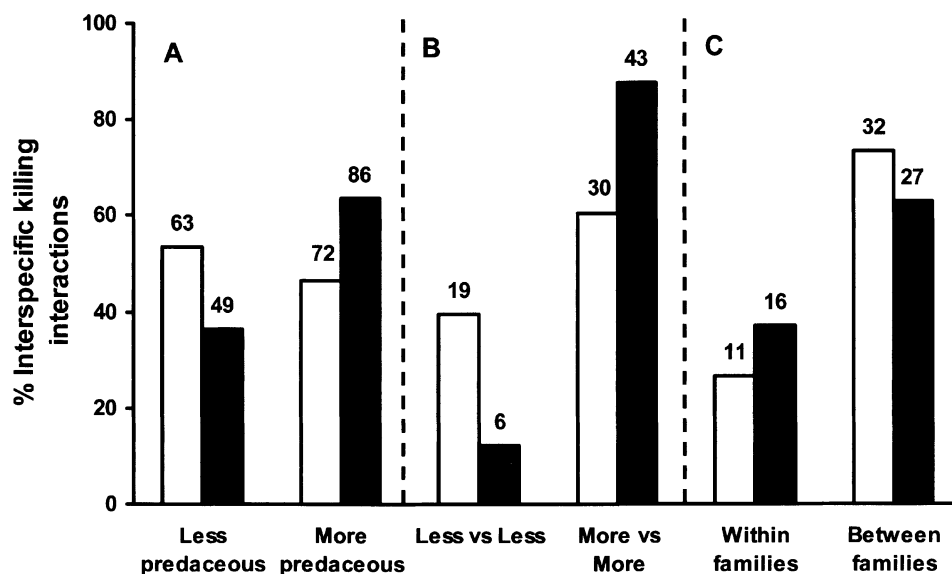


Figure 5: Expected (open bars) and observed (filled bars) frequencies of percentage of killing interactions as a function of predatory categories and taxonomy. For all statistical comparisons, α was set at 0.05; numbers of observed and expected observations are displayed above bars. *A*, Expected interactions were estimated from geographic range overlap of species regardless of their predatory habits; less predaceous carnivores (relative blade length [RBL] < 0.65) and more predaceous ones (RBL > 0.65) participated in killing interactions less and more than expected, respectively. *B*, Expected interactions were estimated from geographic range overlap of species belonging to the same predatory category; more predaceous species were more prone to interact with species in the same category than less predaceous ones were. *C*, Only more predaceous carnivores were analyzed; species in this predatory category interacted with species of the same or different families as expected from their overlapping ranges.

species pair, leading to character convergence, is a possible consequence (fig. 1). In fact, several theoretical models predict character convergence rather than divergence between potential competitors (reviewed in Dayan and Simberloff 2005). Although strong empirical support for this hypothesis is lacking, data on European minks (*Mustela lutreola*) suggest that this alternative is at least plausible. A significant increase in the body sizes of European minks was observed after the introduction of the larger American mink (*Mustela vison*) in Eastern Europe. This increment in body size in the smaller European minks has been interpreted as a response to direct aggression from the larger exotic species (Sidorovich et al. 1999).

Interspecific killing is an important mortality factor, accounting for as much as 89% of total deaths in the victim population (Kamler et al. 2003). We have shown that this force is strongly mediated by body size and morphology. We speculate that such forces exert powerful selective pressures, potentially causing character displacement among sympatric Carnivora, particularly in body size, and spatially structuring communities. For instance, character displacement (either divergence or convergence) in body size due to killing interactions probably affects the potential for exploitative competition and could ultimately influence habitat use and distribution of competing species. In the

long term, this should play an important role in determining patterns of geographic range overlap, as has been suggested for some Palearctic and British mammals (Letcher et al. 1994) and North American desert rodents (Bowers and Brown 1982).

