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Carnivory in the Oligo-Miocene:
Resource Specialization, Competition, and Coexistence
Among North American Fossil Canids

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Biology

by

Mairin Francesca Aragonés Balisi

2018

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2018

ABSTRACT OF THE DISSERTATION

Carnivory in the Oligo-Miocene:
Resource Specialization, Competition, and Coexistence
Among North American Fossil Canids

by

Mairin Francesca Aragonés Balisi
Doctor of Philosophy in Biology
University of California, Los Angeles 2018
Professor Blaire Van Valkenburgh, Chair

Competition likely shaped the evolution of the mammalian family Canidae (dogs and their ancestors; order Carnivora). From their origin 40 million years ago (Ma), early canids lived alongside potential competitors that may have monopolized the large-carnivore niche—such as bears, bear-dogs, and nimravid saber-toothed cats—before becoming large and hypercarnivorous (diet of >70% meat) later in their history. This ecomorphological context, along with high phylogenetic resolution and an outstanding fossil record, makes North American fossil canids an ideal system for investigating how biotic interactions (e.g. competition) and ecological specialization (e.g. hypercarnivory) might influence clade evolution.

Chapter 1 investigates whether ecological generalization enables species to have longer durations and broader geographic range. I developed and applied a carnivory index to 100+

species, processing 3708 occurrences through a new duration-estimation method accounting for varying fossil preservation. A non-linear relationship between duration and carnivory emerged: both hyper- and hypocarnivores have shorter durations than mesocarnivores.

Chapter 2 tests the cost of hypercarnivory, quantified as elevated extinction risk. Large hypercarnivorous canids experienced extinction rates on par with other canids. However, in each canid subfamily, extinction rates rose after the first occurrence of large hypercarnivores, supporting the idea of hypercarnivory as a “macroevolutionary ratchet” for individual clades. Large hypercarnivores originated just over 10 Ma after the origin of Canidae, exhibiting constant diversification rates and peaking in richness around 12 Ma. Relationships emerge between diversification rates of canid subfamilies and temperature, suggesting future hypotheses to be investigated.

Chapter 3 quantifies functional morphology in 114 fossil canids and non-canid competitors from 40 to 15 Ma, testing for ecological congruence between continental and regional scales and whether ecomorphological disparity reflects taxonomic diversity. Disparity appears inversely related to diversity. All four geographic regions examined preserved a narrower range of ecomorphology than at the continental scale. These results suggest that partitioning dietary as well as geographic resources, despite constraints to size, permitted canids to minimize competition and diversify.

These macroecological and macroevolutionary studies of early canids and their potential competitors improve understanding of the resilience of the carnivore niche over long timescales, including periods of accelerated global change.

The dissertation of Mairin Francesca Aragonés Balisi is approved.

Michael Edward Alfaro

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University of California, Los Angeles

2018

I dedicated my master's thesis to the memory of my mother, Fe Aragonés Balisi, who gave me my first biology lesson, and to the memory of my grandfather, Benjamin Aragonés, who left me his *National Geographic* collection. I now dedicate my Ph.D. dissertation to my father, Mario Luczon Balisi, and my brother, John Paul Aragonés Balisi, who have supported me in the pursuit of this degree even when memory faltered.

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I am thankful that my Ph.D. brought me back to Southern California so that I could be close to my family after being away for nearly a decade. Thanks to my father, who always welcomes my visits and sends me back to Los Angeles with food, and who has given me absolute freedom, never judging my life decisions. Thanks to my brother, 12 years younger: we are both immigrant children who lost our mother, an awareness that keeps me grounded, because I need to succeed not only for my own sake but also to model for him that success is possible.

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I am grateful to friends. Too many people talk about how graduate students are depressed, about how graduate school is isolating. It's isolating from society—because how many people care about our thesis topics? Particularly in this city so dominated by the media industry: “No one moves to Los Angeles to become a paleontologist,” a Los Angeles paleontologist colleague said recently, or to become an academic in general. Graduate school is also isolating from our peers: we chip away at thesis topics so apparently specialized; who even would read these? Friends have been my antidote to this isolation.

I am lucky to have attended high school and college in the same state, retaining contacts from those life chapters: Hong Hoa, Jana, Linda, Minna, Natalie, Brandon, Sarah G, Yumi, Jenny, Shawn, Yan. A few Michigan associates moved to San Francisco, where they introduced me to other cool folks: Brennan, Cat, Eytan, Rocío, Tamara. I made and reconnected with acquaintances during two research visits to New York City: Dan, Elita, Mari, Sam G, Shaista. Los Angeles is a cultural hub and home to many folks, so comrades often pass through: Albert, Brian, Missy, Sam P, Tara, Theresa. The Internet also facilitates long-distance friendships: Alexa and many others who ‘like’ every social media post. These friends expressed curiosity in my work as a scientific and creative pursuit and, just as importantly, shared non-academic interests with me.

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- 2018 **Balisi, M.**, X. Wang, J. Sankey, J. Biewer, and D. Garber. Fossil canids from the Mehrten Formation, late Cenozoic of northern California. *Journal of Vertebrate Paleontology* 37(6). (doi:10.1080/02724634.2017.1405009)
- 2018 Wang, X., S. C. White, **M. Balisi**, J. Biewer, J. Sankey, D. Garber, and Z. J. Tseng. First bone-cracking dog coprolites provide new insight into bone consumption in *Borophagus* and their unique ecological niche. *eLife* 7:e34773. (doi:10.7554/eLife.34773)
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I.
DIETARY SPECIALIZATION
IS LINKED TO REDUCED SPECIES DURATIONS
IN NORTH AMERICAN FOSSIL CANIDS

Abstract

How traits influence species persistence is a fundamental question in ecology, evolution, and paleontology. We test the relationship between dietary traits and both species duration and locality coverage over 40 million years in North American canids, a clade with considerable ecomorphological disparity and a dense fossil record. Because ecomorphological generalization—broad resource use—may enable species to withstand disturbance, we predicted that canids of average size and mesocarnivory would exhibit longer durations and wider distributions than specialized larger or smaller species. Second, because locality coverage might reflect dispersal ability and/or survivability in a range of habitats, we predicted that high coverage would correspond with longer durations. We find a non-linear relationship between species duration and degree of carnivory: species at either end of the carnivory spectrum tend to have shorter durations than mesocarnivores. Locality coverage shows no relationship with size, diet, nor duration. To test whether generalization (medium size, mesocarnivory) corresponds to an adaptive optimum, we fit trait evolution models to previously generated canid phylogenies. Our analyses identify no single optimum in size or diet. Instead, the primary model of size evolution is a classic Cope's Rule increase over time, while dietary evolution does not conform to a single model.

Background

The potential to predict emergent species- and community-level patterns and processes from functional traits is of great ecological and evolutionary interest [1–3]. For example, which traits cause some species to be more widespread and last longer than others? Using geographic breadth and species longevity as measures of success, how do a species' traits interact to make it successful over evolutionary time?

In extant mammals, abundance, range size, and population size are measures of success that can be influenced by a variety of factors, such as body size [4,5], diet or prey choice [6], and dispersal ability [7]. Fossil ecosystems provide another dimension—time—and permit the analysis of taxon longevity in addition to geographic range as a metric of success. In this study, we examine the impact of body size and diet on patterns of success in the family Canidae of the order Carnivora, which spans over two orders of magnitude in mass [8] and varies widely in diet from hypocarnivores with diets comprising less than 50% meat, to mesocarnivores with diets comprising 50-70% meat, to hypercarnivores with diets comprising over 70% meat [9]. On an ecomorphological spectrum from generalization to specialization, small-bodied hypocarnivory and large-bodied bone-cracking hypercarnivory form opposite specialized extremes.

Ecomorphological specialization in body size

Body size exerts pervasive effects on a variety of traits, such as habitat selection and resource use. As these traits form a species' niche [10,11], they may ultimately influence interactions at various scales ranging from community species assembly to continental clade dynamics [12].

Because energetic requirements scale allometrically with body size, animals tend to specialize on prey sizes that maximize their net energy gain while foraging [13]. To sustain high

metabolic rates, small carnivorans and other small mammals spend most of their time foraging, specializing on high-energy foods—such as insects—that are available in sufficient supply and accompanied by low costs [12,14]. Additionally, small carnivorans are biomechanically and morphologically limited to small prey [15]; mid-sized and larger carnivorans are better equipped to eat a wider range of prey sizes [16]. Meanwhile, large predators specialize on large prey because small prey are insufficient to sustain the energetic costs of large size [13,15,17]. Therefore, while mammals on the size extremes might approach morphological and physiological constraints, mid-sized mammals are well within these limits [18,19].

Additionally, mid-sized mammals tend to inhabit a wide range of habitats, while large and small species are distributed relatively narrowly [20]. This is likely because small size limits the dispersal of small species, while the energetic costs associated with large size [17] constrains large species to live in habitats with high productivity. Small mammals also exhibit greater turnover among habitats, suggesting that—because of energetic and physiological constraints—they are limited by environmental variation or biotic effects more than are mid-sized and large mammals [12]. In these ways, medium size might be considered a generalist strategy, and small and large body sizes as specialist strategies.

Ecomorphological specialization in diet

Many previous workers have examined dietary ecomorphological specialization in extant and extinct carnivorans [9,21–24], including not only hypercarnivory but also hypocarnivory [25–28]. While hypocarnivores tend to have a varied diet, hypocarnivory—like hypercarnivory—constitutes an ecomorphological specialization for carnivorans, the earliest of whom originated with a full complement of teeth (6 molars, 8 premolars, 4 canines, 12 incisors). This ancestral dentition was equipped with blades to slice meat and basins to grind plant matter,

enabling early canids to be as omnivorous as raccoons today. This ecomorphologically generalized toolkit provided the foundation for carnivorans to diversify into a range of diets.

Over evolutionary time, carnivorans could deviate from this generalized mesocarnivorous morphology by modifying the toolkit, largely by tooth loss, to emphasize some functions over others. A few carnivoran lineages reduced their premolars but enlarged the grinding area, with some clades flattening and co-opting the blades as grinding surfaces, reducing their ability to process significant portions of meat: the hypocarnivorous specialization (e.g. bears). By losing posterior molars, other carnivoran lineages reduced grinding area and therefore their ability to process plant matter: the hypercarnivorous specialization (e.g. cats). A further specialization of hypercarnivory is bone-cracking, a behavior that provides access to nutritious marrow [29] but also requires a robust skull and dentition (e.g. hyenas) [30,31].

Because lost structures rarely re-evolve (Dollo's Law) [32], the loss of dental cusps and of teeth themselves is often irreversible. Lineages that have begun to venture down the path of ecomorphological specialization tend to be able to modify only features that remain. Therefore, carnivoran lineages that modify the mesocarnivorous morph—whether in the hyper- or hypocarnivorous direction—tend to become progressively more specialized over evolutionary time (Figure S1.1). As a consequence, relative to their ancestors, ecomorphological specialists may have reduced evolvability, or capacity to generate heritable phenotypic variation [33,34], which narrows their response to selection in evolutionary time.

Canidae

The fossil record of the carnivoran family Canidae includes a diversity of species that span and perhaps surpass the size and dietary spectrum of extant caniforms. Fossil canids (dogs) arose in North America in the late Eocene (~40 million years ago, Ma), radiating into over 130

species in three subfamilies [35–37]: the extant Caninae; and Hesperocyoninae and Borophaginae, both of which are extinct. Originating as small-bodied forms with omnivorous adaptations, Hesperocyoninae and Borophaginae evolved toward large size (> 90 kg) [38] and hypercarnivory prior to extinction, suggesting a macroevolutionary ratchet in which dietary specialization along with reduced population densities heightened extinction risk [23,39]. Preliminary work suggests that Caninae follows a similar trend over its recent history, raising the question of their current vulnerability to extinction.

Ecomorphological specialization is readily observable in the canid cranio-dentition. The most hypercarnivorous canids (e.g. *Enhydrocyon*, *Epicyon*) have drastically reduced or lost the grinding molars, losing a cusp on the grinding basin of the lower carnassial to co-opt the now-trenchant basin as an extension of the carnassial blade. Meanwhile, the most hypocarnivorous canids (e.g. *Cynarctoides*, *Cynarctus*) bear dentition quite odd for canids: instead of cusps that could hold or pierce vertebrate meat, their teeth bear ridges that converge on ungulate selenodont morphology: a specialization for chewing tough plant matter (Figure S1.2). The existence of large-bodied hypercarnivorous adaptations as well as less studied hypocarnivorous specializations makes fossil Canidae an ideal system within which to explore the effects of ecomorphological specialization on taxon success.

Aims

Previous work [39] has suggested that specialization for hypercarnivory heightened extinction risk in Hesperocyoninae and Borophaginae. However, these authors did not look at the opposite end of the spectrum: hypocarnivores. Additionally, this study found a positive correlation between carnivory and body size, but only a negative qualitative association—no significant statistical correlation—between carnivory and species duration [39]. Larger canids

tend to be more carnivorous, and more carnivorous canids appear to have shorter durations, but the signal is noisy. Here, we follow up on this work by a) refining estimates of duration, b) doubling the number of species analyzed, c) including the third canid subfamily, fossil Caninae, d) examining hypocarnivores as well as hypercarnivores, e) tracking a geographic metric of success, locality coverage, and f) analyzing the data within a phylogenetic context.

We test the null hypothesis that a) body size and b) diet (carnivory) have no relationship with either a) species duration, a measure of success in time, or b) occupancy or fossil locality coverage, a measure of success in space. We expect that generalized species of average size and mesocarnivorous diet will survive longer and have broader distributions than more specialized species because their flexibility allows them to better survive times of disturbance and exist over a wider range of environmental conditions. Moreover, using locality coverage (a measure of geographic range) as a proxy for dispersal ability, we predict that the combined effects of size, diet, and locality coverage will better describe patterns of duration than the individual and combined effects of size and diet alone. Lastly, if generalization were advantageous, then medium size and mesocarnivory would correspond to an adaptive optimum, and the best-supported evolutionary model for both body mass and carnivory would be a single-peak Ornstein-Uhlenbeck model, where species traits would be constrained around optimum values.

Methods

Calculating species traits

Body size

We estimated fossil canid body masses from the length of the lower first molar (m1L) using a previously published regression equation based on extant Canidae [40].

Carnivory

We collected measurements of six commonly used characters [27,41,42] of the skull, jaw, and dentition for a comparative dataset of 45 extant caniform and hyaenid species and a dataset of 131 fossil canid species. Following Van Valkenburgh *et al.* [39], we combined the species means of these characters into three ratios of dietary significance: RBL, relative blade length (trigonid blade length relative to total length of lower first molar); RUGA, relative upper grinding area (square root of upper molar grinding area relative to upper fourth premolar length); and JD/DL, jaw depth relative to dentary length. For species that we could not measure ourselves, we obtained character means or dietary indices from published work [35–37,39,43,44], permitting expansion of our analysis to a broad range of extant carnivorans and fossil canids. Because fossils are often fragmentary, recording all characters for all species was not possible; our largest sample size is 117 species for the characters RBL and m1L. The extant taxa, coded dietary categories, and references for dietary categories are in Table S1.1.

The dietary ratio JD/DL requires complete dentaries, which are often not available for fossil species. To maximize recovery of this ratio, we developed an equation relating the length of the lower first molar to dentary length for each canid subfamily and used this to estimate dentary length in species without complete dentaries (Supplementary Information), a process that revealed subtle differences in the jaw morphologies of the three subfamilies. In comparison to hesperocyonines and canines, borophagines—including smaller, putatively non-bone-cracking members of the subfamily—tend to have shorter jaws relative to the length of the lower first molar (Figure S1.3).

We ran principal components analysis (PCA) on the three ratios for the 45 extant taxa (Table S1.1) using the R function `prcomp()`, and used the first principal component axis as a

“carnivory index”. The variances of the ratios differ by an order of magnitude (median absolute deviations for extant-species ratios: RBL, 0.039; RUGA, 0.203; JD/DL, 0.027) and would be disproportionately weighted in a PCA using the covariance matrix. Because of this, we used the correlation matrix instead, which rescales and standardizes the data. The principal component analysis based on extant taxa of known diet generated a multivariate linear model, which we then used with the R function `predict()` to predict numerical values of the fossil taxa of unknown diet. These numerical predictions for extinct taxa were graphically superimposed onto the model of the extant taxa. In this visualization, extinct taxa are most similar in dietary ecomorphology to the closest-plotting extant taxa.

A discriminant function analysis would be appropriate if classifying taxa of unknown diet according to a comparative dataset of discrete categories; however, because extant dietary categories may not adequately describe fossil species’ dietary adaptations, we did not classify fossil taxa to the extant categories. Therefore, identification of dietary categories for extant taxa was only for visualization. While not correcting for phylogeny during preliminary data reduction (e.g. standard PCA) can produce misleading results in subsequent phylogenetic comparative analysis [45], phylogenetic PCA requires assuming an evolutionary model to generate the principal component scores, which may also distort subsequent phylogenetic comparative analysis if the true model differs from the assumed model [46]. Therefore, we performed standard PCA followed by phylogenetic comparative methods.

Calculating success in space and time for fossil canids

We compiled occurrence data for North American fossil canids from the Neogene Mammal Mapping Portal (NeoMap, <http://ucmp.berkeley.edu/neomap> [47,48]) and Fossilworks / Paleobiology Database (<http://www.fossilworks.org>; <http://www.paleobiodb.org>). We last

accessed the databases on March 24, 2017, cross-checking database records against the canid monographs by Wang *et al.* [35–37] and more recent occurrences in the literature [49–51]. In cases of overlap between the two databases, we used the occurrence record from NeoMap because NeoMap’s maximum and minimum age records, when cross-checked against the literature, were more precise than those of Fossilworks / the Paleobiology Database, which assigns dates based on the occurrence or locality’s time interval and therefore tends to be of more variable precision.

We calculated two emergent properties for each species: a) sampling-adjusted species duration, a measure of success in time, and b) maximum occupancy or locality coverage, a measure of success in space. We excluded singletons ($n = 23$), or species that occur at only one locality, because calculations of duration and locality coverage for these would be disproportionately biased by poor preservation. We also excluded extant species ($n = 8$), because their geographic ranges likely have been constrained by anthropogenic activities and structures. Altogether, 107 non-singleton extinct species were included in the maximum data set. These, the excluded singletons, and extant species totaled 3710 fossil occurrences ranging from 38.713 (+/- 0.951) to 0.0 (+/- 0.0) Ma.

Species duration

Because the fossil record does not preserve all individuals that have ever existed, the first appearance date (FAD) is unlikely to capture the first individual after a given species originated, and the last appearance date (LAD) is unlikely to capture the last individual before a given species goes extinct. To account for this incomplete preservation, we calculated sampling-adjusted species durations using the open-source Python program PyRate [52] and a Markov Chain Monte Carlo birth-death model run for the default setting of 10,000,000 iterations, with

the first 200,000 discarded as burn-in. This process yielded skewed distributions of times of speciation (TS, right-skewed) and extinction (TE, left-skewed) for each species. We chose the medians of these distributions as unbiased estimates of TS and TE [5], and calculated the sampling-adjusted duration for each species as median(TE) minus median(TS).

Maximum locality coverage (occupancy)

Similarly, because not all environments are conducive to fossilization, the fossil record likely captures only part of the geographic range that a species has occupied over its duration. Additionally, some fossil localities are clustered more closely than others, so that counting only the number of localities where a species is found would overestimate the range of species abundant at a given cluster even if the species is not actually widespread [6,53]. To account for preservational bias and clustering of localities, we divided the North American continent into standardized half-degree by half-degree “cells” and calculated occupancy as a proportion of the number of cells occupied by a given species out of the number of cells occupied by all canid species for a given time period [54,55]. Calculating geographic occupancy as a proportion of available localities for a given time interval provides results more robust than convex-hull or similar estimates of geographic range that may be sensitive to varying environmental constraints, such as ice sheets and changing sea level. We collected these data for 18 time-slices representing subdivisions of North American Land Mammal Ages (Table S1.2) and chose the time slice with the highest occupancy to represent maximum locality coverage for that species.

Statistics

To test for phylogenetic signal in the two intrinsic traits (body size, diet) and two emergent properties (duration, occupancy), we computed Pagel’s λ [56] and Blomberg’s K [57] using the R package `phytools` [58]. To account for phylogenetic signal if present, we

conducted phylogenetic generalized least squares (PGLS) analyses using the `gls()` function in the R package `nlme` [59], computing lambda using maximum likelihood, and the best tree from the set of 500 fossil canid phylogenies generated by Slater [43] (Figure S1.4). We compared results with Brownian motion ($\lambda=1$) and null ($\lambda=0$) models using AICc and small-sample Akaike weights.

Preliminary observations showed a triangular relationship between our carnivory index and species longevity, with peak longevity occurring at mesocarnivorous values. To quantify the relationship on either side of the peak—for hypocarnivorous and hypercarnivorous taxa—we divided the data along the median carnivory value and tested for a linear correlation between longevity and carnivory for less and more carnivorous taxa separately.

A linear relationship between two variables may be obscured if variance in the sample varies with the independent variable (heteroscedasticity), possibly because a third unaccounted-for variable confounds the signal. Heteroscedasticity violates the constant-variance assumption of linear regression; therefore, linear regression is inappropriate to use in this case. Despite having refined our estimates of duration by factoring in sampling, the variance in duration values differs along the carnivory axis, with mesocarnivorous values having not only the highest longevity but also the greatest variation in longevity. The confounding variable is likely fossil preservation, which tends to vary with body size (larger species are more likely to be preserved than smaller species) and geographic range size (species dispersed more widely, in a variety of environments of differing likelihoods of preservation, tend to be more widely preserved than more localized species). To quantify the relationship between longevity and specialization for the best-preserved species—i.e. the relationship between maximum potential longevity and carnivory—we used quantile regression (R package `quantreg` [60]), which identifies the

relationship between the response and predictor variables at certain quantiles (τ) [61–65]. In our case, linear regression (regression through the mean; $\tau = 0.5$) provides a good estimate of duration when carnivory is close to the extremes (hypo- and hypercarnivory) and duration is restricted to low values; but, as diet approaches mesocarnivory, variance in duration increases, and carnivory loses power to predict duration in a linear regression model. However, even though regression at $\tau = 0.5$ in this case does not provide useful information, regression at other quantiles may be meaningful. For this study, we modeled the slope of the relationship at $\tau = 0.6$, 0.7, 0.8, and 0.9; $\tau = 0.9$ represents the upper bound of the distribution, putatively when preservation is best. We bootstrapped the analysis for 10,000 replications to generate standard errors and p -values.

We explored the individual and combined effects of body mass, carnivory, and maximum locality coverage on duration by running nested linear regressions on a subset of 77 fossil canid species for which we could record all four variables. We compared the nested models using AICc, Akaike weights, and R^2 .

Models of trait evolution

To test if the evolution of body mass and carnivory in canids gravitated toward certain values (“optima”) or progressed by other modes, we used maximum likelihood to fit six models of trait evolution to observed body-size and carnivory values, with best fit determined using small-sample Akaike weights. The six models include Brownian motion (BM), Accelerating Decelerating (ACDC), Trend, Drift, Diversity Dependence (Div), and Ornstein-Uhlenbeck (OU). BM is the null phylogenetic model, a random walk with no consistent trends; change is independent of past character states. ACDC refers to a rapid trait divergence at the beginning of a clade followed by slowed evolution toward the tips of the clade. Trend is BM incorporating a

linear shift in evolutionary rate, while Drift is a trend toward larger or smaller trait values rather than rates. Div has rates varying as a function of past diversity [43], possibly resulting from competition increasing with species richness, which then propels trait convergence or divergence. Lastly, OU may be conceptualized as a “rubber band” model: species may evolve away from “optimal” values but would be constrained close to the optimum by the rubber band.

