Iterative evolution of large-bodied hypercarnivory in canids benefits species but not clades

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Ecological specialization has costs and benefits at various scales: traits benefitting an individual may disadvantage its population, species or clade. In particular, large body size and hypercarnivory (diet over 70% meat) have evolved repeatedly in mammals; yet large hypercarnivores are thought to be trapped in a macroevolutionary “ratchet”, marching unilaterally toward decline. Here, we weigh the impact of this specialization on extinction risk using the rich fossil record of North American canids (dogs). In two of three canid subfamilies over the past 40 million years, diversification of large-bodied hypercarnivores appears constrained at the clade level, biasing specialized lineages to extinction. However, despite shorter species durations, extinction rates of large hypercarnivores have been mostly similar to those of all other canids. Extinction was size- and carnivory-selective only at the end of the Pleistocene epoch 11,000 years ago, suggesting that large hypercarnivores were not disadvantaged at the species level before anthropogenic influence.
Modern mammal communities are depauperate in 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 such as Rancho La Brea included as many as five more: the extinct dire wolf, American lion, short-faced bear, and two saber-tooth cats. Even more rare is bone-cracking, 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. The current paucity of large hypercarnivores encourages the perception that the costs of carnivory make diverse predator assemblages unsustainable. 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.

Extant large carnivores tend to be hypercarnivores that consume prey of large or larger than themselves. This strategy is costly for several reasons. Large prey are less abundant and have patchier distributions than smaller prey, lengthening predators’ search and pursuit times. They are difficult to take down, making a carcass worth fighting over, which can lead to injury and death. And, they often are more dangerous than small prey. Cracking large bones incites fracture and wear on teeth, the main tools of prey capture and food processing. Juveniles must grow large enough to be able to learn attack behaviors and catch large prey, delaying acquisition of foraging skills. On macroevolutionary scales, hypercarnivorous adaptations—e.g., loss of dental features to create slicing blades—are likely to be irreversible, limiting further morphological diversification.

Yet, hypercarnivory presents benefits that likely offset its costs. Barrington predator specialization on a few prey species, meat is readily available. It has high energy content and is more efficiently digested than plants, permitting high basal metabolic rates, growth rates, and fecundity. Hypercarnivores tend to be larger-bodied than non-hypercarnivorous relatives, affording greater dispersal ability across environments of variable resource availability. Despite hypercarnivore’s apparent irreversibility, it repeatedly punctuates the evolutionary history of the Carnivora, suggesting that it is successful.

The fossil record of North American dogs (Carnivora: Canidae) presents an ideal system for testing the impact of this specialization on the diversification of large predators. Fossil dogs arose in North America ~40 million years ago (Ma), radiating into over 130 species in three subfamilies: Hesperocyoninae, Borophaginae, and Caninae. The extinct species surpass the extant species in ecomorphological range, including many large hypercarnivores. Competitive interactions have been hypothesized among the subfamilies, and habitat changes over the Neogene may have precipitated morphological and behavioral shifts; the roles of climate and competition in the rise and fall of canids remain an area of active study.

Negative relationships have emerged between dietary specialization (including hypercarnivory) and species duration in Hesperocyoninae, Borophaginae, and Caninae, suggesting that specialization negatively impacts canid success. Here, we investigate further by (a) quantifying turnover rates at intervals to pinpoint differences in body mass and diet between extinction survivors and victims, (b) comparing rates of diversification (origination, extinction, and origination minus extinction, all relative to the total history of the group in question) between large hypercarnivores and all other canids as well as among subfamilies, and (c) tracking diversification rates in correlation with, first, traits as potential intrinsic drivers and, second, global temperature estimated by oxygen isotopes as a possible extrinsic driver of canid diversification.

How have the costs and benefits of large-bodied hypercarnivory impacted extinction risk at the species level and, further, at the clade level? If being a large hypercarnivore increases the probability of going extinct, then we predict that, relative to smaller and/or less carnivorous canids, large hypercarnivores would have higher extinction frequencies, calculated as the proportion of species that become extinct relative to the total number of species in the interval. Alternatively, if the short-term benefits of large-bodied hypercarnivory outweigh the costs in the long-term, then large hypercarnivores may exhibit constant extinction rates on par with or lower than non-hypercarnivores.