Conclusions

Overall, carnivores conform to predictions derived from existing theory on interspecific killing. Relative body size, trophic relationships, and taxonomic relatedness were important factors governing the frequency, intensity, and direction of interspecific killing (Case and Gilpin 1974; Polis et al. 1989). Most interestingly, we found that even though interactions are frequent when food overlap is high, as body sizes of competitors become more similar, the frequency and intensity of killing interactions decreases, whereas the potential for food competition remains constant or increases. This counterintuitive finding is explained by the influence of relative body sizes of potential competitors on the outcome of interspecific killing. When the opponents have very similar body sizes, launching an attack carries high risks, and fighting tends to be avoided even if the potential benefits (i.e., freeing an important amount of resource) are large. The importance of this

extreme interaction as a factor influencing character displacement and community structure warrants further investigation.

Acknowledgments

We thank M. Bourgeois, K. Gerow, and C. Martinez del Río for helpful comments on an early version of this manuscript. The Smithsonian Institution's National Museum of Natural History granted us access to the mammal collection. E.D. was supported by the University of Wyoming and by the Fulbright Commission through a Fulbright Fellowship and a Professional Enhancement Grant.

Literature Cited

- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- Bowers, M. A., and J. H. Brown. 1982. Body size and coexistence in desert rodents: chance or community structure? *Ecology* 63:391–400.
- Bull, E. L., and T. W. Heuter. 2001. Survival, causes of mortality, and reproduction in the American marten in northeastern Oregon. *Northwestern Naturalist* 82:1–6.
- Buskirk, S. W. 1999. Mesocarnivores of Yellowstone. Pages 165–187 in T. W. Clark, A. Peyton Curlee, S. C. Minta, and P. M. Kareiva, eds. *Carnivores in ecosystems: the Yellowstone experience*. Yale University Press, London.
- Carbone, C., and J. L. Gittleman. 2002. A common rule for the scaling of carnivore density. *Science* 295:2273–2276.
- Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. *Biological Conservation* 110:67–75.
- Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. *Proceedings of the National Academy of Sciences of the USA* 71:3073–3077.
- Corbet, G. B. 1978. The mammals of the Palearctic region: a taxonomic review. British Museum, London, and Cornell University Press, Ithaca, NY.
- Corbet, G. B., and J. E. Hill. 1992. The mammals of the Indomalayan region: a systematic review. Oxford University Press, Oxford.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563–566.
- Dayan, T., and D. Simberloff. 2005. Ecological and community-wide character displacement: the next generation. *Ecology Letters* 8:875–894.
- Dayan, T., D. Simberloff, E. Tchernov, and Y. Yom-Tov. 1989. Inter- and intraspecific character displacement in mustelids. *Ecology* 70:1526–1539.
- . 1992. Canine carnassials: character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society* 45:315–331.
- Dragoo, J. W., R. D. Bradley, R. L. Honeycutt, and J. W. Templeton. 1993. Phylogenetic relationships among the skunks: a molecular perspective. *Journal of Mammalian Evolution* 1:255–267.