Slater [43] used a Bayesian fossil tip-dating approach on morphological data to generate a distribution of time-calibrated phylogenies for 121 canids, including extant and non-North American species. We pruned the phylogenies to the species also present in our fossil trait dataset (Figure S1.4). Slater’s time calibration uses species stratigraphic ranges recorded from Wang *et al.* [35–37], closely reflecting our species temporal ranges inferred directly from occurrence data using PyRate and checked also using the monographs by Wang *et al.* Using the 500 canid phylogenies randomly sampled by Slater from the posterior distribution, we fit constant-rate BM, ACDC, Trend, Drift, and OU models with the `fitContinuous()` function in the R package `geiger` [66], and the Div model with the `fitDiversityModel()` function in `phytools` [58]. Given previous work showing iterative occurrences of large body size and hypercarnivory within the three subfamilies [67], analyzing traits on the family level may conflate iterative occurrences and obscure relationships between ecological traits and success; therefore, we also analyzed trait evolution on subfamily trees extracted from the 500 randomly sampled phylogenies. We conducted statistical and phylogenetic analysis in R version 3.4.1 [68].

Results

Figure 1.1 shows the first two axes of the principal component analysis run on the three dietary indices (Table S1.1) of the extant comparative dataset. Species that score highly on the

first axis, such as the three extant hyaenids (*Crocuta crocuta*, *Hyaena brunnea*, and *Hyaena hyaena*), have high relative blade length, deep jaws relative to dentary length, and small upper molar grinding areas relative to upper fourth premolar length. PC 1 therefore ranges from less carnivorous on the left to more carnivorous on the right. PC 2 approximates durophagy—consumption of tough food items, such as bone—with less durophagous above and more durophagous below. Because the loading of RUGA (grinding area on the upper teeth relative to upper carnassial length) runs nearly parallel to PC 1 (Figure S1.5), it contributes little to PC 2; instead, PC 2 is driven by long blades on the positive side and deep jaws on the negative side.

The three dietary indices were preserved in 93 fossil canids of unknown diet (hollow shapes), whose predicted principal component values are superimposed onto the extant plot (Figure 1.1). While most extant caniform carnivorans lie on the left of the plot, most fossil canids lie on the right, suggesting that fossil canids tend to have been more carnivorous and more durophagous than extant caniforms. In addition, the dietary diversity in fossil canids tends to surpass that of extant canids (filled squares, Figure 1.1) and is shifted towards the robust morphologies of the wolverine (*Gulo gulo*) and the hyaenids.

Rather than a linear correlation, a triangular pattern emerges when duration is plotted against carnivory index (Figure 1.2A). Our dataset shows short durations occurring at values throughout the carnivory index; short durations are equally likely for less and more carnivorous canids. However, long durations occur only at mid-carnivory values. The upper left and upper right quadrants of Figure 1.2A—the quadrants for long-lived hypo- and hypercarnivores, respectively—remain empty. There are three outliers on the hypercarnivorous side that are long-lived for their degree of specialization: the hesperocyonines *Enhydrocyon basilatus* (estimated duration = 6.16 Ma) and *Enhydrocyon crassidens* (8.73 Ma), and the borophagine *Epicyon*

haydeni (6.83 Ma). These durations are still much shorter than the maximum duration, represented by the mesocarnivore *Cormocyon copei* at 13.07 Ma. A gap in carnivory values separates the rest of the canid distribution from the three most hypocarnivorous species, which are relatively short-lived: the borophagines *Cynarctus crucidens* (2.58 Ma) and *Cynarctoides luskensis* (2.72 Ma), and the canine *Urocyon minicephalus* (1.59 Ma).

Without correcting for phylogeny, there is a weak but significant negative relationship between body mass and species duration (Figure 1.2B: $R^2 = 0.060$, $p = 0.013$). However, this significance disappears after phylogenetic corrections (PGLS under BM with λ estimated by ML; $\lambda = 0.853$, $p = 0.107$). No linear relationship is apparent between carnivory and species duration, whether using raw trait values ($R^2 = 0.012$, $p = 0.942$) or correcting for phylogeny (PGLS under BM with λ estimated by ML; $\lambda = 0.879$, $p = 0.297$). Maximum locality coverage also has no relationship with either body mass or carnivory (Figure 1.2C: $R^2 = 0.009$; $p = 0.584$; Figure 1.2D: $R^2 = 0.002$; $p = 0.37$).

We analyzed how species duration may vary with specialization on both dietary extremes (Figure 1.3). The relationship between duration and specialization in less carnivorous taxa, having no phylogenetic signal, was analyzed by an Ordinary Least Squares (OLS) regression; more carnivorous taxa, having moderate phylogenetic signal ($\lambda=0.538$), was analyzed by PGLS. On the more-carnivorous side, we excluded the three outlying hypercarnivorous species (*Enhydrocyon basilatus*, *Enhydrocyon crassidens*, and *Epicyon haydeni*) from the regression analyses (resulting $n = 40$). The OLS result for lesser carnivory showed a negative association but no significant relationship between duration and hypocarnivorous specialization ($p > 0.05$); the PGLS result for greater carnivory showed a significant negative relationship between duration and hypercarnivorous specialization ($p = 0.044$).

We reinforced the standard regressions and accounted for heteroscedasticity by using quantile regressions. The relationship between duration and specialization for lesser carnivory is not significant at any quantile (τ), although duration tends to decrease as specialization approaches less carnivory; this tendency is strongest although still not significant at $\tau = 0.8$ (Table 1.2A; Figure 1.3A). The tendency of duration to decrease with specialization for greater carnivory is more definitive: at $\tau \geq 0.8$, like the phylogenetic regression, there is a significant negative relationship between duration and greater carnivory (Table 1.2B; Figure 1.3B).

Size and diet together—not as isolated traits—influence an animal’s ecology, so it is not surprising that a model combining these two traits (logmass, carnivory) better explains species duration than does each of them separately (Table 1.3; Figure 1.4; hypercarnivorous outliers included). Visualizing duration color-mapped onto bivariate plots of carnivory and body mass highlights key differences between hypocarnivory and hypercarnivory, the two extremes of dietary specialization examined here. The distribution defined by body mass, lesser degrees of carnivory, and duration is straightforward: duration tends to decline with increasing mass and with increasing hypocarnivory (Figure 1.4A). The distribution defined by body mass, greater degrees of carnivory, and duration is more nuanced, showing longer durations at the highest carnivory values even as the prevailing trend is for decreased duration with higher carnivory (Figure 1.4B) and suggesting that large body size combined with hypercarnivory biases species to shorter durations, to a point.

Could high occupancy allow a dietary specialist to last in the record longer, despite a heightened extinction risk that may be conferred by its specialization? Adding locality coverage to the interactive model as a proxy for dispersal ability increases the model’s explanatory power (Table 1.3). Despite high carnivory, species may endure when they have small to medium body

size and wide geographic distribution: a combination of dietary specialization and geographic generalization.

The Ornstein-Uhlenbeck “rubber band” model does not fit the evolution of mass or carnivory in the sampled canids. For the family Canidae sampled together, the best supported model of **body mass** evolution is Drift, a directional shift in trait values (Figure 1.5A). This shift is positive (Table S1.2), corroborating previous work documenting size increase in Canidae over time in a classic example of Cope’s Rule [39]. Restricting the analysis to the subfamily level, the best supported model of body mass evolution in both Hesperocyoninae and Borophaginae is again Drift toward larger body sizes; Drift is also the best supported model of body mass evolution in fossil Caninae, although more equivocally than in the two extinct subfamilies (Figure 1.5A). Including extant species in Caninae, no single model emerged to support the evolution of body mass. For the family Canidae sampled together, all tested models are poorly supported for the evolution of **carnivory** (Figure 1.5B). Within Hesperocyoninae, the two best supported models are BM and Drift. Within Borophaginae, ACDC is the best supported model for the evolution of carnivory; the positive rate change parameter indicates an accelerating rate through time, or a late burst of evolution (Table S1.3). Within fossil Caninae, BM is marginally favored over the other models (Figure 1.5B), a result that also emerges when extant Caninae are included.

Discussion

Specific to canids, Van Valkenburgh *et al.* [39] showed a qualitative association, although no statistical correlation, between the evolution of large body size, a dietary shift to hypercarnivory, and a decline in species durations in Hesperocyoninae and Borophaginae, the

two extinct subfamilies of North American canids. This lack of correlation stemmed in part from asymmetrical bias in the fossil record between short durations and long durations. Long durations are more verifiable as being long; short durations may be truly short or merely a signal of poor preservation. This asymmetry is visible as heteroscedasticity in the “filled triangle” pattern emergent in the relationship between carnivory and duration (Figure 1.2A), where a triangular upper bound is clearly delineated but a lower bound is not. Focusing on the upper bound of the data using quantile regression enabled us to bypass this asymmetry.

Body mass alone, when corrected for phylogeny, was not implicated as a correlate of **duration**. However, the dietary measures examined tend to correlate with body mass (Figure S1.6) because prey size correlates with predator size. Fox-sized canids, for example, may be hypercarnivorous but generally do not hunt prey larger than themselves, a distinction stemming from energetic requirements differing between species below and above ~21 kg [16,44]. Therefore, the jaws of fox-sized canids are proportioned less robustly than wolf-sized canids. Fox-sized canids also do not have the same bone-cracking adaptations as hyenas and hyena-like borophagine dogs [31], and consequently their jaws are relatively long and shallow rather than short and deep. While most of the measures were standardized to account for body mass (e.g. RBL is a measure of the lower slicing blade divided by lower carnassial length, our proxy for mass), the morphological differences between hunters of small versus large prey remain in proportions of linear traits, such as relative jaw depth.

Our analysis makes visible two patterns in the relationship between **duration** and **diet**: one for more carnivorous species and another for less carnivorous species. Rather than a simple linear correlation between duration and carnivory, the relationship is between duration and *specialization*: the more diet-specialized a species, either for greater or lesser carnivory, the

shorter its duration in the fossil record is likely to be. While only the negative relationship between duration and hypercarnivorous specialization is significant, duration and hypocarnivory are still negatively associated. The lack of statistical support for this association may stem from the sparse record of species between the mesocarnivorous and hypocarnivorous range. Few species have values between one and two on the hypocarnivory scale (Figure 1.3). This is likely because many putatively less-carnivorous species—e.g. several members of the genera *Cynarctoides* (4 of 8 species), *Leptocyon* (3 of 9), *Phlaocyon* (5 of 10), and *Urocyon* (3 of 5)—were preserved as fossils too fragmentary for calculation of the carnivory index. This poor preservation may itself suggest reduced persistence conferred by hypocarnivorous specialization.

Body size and dietary specialization were not correlated with **locality coverage** as estimated here. This result runs contrary to expectations that large species would have larger geographic ranges than small taxa because of better dispersal ability afforded by large body size, or that hypercarnivores would have larger ranges than hypocarnivores because meat is a constant resource not as restricted by environment as plant matter. Accurately quantifying geographic range is a particular challenge in the fossil record; other geographic measures such as abundance, or other methods of quantifying range, may provide better estimates of geographic success [6,54,55] and are currently being evaluated in a follow-up study. The moderate positive correlation between locality coverage and duration might reflect taphonomy in that species preserved over longer timespans also may be preserved more broadly. However, it likely also represents a signal of biological success that might be resolved with better quality data: the same generalist traits that lead to longer durations might also lead to greater geographic coverage.

In modern ecosystems, species success is often defined as large geographic range, high population density, large group size, and high reproductive rate. The interaction of these traits

with each other complicates predictions of extinction risk [69]. Risk does not scale simply with body size; rather, complex interactions among correlated traits produce multiple pathways to extinction or persistence. For example, smaller species tend to have lower extinction risk than do larger species, in part because small mammalian body size correlates with large litter size and population size [70]. In the current analysis, smaller canid species also tend to live longer than larger canids, although the correlation disappears when corrected for phylogeny. Litter size is a trait that we are unable to measure in the fossil record, and thus remains an unmeasured possible covariate in our study.

We identified no movement toward a single evolutionarily optimal value for body size or carnivory across all Canidae. Rather, Cope's Rule—a phenomenon of body size increase within a lineage over time, well-documented among North American canids [39,71]—is echoed in our selection of the Drift model with a positive parameter for the body mass evolution of all canids, hesperocyonines only, and borophagines only (Figure 1.5; Table S1.3). This model is selected more ambiguously in fossil Caninae likely because of biogeographic differences: Caninae began to migrate outside North America approximately 7 Ma, while the two subfamilies remained endemic to the continent for the entirety of their durations [35–37]. It is possible that, had we not restricted our analyses to North America and instead included all fossil canids globally, we might have recovered an unambiguous Drift model as with the two extinct subfamilies. However, the expansion of habitats available to Caninae upon migration likely impacted trait evolution in this clade.

For all Canidae and Hesperocyoninae only, no single model was best-supported for the evolution of carnivory. The conflation of different subfamily-level patterns likely caused the lack of resolution at the family level. Within Borophaginae, the best supported model is ACDC, with

a positive parameter indicating accelerating rate of evolution over time (Table S1.3). The selection of ACDC may be a statistical artifact: if traits evolved under constant-rate multivariate Brownian motion, but these traits were then reduced by standard rather than phylogenetic PCA as we have done, the first few principal component axes will appear to have evolved by an Early Burst process, a specific case of ACDC where rates decelerate through time [46]. Future studies of a multivariate trait such as carnivory would benefit from truly multivariate models of trait evolution. However, this result likely signals the directionality of the evolution of carnivory in Borophaginae: despite the early dominance of hypocarnivores in this subfamily, preliminary work shows that after approximately 16 Ma the subfamily shows a concerted movement toward hypercarnivory. The selection of Trend with a positive parameter—a linear increase in evolutionary rate—as the second-best model supports the primary selection of the ACDC model in suggesting increase in evolutionary rate of borophagine carnivory over time. Determining rate-shift points would represent a subsequent step toward identifying potential ecological drivers of the extreme dietary adaptations in this clade.

While examining abiotic influences such as topographic complexity [72–74] is outside the scope of this study, research into the diversity dynamics of specialization would benefit from teasing apart possible interactions between abiotic and biotic processes in determining species success [4]. The spread of grasslands and opening of habitats after the Middle Miocene Climatic Optimum [75,76] likely impacted trait evolutionary rate, potentially accelerating the rise of large-bodied, bone-cracking, and cursorial morphologies. Future work aims to test these hypotheses. The impact of congener competition on the ranges of young radiating lineages of mammalian carnivores, which our current dataset and methods lack the resolution to address, also presents an exciting opportunity for future study.

Conclusion

A negative relationship exists between species duration and dietary specialization, although no phylogenetically informed relationship exists between duration and body mass, between occupancy and body mass, and between occupancy and diet. Bone-cracking hypercarnivores tend to have shorter durations than small mesocarnivores, although we also identify an inflection point in the hypercarnivore morphospace beyond which some species appear to have surpassed constraints conferred by hypercarnivory. The negative relationship between duration and specialization may be mediated by geographic range and dispersal ability in an interplay between geographic range and taxonomic duration [77]: if they could disperse, even species of narrow resource use can be successful in time.

Jack of all trades or master of one? Our study of macroecological patterns in North American fossil canids provides evidence that small to medium-sized species with more generalized diets persisted longer on average than both small hypocarnivores and large bone-cracking hypercarnivores. The apparently greater success of dietary generalists relative to specialists may result from the generalist ability to take advantage of a wider range of resources and thereby better withstand environmental and biotic perturbations.

Tables and Figures

Table 1.1. Summary statistics and measures of phylogenetic signal for the two intrinsic traits and two emergent properties.

Metric	Median	Median absolute deviation	Pagel's λ	Pagel's λ p	Blomberg's K	Blomberg's $K p$
\log_{10} body mass	$\log_{10}0.971$ (9.354 kg)	$\log_{10}0.383$ (7.611 kg)	0.992	$7.42e-39$	3.06	0.001
Carnivory	0	0.8827668	0.891	$4.89e-16$	0.947	0.001
Duration	3.688 Ma	3.117 Ma	0.891	0.00291	0.34	0.012
maxLocCover	0.1483515	0.1272834	$6.61e-05$	1	0.262	0.279

Table 1.2. Quantile regression results at four levels comparing species duration as a function of degree of specialization. All canids below the median carnivory value are less carnivorous (A); above the median, more carnivorous (B).

Intercept					Slope				
Quantile (τ)	Value	SE	T	p	Value	SE	t	p	
A. Less carnivorous taxa									
0.6	6.127	1.854	3.304	0.002	-1.740	1.841	-0.945	0.350	
0.7	6.863	1.700	4.036	0.000	-1.022	1.975	-0.517	0.608	
0.8	9.274	1.869	4.963	0.000	-3.085	2.535	-1.217	0.230	
0.9	10.409	1.983	5.248	0.000	-3.926	3.259	-1.205	0.235	
B. More carnivorous taxa									
0.6	4.767	1.297	3.677	0.001	-0.975	0.963	-1.012	0.318	
0.7	6.908	1.749	3.949	0.000	-2.174	1.318	-1.649	0.107	
0.8	8.884	1.792	4.960	0.000	-3.280	1.453	-2.257	0.030	
0.9	11.474	1.336	8.591	0.000	-4.656	1.184	-3.933	0.000	

Table 1.3. Results from the nested linear regressions concerning effects of body mass, carnivory, maximum locality coverage, and their combinations on the durations of 77 fossil canid species.

Variable	loglik	AICc	AICw	Adj. R^2	p
Body mass only	-182.2848	368.7387	0.035979806	0.0511	0.02952
Carnivory only	-184.7015	373.5720	0.003210084	-0.01295	0.7965
maxLocCover only	-182.8161	369.8013	0.021150124	0.03738	0.05409
Body mass and carnivory	-178.0272	364.6341	0.280132853	0.1301	0.005135
Body mass, carnivory, and maxLocCover	-172.3531	362.9215	0.659527134	0.2085	0.00178

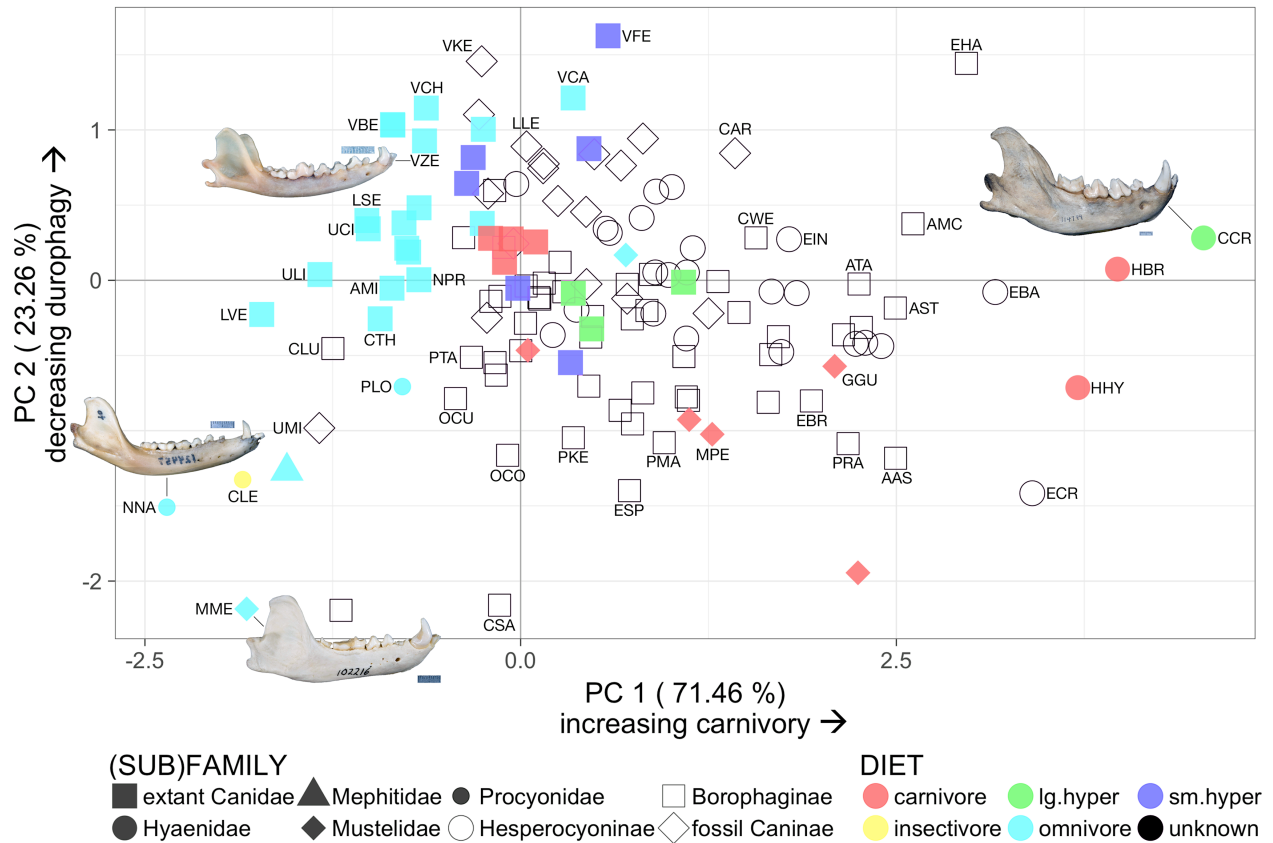


Figure 1.1. First two axes of principal component analysis run on three dietary indices of 45 extant caniform carnivorans and hyaenids, with extinct canids superimposed. “lg.hyper” denotes large hypercarnivores; “sm.hyper” denotes small hypercarnivores. Species are labeled where space permits. Representative images of lower jaws are included to illustrate extreme ecomorphologies. Species abbreviations: AAS, *Aelurodon asthenostylus*; AMC, *Aelurodon mcgrewi*; AMI, *Atelocynus microtis*; AST, *Aelurodon stirtoni*; ATA, *Aelurodon taxoides*; CAR, *Canis armbrusteri*; CCR, *Crocota crocuta*; CLU, *Cynarctoides luskensis*; CLE, *Conepatus leuconotus*; CSA, *Cynarctus saxatilis*; CTH, *Cerdocyon thous*; CWE, *Carpocyon webbi*; EBA, *Enhydrocyon basilatus*; EBR, *Euoplocyon brachygnathus*; ECR, *Enhydrocyon crassidens*; EIN, *Ectopocynus intermedius*; EHA, *Epicyon haydeni*; ESP, *Euoplocyon spissidens*; GGU, *Gulo gulo*; HBR, *Hyaena brunnea*; HHY, *Hyaena hyaena*; LLE, *Leptocyon leidy*; LSE, *Lycalopex sechurae*; LVE, *Lycalopex vetulus*; MME, *Meles meles*; MPE, *Martes pennanti*; NNA, *Nasua nasua*; NPR, *Nyctereutes procyonoides*; OCO, *Otarocyon cooki*; OCU, *Oxetocyon cuspidatus*; PKE, *Paracynarctus kelloggi*; PLO, *Procyon lotor*; PMA, *Psalidocyon marianae*; PRA, *Protepicyon raki*; PTA, *Phlaocyon taylori*; UCI, *Urocyon cinereoargenteus*; ULI, *Urocyon littoralis*; UMI, *Urocyon minicephalus*; VBE, *Vulpes bengalensis*; VCA, *Vulpes cana*; VCH, *Vulpes chama*; VFE, *Vulpes ferrilata*; VKE, *Vulpes kernensis*; VZE, *Vulpes zerda*. Specimen images from Animal Diversity Web (<http://www.animaldiversity.org/>).