In Hesperocyoninae and Borophaginae, the two canid subfamilies that are completely extinct, we find that diversification of large-bodied hypercarnivores appears constrained at the clade level, biasing specialized lineages to extinction. However, despite shorter species durations, extinction rates of large hypercarnivores have been mostly similar to those of all other canids. Extinction was size- and carnivory-selective only at the end of the Pleistocene epoch 11,000 years ago, suggesting that large hypercarnivores were not disadvantaged at the species level before anthropogenic influence.

Results

Large hypercarnivores. The majority (100/132 analyzed species) of North American fossil canids over the last 40 Ma were <20 kg and fed on prey smaller than themselves (Fig. 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 wide dietary range, including mesocarnivory and hypocarnivory. Small- to medium-sized hypercarnivores exist—e.g., some extant foxes—but, because the energetic costs differ between smaller and larger hypercarnivores, we included these smaller species with all other canids. Based on our estimates of predator and prey body sizes, we categorized 32 species as large hypercarnivores, including Enhydrocyon (four species), Ectopocynus simplicidens, and Osbornodon fricki in Hesperocyoninae; Aeluroidon (six species), Paratomarctus euhos, Carpocyon webbi and robustus, Protepiyon + Epicyon (three species), and Borophagus (eight species) in Borophaginae; and Theriodictis floridanus, Xenocyon (two species) and two extinct species of Canis in Caninae.

Survivor–victim analysis. Figure 2 shows large hypercarnivorous species in the upper right quadrant (gray-shaded region) of each morphospace time slice. If being large and hypercarnivorous increases extinction risk, then, for each time slice, more extinct species (hollow shapes) would be in the gray-shaded region, and fewer extinctions representing smaller non-hypercarnivores would be in the unshaded region. Our analyses do not support this hypothesis. We found negligible differences in carnivory and body mass for most time intervals (Table 1). Particularly after correcting for multiple comparisons, the only significant difference between survivors and victims occurred at the end of the Pleistocene epoch (0.01 Ma; P = 0.011). At this time, three large hypercarnivores became extinct or were extirpated from North America—Cuon alpinus; Canis armbrusteri; and the dire wolf, Canis dirus—leaving behind a radiation of small and relatively hypocarnivorous foxes.

Subfamily trends. Despite minimal support for size- and carnivory-selective extinction, trends emerge within each subfamily. Starting 10 My after origin, Hesperocyoninae populated the large-hypercarnivore space (Fig. 2); the last surviving hesperocyonine, the large hypercarnivore Osbornodon fricki,
Hesperocyoninae accelerated at 29 Ma and again around 20 Ma; over the subfamily Borophagine origination rate, meanwhile, was nearly constant over the last 40 Ma were ≤20 kg and fed on prey smaller than themselves.

Support for a rate decrease occurs at about 30 Ma (Fig. 4d) suggesting at least two origination rates in this subfamily; positive Axes are log10-transformed. Gray-shaded area marks estimated predator mass ≥20 kg. Orange line represents a 1:1 ratio, or 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. Most North American fossil canids over the last 40 Ma were <20 kg and fed on prey smaller than themselves.

became extinct ~14.8 Ma. Borophagines boarded an evolutionary conveyor belt toward the niche left open by O. fricki’s extinction, eventually also becoming extinct ~2 Ma. Canines appear to follow this pattern most recently, until experiencing the only hypercarnivore-selective extinction ~0.01 Ma.

Extinction dynamics of large hypercarnivores. Starting with the hesperocyonine Enhydrocyon 30–27.9 Ma (Fig. 3), large hypercarnivores numbered fewer than all other canids for much of their history, except 13–8 Ma when their richness peaked (Figs. 2 and 3a). Large-hypercarnivore extinction started marginally higher than observed for all other canids but was surpassed by extinction of the latter at 20 Ma, although both rates are now statistically indistinguishable because of an increase in both large-hypercarnivore extinction rate and its credible interval starting ~7 Ma (Fig. 3b; Supplementary Table 1, Supplementary Fig. 1).