- Eaton, R. L. 1979. Interference competition among carnivores: a model for the evolution of social behavior. *Carnivore* 2:9–16.
- Eisenberg, J. F. 1989. *Mammals of the Neotropics*. Vol. 1. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago.
- Eisenberg, J. F., and K. H. Redford. 1999. *Mammals of the Neotropics*. Vol. 3. Ecuador, Peru, Bolivia, Brazil. University of Chicago Press, Chicago.
- Emmons, L. H., and E. Feer. 1997. *Neotropical rainforest mammals: a field guide*. University of Chicago Press, Chicago.
- Fedriani, J. M., T. K. Fuller, R. M. Sauvajot, and E. C. York. 2000. Competition and intraguild predation among three sympatric carnivores. *Oecologia (Berlin)* 125:258–270.
- Feldhamer, G. A., B. C. Thompson, and J. A. Chapman. 2003. *Mammals of North America: biology, management and conservation*. 2nd ed. Johns Hopkins University Press, Baltimore.
- Gittleman, J. L. 1985. Carnivore body size: ecological and taxonomic correlates. *Oecologia (Berlin)* 67:540–554.
- . 1986. Carnivore life history patterns: allometric, phylogenetic, and ecological associations. *American Naturalist* 127:744–771.
- Gittleman, J. L., and P. H. Harvey. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology* 10:57–63.
- Greene, H. W., and F. M. Jaksic. 1983. Food-niche relationships among sympatric predators: effects of level of prey identification. *Oikos* 40:151–154.
- Hall, E. R. 1981. *The mammals of North America*. Vol. 2. Wiley, New York.
- Johnson, W. E., and W. L. Franklin. 1994. Conservation implications of South American grey fox (*Dusicyon griseus*) socioecology in the Patagonia of southern Chile. *Vida Silvestre Neotropical* 3:16–23.
- Johnson, W. E., T. K. Fuller, and W. L. Franklin. 1996. Sympatry in canids: a review and assessment. Pages 189–218 in J. L. Gittleman, ed. *Carnivore behavior, ecology, and evolution*. Vol. 2. Cornell University Press, Ithaca, NY.
- Jones, M. 1997. Character displacement in Australian dasyurid carnivores: size relationships and prey size patterns. *Ecology* 78:2569–2587.
- Kamler, J. F., W. B. Ballard, R. L. Gilliland, P. R. Lemons, and K. Mote. 2003. Impacts of coyotes on swift foxes in northwestern Texas. *Journal of Wildlife Management* 67:317–323.
- Koehler, G. M., and M. G. Hornocker. 1991. Seasonal resource use among mountain lions, bobcats, and coyotes. *Journal of Mammalogy* 72:391–396.
- Krebs, C. J. 1989. *Ecological methodology*. Harper & Row, New York.
- Krebs, C. J., E. Loforth, J. Copeland, V. Banci, D. Cooley, H. Golden, A. Magoun, and R. Mulders. 2004. Synthesis of survival rates and causes of mortality in North American wolverines. *Journal of Wildlife Management* 68:493–502.
- Laurenson, M. K. 1995. Implications of high offspring mortality for cheetah population dynamics. Pages 385–399 in A. R. E. Sinclair and P. Arcese, eds. *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago.
- Letcher, A. J., A. Purvis, S. Nee, and P. H. Harvey. 1994. Patterns of overlap in the geographic ranges of Palearctic and British mammals. *Journal of Animal Ecology* 63:871–879.
- Lindström, E. R., S. M. Brainerd, J. O. Helldin, and K. Overskaug. 1995. Pine marten–red fox interactions: a case of intraguild predation? *Annales Zoologici Fennici* 32:123–130.
- Logan, K. A., and L. L. Sweanor. 2001. *Desert puma: evolutionary ecology and conservation of an enduring carnivore*. Island, Washington, DC.