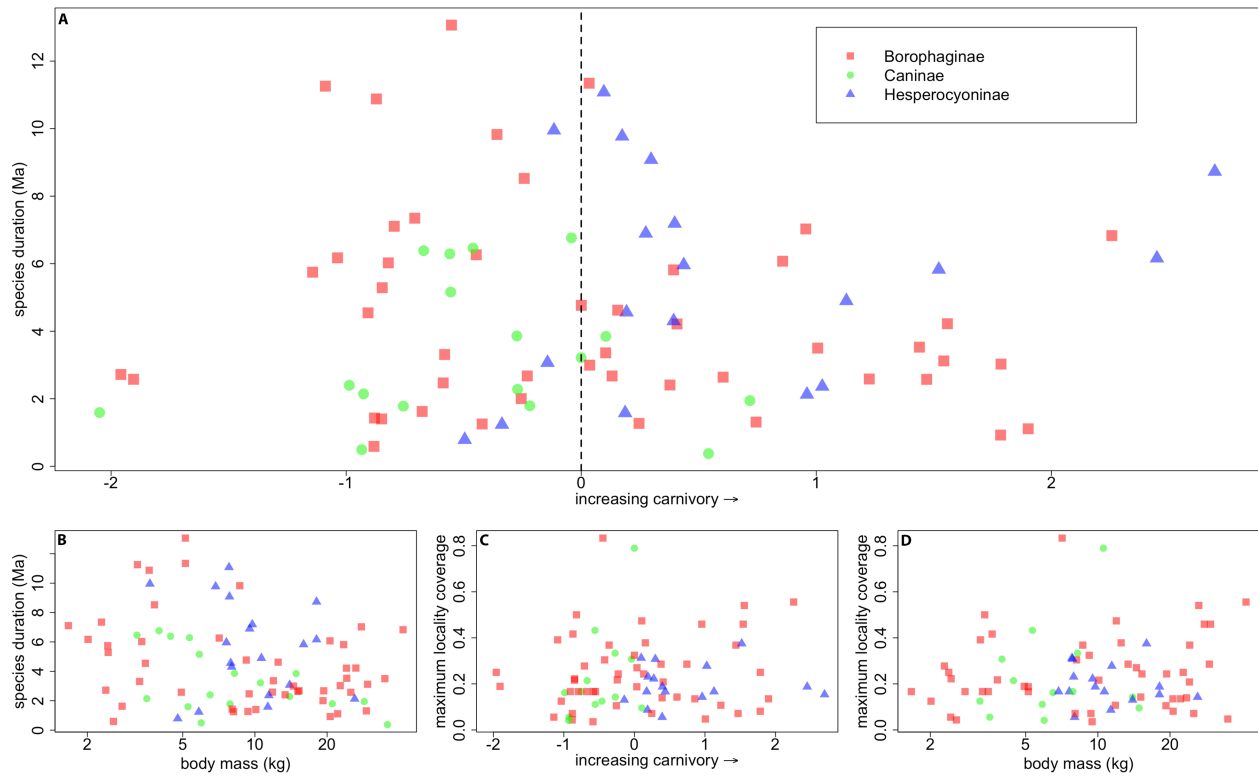


Figure 1.2. Bivariate plots of emergent properties against intrinsic traits of North American fossil canids. **A**, species duration (Ma) against carnivory increasing to the right. Carnivory is PC 1 re-centered around median = 0 (dashed line). Excepting a few outliers, the upper bounds of the data form a triangular shape. **B**, species duration against log10 body mass. **C**, maximum locality coverage against carnivory increasing to the right. **D**, maximum locality coverage against log10 body mass.

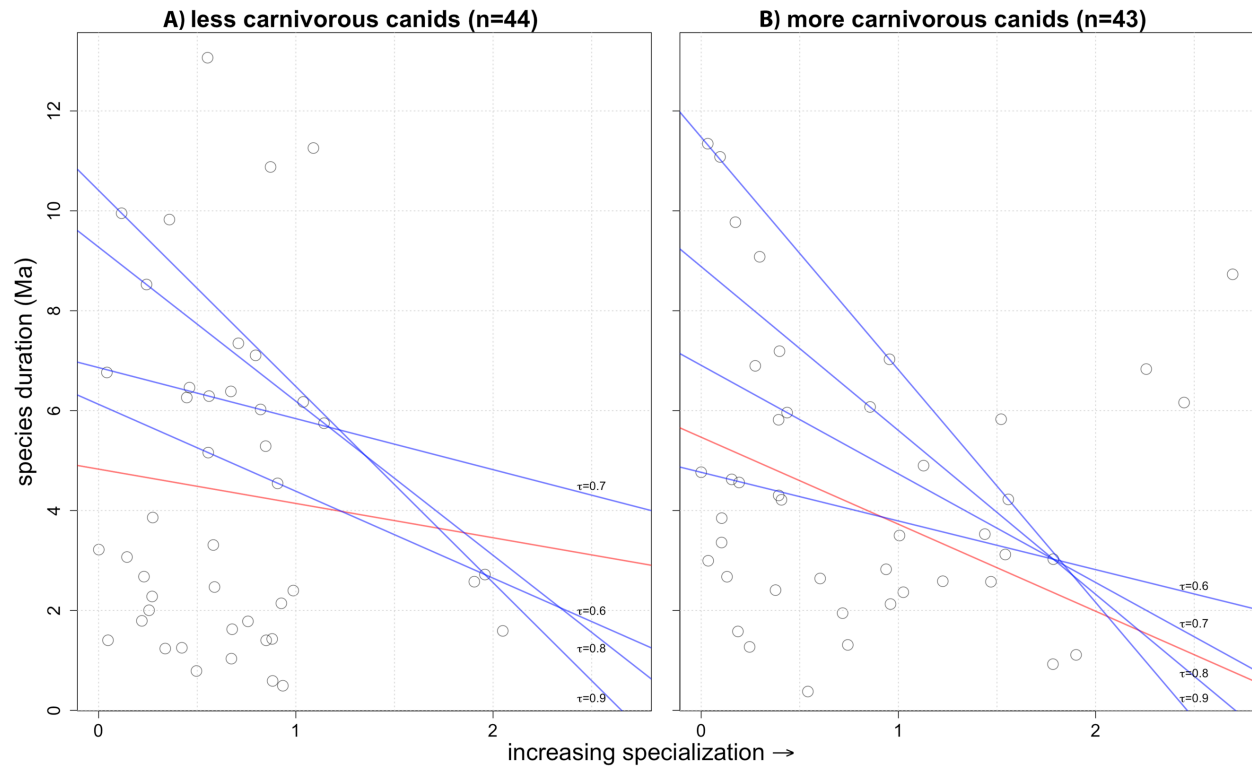


Figure 1.3. Relationship between species duration and specialization. **A**, less carnivorous, **B**, more carnivorous canids. The red line signifies an Ordinary Least Squares regression for less carnivorous canids and a Phylogenetic Generalized Least Squares regression with $\tau=0.538$ for more carnivorous canids. Quantile regression lines in blue are shown for the 0.6th, 0.7th, 0.8th, and 0.9th quantiles of duration versus specialization.

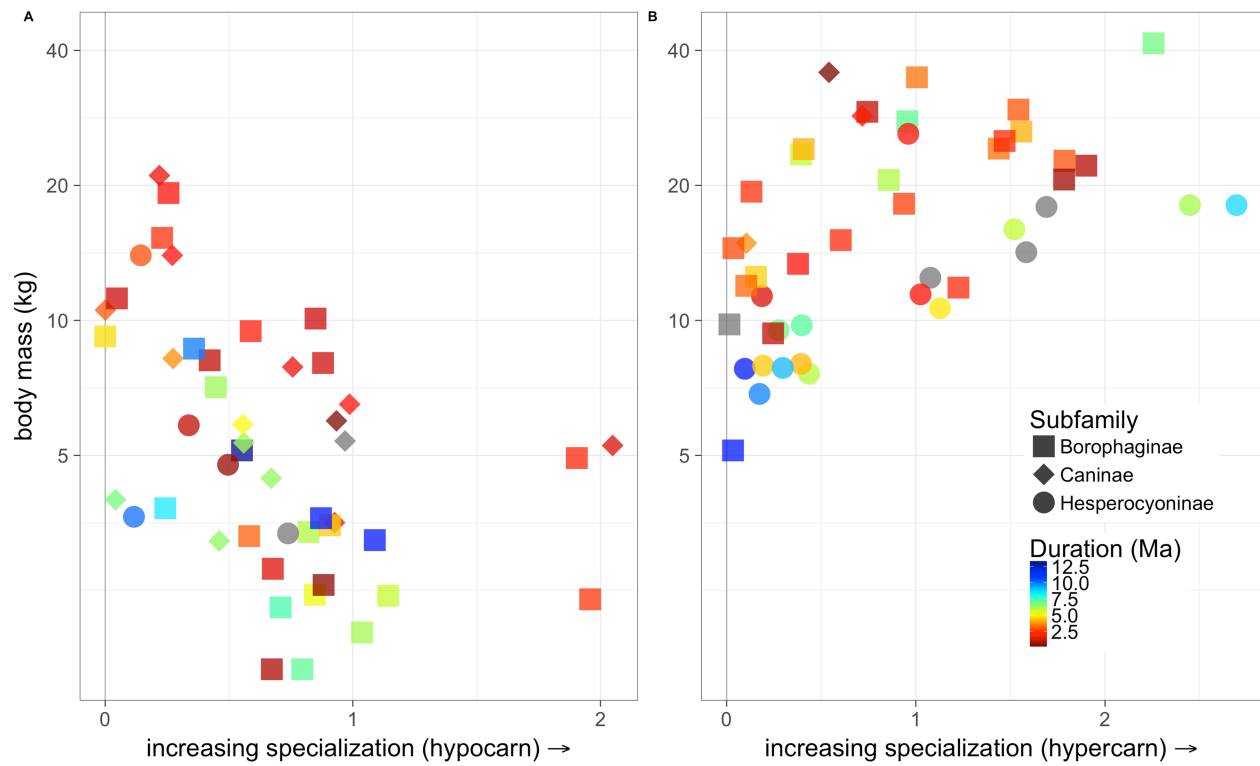


Figure 1.4. Bivariate plots visualizing species duration as a function of the combined effects of body size and specialization. Duration is mapped as color. **A**, for hypocarnivorous species; **B**, for hypercarnivorous species.

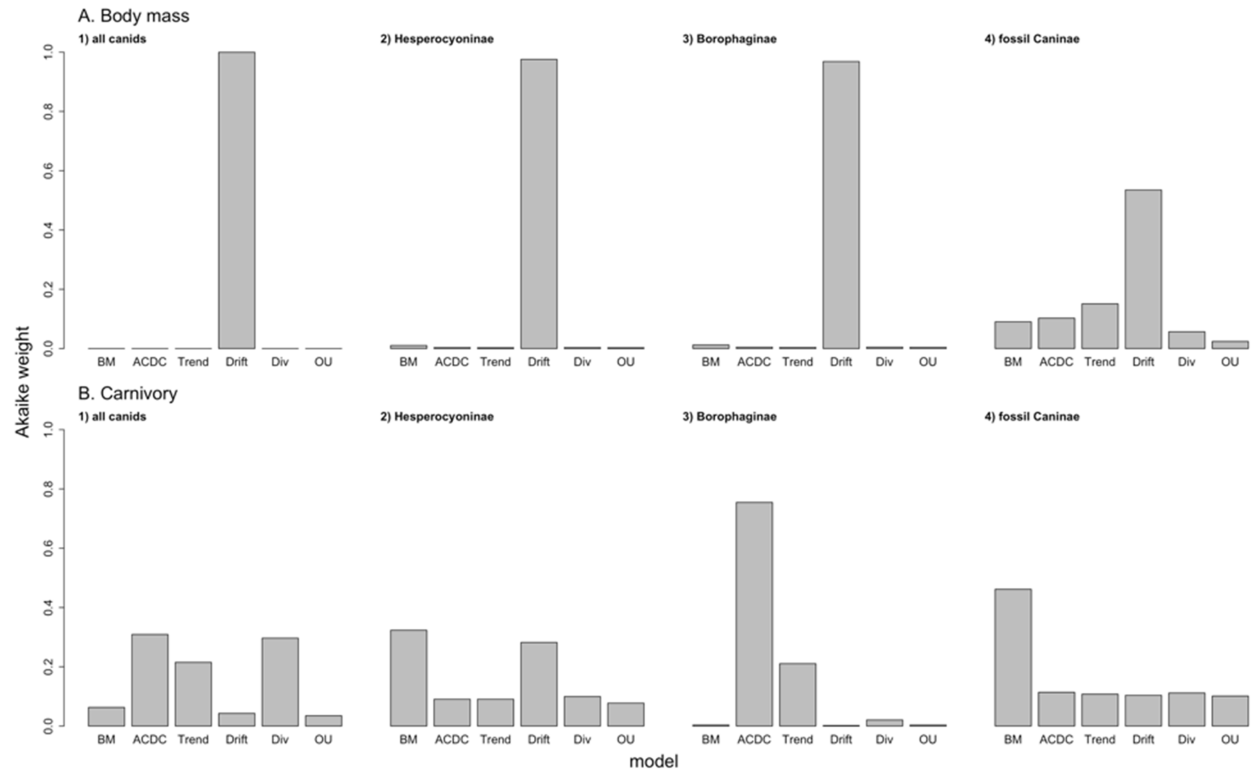


Figure 1.5. Median Akaike weights derived from model fits to 500 trees drawn randomly from the posterior distribution of trees. “Caninae” in this sample includes only fossil North American Caninae. **A**, body mass; **B**, carnivory.

Supplementary Information

Table S1.1. Comparative database of 45 extant carnivoran species used to define the dietary morphospace. “Sm.hyper” denotes small (< 20 kg) hypercarnivore; lg.hyper denotes large (\geq 20 kg) hypercarnivore.

Family	Genus	Species	Mass (kg)	RBL	RUGA	JD/DL	Diet	Diet references
Canidae	<i>Vulpes</i>	<i>lagopus</i>	4.9	0.622	0.851	0.145	sm.hyper	[78–81]
Canidae	<i>Atelocynus</i>	<i>microtis</i>	9.5	0.608	1.127	0.136	omnivore	[82,83]
Canidae	<i>Canis</i>	<i>adustus</i>	9.5	0.611	1.032	0.128	omnivore	[84–88]
Canidae	<i>Canis</i>	<i>aureus</i>	9	0.639	0.949	0.143	carnivore	[85,89,90]
Canidae	<i>Canis</i>	<i>latrans</i>	14	0.643	0.847	0.14	carnivore	[91–95]
Canidae	<i>Canis</i>	<i>lupus</i>	51.5	0.646	0.862	0.166	lg.hyper	[96,97]
Canidae	<i>Canis</i>	<i>mesomelas</i>	7.5	0.642	0.906	0.138	carnivore	[85,88,90,98]
Canidae	<i>Canis</i>	<i>simensis</i>	15.25	0.664	1.006	0.122	sm.hyper	[99–101]
Canidae	<i>Cerdocyon</i>	<i>thous</i>	6.5	0.59	1.104	0.138	omnivore	[102–106]
Canidae	<i>Chrysocyon</i>	<i>brachyurus</i>	21.5	0.624	1.112	0.131	omnivore	[102,107]
Canidae	<i>Cuon</i>	<i>alpinus</i>	19	0.681	0.731	0.168	lg.hyper	[108,109]
Canidae	<i>Lycalopex</i>	<i>culpaeus</i>	8.7	0.633	0.905	0.13	omnivore	[101,110–114]
Canidae	<i>Lycalopex</i>	<i>griseus</i>	3	0.617	1.03	0.122	omnivore	[105,111,112,115]
Canidae	<i>Lycalopex</i>	<i>gymnocercus</i>	5.35	0.628	1.028	0.122	omnivore	[105,106,110]
Canidae	<i>Lycalopex</i>	<i>sechurae</i>	3.6	0.617	1.133	0.12	omnivore	[116]
Canidae	<i>Lycalopex</i>	<i>vetulus</i>	4	0.566	1.288	0.125	omnivore	[117,118]
Canidae	<i>Lycaon</i>	<i>pictus</i>	27	0.659	0.932	0.16	lg.hyper	[119–122]
Canidae	<i>Nyctereutes</i>	<i>procyonoides</i>	7	0.612	1.059	0.136	omnivore	[98,123,124]
Canidae	<i>Speothos</i>	<i>venaticus</i>	6	0.636	0.922	0.171	sm.hyper	[102,103,125]
Canidae	<i>Urocyon</i>	<i>cinereoargenteus</i>	4.5	0.613	1.119	0.121	omnivore	[126]
Canidae	<i>Urocyon</i>	<i>littoralis</i>	4	0.577	1.116	0.12	omnivore	[127–129]
Canidae	<i>Vulpes</i>	<i>bengalensis</i>	2.5	0.666	1.192	0.111	omnivore	[130,131]
Canidae	<i>Vulpes</i>	<i>cana</i>	0.8	0.712	0.91	0.125	omnivore	[132–134]
Canidae	<i>Vulpes</i>	<i>chama</i>	3	0.676	1.127	0.111	omnivore	[101,135]
Canidae	<i>Vulpes</i>	<i>corsac</i>	5	0.693	0.837	0.133	sm.hyper	[101,136]
Canidae	<i>Vulpes</i>	<i>ferrilata</i>	7	0.738	0.859	0.118	sm.hyper	[101,137]
Canidae	<i>Vulpes</i>	<i>macrotis</i>	2.1	0.643	0.94	0.122	sm.hyper	[101,138]
Canidae	<i>Vulpes</i>	<i>pallida</i>	2.8	0.656	1.129	0.108	omnivore	[101]
Canidae	<i>Vulpes</i>	<i>rueppellii</i>	3.3	0.677	1.007	0.119	omnivore	[139]
Canidae	<i>Vulpes</i>	<i>vulpes</i>	6	0.629	0.883	0.133	carnivore	[101,140]
Canidae	<i>Vulpes</i>	<i>zerda</i>	1.2	0.655	1.06	0.113	omnivore	[90,141]
Hyaenidae	<i>Crocuta</i>	<i>crocuta</i>	62.5	0.817	0	0.218	lg.hyper	[142–145]
Hyaenidae	<i>Hyaena</i>	<i>brunnea</i>	53.4	0.807	0.243	0.22	carnivore	[134,146–148]
Hyaenidae	<i>Hyaena</i>	<i>hyaena</i>	35	0.766	0.316	0.237	carnivore	[143]
Mephitidae	<i>Conepatus</i>	<i>leuconotus</i>	1.8	0.53	1.274	0.156	omnivore	[149]
Mustelidae	<i>Eira</i>	<i>barbara</i>	4.8	0.658	0.611	0.244	carnivore	[150,151]
Mustelidae	<i>Gulo</i>	<i>gulo</i>	21.5	0.685	0.472	0.197	carnivore	[152–154]
Mustelidae	<i>Martes</i>	<i>pennanti</i>	3.4	0.642	0.68	0.197	carnivore	[155]
Mustelidae	<i>Meles</i>	<i>meles</i>	13	0.514	1.541	0.186	omnivore	[156–158]
Mustelidae	<i>Mellivora</i>	<i>capensis</i>	10.3	0.603	0.475	0.18	carnivore	[84,159,160]
Mustelidae	<i>Melogale</i>	<i>moschata</i>	2	0.647	0.635	0.148	omnivore	[161,162]
Mustelidae	<i>Taxidea</i>	<i>taxus</i>	8.4	0.629	0.979	0.164	carnivore	[134,149]
Procyonidae	<i>Nasua</i>	<i>narica</i>	5	0.531	1.424	0.157	insectivore	[163,164]
Procyonidae	<i>Nasua</i>	<i>nasua</i>	4.6	0.469	1.304	0.142	omnivore	[134,165]
Procyonidae	<i>Procyon</i>	<i>lotor</i>	6.5	0.632	1.427	0.17	omnivore	[134,149]

Table S1.2. Time intervals used for analysis of maximum geographic range area. Intervals follow the age bounds defined on the MIOMAP / FAUNMAP database, except for the Early / Late Clarendonian pair of intervals, which were assigned to be of equal size after preliminary analysis showed that using MIOMAP's original Early / Middle / Late Clarendonian subdivisions produced extreme unevenness in number of localities across the Clarendonian.

Interval name	Abbreviation	Lower bound (million years ago)	Upper bound (million years ago)
Early Early Arikareean	EEAK	30	27.9
Late Early Arikareean	LEAK	27.9	23.8
Early Late Arikareean	ELAK	23.8	19.5
Late Late Arikareean	LLAK	19.5	18.8
Early Hemingfordian	EHMF	18.8	17.5
Late Hemingfordian	LHMF	17.5	15.9
Early Barstovian	EBAR	15.9	14.8
Late Barstovian	LBAR	14.8	12.5
Early Clarendonian	ECLA	12.5	10.75
Late Clarendonian	LCLA	10.75	9
Early Early Hemphillian	EEHP	9	7.5
Late Early Hemphillian	LEHP	7.5	6.7
Early Late Hemphillian	ELHP	6.7	5.9
Late Late Hemphillian	LLHP	5.9	4.7
Blancan	BLAN	4.7	1.7
Irvingtonian	IRVI	1.7	0.45
Rancholabrean	RANC	0.45	0.01
Holocene	HOLO	0.01	0

Table S1.3. Median results from models of trait evolution fitted to 500 trees sampled at random from the Bayesian posterior distribution by Slater [43].