Subfamily diversification rates. For origination of Hesperocyoninae, the two-rate model showed highest support (Table 2), suggesting at least two origination rates in this subfamily; positive support for a rate decrease occurs at about 30 Ma (Fig. 4d–f). Borophagine origination rate, meanwhile, was nearly constant over the subfamily’s duration (Fig. 4g–i, Table 2). Extinction of Hesperocyoninae accelerated at 29 Ma and again around 20 Ma; for Borophaginae, extinction exceeded origination around 20 Ma. Different patterns characterize Caninae: origination and extinction rates have been approximately equal—producing zero to positive net diversification for much of North American canine history—and both rose gradually from 10 Ma to the present (Fig. 4j–l, Table 2).

Correlation between rates and traits. Origination and extinction rates do not correlate significantly with body mass, carnivory or a combination of the two traits in all Canidae or in any subfamily (Supplementary Table 2), although some rates appear to be weakly correlated (Supplementary Fig. 2).

Correlation between rates and temperature. Extinction rates for all canids, smaller non-hypercarnivores, and Caninae correlated positively with the oxygen-isotope record. Higher δ18O values correspond to lower temperatures; therefore, there was higher turnover among species as global temperature decreased. All other correlations were not significant (Supplementary Fig. 3, Supplementary Table 3).

Discussion
The costs and benefits of hypercarnivory are well known at the individual level. At the species level, specialization may confer a short-term advantage by optimizing an organism for its environment and available resources; but, over long timescales, specialization can be an evolutionary trap for entire clades.

Hypercarnivorous adaptations that simplify the dentition to maximize the slicing surface—such as loss of cusps on teeth (e.g., canids with trenchant talonids) or loss of grinding teeth (e.g., feliforms)—exemplify Dollo’s law: that a structure, once lost, is unlikely to be regained. Relative to generalists bearing the ancestral condition, specialists with derived and reduced morphologies provide less material for evolvability and a narrower range of “next steps” for descendant species.

Consequently, on macroevolutionary timescales, canids appear repeatedly to board a conveyor belt toward progressively greater specialization, with few or no reversals. Therefore, hypercarnivory evolving under Dollo’s law inevitably will increase the relative frequency of hypercarnivory in the later history of a clade—until the clade vanishes, even if the possibility remains that the dietary shift is not the ultimate cause of extinction.

This evolutionary conveyor belt or macroevolutionary ratchet is apparent in the survivor–victim analysis (Fig. 2). Each subfamily originates as small mesocarnivores, increasing in size and carnivory over time until—in the two extinct canid radiations—species enter and eventually vanish from the extreme quadrant of morphospace. Accordingly, clade extinction rates increase and eventually exceed origination rates after the rise of lineages leading to the first large hypercarnivores (Enhydrocyon in Hesperocyoninae ~29 Ma, followed by Osbornodon ~20 Ma; Borophagini in Borophaginae ~20 Ma) (Fig. 4).

Specialization signals the beginning of clade decline. Given this, and given the tendency of canid specialists toward shorter species durations (Fig. 2 in ref. 27), one might expect higher extinction rates for large hypercarnivores, because extinction rate is the reciprocal of mean species longevity. This is not what we observed (Fig. 3; Supplementary Fig. 1, Table 1). The lack of evidence for higher extinction rates for large hypercarnivores (Fig. 3) might be due, at least partially, to how we binned the data in the analysis, comparing “large hypercarnivores” to “all other Canidae” in order to (1) focus not just on specialists but specifically on large hypercarnivores and (2) circumvent the problem of small sample sizes and poor fossil preservation for small hypocarnivores. Highly specialized species on the other end...
of the spectrum—small hypocarnivores—also tend to have shorter durations and therefore should have higher extinction rates, hence potentially inflating the extinction rate of "all other Canidae". Nonetheless, neither size nor carnivory was correlated with diversification rates for all canids or any subfamily (Supplementary Table 2). Therefore, for most of canid history, large-bodied hypercarnivory appears to have been a liability to clades, but not to species.