- Macdonald, D. W., and P. Barret. 2004. *Mammals of Europe*. Princeton University Press, Princeton, NJ.
- McDonald, R. A. 2002. Resource partitioning among British and Irish mustelids. *Journal of Animal Ecology* 71:185–200.
- McNab, B. K. 1989. Basal rate of metabolism, body size, and food habits in the order Carnivora. Pages 335–354 in J. L. Gittleman, ed. *Carnivore behavior, ecology, and evolution*. Vol. 1. Cornell University Press, Ithaca, NY.
- Meester, J. A. J., I. L. Rautenbach, N. J. Dippenaar, and C. M. Baker. 1986. Classification of southern African mammals. *Transvaal Museum Monographs* 5:1–359.
- Mills, M. G. L., and H. C. Biggs. 1993. Prey apportionment and related ecological relationships between large carnivores in Kruger National Park. Pages 253–268 in N. Dunstone and M. L. Gorman, eds. *Mammals as predators*. Clarendon, Oxford.
- Novaro, A. J. 1997a. *Pseudalopex culpaeus*. *Mammalian Species* 558: 1–8.
- . 1997b. Source-sink dynamics induced by hunting: a case study of Culpeo foxes on rangelands in Patagonia, Argentina. PhD diss. University of Florida, Gainesville.
- Nowak, R. M. 1999. *Walker's mammals of the world*. Vol. 2. 5th ed. Johns Hopkins University Press, Baltimore.
- Nowell, K., and P. Jackson. 1996. Wild cats: status survey and conservation action plan. World Conservation Union/Species Survival Commission Cat Specialist Group, Muri, Switzerland.
- Núñez, R. 1999. Hábitos alimentarios del jaguar (*Panthera onca*, Linnaeus 1758) y del puma (*Puma concolor*, Linnaeus 1771) en la Reserva de la Biosfera Chamela-Cuixmala, Jalisco, México. Tesis de Licenciatura, Universidad Michoacana de San Nicolás de Hidalgo, Morelia.
- Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. *American Naturalist* 153:492–508.
- Palomares, F., and M. Delibes. 1994. Spatio-temporal ecology and behavior of European genets in southwestern Spain. *Journal of Mammalogy* 75:714–724.
- Palomares, F., P. Gaona, P. Ferreras, and M. Delibes. 1995. Positive effects on game species of top predators by controlling smaller predator populations: an example with lynx, mongooses, and rabbits. *Conservation Biology* 9:295–305.
- Parera, A. 2002. Los mamíferos de Argentina y la región austral de Sudamérica. Ateneo, Buenos Aires.
- Pocock, R. I. 1951. Catalogue of the genus *Felis*. British Museum of Natural History, London.
- Polis, G. A. 1988. Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size-structured populations. Pages 185–202 in B. Ebenman and L. Persson, eds. *Size-structured populations*. Springer, Berlin.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Ray, J. C., and M. E. Sunquist. 2001. Trophic relations in a community of African rainforest carnivores. *Oecologia (Berlin)* 127:395–408.
- Redford, K. H., and J. F. Eisenberg. 1992. *Mammals of the Neotropics*. Vol. 2. Chile, Argentina, Uruguay, Paraguay. University of Chicago Press, Chicago.
- Reid, F. A. 1997. *A field guide to the mammals of Central America and southeast Mexico*. Oxford University Press, New York.
- Renkonen, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische Käferwelt der finnischen Bruchmoore. *Annales Zoologici Societatis Zoologicae Botanicae Fennicae Vanamo* 6:1–226.
- Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. *Journal of Mammalogy* 47:602–612.
- Schaller, G. B. 1967. *The deer and the tiger*. University of Chicago Press, Chicago.
- . 1972. *The Serengeti lion: a study of predator-prey relations*. University of Chicago Press, Chicago.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- . 1983. Field experiments on interspecific competition. *American Naturalist* 122:240–285.
- Sidorovich, V., H. Kruuk, and D. W. Macdonald. 1999. Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. *Journal of Zoology* 248: 521–527.
- Silva, M., and J. A. Downing. 1995. *Handbook of mammalian body masses*. CRC, Boca Raton, FL.
- SPSS. 1999. SPSS, release 10.0 for Windows. Chicago.
- Stuart, C., and T. Stuart. 1997. *Field guide to the larger mammals of Africa*. Struik, Cape Town.
- Sunde, P., K. Overskaug, and T. Kvam. 1999. Intraguild predation of lynxes on foxes: evidence of interference competition? *Ecography* 22:521–523.
- Tannerfeldt, M., B. Elmhagen, and A. Angerbjörn. 2002. Exclusion by interference competition? the relationship between red and arctic foxes. *Oecologia (Berlin)* 132:213–220.
- Thornton, W. A., and G. C. Creel. 1975. The taxonomic status of kit foxes. *Texas Journal of Science* 26:127–136.
- Van Valkenburgh, B. 1989. Carnivore dental adaptations and diet: a study of trophic diversity within guilds. Pages 410–436 in J. L. Gittleman, ed. *Carnivore behavior, ecology, and evolution*. Vol. 1. Cornell University Press, Ithaca, NY.
- Wilson, D. E., and D. A. M. Reeder. 1993. *Mammal species of the world: a taxonomic and geographic reference*. 2nd ed. Smithsonian Institution Press, Washington, DC.
- Yañez, J. L., J. C. Cardenas, P. Gezele, and F. M. Jaksic. 1986. Food habits of the southernmost mountain lions (*Felis concolor*) in South America: natural versus livestocked ranges. *Journal of Mammalogy* 67:604–606.
- Youngman, P. M. 1990. *Mustela lutreola*. *Mammalian Species* 362:1–3.
- Zar, J. H. 1998. *Biostatistical analysis*. 4th ed. Prentice Hall, Englewood Cliffs, NJ.

Associate Editor: Peter J. Morin

Editor: Jonathan B. Losos