Model	Log likelihood	AICc	AICw	σ^2	parameter
A. All canids					
A. Body mass					
BM	44.66475	-85.21069	9.157756e-05	0.003137757	NA
ACDC	44.82939	-83.41878	3.961611e-05	0.002973134	2.162607e-03
Trend	44.19477	-82.14953	3.065730e-05	0.002961913	2.894189e-03
Drift	54.88301	-103.52601	9.997347e-01	0.002574601	1.827889e-02
Diversity	44.91393	-83.58786	4.295418e-05	0.002830693	6.421031e-06
OU	44.66091	-83.08183	3.446327e-05	0.003138818	5.638945e-11
B. Carnivory					
BM	-85.58034	175.3145	0.06286337	0.05542281	NA
ACDC	-82.93337	172.1784	0.30904457	0.02338048	3.757759e-02
Trend	-83.59806	173.5078	0.21499314	0.01879732	2.894189e-03
Drift	-84.89842	176.1085	0.04285114	0.05429989	2.199654e-02
Diversity	-82.93179	172.1753	0.29672574	0.03478219	4.402561e-04
OU	-85.15941	176.6305	0.03487011	0.06291428	5.638945e-11
B. Hesperocyoninae					
A. Body mass					
BM	10.72104	-16.89664	0.010247768	0.002784072	NA
ACDC	10.90481	-14.66677	0.003364927	0.003324918	-1.554880e-02
Trend	10.69501	-14.24717	0.002814115	0.003080303	-8.770118e-03
Drift	16.56953	-25.99621	0.975773477	0.001726929	2.229475e-02
Diversity	10.92228	-14.70171	0.003365869	0.003019731	-1.813923e-05
OU	10.73479	-14.32673	0.002868430	0.003019731	4.874302e-11
B. Carnivory					
BM	-16.80593	38.41185	0.32331540	0.03979974	NA
ACDC	-16.57325	40.86079	0.09059419	0.04690875	-1.791413e-02
Trend	-16.74146	41.19720	0.09059419	0.04389444	-8.770118e-03
Drift	-15.43745	38.58919	0.28213640	0.03413788	4.820888e-02
Diversity	-16.50592	40.72612	0.09957292	0.03664228	4.999463e-04
OU	-16.81839	41.35107	0.07754502	0.03981831	4.874302e-11
C. Borophaginae					
A. Body mass					
BM	24.40350	-44.58059	0.012110790	0.003053074	NA
ACDC	24.49023	-42.51892	0.004613334	0.002941919	1.023808e-03
Trend	24.06219	-41.66283	0.003805079	0.002739413	4.655062e-03
Drift	29.88019	-53.29883	0.968437135	0.002526532	2.142011e-02
Diversity	24.55110	-42.64065	0.004800221	0.002730486	1.277821e-05
OU	24.40370	-42.34586	0.004210236	0.003049184	3.025531e-11
B. Carnivory					
BM	-53.39299	111.05871	0.003421490	6.526654e-02	NA
ACDC	-46.60766	99.77347	0.754624015	4.906135e-03	1.062904e-01
Trend	-48.03736	102.63287	0.210585899	2.675498e-05	3.488621e-03
Drift	-52.81768	112.19350	0.001821449	6.379503e-02	3.459980e-02
Diversity	-50.36962	107.29738	0.020662595	3.881006e-02	8.624105e-04
OU	-52.30791	111.17395	0.003301093	8.701984e-02	4.405020e-11

D. Fossil Caninae						
A. Body mass						
BM	13.76979	-22.93958	0.09041973	2.941388e-03		NA
ACDC	14.99181	-22.72046	0.10259634	7.382779e-04	6.495250e-02	
Trend	15.35436	-23.44556	0.15091620	4.799969e-06	5.096073e+01	
Drift	16.86994	-26.47673	0.53512705	2.244663e-03	1.748150e-02	
Diversity	14.52832	-21.79348	0.05662464	1.877707e-03	8.941093e-05	
OU	13.76245	-20.26174	0.02399209	2.938599e-03	4.348186e-11	
B. Carnivory						
BM	-11.22622	27.37552	0.4616176	0.03449126		NA
ACDC	-11.05996	30.11993	0.1138682	0.02490613	1.662639e-02	
Trend	-11.19122	30.38243	0.1077072	0.02484354	5.096073e+01	
Drift	-11.17205	30.34409	0.1037565	0.03419290	-2.057593e-03	
Diversity	-11.08674	30.17349	0.1116702	0.02626673	1.116238e-03	
OU	-11.21163	30.42325	0.1013317	0.03648666	4.348186e-11	

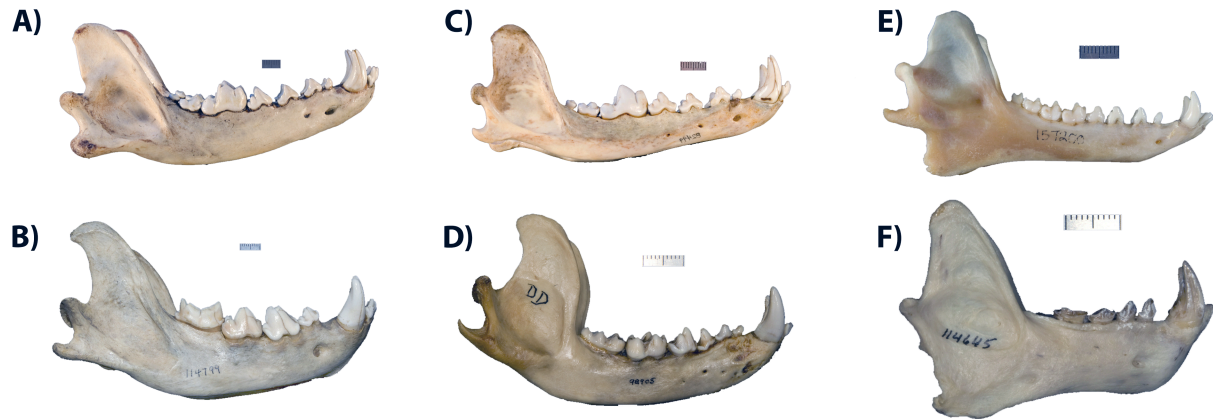


Figure S1.1. Lower jaws of representative extant carnivoran species across the hypercarnivory-mesocarnivory-hypocarnivory spectrum. **A, B**, hypercarnivores; **C, D**, mesocarnivores; **E, F**, hypocarnivores. **A**, grey wolf, *Canis lupus*; **B**, spotted hyena, *Crocuta crocuta*; **C**, coyote, *Canis latrans*; **D**, raccoon, *Procyon lotor*; **E**, bat-eared fox, *Otocyon megalotis*; **F**, kinkajou, *Potos flavus*. To highlight the differences in skeletal proportions corresponding to functional and dietary divergence among these animals, the lower jaws have been scaled to the same length from mandibular condyle to anterior end. Scale bars = 10 mm. Original specimen photos from Animal Diversity Web: <https://animaldiversity.org>.

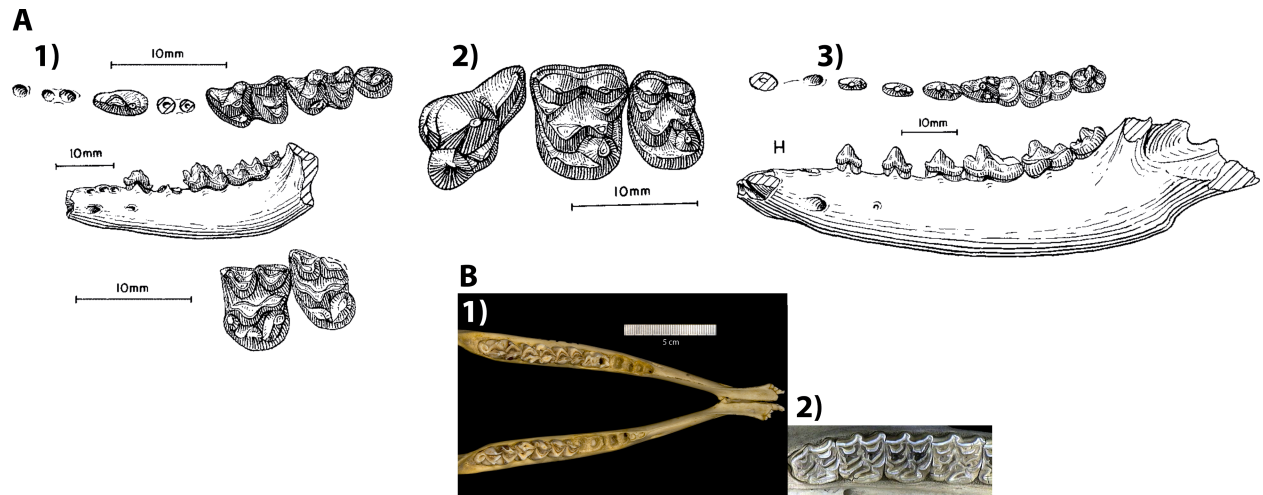


Figure S1.2. Comparison of the dentition of putatively hypocarnivorous fossil canids with the dentition of known extant herbivorous ungulates. **A**, hypocarnivorous fossil canids; **1)** *Cynarctoides emryi*: occlusal view of lower dentition (top), labial view of lower jaw (middle), and occlusal view of upper molars (bottom); **2)** *Phlaocyon achoros*: occlusal view of upper carnassial and molars; **3)** *Cynarctus crucidens*, occlusal view of lower dentition (top) and labial view of lower jaw (bottom). **B**, hypocarnivorous fossil canids; **1)** occlusal view of lower jaw of impala, *Aepyceros melampus*, and **2)** occlusal view of dentition of horse, *Equus caballus*. Putatively hypocarnivorous fossil canids exhibit ecomorphological specialization in their teeth, with dental wear creating ridges converging on ungulate selenodont or bunodont dental morphology. Fossil-canid illustrations are from Wang *et al.* [36] and included with permission; extant-ungulate specimen photographs are from Animal Diversity Web (<https://animaldiversity.org>).

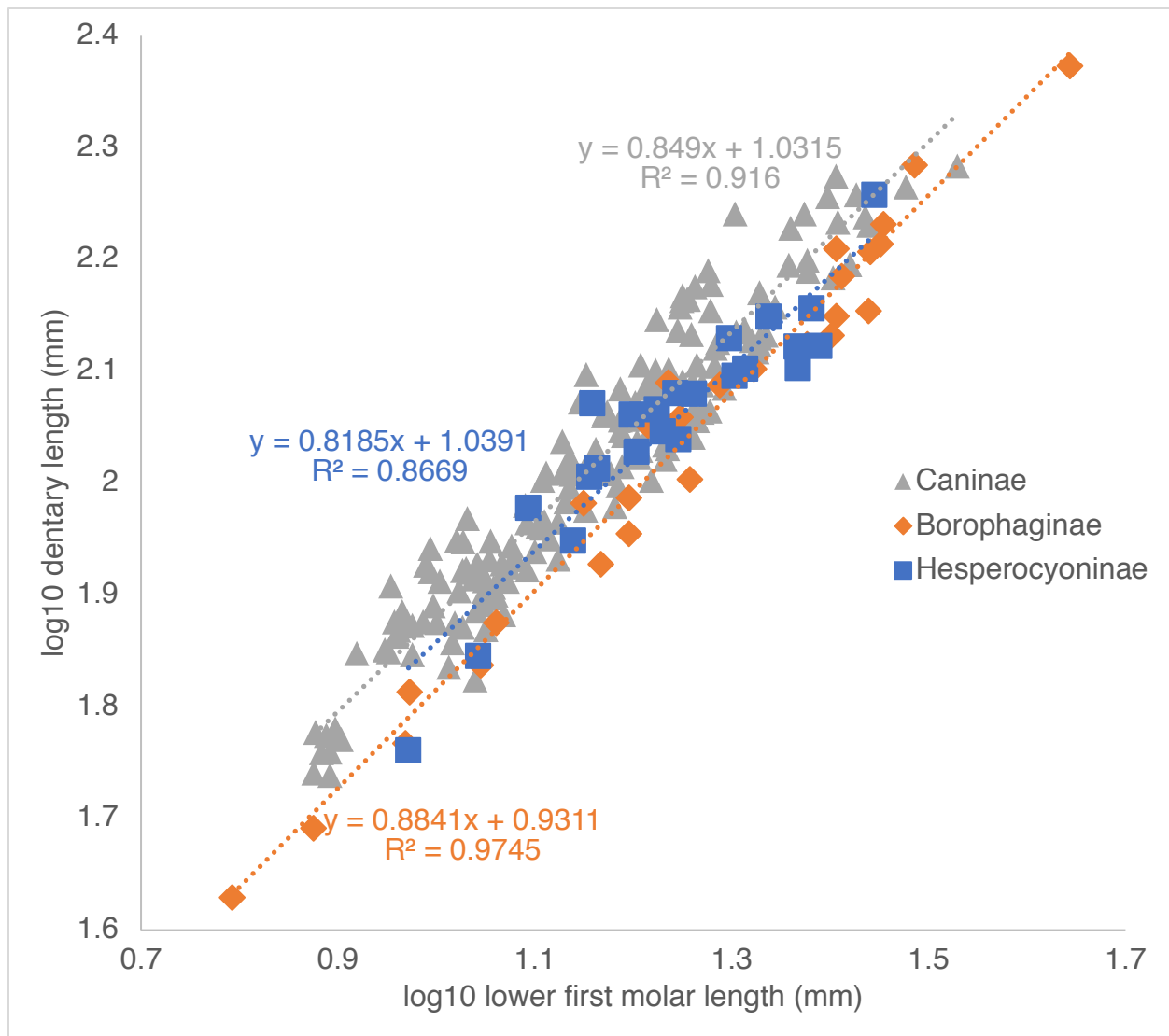


Figure S1.3. Per-subfamily regressions of log10 dentary length on log10 lower first molar length used to estimate dentary length of fragmentary fossil species. Based on intact dentaries of 24 hesperocyonine individuals, 27 borophagine individuals, and 175 canine (extinct and extant) individuals. Borophagine dentaries tend to be shorter for a given molar length than dentaries of other subfamilies, even for borophagines of smaller body size that would not be expected to use a robust dentary to process bone.

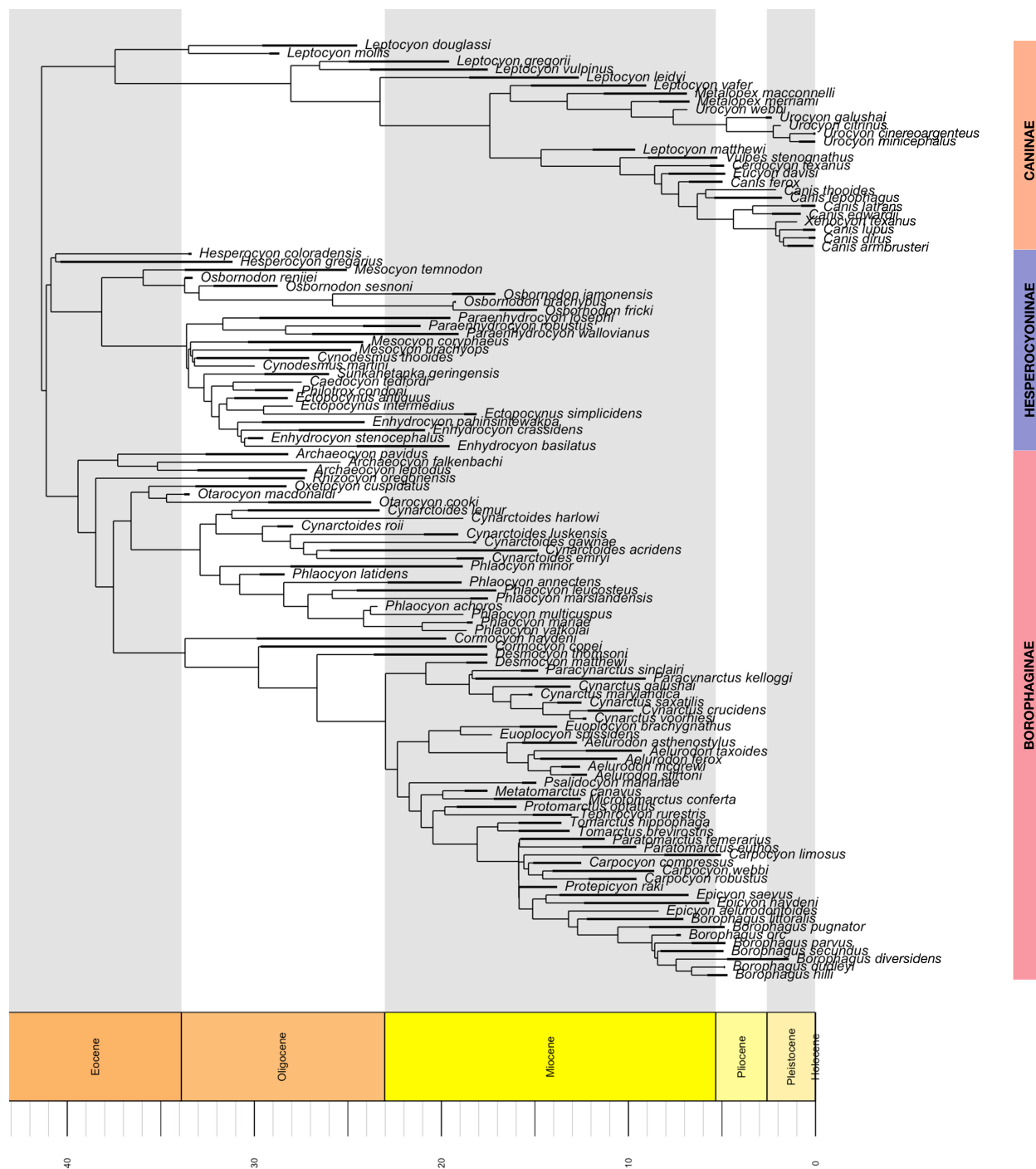


Figure S1.4. Time-scaled canid tree. Topology from tree with the highest log-likelihood from the Bayesian posterior probability distribution of Slater [43]. Black bars on branches indicate stratigraphic range recorded by occurrences. Branches lacking black bars indicate singletons, or species with only one occurrence. Time units are millions of years ago.



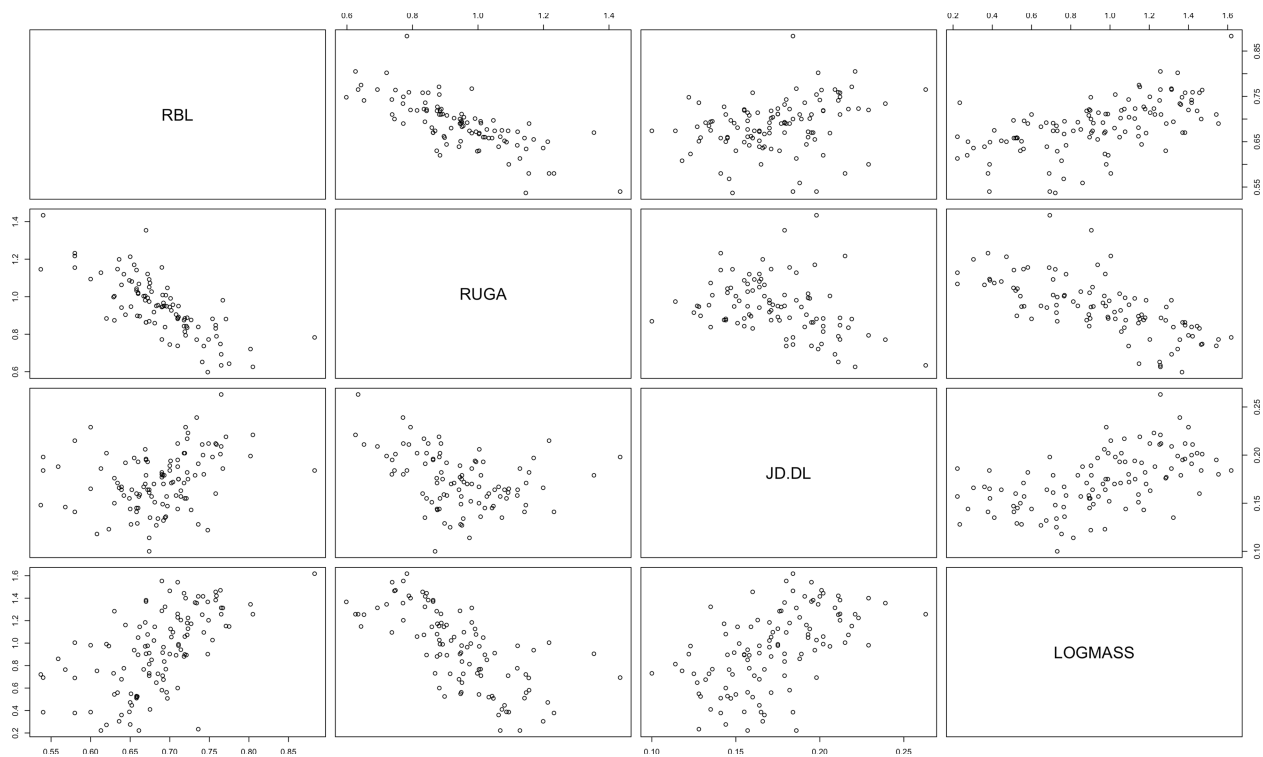


Figure S1.6. Bivariate plots showing correlated patterns among dietary measures and body mass.

II.

LARGE-BODIED HYPERCARNIVORY AS CONVEYOR BELT TO EXTINCTION? DIVERSIFICATION DYNAMICS OF NORTH AMERICAN FOSSIL CANIDS

Abstract

Large-bodied hypercarnivory and bone-cracking are costly; their appearance in a lineage constitutes an irreversible macroevolutionary “ratchet”. While modern ecosystems harbor few large hypercarnivores, this specialization repeatedly appears in the fossil record, permitting exploration of how it correlates with extinction risk in a world predating human effects. Here, we track this specialization in North American fossil dogs (Canidae), a family of over 130 species spanning a range of ecomorphologies, including iterative occurrences of large-bodied hypercarnivory. Comparing extinction victims and survivors over 40 million years of canid history, we identify an association with body size and carnivory only at the end-Pleistocene ~10 ka, when all extinct canids were large and hypercarnivorous. Otherwise, victims and survivors are similar in size and diet, suggesting little elevated extinction risk from bone-cracking or large-bodied hypercarnivory alone. Diversification rates corroborate this result. Large hypercarnivores originated within 10 million years of the origin of the Canidae, exhibiting constant speciation and extinction rates and peaking in richness around 12 Ma. Hesperocyoninae and Borophaginae, the two extinct canid subfamilies, also display constant speciation rates but extinction rates surpass speciation rates at the time of origin of lineages leading to large hypercarnivores. Previous work has advanced competition as a primary driver of canid diversification, although environmental changes propagating through trophic webs likely also influenced their diversity dynamics. We find significant relationships between large-hypercarnivore extinction rate and temperature, and between diversification rates of individual canid subfamilies and temperature, suggesting links to be investigated between climate and canid evolution.

Background

Modern mammal ecosystems are bottom-heavy and depauperate of apex predators. Most regions except Africa harbor few coexisting large hypercarnivores (species ≥ 21 kg with diets that are $>70\%$ vertebrates). Extant North American ecosystems include at most two, the gray wolf and mountain lion, whereas late Pleistocene ecosystems included as many as six: gray wolf, mountain lion, the extinct dire wolf, American lion, and two sabertooth cats [166]. The current big-predator paucity makes this dietary specialization difficult to study in the modern world and may encourage the perception that the costs of hypercarnivory make diverse predator assemblages unsustainable [167,168]. Even more rare are specialized bone-crackers, a modification of hypercarnivory that involves breaking open bones to obtain nutritious marrow. At present, the spotted and brown hyenas are our only extant bone-crackers [142]. The fossil record, however, preserves a richness of large-bodied mammalian hypercarnivores and bone-crackers, inviting inquiry into how these specializations may propagate through lineages and ecosystems, and why they are so rare today.

Carbone *et al.* [17,167] found that, among living carnivorans, most species larger than 20 kg tend to be hypercarnivores that typically consume prey as large or larger than themselves. Such a strategy is costly for several reasons. First, because large prey are less abundant, they have patchier prey distributions that lengthen search and pursuit times [169,170]. Moreover, large prey are dangerous and difficult to kill, making a carcass worth fighting over, all of which can lead to injury and death [171–175]. Larger or social prey can require greater time to stalk, pursue, and kill [176–179]. The bone-cracking that may accompany feeding on large vertebrate prey inflicts fracture and wear on teeth, the main tools of prey capture and food processing [180–182]. The acquisition of foraging skills in juveniles is delayed because they must grow large

enough to be able to catch large prey, as well as learn successful attack behaviors [183,184]. Adaptations for hypercarnivory—such as a loss of dental features to create simple slicing blades—are likely to be irreversible on the macroevolutionary scale [22], so that hypercarnivores tend to evolve into a corner and the end of a lineage.

Yet hypercarnivory presents benefits that may offset its costs. Barring predator specialization on a few prey species, meat is a readily available resource [185]. It has high energy content [17] and is more rapidly and efficiently digested than plant matter [186,187], permitting high basal metabolic rates, high growth rates, and high fecundity [185,188–193]. Hypercarnivores tend to be larger-bodied than non-hypercarnivorous relatives, affording greater ability to disperse across environments that vary in resource availability [193,194]. Despite hypercarnivory’s apparent irreversibility, it repeatedly punctuates the evolutionary history of the order Carnivora [67], an iterative evolutionary pattern that suggests it is successful [23].

The fossil record of North American dogs (Carnivora: Canidae) presents an ideal system in which to test how the costs and benefits of this specialization have impacted the diversification of large hypercarnivores. Fossil dogs arose in North America approximately 40 million years ago (Ma), radiating into over 130 species in three subfamilies: Hesperocyoninae, Borophaginae, and Caninae [35–37]. Originating as small mammals with omnivorous adaptations, Hesperocyoninae and Borophaginae demonstrated trends toward large size and hypercarnivory prior to extinction. Caninae, while still extant, may be on the same trajectory, given that large hypercarnivores appear late in the subfamily’s history. Competitive interactions have been hypothesized among the subfamilies [195], and habitat changes over the Neogene have been posited to have precipitated morphological and behavioral shifts [196]. The differential roles of climate and competition in the rise and fall of large hypercarnivorous canids

remain an area of active study [197].