The lack of correlation between rates and traits presented here contrasts with recent work showing increased extinction rates in saber-toothed cats relative to other felids. However, this difference makes sense considering that hypercarnivory in canids is

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**Table 1 Results of survivor–victim analysis over 17 time slices.**

| Time slice (millions of years ago) | A | B | C |
|-----------------------------------|---|---|---|
| F | P | BH sig | Akaike weight, carnivory | Akaike weight, body mass | Akaike weight, carn:mass | $\chi^2$ | P | BH sig |
| 32.2 | 0.38 | 0.664 | No | 0.528 | 0.459 | 0.012 | NA | NA | NA |
| 30.0 | NA | NA | NA | 0.450 | 0.327 | 0.223 | NA | NA | NA |
| 27.9 | 1.454 | 0.227 | No | 0.426 | 0.478 | 0.096 | 0.027 | 0.864 | No |
| 23.8 | 0.27 | 0.698 | No | 0.475 | 0.476 | 0.050 | 0.014 | 0.919 | No |
| 19.5 | 1.581 | 0.215 | No | 0.768 | 0.182 | 0.050 | 1.626 | 0.303 | No |
| 18.8 | 0.77 | 0.415 | No | 0.516 | 0.476 | 0.008 | NA | NA | NA |
| 17.5 | 0.653 | 0.489 | No | 0.404 | 0.569 | 0.027 | 0.407 | 0.661 | No |
| 15.9 | 0.12 | 0.713 | No | 0.477 | 0.521 | 0.002 | 0.381 | 0.663 | No |
| 14.8 | 0.567 | 0.488 | No | 0.561 | 0.411 | 0.027 | 0.377 | 0.581 | No |
| 12.5 | 1.152 | 0.289 | No | 0.321 | 0.621 | 0.058 | 3.909 | 0.062 | No |
| 10.75 | 0.061 | 0.899 | No | 0.486 | 0.499 | 0.015 | 0.417 | 0.603 | No |
| 9.0 | 1.219 | 0.291 | No | 0.643 | 0.298 | 0.059 | 0.244 | 0.686 | No |
| 6.7 | 4.709 | 0.047 | No | 0.457 | 0.520 | 0.024 | 0.219 | 0.711 | No |
| 4.7 | 0.219 | 0.667 | No | 0.499 | 0.496 | 0.005 | 0.020 | 0.891 | No |
| 1.7 | 0.053 | 0.887 | No | 0.443 | 0.556 | 0.002 | 0.625 | 0.547 | No |
| 0.45 | 1.099 | 0.309 | No | 0.560 | 0.418 | 0.022 | 0.627 | 0.586 | No |
| 0.01 | 14.716 | 0.011 | Yes | 0.956 | 0.034 | 0.010 | 4.688 | 0.041 | No |

*BH sig* stands for significance after adjusting for multiple comparisons using the Benjamin–Hochberg (BH) method; results significant with the BH correction are in bold. (A) Results from permutational MANOVA indicating lack of significant differences between survived and extinct over most time slices. "NA" indicates no analysis possible because of only one survivor from the preceding time interval. (B) Akaike weights from logistic regressions with both body mass (log10mass) and carnivory (m1BS) coded as continuous variables. carn:mass is the interaction between carnivory and body mass. (C) Results of contingency tests with large-bodied hypercarnivory coded as a binary variable (yes/no). "NA" indicates no analysis possible because of a lack of large hypercarnivores in the preceding time interval.
less extreme than that in felids. For example, while hypercarnivor- 
ous canids tend to have altered their lower molar tooth row to 
 enhance slicing over grinding, they have retained the component 
 teeth (m1–3). By contrast, saber-toothed cats tend to have lost the 
 entire module of the dentition capable of chewing and grinding 
 food: from the talonid basin of the lower carnassial to the post- 
carnassial molars (m2–3). By simplifying yet retaining structures, 
 hypercarnivorous canids theoretically maintain a wider range of 
 prey-consumption tools than did saber-toothed cats, which were 
 more severely limited in their ability to process anything but 
 meat. Many saber-toothed cats also had larger body sizes—some 
 being the largest predators in their communities37—than 
 contemporaneous hypercarnivorous canids, as seen in Smilodon 
 fatalis and the dire wolf Canis dirus at the Pleistocene Rancho La 
 Brea asphalt seeps38. The Rancho La Brea example introduces 
 another difference between canids and felids that may play a role 
 in extinction risk: hypercarnivorous canids tend to be pack 
hunters39, while many extant felids tend to be solitary40 (though 
 Smilodon itself has been interpreted largely to have been social41,42). Among canids such as the African wild dog (Lycaon 
pictus), the ability to hunt in groups expands the range of prey 
sizes and enhances their ability to successfully defend their kills 
from theft43. These various considerations may explain the lack of 
increased risk in large hypercarnivorous canids, despite increased 
risk in hyper-specialized felids.