Van Valkenburgh *et al.* [39] found a negative association, although no statistical correlation, between hypercarnivory and species duration in Hesperocyoninae and Borophaginae: larger canids tend to be more carnivorous, and more carnivorous canids appear to have shorter durations. Balisi *et al.* [198] clarified this association, finding a significant negative relationship between dietary specialization (including hypercarnivory) and species duration within all three subfamilies combined, although body size and species geographic range appeared to modulate the negative effect of hypercarnivory on duration. Here, we follow up on these studies by a) examining the canid fossil record in intervals to identify differences in body mass and diet between extinction survivors and victims, b) comparing rates of diversification between large hypercarnivores and all other canids, as well as among the three canid subfamilies, and c) tracking diversification rates in correlation with an environmental measure: global temperature estimated by the oxygen isotope record.

How have the costs and benefits of being a large-bodied hypercarnivore on the individual level impacted success and extinction risk at the species level and, further, at the clade level? **If being a large hypercarnivore increases extinction risk**, then we predict that, **relative to smaller and/or less carnivorous canids, large hypercarnivorous canids would**: 1) become extinct at greater frequencies per given time interval, and 2) have higher rates of extinction. Alternatively, if the short-term benefits of large-bodied hypercarnivory outweigh the costs in the long term, then large hypercarnivores may exhibit extinction rates on par with or lower than those of non-hypercarnivores. We also predict that, in accordance with previous work concluding that incipiently and fully cursorial predator morphologies arose in response to habitat shifts in the Miocene [196], diversification rates of large hypercarnivores might correlate with changes in

climate over the past 40 million years.

Methods

Measurement of species traits. We measured carnassial blade length, jaw depth, and jaw length on specimens located at the American Museum of Natural History (New York, NY), University of California Museum of Paleontology (Berkeley, CA), Los Angeles County Natural History Museum (Los Angeles, CA), and Yale Peabody Museum (New Haven, CT). When specimens were not easily accessible, we obtained measurements from the literature [35–37,51].

Estimation of canid body size. Because fragmentary fossils rarely preserve enough of the organism to provide a direct measurement of body size, we estimated body size using Van Valkenburgh’s regression on lower first molar length in extant canids [40]. Because carnivorans over 20 kg have increased energetic costs and prey on larger species than do carnivorans below 20 kg [17,167], we defined “large” body size as an estimated species mean mass over 20 kg.

Estimation of prey body size. A number of species (e.g. some *Enhydrocyon*) yielded mass estimates just under 20 kg, even though other morphological evidence suggests that they were large and hypercarnivorous. The regression estimates account only for mean mass; these species may have easily been over 20 kg in life. Additionally, the mass regressions are based only on extant canids, all of whom belong to subfamily Caninae. Considering that Hesperocyoninae and Borophaginae tend to be built slightly more robustly than Caninae [199], the estimates based on extant Caninae likely underestimate mass for the two extinct subfamilies. Given this, we supplemented the body mass estimates by estimating prey body size using Van Valkenburgh *et al.*’s regression on jaw depth for extant canids [44]. In this way, species that fall just under an estimated 20 kg may still be categorized as “large hypercarnivores” based on an estimated prey

size larger than themselves.

Quantification of carnivory using a single metric. A suite of traits associated with increased bite forces and greater masticatory loads characterizes hypercarnivorous morphologies: deep jaws, broad skulls, large canines and incisors, reduced post-carnassial molars, long shearing blades on lower carnassials, and increased mechanical advantage of the jaw-closing muscles [41–43]. However, fragmentary fossils rarely preserve many, much less all, of these traits. To maximize sample size, we quantified degree of carnivory by a single metric: the length of the blade on the lower first molar (carnassial) relative to dentary length (m1BS). m1BS provides a more comprehensive quantification than other carnivory proxies, such as the blade length of the lower carnassial relative to the total lower carnassial length (RBL), because the calculation of m1BS relative to dentary length accounts for the shortening of the rostrum that occurs in some hypercarnivorous taxa (e.g. hyaenids) that aids them in cracking bone [44]. Because not all species preserve intact dentaries, we estimated dentary length when needed using within-subfamily regression equations based on the length of the lower first molar and calculated from fossil canid specimens with intact dentaries [198]. Quantifying carnivory as m1BS permitted inclusion of 127 fossil canid species in the sample. Based on the minimum value in extant large hypercarnivorous canids, we defined “hypercarnivory” in the fossil taxa as species mean m1BS \geq 0.107.

Databases. We compiled occurrence data for North American fossil canids over the past 40 million years from the Neogene Mammal Mapping Portal (NeoMap, <http://ucmp.berkeley.edu/neomap>) and Fossilworks / Paleobiology Database (<http://www.fossilworks.org>; <http://www.paleobiodb.org>). NeoMap links the Miocene Mammal Mapping Project (MioMap, <http://miomap.berkeley.edu> [47]) and the Quaternary Faunal

Mapping Project (FaunMap, <http://ucmp.berkeley.edu/faunmap> [48]), providing occurrence data for all published late Oligocene through Holocene mammals in the United States and for many Quaternary localities in Canada. PBDB is a wider-ranging database, providing global occurrence data for organisms of all geologic ages. For the taxa and time periods of interest in this study, records of minimum and maximum locality age are more precise in MioMap and FaunMap than in PBDB; therefore, MioMap and FaunMap form the bulk of the occurrence data used here. PBDB was used for occurrences prior to the late Oligocene or occurrences not otherwise found in MioMap and FaunMap. Occurrence data from both databases were cross-checked for reliability against the published literature (e.g. 36–38, 43, 49–51). We compiled 3708 fossil occurrences for all Canidae: 314 for Hesperocyoninae, 1265 for Borophaginae, and 2129 for Caninae.

Testing extinction selectivity per time interval. For survivor-victim analyses, we examined 18 unequal-length time intervals over the past 40 million years. The time intervals are subdivisions of North American Land Mammal Ages (NALMAs), ranging from the Orellan NALMA to the Recent (Table S2.1). Each time slice compares the intervals before and after, amounting to 17 slices. Species were categorized as winners (survivors) or losers (non-survivors) based on whether they were present in the subsequent interval. Lazarus taxa—taxa that disappear for one or more periods but later reappear—are included as having continuous records through the intervening interval/s in which they may have no record. For each slice, we combined all taxa into a single pool, sampling this pool with replacement to generate two bootstrap samples equal in size to the number of survived and the number of extinct species. We resampled 10000 times, generating a null distribution of F ratios against which to assess significance of our observed test statistic. We also examined three models for each slice using logistic regression: a) extinction ~

body mass, b) extinction \sim carnivory [m1BS], and c) extinction \sim body mass * carnivory [m1BS]. Additionally, given the sharp difference in energetic cost between large hypercarnivores (e.g. wolves) and all other species (e.g. coyotes) [17,167,201], we ran contingency tests with the independent variable as an ecomorphological category with two levels—large hypercarnivore, or not—and the dependent variable as extinction. These procedures were executed in R version 3.4.1 [68].

Calculation of diversification rates. Using fossil occurrences as input data, we used the open-source Python program PyRate for joint estimation of species richness, preservation rates, speciation and extinction rates (number of speciations or extinctions per million years), and longevity [52,197]. We partitioned the full canid dataset into two subsets: large hypercarnivores, and all other canids. To account for uncertainty in the age of each occurrence, we generated 100 randomized sets of ages for each of the three datasets (all canids, large hypercarnivores, and canids excluding large hypercarnivores) by resampling the age of each occurrence uniformly within the respective temporal range. We then analyzed the full dataset and the two subsets independently under a Markov Chain Monte Carlo birth-death model with rate shifts (BDMCMC). We ran the analysis for the default of 10,000,000 BDMCMC iterations, sampled every 1000th iteration to obtain posterior estimates of the parameters, monitored effective sample sizes by visualizing the log files in Tracer [202], and discarded the first 200,000 iterations as burn-in. We also estimated diversification rates for the three canid subfamilies separately and compared our results with those of Silvestro *et al.* [197].

Accounting for potential shifts in preservation rate. Canid species before the Arikareean-Hemingfordian boundary (18.8 Ma) tend to last 5 million years longer on average than canid species after the boundary, in part possibly because uncertainty of dates for Arikareean

localities—quantified as stratigraphic range per occurrence—tends to be greater than for locality dates from other NALMAs (Figure S2.1). To account for this potential discrepancy in the canid fossil record, we used the Time-variable Poisson Process (TPP) + Gamma (G) model in PyRate, which assumes both that preservation rates are constant within a predefined time interval but can vary across time intervals (TPP) and that preservation can vary across lineages (G). We designated the NALMAs as the time intervals for this analysis, allowing PyRate to account for the possibility of preservational rate shift not only at the Arikareean-Hemingfordian boundary but also as NALMAs progress to the present. Preservation rates are estimated using the abundance of occurrences per lineage per time bin.

Covariance of diversification rates with traits. Using the Covar birth-death model in PyRate, we also tested whether diversification rates for all Canidae and per subfamily may be linked with shifts in body mass and degree of carnivory. In this model, the parameters α_λ (correlation with speciation rate) and α_μ (correlation with extinction rate) are estimated from the data, quantifying the relationship between shifts in diversification rates and shifts in trait value. We ran the default of 10,000,000 iterations, sampled every 1000th, and discarded the first 2,000 samples as burn-in. $\alpha > 0$ indicates a positive relationship between the trait value and the birth-death rates, and $\alpha < 0$ indicates a negative relationship. We considered the relationship significant if the distribution of 95% highest posterior densities of α did not overlap 0.

Relationship with global temperature. PyRate also incorporates analysis of data under birth-death models where diversification rates change through time as an exponential or linear function of a time-continuous correlate, such as temperature. Following Slater *et al.* [203], we fit a cubic spline to oxygen isotope records published by Zachos *et al.* [204] using the `smooth.spline` R function and 15 degrees of freedom. We tested the resulting curve for

relationships with diversification rates. Higher $\delta^{18}\text{O}$ values signify lower temperature. We ran the default of 1,050,000 MCMC iterations, sampled every 1000th, and discarded the first 210,000 iterations as burn-in to obtain posterior estimates of the parameters γ_λ (correlation with speciation rate) and γ_μ (correlation with extinction rate). $\gamma > 0$ indicates positive correlation between speciation or extinction rate and temperature; $\gamma < 0$ indicates negative correlation. We considered the relationship significant if the distribution of 95% highest posterior densities of γ did not overlap 0.

Results

Large hypercarnivores. The overwhelming majority (99/127 species) of North American fossil canid species over the last 40 million years were under 20 kg and likely did not feed on prey larger than themselves (Figure 2.1). Fossil canids spanned over an order of magnitude in mean size (from *Otarocyon cooki*, 1.67 kg; to *Epicyon haydeni*, 41.49 kg) and a wide range of diets including mesocarnivory and hypocarnivory (43). Small- to medium-sized hypercarnivores exist—e.g. extant foxes—but, because the energetic costs of carnivory differ between smaller and larger hypercarnivores [167], we included these smaller species with all other canids. Based on our estimates of predator and prey body sizes, we categorized 33 species as large hypercarnivores, including the genus *Enhydrocyon* (four species), *Ectopocynus simplicidens*, and *Osbornodon fricki* in the subfamily Hesperocyoninae; *Aelurodon* (six species), *Paratomarctus euthos*, *Carpocyon webbi* and *robustus*, *Protepicyon* + *Epicyon* (three species), and *Borophagus* (eight species) in the subfamily Borophaginae; and *Chrysocyon nearcticus*, *Theriodictis? floridanus*, *Xenocyon* (two species) and two extinct species of *Canis* in the subfamily Caninae. Large hypercarnivores comprise a quarter of all currently known North American fossil canid

diversity.

Preservation rates. The tempo of preservation varies among NALMAs. Preservation rates in early canid history (Duchesnean to Orellan NALMAs) are significantly lower than those in canid mid-history (Whitneyan to Irvingtonian), which are significantly lower than those in the Rancholabrean and Recent records (Figure S2.2). Earlier in canid history, the low “preservation rates”—as seen in the wide confidence interval of the Duchesnean record—may be biased by the low diversity at the base of the family’s radiation. This heterogeneity in preservation necessitates our use of the TPP+G model for calculation of diversification rates in PyRate.

Survivor-victim analysis. Figure 2.2 shows large hypercarnivorous species populating the upper right quadrant of each morphospace time-slice. If being large and hypercarnivorous increases extinction risk, then, for each time-slice, we would tend to see extinct species—more hollow shapes—toward the upper right, and fewer extinctions for smaller non-hypercarnivores toward the bottom left. Our analysis does not support this hypothesis. We found negligible differences in carnivory, body mass, or the interaction between carnivory and body mass between extinct and surviving species for most time intervals. The only significant difference in both carnivory and body mass (model $p = 0.005$) occurred at the end of the Pleistocene, at 0.01 Ma. At this time, three large hypercarnivores became extinct or at least extirpated from North America—*Cuon alpinus*; *Canis armbrusteri*; and the dire wolf, *Canis dirus*—and left behind a radiation of foxes.

Subfamily trends. Despite minimal support for our prediction of differential extinction outcomes based on differences in body size and carnivory, we observe trends within each subfamily. About 10 million years after the origin of canids, Hesperocyoninae began to enter the large-hypercarnivore space (Figure 2.2). With time, they populated this niche; the last surviving

hesperocyonine, the large hypercarnivore *Osbornodon fricki*, became extinct about 14.8 Ma, between the Early and Late Barstovian. Borophagines followed the same trajectory, boarding an evolutionary conveyor belt toward the niche of large body size and hypercarnivory left open by the extinction of *O. fricki*, and eventually also stumbling over an evolutionary cliff into extinction. Most recently, canines appear to be following a similar pattern, so far culminating in the only selective extinction of hypercarnivores in this analysis.

Diversification metrics of large hypercarnivorous canids. Hesperocyonines, and canids as a whole, broke into the large-hypercarnivore niche with the appearance of *Enhydrocyon* in the Early Early Arikareean, between 30 and 27.9 Ma, marking the beginning of the large-hypercarnivore diversification curves (Figure 2.3). Large hypercarnivores were vastly outnumbered by all other canids for much of their history, with the exception of the period between approximately 12 and 7 Ma when they reached peak richness and surpassed the diversity of all other canids (Figure 2.3A). Confirming the results from the survivor-victim analyses, large hypercarnivores have experienced constant speciation and extinction rates, in contrast to the more heterogeneous rates for all other canids. Speciation rates were low but largely on par with those for all other canids until ~5 Ma, when smaller non-hypercarnivore speciation accelerated (Figure 2.3B). Large-hypercarnivore extinction rate was initially higher than for all other canids, but extinction of all other canids accelerated and began to surpass that for large hypercarnivores ~20 Ma. However, the confidence interval for large-hypercarnivore extinction rate also increased ~8 Ma, so that the extinction rates for large hypercarnivores and all other canids are now statistically indistinguishable (Figure 2.3C). Net diversification rate of large hypercarnivores was low but positive on average until ~7 Ma (Figure 2.3D). Average longevity of large hypercarnivores was initially lower than that for all other canids; however, average

longevity for all other canids crashed ~20 Ma to a duration lower than that of large hypercarnivores (Figure 2.3E).

Per-subfamily diversification rates. Under the TPP+G model of preservation, speciation rates of Hesperocyoninae and Borophaginae were constant over the duration of the two subfamilies (Figure 2.4). Extinction rates exceeded speciation rates at approximately 29 Ma and 20 Ma, respectively, after which the two subfamilies began to decline in diversity. Different diversification patterns characterize Caninae, the only extant subfamily: both speciation and extinction rates have been rising gradually from approximately 11 Ma to the present, so that net diversification rate thus far has been positive throughout the subfamily's duration.

Correlation with traits. Speciation and extinction rates largely do not correlate with either body mass or degree of carnivory in all Canidae or among the three subfamilies, with the exception of Borophaginae (Table 2.1). Among borophagines, extinction rates are significantly related to both body mass and carnivory, but negatively so: smaller non-hypercarnivorous borophagines tended to go extinct more quickly than large hypercarnivorous borophagines.

Correlation with temperature. Extinction rate for large hypercarnivorous canids, speciation and extinction rates for all canids that were not large and hypercarnivorous, extinction rates for Borophaginae, speciation and extinction rates for Caninae, and speciation and extinction rates for all Canidae were positively correlated with the oxygen-isotope record. Higher $\delta^{18}\text{O}$ values correspond to lower temperatures; these diversification rates therefore increased as global temperature decreased. Extinction rates for Hesperocyoninae were negatively correlated with the oxygen-isotope curve and thus positively correlated with temperature. All other correlations were not significant (Table 2.2).

Discussion

The costs and benefits of hypercarnivory and bone-cracking are well known at the individual level [167,168,171,176,201]. At the species level, specialization appears to confer a short-term advantage in optimizing an organism for its environment and available resources; but, over longer time scales, specialization can act as an evolutionary trap for entire clades [67,205,206]. Hypercarnivorous adaptations that simplify the dentition to maximize the meat-slicing surface—such as loss of cusps on teeth (e.g. canids with trenchant talonids) or loss of grinding teeth altogether (e.g. feliforms)—tend to be irreversible. As such, they are an example of Dollo’s law, which states that a structure, once lost, is not likely to be regained [22]. Specialists with derived morphologies (e.g. felids) are less morphologically variable than generalists that retain the ancestral condition (e.g. canids with non-trenchant lower carnassials) [67]. Less morphological variability may signify less evolvability: a smaller range of potential “next steps” for descendant species to take [207]. Therefore, on evolutionary timescales, there appears to be a conveyor belt toward greater and greater specialization until a clade vanishes [205]. This conveyor belt is apparent in the survivor-victim analysis (Figure 2.2). Each subfamily originates as small-bodied mesocarnivorous species, increasing in size and carnivory over time. In the two extinct canid radiations, extinction of the subfamily happens only after species enter the extremes of the large-bodied and hypercarnivorous quadrant of morphospace.

Given the repeated association between specialization for hypercarnivory and clade (subfamily) decline in at least two of the three canid subfamilies, it might be expected that hypercarnivorous taxa would exhibit shorter species durations, lower speciation rates and higher extinction rates. However, this is not what we observed at the species level. Although the extinction rate for hypercarnivorous species was initially higher than that for all other canids, it

was surpassed by the extinction rate for all other canids approximately 20 Ma (Figure 2.3C). Overall, net diversification rates for large hypercarnivorous canids have been on par with those for all other canids until recently (Figure 2.3D). Thus, at the species level, large-bodied hypercarnivory does not appear to have been a liability for much of canid history. At the clade level, however, extinction rates exceed speciation rates for both Hesperocyoninae and Borophaginae in concert with the appearance of lineages leading to the first large hypercarnivores in each subfamily (*Enhydrocyon* in Hesperocyoninae; Borophagini in Borophaginae) (Figure 2.4). In these two cases, the first appearance of lineages culminating in large-bodied hypercarnivorous specialization signals the beginning of clade decline.

Analyzed as time-continuous variables, neither body size nor degree of carnivory showed a significant relationship with diversification rates for all canids, hesperocyonines, or canines (Table 2.1). However, both traits were significantly correlated with borophagine extinction rate, although the negative relationship is the inverse of what was expected under a hypothesis of large-bodied hypercarnivory increasing extinction risk. Rather, the larger and more carnivorous the canid, the lower its extinction rate. Many of these small non-hypercarnivorous borophagines were hypocarnivores (e.g., *Cynarctoides*, *Cynarctus*, *Phlaocyon*), and the combination of small size and dietary and/or habitat specialization could have led to lower preservation potential and therefore an underestimate of their duration.

The constant speciation rate of large-bodied hypercarnivores (Figure 2.3B) suggests that selection favored the evolution of this ecomorph, and yet the first species, the hesperocyonine *Enhydrocyon*, did not appear until ~10 Ma into canid history. Large hypercarnivorous dogs reached their peak richness nearly 18 million years later, approximately 12 Ma (Figure 2.3A). What could have freed this niche for canids? Alternatively, what could have prevented canids

from dominating this niche sooner?

In addition to intrinsic constraints, interspecific competitive effects likely regulated the population density and species richness of large hypercarnivores in fossil communities, acting as another constraint on the production of new predator taxa. Much previous work has pointed to inter-family competition as a driver of diversity dynamics in carnivorans [67,197,206,208]. Canids are far from the only large hypercarnivores during their early history: amphicyonids (bear-dogs), felids (cats), mustelids (weasels and allies), nimravids and barbourfelids (false saber-toothed cats), procyonids (raccoons and allies), and ursids (bears) overlap temporally with canids throughout the duration of the family and also include large hypercarnivorous members [67]. Overlapping diversity patterns have led to inferences of inter-clade competition suppressing the evolution of large hypercarnivorous canids until later in canid history [197]: nimravids had gone extinct and amphicyonids were declining when large canid hypercarnivores became dominant ~16 Ma, leaving carnivore niches open for canids—the “cat gap”—until felids arrived and started to become common in North America ~10 Ma [9,67,195]. However, overlapping diversity patterns alone are insufficient to infer competition and must be supported by evidence of overlapping ecomorphologies. While ecomorphological overlap among these groups has been quantified [67,206,208], the resolution of canid taxonomy and phylogeny surpasses that of these groups, hindering comparison at the species level. Taxon-free approaches (e.g. analyzing the distributions of raw traits not averaged by species or taxonomic units) are outside the scope of this current study but might confirm the role of inter-clade competition in canid diversification, particularly within a restricted context such as a single locality or paleo-community.

Whereas competition has often been used to explain predator evolutionary divergence, climate might also influence the evolutionary trajectory of predator clades through bottom-up

effects that propagate successively as energy flow through vegetation and prey species [209–211]. The PyRate analysis of correlation with the oxygen isotope record appears to support this hypothesis, yielding significant relationships between this global temperature proxy and some subsets of the canid dataset (Table 2.3). However, the clades respond differently: a cooling climate appears correlated with decreasing extinction rate for Hesperocyoninae and increasing extinction rate for Borophaginae, and with both increasing speciation and increasing extinction rates for Caninae and all Canidae (Table 2.2; Figure S2.3). These conflicting results among the subfamilies suggest that climate, though an intriguing hypothesis, may be less important than biotic interactions. Future work in this area would benefit from compiling regional and local environmental proxies to be assessed alongside changes in faunal diversity (e.g. [212]).

Our results differ slightly from those of Silvestro *et al.* [197], who first used PyRate to quantify diversification rates in North American fossil canids. Silvestro *et al.* found significant temporal changes in both speciation and extinction rates for Hesperocyoninae and Borophaginae, in contrast to our findings of constant speciation rates eventually being surpassed by extinction rate for both. This discrepancy likely stems from two differences: in the model used for analysis, and in the source of occurrence data. First, Silvestro *et al.* modeled preservation as a non-homogeneous Poisson process (NHPP), allowing for preservation heterogeneity only among lineages using the Gamma model. In contrast, taking into account the variability of the fossil record over time in terms of preservation quality and number of localities (Figures S2.1, S2.2), we modeled the preservation process as a realistic time-variable Poisson process (TPP) coupled with the Gamma model to incorporate both temporal and across-lineage variation in preservation rate. Second, Silvestro *et al.* drew their occurrence data from the Paleobiology Database (PBDB). While we used some occurrence data from the PBDB, we primarily drew from

NEOMAP, which records occurrence-specific dates as opposed to interval-specific dates as the PBDB does.

The family Canidae has served as a model system for studying the macroevolution of large hypercarnivores [43,197]. However, they are far from the only clade to have populated this niche. Exploration of the possible association between hypercarnivory and extinction risk using another study system—for example, the Miocene hyenas of Europe, or amphicyonids—would permit confirmation of whether the patterns quantified here are restricted to canids or represent a general phenomenon among clades that grow to large body sizes and hypercarnivory. Future work also needs to examine the intersection of traits and environment—and mechanisms for this intersection—explored preliminarily in this study. Despite their decreased evolvability on the clade level, at the species level large hypercarnivores appear not always doomed to failure. Future work needs to ask: which environments, which climates, may promote the diversification of large hypercarnivores? Under what environmental conditions may animal lineages cross a threshold into this specialization, and still succeed?

Conclusions

Taxa specialized for large-bodied hypercarnivory do not appear to be disadvantaged at the species level: with the exception of the late Pleistocene, large hypercarnivorous canids become extinct at rates comparable to all other canids. Accordingly, despite the apparent advantages of generalization [198], the canid fossil record reveals that lineages iteratively evolve toward its opposite, specialization. In at least one instance in each of the three canid subfamilies, species become larger and more carnivorous over time. However, specialization tends to restrict subsequent morphological variability, particularly in the jaws and dentition, so that reversals to

generalization are rare. As a result, despite apparent success at the species level, the subsequent progress of an incipiently specialized clade tends to be a unilateral march toward extinction rather than toward further diversification.

Speciation rate is constant once canids enter the large-hypercarnivore niche, yet canids enter and fill the niche relatively late—why? Previous work has inferred competitive effects among carnivoran clades, although an in-depth analysis of potential competition from coeval carnivoran families is outside the scope of this study. Considering environmental effects, we find support for a relationship between some aspects of canid diversification and shifts in global temperature. Large hypercarnivorous canids reached their peak after the Middle Miocene Climatic Optimum and subsequently have been declining, highlighting the need to take into account possible interactions between intrinsic traits and extrinsic environment in shaping the evolutionary trajectory of clades.

Tables and Figures

Table 2.1. Median posterior estimates of the parameters α_λ (correlation with speciation rate) and α_μ (correlation with extinction rate) quantifying the relationship between traits and diversification rates. 95% highest posterior densities (HPD) are in parentheses. Parameters displaying a significant relationship (95% HPD does not span 0) are in bold.

Group	Body mass		Degree of carnivory (m1BS)	
	α_λ	α_μ	α_λ	α_μ
Hesperocyoninae	0.9784 (-0.4746, 2.4389)	0.6905 (-0.8755, 2.1639)	0.9686 (-0.5252, 2.3902)	0.7654 (-0.7576, 2.1813)
Borophaginae	0.5847 (-0.2242, 1.7212)	-1.1085 (-1.8692, -0.3853)	0.5797 (-0.1982, 1.7704)	-1.1174 (-1.897, -0.3972)
Caninae	-0.5091 (-1.8731, 0.9582)	0.1059 (-1.3549, 1.7116)	-0.562 (-1.8958, 0.8891)	0.1108 (-1.4104, 1.6937)
All Canidae	-0.1727 (-0.7398, 0.4296)	-0.537 (-1.1297, 0.0359)	-0.2102 (-2.1189, 1.7859)	-0.2528 (-2.2323, 1.5599)

Table 2.2. Median posterior estimates of the parameters γ_λ and γ_μ quantifying the correlation between the global oxygen isotope record [204] and diversification rates. 95% highest posterior densities (HPD) are in parentheses. Parameters displaying significant correlation (95% HPD does not span 0) are in bold.

Group	Exponential model		Linear model	
	γ_λ	γ_μ	γ_λ	γ_μ
Lg. hypercarn.	0.1921 (-1.3023, 1.7868)	1.5839 (0.035, 3.2371)	0.1719 (-1.1366, 1.4797)	1.374 (-0.0397, 3.1297)
All other canids	2.4364 (1.3797, 3.4151)	2.1215 (1.0341, 3.1921)	1.588 (0.9061, 2.1302)	2.2538 (0.9029, 3.2576)
Hesperocyoninae	-0.1141 (-0.8408, 0.5443)	-1.0078 (-1.7091, -0.3496)	0.0197 (-0.4574, 0.7107)	-0.4717 (-0.6484, -0.178)
Borophaginae	-0.313 (-0.9768, 0.3635)	0.6628 (0.1302, 1.2226)	-0.3808 (-1.197, 0.2153)	0.2865 (0.0119, 0.4078)
Caninae	2.6788 (1.4546, 3.8467)	2.1667 (0.739, 3.533)	3.1997 (1.8205, 4.3107)	2.6328 (1.0678, 4.0907)
All Canidae	1.9535 (1.0372, 2.7337)	2.0747 (1.1553, 2.8357)	1.527 (0.7029, 2.3195)	2.0021 (1.0223, 2.8276)

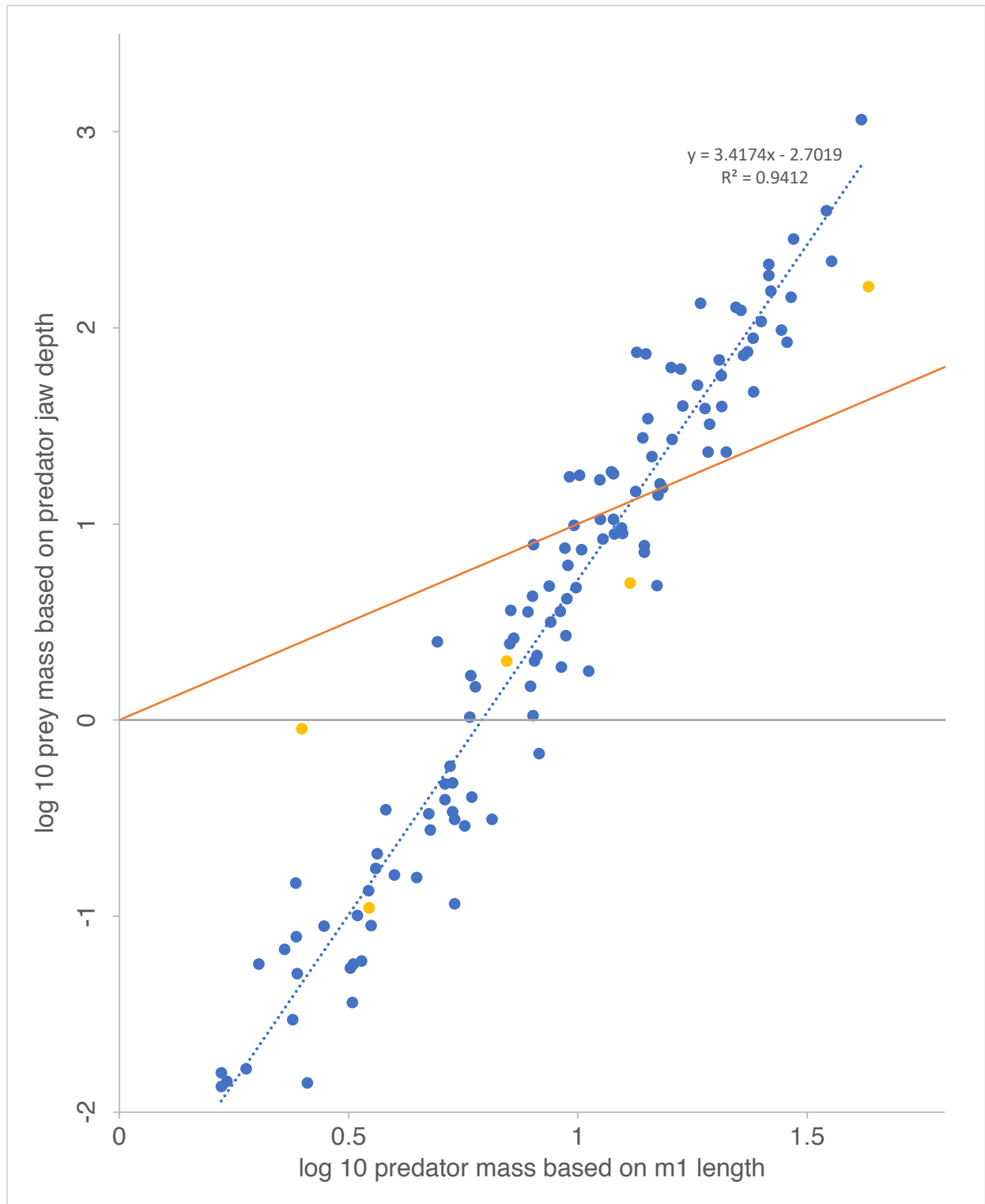


Figure 2.1. Log₁₀-log₁₀ plot of typical prey mass (kg) against canid mass (kg) for 130 species of extinct canids (blue points) and five species of extant canids (yellow points). All plotted species are North American. Orange line represents a 1:1 ratio: prey mass equal to canid mass. Canid species falling above the orange line likely consumed prey larger than themselves, lending support to the categorization of “large hypercarnivore” based on size alone.

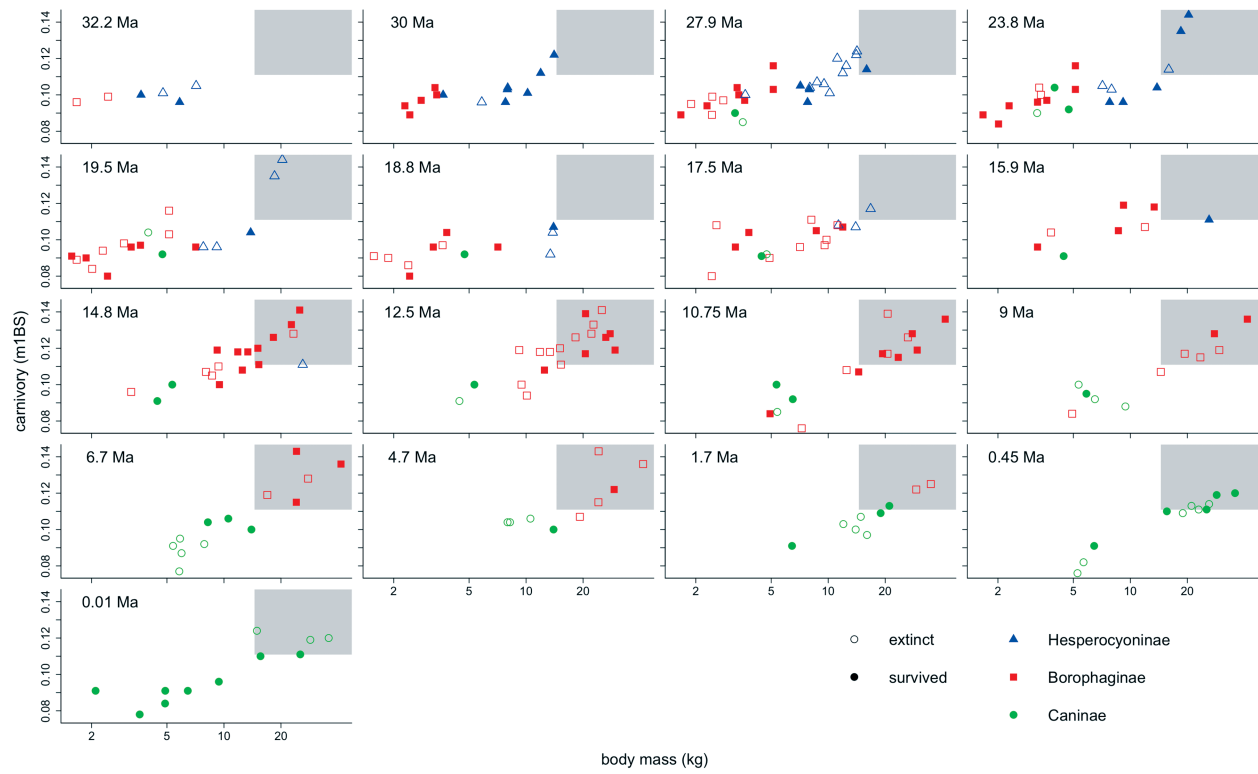


Figure 2.2. Ecomorphology of extinct and survived canid species over 17 time slices. The gray boxes designate the large-hypercarnivore niche. Only the end-Pleistocene extinction, at 0.01 Ma, shows a significant difference in body mass and carnivory between extinct and survived.

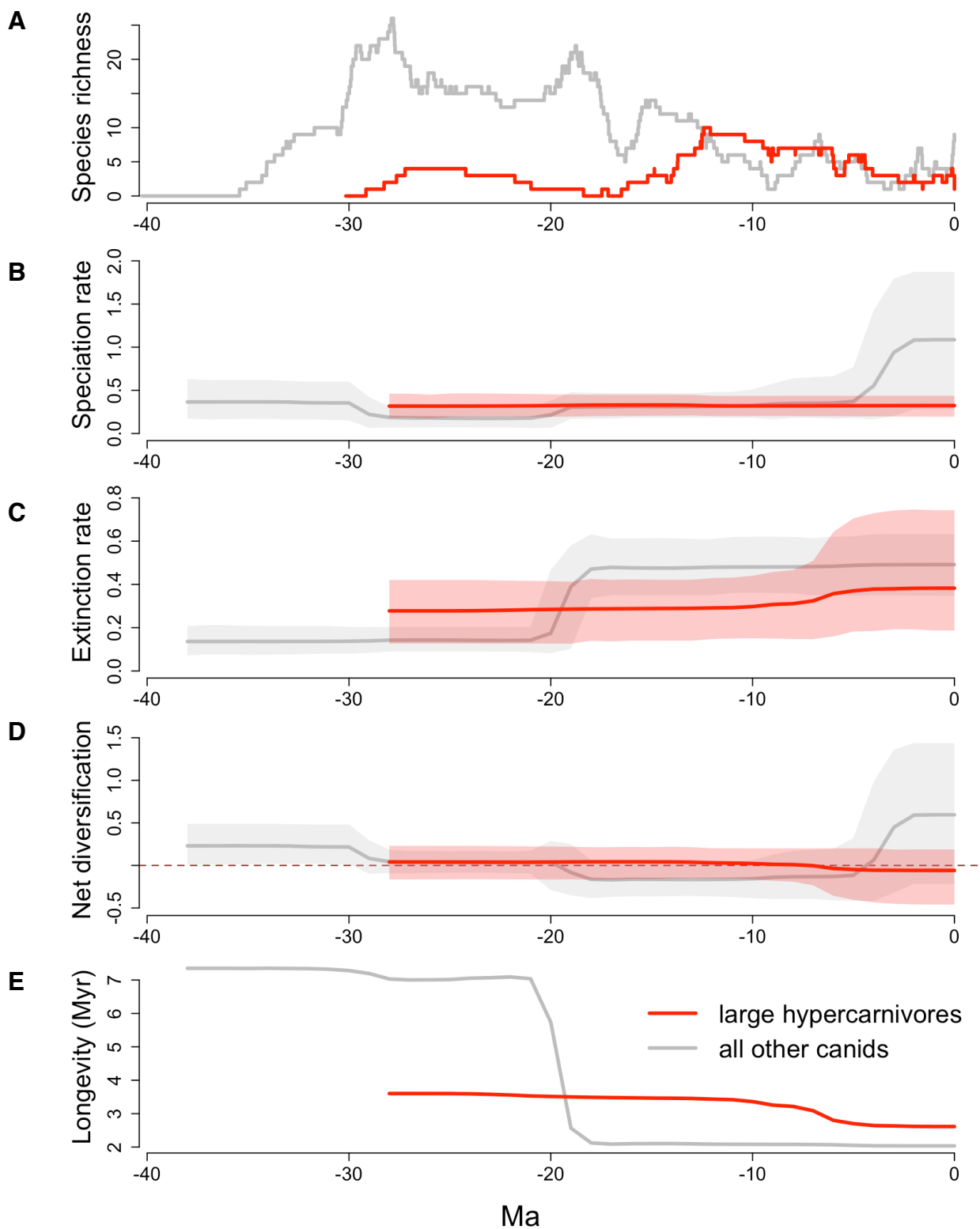


Figure 2.3. Average species richness (A), speciation rates (B), extinction rates (C), net diversification rates (D), and average longevity (E) for large hypercarnivorous North American fossil canids and all other North American fossil canids. Solid lines denote mean values; shading denotes 95% confidence intervals.

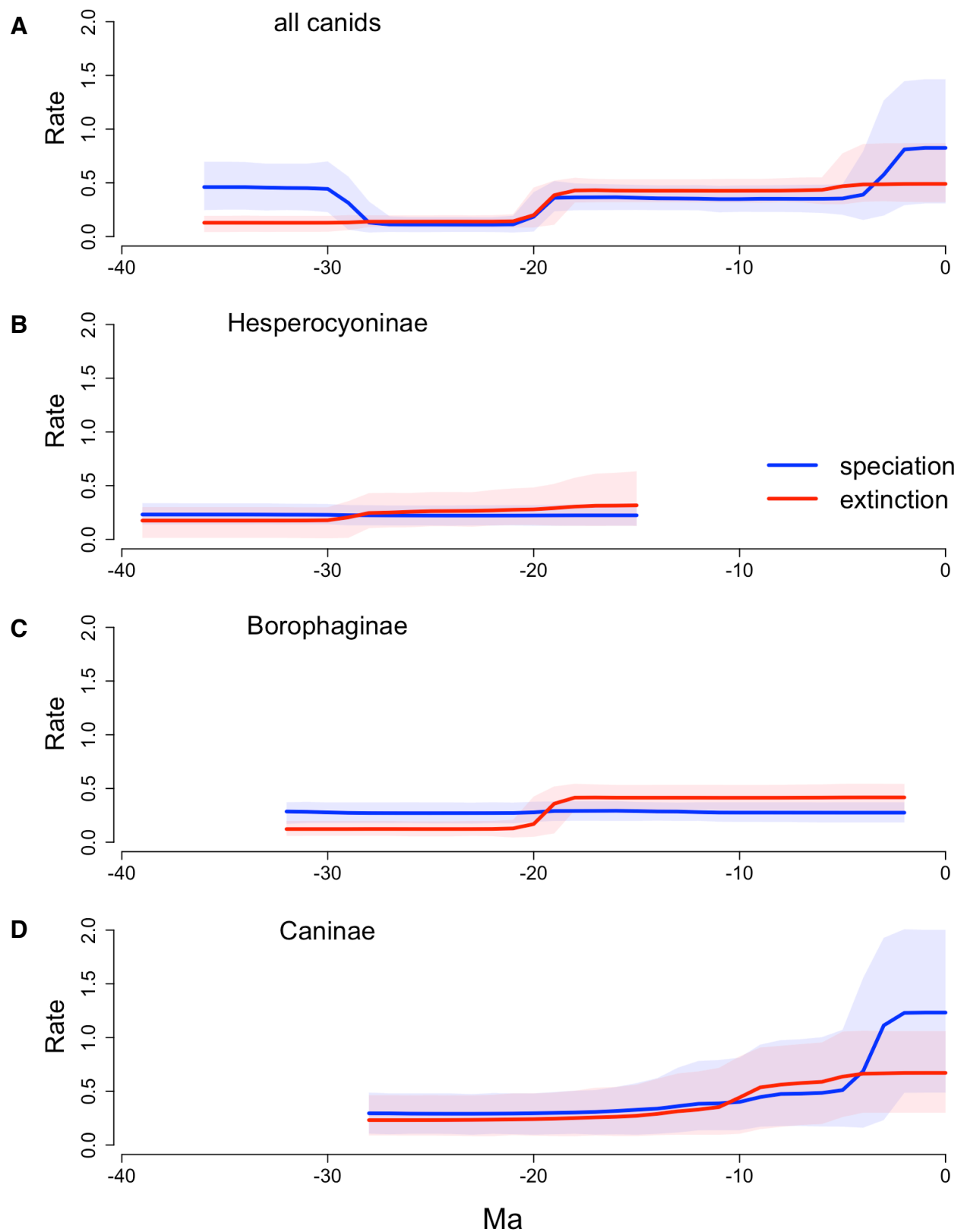


Figure 2.4. Speciation and extinction rates for all canids (A) and the three canid subfamilies: Hesperocyoninae (B), Borophaginae (C), and Caninae (D). Solid lines denote mean rates; shading denotes 95% confidence intervals.

Supplementary Information

Table S2.1. Subdivisions of North American Land Mammal Ages used to delineate time intervals for this study, based partly on MioMap (ucmp.berkeley.edu/miomap/about/lookuptables.html) and FaunMap (ucmp.berkeley.edu/faunmap/about/lookuptables.html) lookup tables.

Acronym	NALMA subdivision	Time
OREL	Orellan	33.9 – 32.2 Ma
WHIT	Whitneyan	32.2 – 30 Ma
EEAK	Early Early Arikareean	30 – 27.9 Ma
LEAK	Late Early Arikareean	27.9 – 23.8 Ma
ELAK	Early Late Arikareean	23.8 – 19.5 Ma
LLAK	Late Late Arikareean	19.5 – 18.8 Ma
EHMF	Early Hemingfordian	18.8 – 17.5 Ma
LHMF	Late Hemingfordian	17.5 – 15.9 Ma
EBAR	Early Barstovian	15.9 – 14.8 Ma
LBAR	Late Barstovian	14.8 – 12.5 Ma
ECLA	Early Clarendonian	12.5 – 10.75 Ma
LCLA	Late Clarendonian	10.75 – 9 Ma
EHMP	Early Hemphillian	9 – 6.7 Ma
LHMP	Late Hemphillian	6.7 – 4.7 Ma
BLAN	Blancan	4.7 – 1.7 Ma
IRVI	Irringtonian	1.7 – 0.45 Ma
RANC	Rancholabrean	0.45 – 0.01 Ma
HOLO	Holocene	0.01 Ma onwards

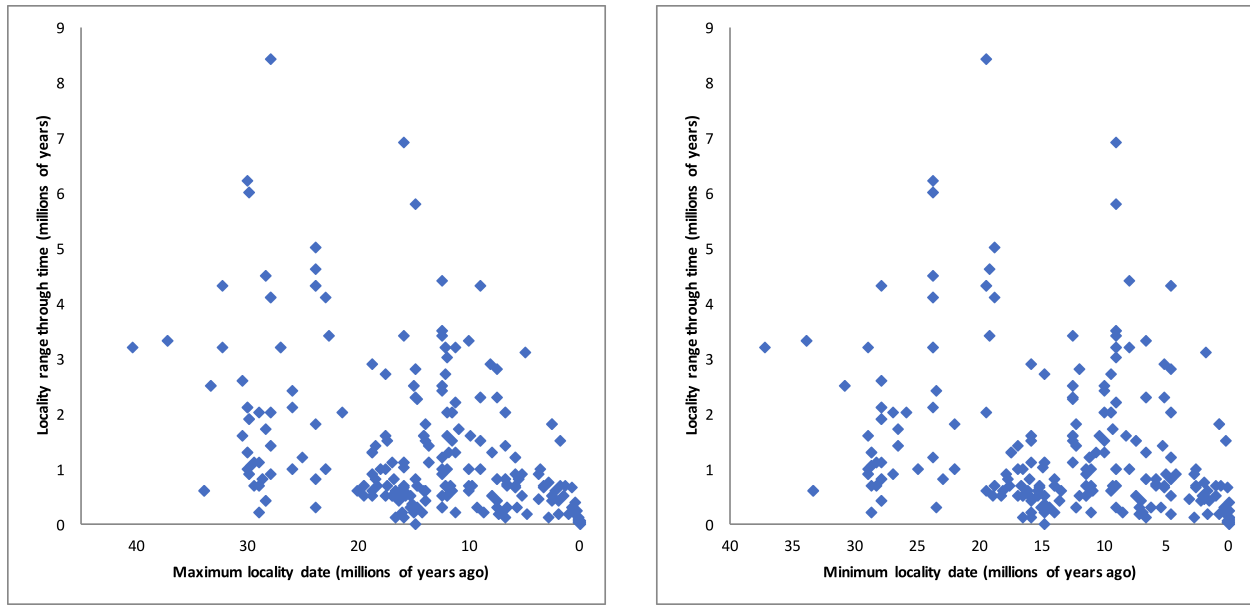


Figure S2.1. Variance in locality range through time (the length of each locality's stratigraphic range, in millions of years) decreasing toward the present, whether the x-axis is maximum or minimum locality date. Younger localities are dated more precisely. Some older localities are dated as precisely as younger localities, but some older localities are dated with much less precision than younger localities.