Apart from intrinsic ecomorphological constraints, over- 
lapping diversity patterns suggest that inter-clade competition 
suppressed the evolution of large hypercarnivorous canids until 
 later in canid history30. Amphiocyonids (bear-dogs), felids, mus- 
telids, nimravids and barbourofelids (false saber-toothed cats), 
 procyonids, and ursids overlapped temporally with canids and 
 also included large hypercarnivorous species23. Nimravids had 
 become extinct and amphicyonids were declining by ~16 Ma, 
 creating a “cat gap”23 and leaving large-hypercarnivore niches 
 open for canids alone until felids arrived in North America 
 ~10 Ma23,28. However, overlapping diversity patterns alone are 
 insufficient to infer competition and must be supported by evi- 
dence of similar ecomorphologies as a proxy for similar resource 
 use. While ecomorphological overlap among these groups has 
 been quantified23,34, the resolution of canid taxonomy and phy- 
 logeny surpasses that of the other carnivoran clades, hindering 
 precise ecomorphological comparison of canid species to non- 
canid carnivoran species. Taxon-free approaches (e.g., analyzing 
 raw trait distributions not averaged by taxonomic units) might 
 confirm the role of inter-clade competition in carnivoran diver- 
sification, particularly within a restricted context such as a single 
 locality or paleocommunity.

Although competition may explain predator evolutionary 
divergence, climate can also influence predator evolution via 
 bottom-up energy flow44,45. However, dynamics within the two 
 extinct canid subfamilies, both of which increased in body size 
 and carnivory before extinction, show no relationship with tem- 
 perature (Supplementary Table 3; Supplementary Fig. 3). The 
 subsets of the data that do show relationships with temperature 
 (Caninae, Canidae, all other canids) largely comprise smaller 
 non-predatory species. As well, Caninae is the only one of the 
 three canid subfamilies to have radiated outside of North 
 America26, likely impacting its trait evolutionary dynamics by 
 broadening the available niche spaces into which the subfamily 
could expand. Therefore, climate appears less important than

**Fig. 3** Diversification metrics of North American canid predators over 
time. a Species richness and b extinction rates for North American fossil 
canids, both large hypercarnivores and not. Solid lines denote mean values; 
shading denotes 95% credible intervals. Large hypercarnivores numbered 
fewer than all other canids for much of their history. Large-hypercarnivore 
extinction started marginally higher than observed for all other canids but 
was surpassed by extinction of the latter at 20 Ma, although the two rates 
are now statistically indistinguishable because of an increase in both large-
hypercarnivore extinction rate and its credible interval starting ~7 Ma. 
Credible intervals are based on 10,000,000 PyRate iterations.

**Table 2** Relative probabilities of birth-death models with different numbers of rate shifts for all Canidae and each canid 
subfamily.

| Model | Canidae Origination | Canidae Extinction | Hesperocyoninae Origination | Hesperocyoninae Extinction | Borophaginae Origination | Borophaginae Extinction | Caninae Origination | Caninae Extinction |
|-------|---------------------|-------------------|----------------------------|---------------------------|-------------------------|-----------------------|-------------------|------------------|
| 1-rate | 0                   | 0                 | 0.3109                     | 0.1234                    | 0.3986                  | 0.0053                | 0.0252            | 0.0836           |
| 2-rate | 0.0278              | 0.2718            | 0.4096                     | 0.4894                    | 0.2578                  | 0.7109                | 0.6548            | 0.7106           |
| 3-rate | 0.0613              | 0.5047            | 0.2085                     | 0.2946                    | 0.1639                  | 0.2378                | 0.2524            | 0.1836           |
| 4-rate | 0.7044              | 0.1873            | 0.0589                     | 0.0788                    | 0.1159                  | 0.0415                | 0.0605            | 0.0206           |
| 5-rate | 0.1794              | 0.0321            | 0.0107                     | 0.0124                    | 0.0216                  | 0.0042                | 0.0068            | 0.0014           |
| 6-rate | 0.0246              | 0.0037            | 0.0014                     | 0.0013                    | 0.0021                  | 0.0003                | 0.0004            | 0.0001           |
| 7-rate | 0.0024              | 0.0003            | 0.0001                     | 0.0001                    | 0.0001                  | 0.0000                | 0.0000            | 0.0000           |
| 8-rate | 0.0001              | 0                   | 0                          | 0                         | 0                      | 0                     | 0                 | 0                 |
| 9-rate | 0                   | 0                   | 0                          | 0                         | 0                      | 0                     | 0                 | 0                 |

Bolded numbers are the highest probabilities in each column, signifying the most probable model for origination or extinction in each clade.
biotic interactions in the diversification of predator-dominated clades. Future work in this area would benefit from assessing regional environmental proxies alongside changes in faunal ecology and diversity (e.g., refs. 46,47) as well as considering tectonic effects on diversification (e.g., refs. 48,49).

Our results differ from those of Silvestro et al.30, who first developed and tested the Python program PyRate, which we use here to quantify diversification in North American fossil canids. Silvestro et al. found strong support for two-rate models for both origination and extinction in the two extinct canid subfamilies: a decrease in origination rate and concomitant increase in extinction rate at ~26 Ma for Hesperocyoninae and 14 Ma for Borophaginae30. In comparison, our analyses similarly preferred two-rate models in Hesperocyoninae but with different timing of shifts (origination decreasing ~30 Ma and extinction increasing ~20 Ma) and identified a nearly constant origination rate eventually surpassed by extinction rate for Borophaginae ~20 Ma (Fig. 4, Table 2). This discrepancy likely stems from differences in both the analysis model and the source of the occurrence data. First, Silvestro et al.30 modeled preservation as a non-homogeneous Poisson process (NHPP), allowing for rate heterogeneity only among lineages. In contrast, given the variability of the fossil record over time in terms of preservation quality and number of localities (Supplementary Figs. 4–6), we modeled preservation as a time-variable Poisson process (TPP) to incorporate both temporal and among-lineage variation in preservation rate. Second, Silvestro et al. drew fossil occurrences from the Paleobiology Database (PBDB). While we used some occurrences from the PBDB, we primarily drew from the Neogene Mammal Mapping Portal, which records occurrence-specific versus interval-specific dates in the PBDB. Based on previous iterations of this study, interval-specific dates tend to have wider ranges than occurrence-specific dates, producing inflated estimates of stratigraphic range that are exacerbated in time periods with poor resolution (e.g., Arikareean North American Land Mammal Age).