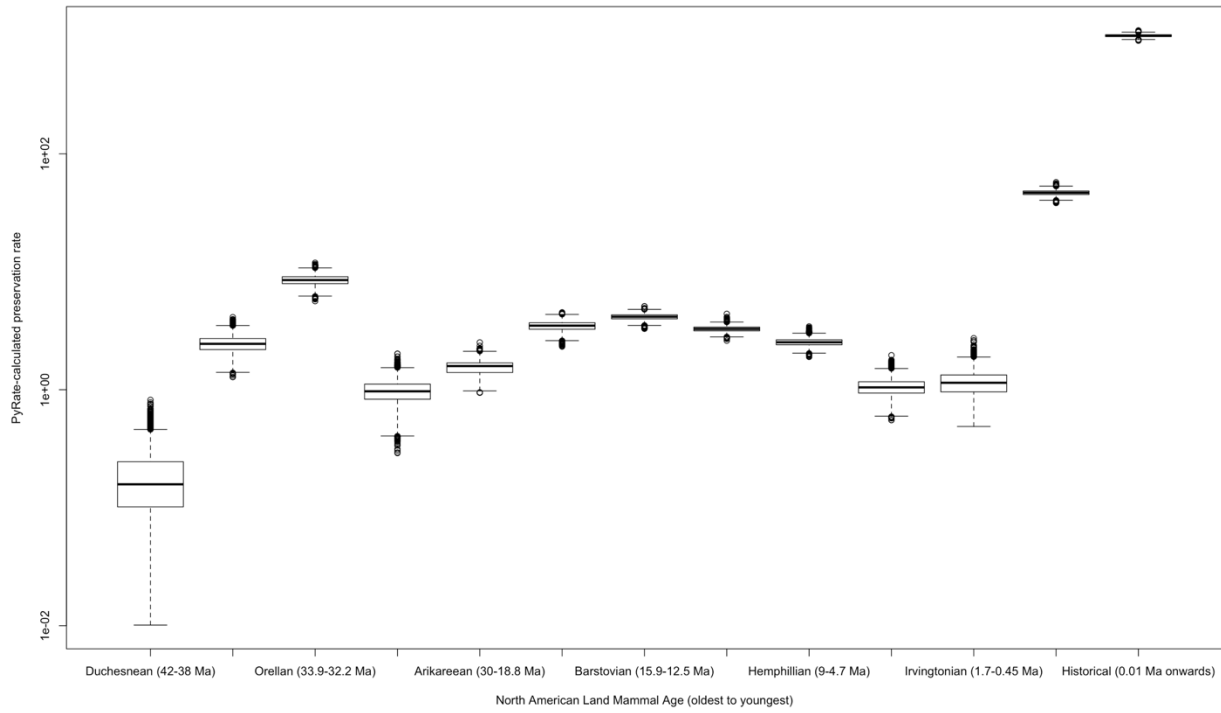


Figure S2.2. PyRate-calculated preservation rate per NALMA. Preservation rates vary from NALMA to NALMA, justifying use of the Time-variable Poisson Process (TPP) to estimate diversification rates in PyRate. Preservation is poorest and most variable in the Duchesnean, the earliest period of canid occurrence. Rates were \log_{10} -transformed to improve visualization.

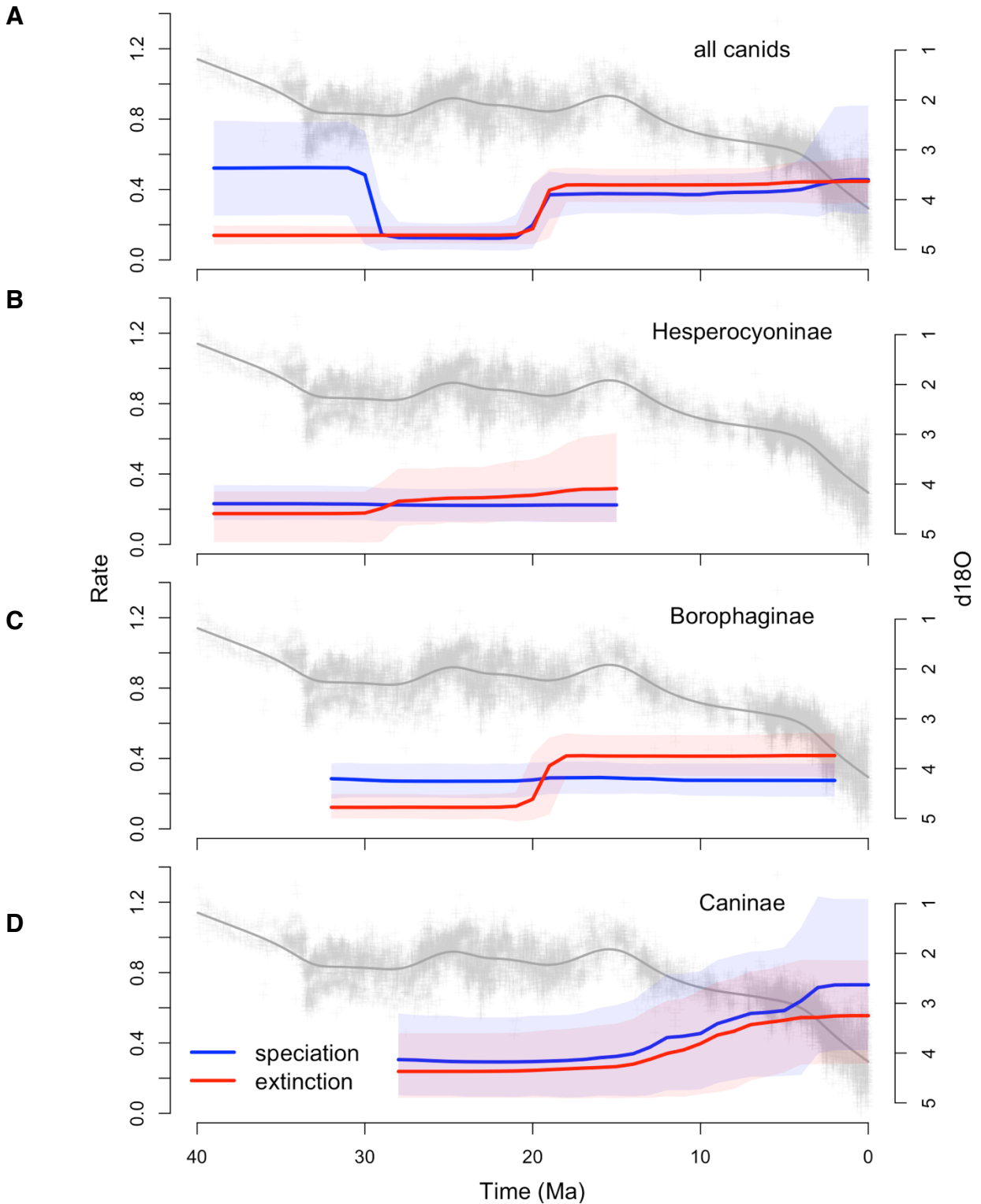


Figure S2.3. Speciation and extinction rates for all canids (A) and the canid subfamilies Hesperocyoninae (B), Borophaginae (C), and Caninae (D) superimposed onto a global temperature proxy, oxygen isotope values, over the past 40 million years. Because higher isotope values indicate lower temperature, the isotope scale is inverted to reflect temperature.

III.
FUNCTIONAL DIVERGENCE
IN BODY SIZE AND DIETARY ADAPTATIONS
WITHIN NORTH AMERICAN FOSSIL
CARNIVORAN COMMUNITIES

Abstract

Among extant taxa, competition between ecologically similar species can lead to character displacement: a divergence in characters, such as body size and skull shape, that relates directly to the way in which the species compete. Character displacement likely acts also at longer time scales, leading to double-wedge diversity patterns in the fossil record of carnivorous mammals, such as canids. We quantified body size and feeding adaptations of 170 Oligo–Miocene carnivorans to: (1) quantify the degree of morphological specialization for feeding abilities such as hypercarnivory; (2) determine the timing of, and potential temporal overlap among, morphological specializations; and (3) examine differences in diversity and disparity among time intervals, with an emphasis on how interactions with potential competitors may have influenced the evolutionary trajectory of Canidae. We generated a functional morphospace of extant carnivorans using estimated body mass and relative blade length of the lower carnassial tooth, against which we analyzed the traits of fossil carnivorans from nine intervals spanning 20 million years. Time intervals of high carnivoran species richness show surprisingly low disparity in body size and blade length, suggesting either that competition was unimportant or that species partitioned resources along another axis. We find evidence for the latter: examining four separate North American regions, we identify similar morphospace occupation and dispersion by different species in each, suggesting geographic partitioning. While we find functional and geographic divergence among carnivorans early in their history, the extent to which competition forced this divergence in the record of early carnivorans remains unclear, highlighting the limitations of studying empirical patterns and necessitating future simulation-based studies of process.

Background

Classic ecological theory posits that competition between two species has two possible outcomes: exclusion, in which one of the two species becomes locally extinct; or coexistence, in which the species evolve to partition resources [213,214]. Over generations, coexistence and resource-partitioning may arise by competitive character displacement: a divergence in characters, such as body size and skull shape, that influences the way in which the species compete [215–218]. On macroevolutionary scales, evolutionary responses to competition have been hypothesized to lead to repeated succession and replacement among ecologically similar clades, recorded as double-wedge patterns of diversity in the fossil record where one clade's richness falls as another clade's rises [195,219,220].

These patterns have been especially evident in the record of carnivorous mammals, such as those in the order Carnivora. The family Canidae originated approximately 40 million years ago in North America and diversified first in the Oligo-Miocene (approximately 34–5 million years ago). Over that 29-million-year span, canids became one of the most taxonomically diverse and morphologically disparate mammal clades, encompassing over 130 species and radiating into a wide range of ecomorphologies that include the large bone-cracking dogs of the later Miocene and the wolf-like and fox-like forms of today [35–37]. However, most of the earliest canids were small mesocarnivorous morphs similar to today's raccoons, with little indication of the diversity in size and dietary mode that they later would reach. The first canid over 20 kg that consumed prey larger than itself, *Enhydrocyon*, appeared 11 million years after the origin of the family, and large hypercarnivorous canids reached peak richness 28 million years after the origin of the clade. Furthermore, in a classic example of Cope's Rule, canids increased not only in average body size but also in minimum body size over their evolutionary history [39].

These two observations—the delayed filling of the large-hypercarnivore niche by canids, and their increase in both average and minimum body size over time—raise questions of ecological suppression. Did biotic interactions with other clades, such as competition, suppress the evolution of large hypercarnivorous canids until these other clades declined? Or, did external factors such as environmental conditions keep canids small and mesocarnivorous until the middle Miocene? Additionally, did the niche of large hypercarnivores remain similar in species richness over the Oligo-Miocene, with different species from different clades filling it; or did the carrying capacity of the predator niche expand or retract over this time?

Several other carnivoran families populated North America from the Oligocene to the Miocene: Felidae (cats), Nimravidae (false saber-toothed cats), Mustelidae (badgers, weasels, martens, wolverines, and allies), Procyonidae (raccoons and allies), Ursidae (bears), and Amphicyonidae (bear-dogs). While these families each existed at lower species richness than canids, their members include putatively carnivorous species that may well have delayed the rise of large hypercarnivorous canids.

Recent work on extinct canids has focused on understanding the dynamics of the three major radiations of Canidae—the subfamilies Hesperocyoninae and Borophaginae (now extinct) and Caninae (the only living subfamily)—from a macroecological and macroevolutionary perspective [43,197,198]. However, competition is an ecological phenomenon that occurs at the level of communities before scaling up to the level of continents. This current study supplements the macroecological and macroevolutionary framework by examining functional trait composition among canids and competitors at the regional level, providing snapshots of competition on the ground. This study focuses on potential carnivoran interactions from the Oligocene to the middle Miocene, an interval during which the three subfamilies of North

American canids overlapped with each other as well as with non-canid carnivorans, and an interval of unsurpassed species richness within the Canidae on a single continent.

For carnivorous mammals, the key parameters for competitive displacement of incumbents by newcomers are body size, diet, and locomotion [221], all of which are reflected in morphology. Here, we quantify and analyze the first two parameters in canids and non-canid competitors in the Oligo-Miocene.

Functional morphology

Carnivoran body mass spans more than four orders of magnitude, a range unsurpassed by any other mammalian order [16]. Extant large predators tend to specialize in larger prey and leave smaller prey to small predators, suggesting that body mass differences evolve to reduce competition [15]. Size divergence is important especially in larger carnivores, which are likely to have difficulty partitioning prey except by size. Additionally, because home-range size scales positively with body size in extant North American mammals [12,222–225], body size can influence partitioning of geographic resources.

Meanwhile, because efficient carnivoran feeding involves specific mechanical requirements, comparison of craniodental adaptations among canids and other carnivorans can reveal feeding behavior. Changes in the robustness of teeth, for instance, allow specialization for different prey sizes. More carnivorous taxa tend to have deep jaws, broad skulls, large canines and incisors, reduced post-carnassial molars, long shearing blades on lower carnassials, and increased mechanical advantage of the jaw-closing muscles: traits associated with increased bite forces and greater masticatory loads. Conversely, more omnivorous taxa tend to have large molar grinding areas, large post-canine dentitions, wide upper and lower fourth premolars, shorter coronoid processes, and longer mandibles: traits that maximize the ability to process a variety of

food items, from soft fruit to hard invertebrates [24,41,42].

Aims, hypotheses, and predictions

To evaluate a hypothesis of competition for the decline and extinction of plesiadapiforms in the Eocene, Maas et al. [220] examined four lines of evidence available in the fossil record: taxonomic richness, relative abundance, paleobiology, and paleobiogeographical history. Because relative abundance for our system is likely biased because of great size disparity leading to differential fossil preservation in carnivorans, we did not attempt to estimate this parameter but instead focused our efforts on quantifying taxonomic richness and paleobiology, and accounted for paleobiogeographical history by examining four geographically separate communities in North America.

Body-size estimates and craniodental metrics of Oligo–Miocene canids across the four regions were recorded to: (1) quantify the morphology of feeding abilities such as hypercarnivory; (2) determine the timing of, and potential temporal overlap among, morphological specializations; and (3) track varying relationships between diversity and disparity over time.

If active competition played an important role in early canid evolution, then there would be functional divergence among carnivoran species. Time intervals of high taxonomic diversity would correspond with time intervals of high ecomorphological disparity; if this occurs at the regional level but not at the continental level, then species would be interpreted to have partitioned geographic resources, sharing similar ecomorphologies across different regions. Additionally, if incumbent, non-canid, coeval taxa competitively suppressed the appearance of large hypercarnivorous canids, then non-canid carnivorans would primarily populate the large-hypercarnivore morphospace while canids would populate all other niche spaces at both

continental and regional scales.

Alternatively, if Oligo-Miocene canids remained small and mesocarnivorous independent of competitive pressures from non-canids, then a) trait values of the combined canid and non-canid dataset would be concentrated in intermediate values, indicating the predominance of a generalized diet across all clades, or b) ecomorphological variables of the combined dataset would span the full possible range of values from hyper- to hypocarnivory, but clades would be distributed evenly throughout the niche space. Disparity would also not track diversity, even at the regional level: times of high richness may coincide with times of medium or low disparity, because many species overlapping in resource use may occupy shared regions of morphospace.

Methods

Comparative database. To interpret the ecology of the fossil carnivorans, we compiled body sizes and raw craniodental measurements of extant carnivorans from Van Valkenburgh and Koepfli ([41]; canids), Van Valkenburgh *et al.* ([44]; hyaenids), Sacco and Van Valkenburgh ([27]; ursids), Friscia *et al.* ([42]; small carnivorans), and Meachen-Samuels and Van Valkenburgh ([226]; felids). The comparative database consists of 76 extant species spanning the range of body sizes and diets of extant terrestrial Carnivora.

Geographic and temporal coverage. We quantified the ecomorphology of fossil canids and potential competitors at two scales: continental and regional. For the regional scale, we concentrated on four North American areas: John Day Basin of Oregon (OR), southwestern South Dakota (SD), southern California (CA), and central New Mexico (NM). These regions, chosen because they preserve long and species-rich fossil records of Canidae and cover much of the geographic breadth of North American canid occupancy, also preserve non-canid

carnivorans. Additionally, the four regions are staggered throughout the Oligo-Miocene: OR and SD best preserve carnivorans from the Early Early Arikareean to Late Late Arikareean North American Land Mammal Ages (NALMAs; 30 to 18.8 million years ago), while CA and NM best preserve carnivorans from the Early Hemingfordian to the Late Barstovian NALMAs (18.8 to 12.5 million years ago). Therefore, the four regions permit different but complementary geographic and temporal vantage points on early canid history. Table 3.1 contains the list of NALMAs and their timespans.

Body size. We estimated \log_{10} body masses of extinct canids and non-canid coevals using regression equations based on the correlation of body mass with lower first molar length [40]. We used the canid regression for canids, the felid regression for felids and nimravids, and the mustelid regression for mustelids and procyonids. For amphicyonids and ursids, we used the all-carnivoran regression rather than the ursid regression because the former has a higher coefficient of determination than the ursid regression.

Diet. While diet is a complex and multivariate trait, many fossils tend to preserve only a few relevant features (e.g. teeth, incomplete dentaries), so that rare and poorly preserved species tend to be excluded from ecological analyses that incorporate several traits. To maximize our number of included species and quantify the ecological role of even rare or poorly preserved species, we analyzed relative blade length (RBL), the ratio of the length of the trigonid blade of the first lower molar to the length of the entire first lower molar (carnassial).

For comparison with the extinct data, we classified the extant data into five dietary categories: 1) hypercarnivory, meat comprising over 70% of the diet; 2) carnivory, meat comprising 50-70%; 3) omnivory, meat comprising less than 50%, or no dominant food type discernible; 4) insectivory, invertebrates comprising over 50%; and 5) herbivory, a diet of

predominantly plant material. These categories were for visualization only; given that extinct ecomorphologies tend to surpass the range of extant ecomorphologies, the extinct data were not classified to these categories.

Taxonomic diversity. To quantify taxonomic diversity, we calculated a number of metrics for each region, including species richness and a diversity index. Because raw species richness of a sample depends on sample size, and because the fossil record has differential preservation and temporal resolution that both affect sample size, we constructed rarefaction curves to assess the effect of sampling. Based on the results of the rarefaction curves, we used the Simpson index—the probability that two individuals randomly drawn from a community will be different species [227]—to incorporate richness and abundance into a single metric. The Simpson index is preferable here because other indices (e.g. Shannon) are susceptible to incomplete sampling, a potential problem in the fossil record. Our measure of abundance was the number of localities per species in each region. While analyzing the minimum number of individuals (MNI) is preferable to number of localities, not all localities have MNI records; additionally, MNI may be biased by differential fossil preservation by body size.

We also calculated similarity in species composition of communities, analyzing the number of localities that preserve each species in each region. Metrics of community taxonomic similarity between two groups include the Jaccard index, the number of taxa shared between the groups divided by the total number of taxa [228]. However, if the communities differ in size, the Jaccard and other common indices (e.g. Bray-Curtis, Sørensen) will underestimate richness in the smaller sample and therefore underestimate similarity. To account for potentially unsampled or undersampled species, we used Chao *et al.*'s [229,230] sample-adjusted Jaccard index, which considers the number of shared taxa known from only one or two localities.

Ecomorphological disparity. To assess the extent of resource-use overlap among carnivorans within each region, with special attention to how potential inter-clade competition may have affected the evolutionary trajectory of North American fossil canids, we (a) for canids, quantified ecomorphological breadth per interval and region by taking the median absolute deviation of \log_{10} body mass and RBL, and tracked expansion or retraction of this breadth; and (b) for all families, bootstrapped ANOVA comparisons of \log_{10} body mass and RBL across families within each interval and region. Competitive suppression against canids may be inferred to be weak at a given time interval or region if there is no significant ecomorphological difference between canids and other clades.

Results

Continental carnivoran diversity and disparity

We were able to estimate body mass and relative blade length for a total of 170 and 114 carnivoran species, respectively, spanning the 20-million-year sampling period from the Early Arikarean (EEAK) to the Late Barstovian (LBAR) (Figure 3.1). Extant and fossil species differed significantly in the distribution of both traits. Fossil carnivorans tended both to be larger (bootstrap $p = 0$) and have relatively longer blades (bootstrap $p = 0.0014$) than extant.

Maxima in continental-scale carnivoran species richness occurred in the EEAK (41 species), Early Hemingfordian (EHMF, 35 species), and Early Barstovian (EBAR, 50 species) (Figure 3.2). Ecomorphological disparity, measured by median absolute deviation, largely did not track taxonomic richness over this time. Disparity in \log_{10} body mass appears inversely related to richness: middling to low values in body-mass disparity correspond to high richness, suggesting high overlap in body mass among species. Body-mass disparity peaked in the Late Late

Arikareean (LLAK), as did disparity in relative blade length; this is remarkable because the LLAK represents a minimum in species richness. RBL disparity overall was high from the Whitneyan (WHIT) to the LLAK before crashing concomitant with the decrease in diversity in the Late Hemingfordian (LHMF). Diversity recovered afterwards and peaked to unprecedented levels in the EBAR; RBL disparity also recovered but far from the same degree (Figure 3.2).

Figure 3.3 tracks continent-wide shifts in body mass and relative blade length per time interval, illuminating the species-level mechanisms behind the disparity analyses. The “cat gap” [195,208,231] from the ELAK to the EHMF—caused by the extinction of nimravids at the end of the LEAK and delayed arrival of true felids in the LHMF—is shown to contribute to the lowered ecomorphological disparity visible in the ELAK and EHMF. The disparity peak during the LLAK, an interval within the cat gap, appears to stem from the entrance of smaller borophagines with relatively shorter blades and, conversely, the advent of very large amphicyonids with relatively longer blades: an expansion of occupied morphospace. For all nine intervals, canids are the most species-rich and also encompass a greater range of morphospace than all other carnivorans.

Regional richness and similarity

The extraordinarily high richness levels at times of middling to low ecomorphological disparity suggest either: 1) that species overlapped significantly in ecomorphology and therefore resource use, or 2) that species partitioned resources along an axis not considered in the analysis. To evaluate habitat region as another potential axis along which species may have partitioned resources, we examined four regions. These four regions reached peak species richness at similar times. The John Day Basin in Oregon reached a height of 20 species in the EEAK, in the same interval as when southwestern South Dakota reached a height of 17 species (Table 3.2). Southern

California peaked at 23 species in the EBAR, in the same interval as when central New Mexico peaked at 13 species (Table 3.2).

While these four regions were chosen because of the high quality of their fossil record, the rarefaction curves per region show little sign of plateauing toward saturation, suggesting that sampling is still incomplete for all regions and will likely be supplemented given more localities (Figure S3.1). Given this, we also quantified the Simpson index as a measure of diversity for each region during their peak diversity interval. Of the four regions, Oregon and California contain the highest number of localities as well as the highest number of species; they also have the highest Simpson indices, suggesting that they are truly more diverse than the two other sites. California also has the highest evenness of species across localities, with the lowest relative abundance of the most abundant taxon (Parker-Berger measure; Table 3.2).

The two EEAK carnivoran communities were less taxonomically similar to each other (Jaccard-Chao similarity = 0.136) than the two younger EBAR carnivoran communities (Jaccard-Chao similarity = 0.588). However, there is no ecomorphological difference between canids from the Oregon and South Dakota EEAK communities and also between canids from the California and New Mexico EBAR communities (bootstrapped $p > 0.05$ for comparisons of $\log_{10}\text{mass}$ and RBL between OR and SD and between CA and NM). Interestingly, there is also no statistically significant ecomorphological difference between EEAK and EBAR communities, whether for all carnivorans or for canids alone: $\log_{10}\text{mass}$ and RBL both earlier and later appear to have come from the same statistical distribution (bootstrapped $p > 0.05$).