No significant correlation emerged between diversification rates and ecomorphological traits across the entire history of canids. In part, this reflects our use of the Covar model in PyRate, which assumes a unidirectional relationship between a trait value and a diversification rate. In a previous study, we identified a nonlinear relationship between species duration and degree of carnivory: species at either end of the ecomorphological spectrum (large hypercarnivores and small hypocarnivores) tend to have shorter durations than mesocarnivores27. We analyzed these categories in the two-trait implementation of the Covar model, coding carnivory as a discrete trait while accounting for the effect of body mass coded as a continuous trait. The resulting lack of evidence for higher extinction rates for large hypercarnivores may stem from small hypocarnivores also having higher extinction rates, averaging out a potential relationship and causing Covar to find no trait-rate correlations significantly different from 0. As well, rather than being temporally explicit, Covar estimates an overall relationship through time without quantifying potential temporal effects, or how a correlation may change through time. This limitation may explain the apparent contradiction between the Covar results and those of the survivor–victim analysis—which divides time into snapshots, recovering ecomorphological selectivity in the most recent time slice—and why previous work...
on North American fossil canids also has found largely no significant effect of ecomorphology on diversification rates39. Regardless, given that most intervals in the survivor–victim analysis display no signature of ecomorphological selectivity, the lack of significant association in the Covar analysis is expected. While nonlinear functions correlating rates to traits and temporal variation in dynamic models would be more complex and computationally intensive to implement, future analytical tools for tracking diversification rates and ecomorphological traits through time would benefit from developing these features.

The lack of size- or carnivory-selective extinction for all but the most recent period of North American canid history is unexpected given the rarity of extant large hypercarnivores and the shorter species durations of fossil hypercarnivores27,21. However, this result is consistent with recent studies of both extant and Pleistocene fauna that document a higher probability of extinction in the largest species, both on land and in the seas65,66. Moreover, this bias toward the removal of the largest species is unprecedented over the past 65 Ma of mammalian extinction events51. While these biodiversity changes began to take place relatively recently in North America, large carnivores started to decline millions of years earlier in Africa, where humans and their hominin ancestors have lived for much longer52. This temporal incongruity implicates anthropogenic impacts—as opposed to factors concurrent between the two continents (e.g., changing forest cover)—in the long-term extinction of large carnivores52. While our data are restricted to a single diverse carnivoran family, our finding of minimal ecomorphological selectivity until the end-Pleistocene supports the idea that modern ecosystems are the product of, and continue to be subject to, trophic downgrading, a process that appears to be largely human-driven with negative effects on biodiversity and ecosystem resilience1,33.

Methods

Estimation of canid body size. We measured carnassial blade length, jaw depth, and jaw length on specimens 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), Yale Peabody Museum (New Haven, CT), and John Day Fossil Beds National Monument (Kimberly, OR). When specimens were not easily accessible, we obtained measurements from the literature24-26,54.

Estimation of prey body size. A few species (e.g., some Enzydroycon) yielded mass estimates just under 20 kg, even though other morphological evidence suggests that they were large and hypercarnivorous (e.g., ref. 58). The regression estimates account only for mean mass; these species may have easily been over 20 kg in life. In addition, the mass regressions are based only on extant canids, all in subfamily Caninae. Hesperocyoninae and Borophaginae tend to have been built slightly more robustly than Caninae;56 therefore, the estimates based on extant Caninae likely underestimate mass for the two extinct subfamilies. Given this, we supplemented the canid body mass estimates by estimating prey body size using a regression on jaw depth for extant canids59: y = 5.383x – 6.482, where y is log10 prey size (kg) and x is log10 jaw depth (mm) between the first and second lower molars. In this way, canid species estimated to have been just under 20 kg might still be categorized as “large hypercarnivores” based on an estimated prey size larger than themselves.

Quantification of carnivory. A suite of traits associated with increased bite forces and greater masticatory loads characterizes hypercarnivorous morphologies37,38. However, fragmentary fossils rarely preserve many of these traits. To maximize sample size, we quantified 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 in some hypercarnivores (e.g., extant hyaenids) that aids them in cracking bone39. Because not all species preserve intact dentaries, we estimated dentary length when needed using within-subfamily regressions based 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 in some hypercarnivores (e.g., extant hyaenids) that aids

on North American fossil canids also has found largely no significant effect of ecomorphology on diversification rates39. Regardless, given that most intervals in the survivor–victim analysis display no signature of ecomorphological selectivity, the lack of significant association in the Covar analysis is expected. While nonlinear functions correlating rates to traits and temporal variation in dynamic models would be more complex and computationally intensive to implement, future analytical tools for tracking diversification rates and ecomorphological traits through time would benefit from developing these features.

The lack of size- or carnivory-selective extinction for all but the most recent period of North American canid history is unexpected given the rarity of extant large hypercarnivores and the shorter species durations of fossil hypercarnivores27,21. However, this result is consistent with recent studies of both extant and Pleistocene fauna that document a higher probability of extinction in the largest species, both on land and in the seas65,66. Moreover, this bias toward the removal of the largest species is unprecedented over the past 65 Ma of mammalian extinction events51. While these biodiversity changes began to take place relatively recently in North America, large carnivores started to decline millions of years earlier in Africa, where humans and their hominin ancestors have lived for much longer52. This temporal incongruity implicates anthropogenic impacts—as opposed to factors concurrent between the two continents (e.g., changing forest cover)—in the long-term extinction of large carnivores52. While our data are restricted to a single diverse carnivoran family, our finding of minimal ecomorphological selectivity until the end-Pleistocene supports the idea that modern ecosystems are the product of, and continue to be subject to, trophic downgrading, a process that appears to be largely human-driven with negative effects on biodiversity and ecosystem resilience1,33.

Methods

Estimation of canid body size. We measured carnassial blade length, jaw depth, and jaw length on specimens 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), Yale Peabody Museum (New Haven, CT), and John Day Fossil Beds National Monument (Kimberly, OR). When specimens were not easily accessible, we obtained measurements from the literature24-26,54.

Estimation of prey body size. A few species (e.g., some Enzydroycon) yielded mass estimates just under 20 kg, even though other morphological evidence suggests that they were large and hypercarnivorous (e.g., ref. 58). The regression estimates account only for mean mass; these species may have easily been over 20 kg in life. In addition, the mass regressions are based only on extant canids, all in subfamily Caninae. Hesperocyoninae and Borophaginae tend to have been built slightly more robustly than Caninae;56 therefore, the estimates based on extant Caninae likely underestimate mass for the two extinct subfamilies. Given this, we supplemented the canid body mass estimates by estimating prey body size using a regression on jaw depth for extant canids59: y = 5.383x – 6.482, where y is log10 prey size (kg) and x is log10 jaw depth (mm) between the first and second lower molars. In this way, canid species estimated to have been just under 20 kg might still be categorized as “large hypercarnivores” based on an estimated prey size larger than themselves.

Quantification of carnivory. A suite of traits associated with increased bite forces and greater masticatory loads characterizes hypercarnivorous morphologies37,38. However, fragmentary fossils rarely preserve many of these traits. To maximize sample size, we quantified 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 in some hypercarnivores (e.g., extant hyaenids) that aids
model with two traits simultaneously. Following Piras et al., we modified the Covar model to estimate the effect of carnivory (coded as a discrete trait: hyper- versus hypencarnivore) on diversification rates while accounting for the effect of body mass (coded as a continuous trait), and ran the analysis using the -discrate and -twotrait flags in PyRate. In the Covar model generally, the parameters \( \alpha \) (correlation with origination rate) and \( \alpha_0 \) (correlation with extinction rate) are estimated from the data, quantifying the relationship between shifts in rates and in trait values. We ran the default of 10,000,000 iterations, sampled every 1000th, and discarded the first 2100 samples as burn-in. \( \alpha > 0 \) indicates a positive relationship between traits and rates; \( \alpha < 0 \) indicates a negative relationship. We considered the relationship significant if the distribution of 95% highest posterior densities of \( \alpha \) did not overlap 0.

**Reporting summary.** Further information on research design is available in the Nature Research Reporting Summary linked to this article.

**Data availability**
The morphometric, occurrence, and PyRate datasets generated and analyzed in this study are available on the Dryad repository: http://doi.org/10.6071/M3M07P8F/2.

**Code availability**
The R code underlying the present analyses and figures are available on the Dryad repository: https://doi.org/10.6071/M3M08F/3.

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Author contributions

M.A.B. conceptualized the study, curated the data, conducted analysis, acquired funding, formulated methodology, administered the project, visualized the results, wrote the original draft, and reviewed and edited the paper. B.V.V. conceptualized the study, provided resources, supervised the project, and reviewed and edited the paper.

Competing interests

The authors declare no competing interests.

Additional information

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