Discussion

Competition is a dominant paradigm explaining divergence in ecomorphology among

carnivorous mammals. The principle of competitive exclusion posits that, given all ecological factors being constant, two species competing for the same resources cannot coexist [213]. Therefore, two ecologically similar species with limited resources in a limited area will result in one species becoming locally extinct, with coexistence resulting only when the species diverge in ecomorphology and cease to compete.

Inferring competition in the fossil record, however, is much more difficult than observing it in living ecosystems. To infer competition, resource use must overlap among a set of coexisting potential competitors. Second, resources must be limited, because organisms do not need to compete for resources that are abundant. Third, competition may occur on one resource axis (for instance, diet) but not in another (for instance, habitat). Overlap in diversity curves is only the first step in inferring competition in the fossil record; one must also establish the above three points and, additionally, establish them at as local a level as possible in order to maximize the likelihood that the species in question did coexist [220].

The mammalian clade Carnivora has been at the forefront of many studies on competition, both in its modern form and in the fossil record. Character displacement inferred to have resulted from competition has been documented in extant small to medium-sized carnivorans, ranging from foxes in the Saharo-Arabian region [215], weasels of North America and mustelids and viverrids of Israel [216], small cats of Israel [232], medium-sized to large canids of Israel [233], jackals in East Africa [218], and mongooses on Pacific islands [234]. Character displacement has also been documented in Miocene hyaenids from Eurasia and Africa [235], and competition (whether active replacement or passive displacement) is commonly hypothesized as a cause for the diversification of some carnivoran clades in contrast to the decline of others [195,236,237]. The rise and fall of Carnivora's many families over its 55-

million-year history present a compelling system for examination of competitive effects over long timescales.

Just as it is difficult to document competition in the fossil record, it is problematic to identify character displacement. Whereas modern animals can be reasonably inferred to have coexisted and therefore potentially affected each other, the problem of time-averaging means that animals found within a single region—unless buried in a single catastrophic event—likely died and were preserved at different points in time. The intervals that we have employed in this study are, by necessity, millions of years long (Table 3.1). Therefore, we hesitate to identify character displacement, as defined by the precise equal ratios commonly referred-to in the literature, and instead refer to *functional divergence*.

The fossil record of mammalian carnivores, as studied here, preserves evidence of functional divergence. Across the time intervals examined, there is a dispersion of trait values throughout the mass-RBL morphospace. Canids tend to have mid-size and mid-RBL values: their ecological generalism and evolutionary lability is observable in the number of species occupying a relatively wider range of morphospace than other families. Other families tend to cluster in high-mass and mid-RBL space (amphicyonids), high-mass and high-RBL space (nimravids and felids), and low-mass and low-RBL space (procyonids). Granted, differences in traits do not always amount to functional differences, and phylogenetic constraints need to be considered. For example, given the ancestral loss of their post-carnassial molars, feliforms (barring further derived loss and modification of teeth, as in the case of aardwolves) are constrained to having $RBL > 0.8$, the hypercarnivorous condition. Given this hypercarnivory, the smaller size of a felid or nimravid compared to a hypercarnivorous amphicyonid does not preclude the two animals' occupancy of overlapping ecological niches, even though their morphological niches appear to

be distinct. Interestingly, mustelids (extant and extinct) occupy similar niches as canids but exist at much lower species richness, in this way likely minimizing competition.

Given the data, it is difficult to conclude that this observed morphological and functional divergence stems from competition. The observed patterns may represent the ghost of competition past: the aftermath of competition recorded in ecomorphology. But, might the patterns recorded here also emerge given an experimental scenario of no competition? Methods of using phylogenetic relatedness as a null hypothesis—in which species traits observed to be more or less divergent than their phylogeny would predict, are interpreted as the result of competition or other ecological mechanisms—are appealing but not easily applicable in this case. Except for canids, most fossil carnivoran families still suffer from poorly resolved phylogeny and, in some instances, taxonomy. Although the empirical approach used here clarifies pattern, simulation-based analyses would likely clarify process [238,239].

What of the differences in taxonomic similarity between the earlier EEAK and later EBAR carnivoran communities? The two EEAK communities, Oregon and South Dakota, are less similar to each other than the two EBAR communities, California and New Mexico. The species shared between Oregon and South Dakota tend to be small mesocarnivorous canids—*Archaeocyon pavidus*, *Cynarctoides lemur*, *Philotrox condoni*—with the exception of the large hypercarnivorous nimravid *Nimravus brachyops*. Meanwhile, the species shared between California and New Mexico tend to be more evenly spread over taxonomic family, body size class, and dietary category: from the large hypercarnivorous *Amphicyon ingens* (a bear-dog), *Osbornodon fricki* (a hesperocyonine canid), and *Protepicyon raki* (a borophagine canid); the medium-sized mesocarnivorous *Microtomarctus conferta*, *Paracynarctus kelloggi*, and *Tomarctus brevirostris* and *hippophaga* (borophagine canids); to the small hypocarnivorous

Cynarctoides acridens (a borophagine canid) and *Leptocyon leidy* (a canine canid). Certainly, Oregon and South Dakota are farther from each other than are California and New Mexico. The increased distance may explain the lower taxonomic similarity, although environmental and topographic shifts over the period from the EEAK to the EBAR may also have eased species dispersal, effectively lowering the limitation on habitat and other resources that would have forced competition.

Conclusions

In our analysis over 20 million years, time intervals of high carnivoran species richness show surprisingly low disparity in body size and blade length, suggesting either that competition was unimportant or that species partitioned resources along another axis. We find evidence for the latter: at peak richness in four separate North American regions, we identify similar morphospace occupation and dispersion by different species in each, suggesting geographic partitioning. While we find functional and geographic divergence among carnivorans early in their history, the extent to which competition forced this divergence in the record of early carnivorans remains unclear, highlighting the limitations of studying empirical pattern and necessitating future simulation-based studies of process.

Tables and Figures

Table 3.1. Subdivisions of North American Land Mammal Ages used to delineate time intervals for this study, based on MioMap (ucmp.berkeley.edu/miomap/about/lookuptables.html) lookup tables.

Acronym	NALMA subdivision	Time
WHIT	Whitneyan	32.2 – 30 Ma
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ELAK	Early Late Arikareean	23.8 – 19.5 Ma
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LHMF	Late Hemingfordian	17.5 – 15.9 Ma
EBAR	Early Barstovian	15.9 – 14.8 Ma
LBAR	Late Barstovian	14.8 – 12.5 Ma

Table 3.2. Diversity metrics for each region.

Region	# localities	# species	Simpson	Evenness	Fisher's α	Parker-Berger
OR.EEAK	97	20	0.911	0.873	7.643	0.134
SD.EEAK	66	17	0.894	0.888	7.415	0.227
CA.EBAR	92	23	0.933	0.919	9.843	0.130
NM.EBAR	39	13	0.840	0.842	6.828	0.308

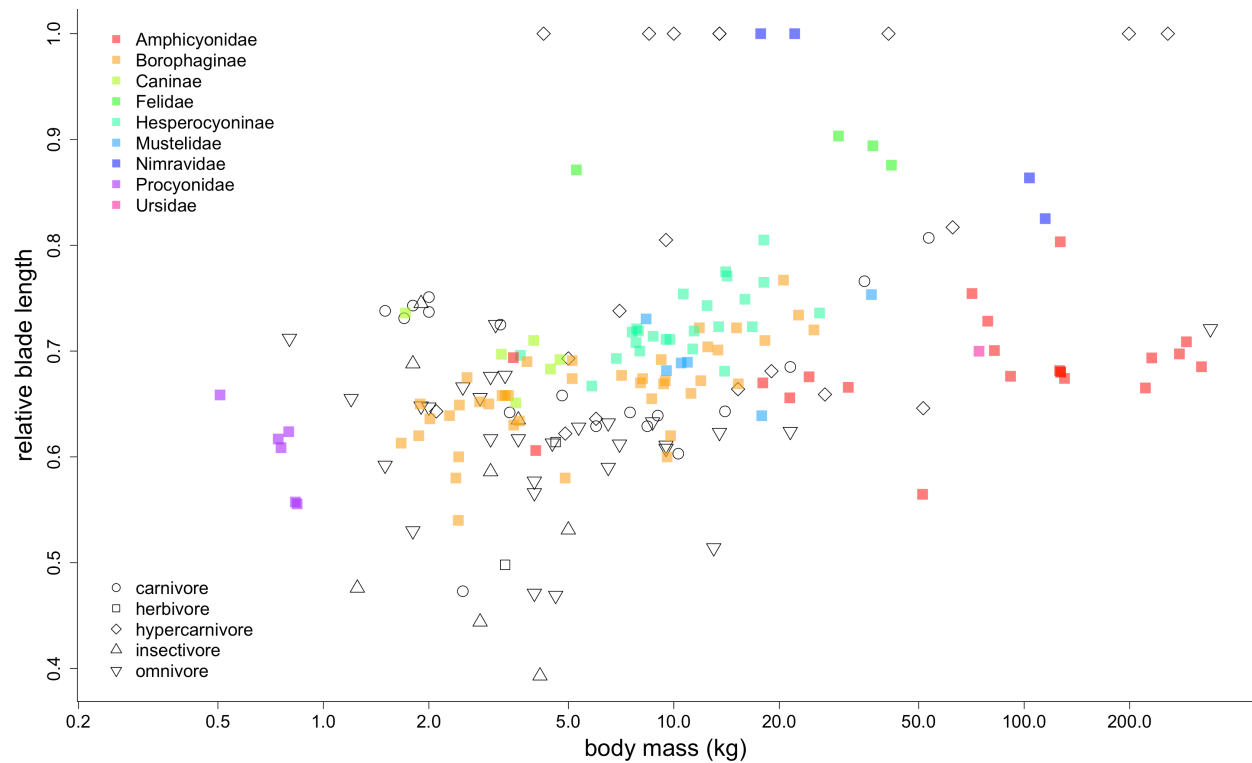


Figure 3.1. Bivariate morphospace (relative blade length v. body mass) of 76 extant carnivorans (hollow shapes) and 114 extinct carnivorans (filled squares). For extant carnivorans, symbol shape indicates diet; for extinct carnivorans, square color indicates family or subfamily assignment. Large-bodied hypercarnivorous carnivorans are to the right.

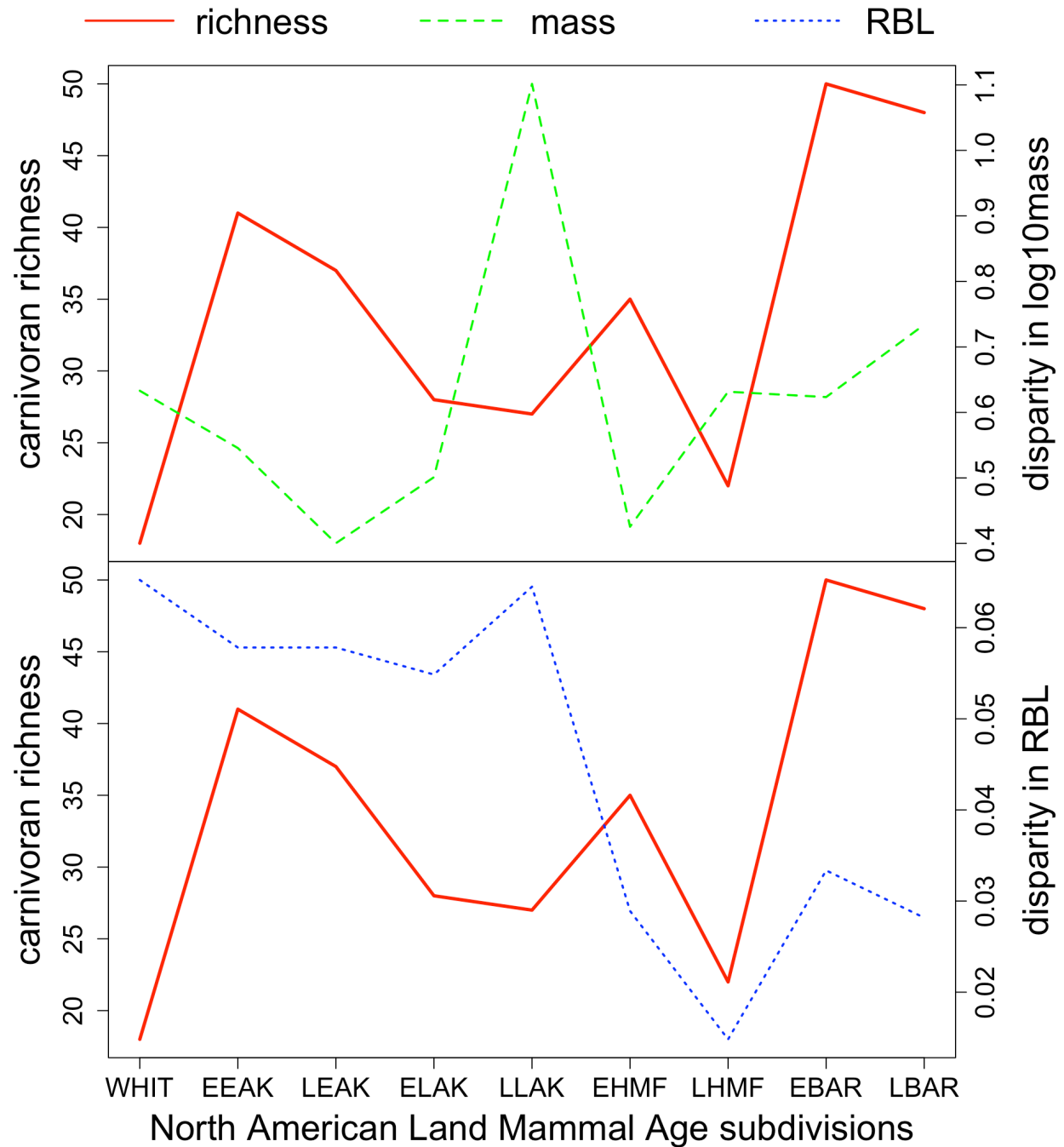


Figure 3.2. Line plots of species richness (red solid), disparity in log10mass (green dashed), and disparity in relative blade length (blue dotted) across the North American carnivoran fossil record over nine subdivisions of North American land mammal ages.

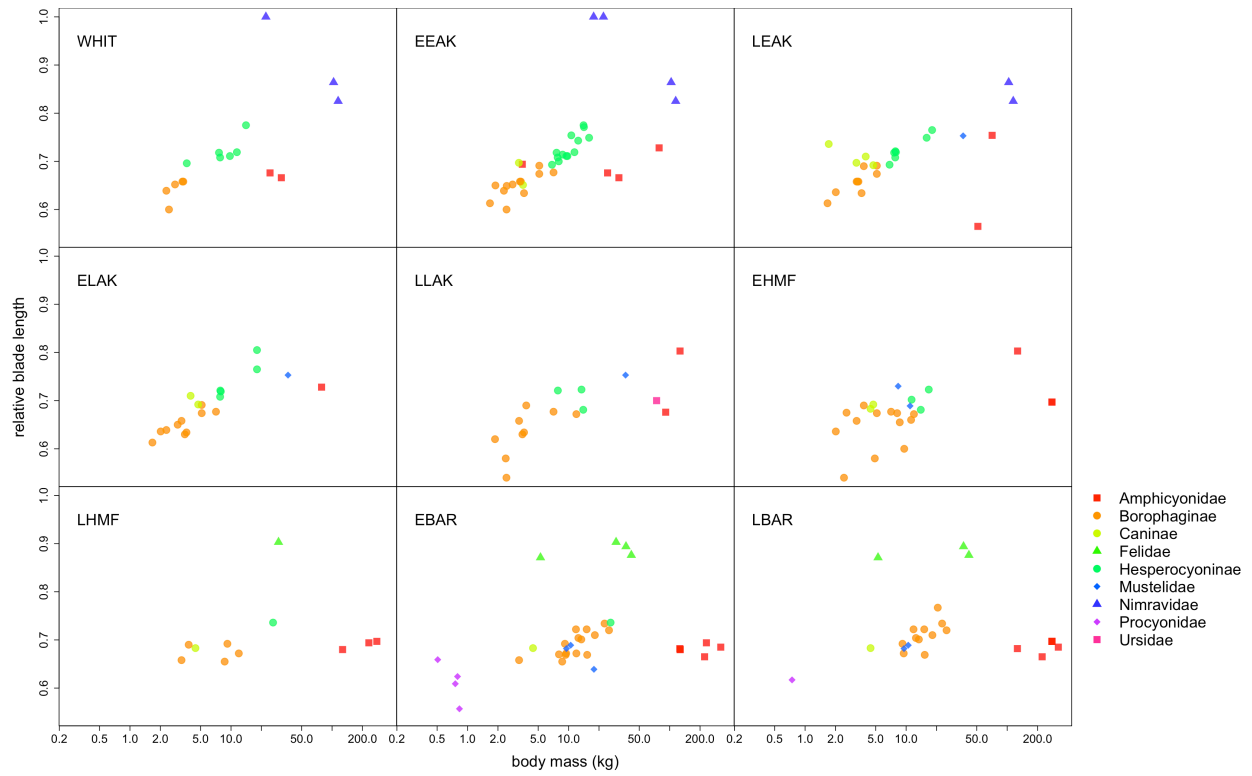


Figure 3.3. Per-interval bivariate morphospaces for carnivorans at the continental scale.

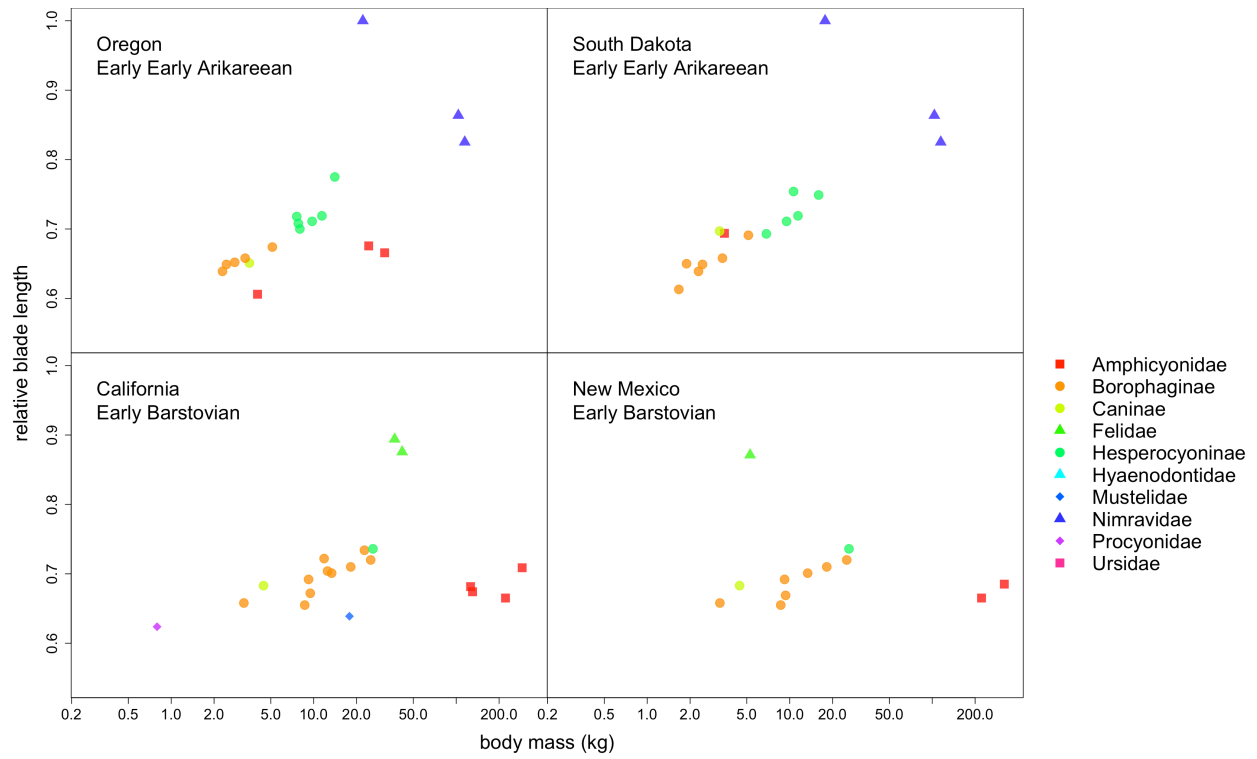


Figure 3.4. Bivariate morphospaces for the peak-richness interval within each region. Canids (hesperocyonines, borophagines, canines) comprise much of the taxonomic diversity and ecomorphological disparity for all four intervals.

Supplementary Information

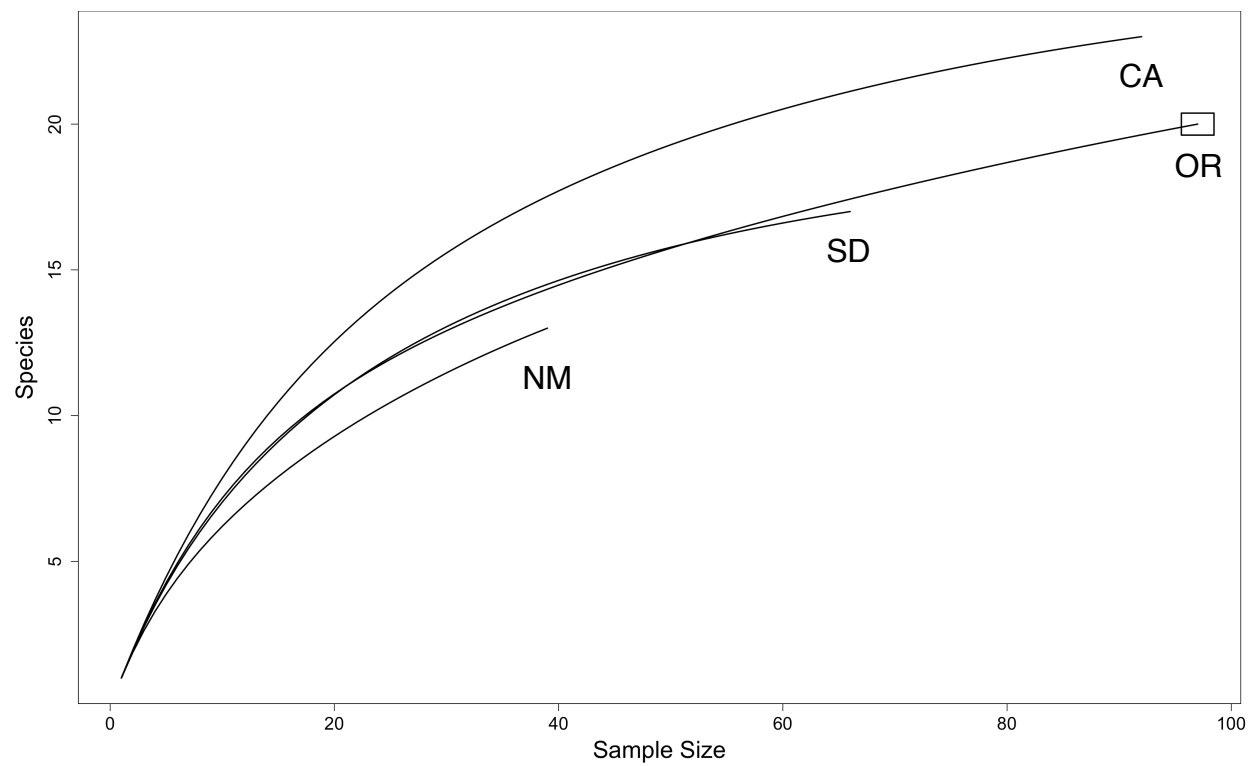


Figure S3.1. Rarefaction curves for each region. Sample size is total number of localities where each species is found.

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