Carnivore extinction in the Late Quaternary

Extinct Pleistocene Carnivores Burned(t?) More Energy

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Science

Ecology letters

Nature eco evo

Pnas

ProcB

125 words

For the last half century, the most prominent/contentious debate in paleoecology has been over the causes of megafaunal extinctions at the end of the Pleistocene. It has been argued that extinct species tended to be larger and have smaller brains. Here we tested these hypotheses using a comprehensive datatset using…

Species, extinct, traits, localities, published literature

We ONLY find BMR, diurnality - predictors of extinction risk

Multiple reg with and without phylo corr concurred yadaydayda…. And corr for multiple comparisons.

Extant carnivores with high bmr and diur are also more likely to be threatened.

General implication

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# Abstract

# Introduction

Drastic megafaunal extinction during the Late Quaternary (~115ka – 500 ya) has been mainly attributed to human activity (*1, 2*) – Martin 67. Many large-bodied land vertebrates that had never encountered humans before were more likely to go extinct even under weak hunting pressures (*3*) – Alroy 2001. This is attested by the fact that continents invaded by humans for the first time (Oceania and the Americas) were more drastically affected by megafaunal extinction than Africa or Eurasia.(*4*). Rapid climate change, even though contested, is also thought to have contributed to extinction – especially between 26k and 12kya when the Earth underwent full glaciation and then rapid deglaciation, affecting the habitat of many species (*5, 6*). A model proposing both human activity and climate change has also been put forward (*7*). Despite the actual cause of extinction, it has been proposed that certain extrinsic and/or intrinsic traits would have been advantageous or detrimental for certain species in order to mitigate the extinction pressures (*8*). Traits such as rate of reproduction, home range, activity pattern, social complexity, locomotor mode, lifespan, brain size, although mostly related to body mass could have affected species’ ability to mitigate extinction pressures (*9*).

GIVE A FEW EXAMPLES and try to cover most variable selected.

In the current study we focus on carnivores (order Carnivora) testing several hypotheses related to extinction propensity. Carnivores comprise more than 290 extant species, and at least 20 other species have been shown to have gotten extinct during the Holocene. Carnivores are, on average, more threatened than other mammals (26.9% endangered species, compared to 22.7% in other mammals) and ~50% of all Carnivores have declining populations (compared to ~30% in other mammals)(*10*).

Being able to identify traits that increase species’ propensity to extinction, this study also has important conservation implications.

Carnivoran evolution and extinction - general

Why carnivores are a good model?

Hypotheses

# Materials and Methods

## Data availability

All data, code and phylogenetic trees used for the analyses in this manuscript are available as electronic supplement and on Github at <https://github.com/orlinst/Carnivores-ext> [still not public]

## Sample

We collated a sample of 128 terrestrial carnivoran species (excluding pinnipeds) available in the Ecological Register (http://ecoregister.org). Four variables of interest were obtained by averaging the observed values per species for 1431 records of species in 382 fossil samples at 260 locations from all continents - body mass, home range, basal metabolic rate (BMR), diet. All sites fell within the last glacial cycle (covering the Late Pleistocene and Holocene) and the final sample contained 11 extinct species (9.7%), and 103 extant species (90.3%) – a coverage of ~42% of all extant species in the order (excluding Pinnipedia). Additionally, we used information on which biogeographic region the species were found from the Ecoregister.

Moreover, we collated data on brain size, EQ, locomotor type, activity period, social complexity, group size, gestation length, interbirth interval, weaning age, and litter size from literature sources (see TABLE X for details and sources) and calculated abundance, and Shannon and Simpson indices of diet diversity based on primary data (scat and camera-traps) from the Ecoregister. Scat categories in the Ecoregister include traces of vertebrates (mammals, birds, reptiles), invertebrates (arthropods, arachnids, insects), fruit, plant, aquatic (annelid, mollusc) and fungi. They were obtained from 134 observations from 103 different sites, based on the composition of between 12 and 3878 scats per site. Scat composition was subsequently recategorized using k-means clustering, resulting in 6 different diet categories: 1-6…[describe]

Shannon and Simpson indices of diet (diversity of food sources in the scat) were calculated using the package vegan (see Table X). Species’ abundance was calculated using data from camera-traps available in the Ecoregister using the following formula:

(count – number of sites) / (count / count per day) [CHECK THIS]

Data are censored at 1 photograph per study – in order to remove censorship we use a standard approach of ….. . This makes it possible for an abundance to approach 0.

<the number of sites is the min number of photos needed>

Due to high collinearity ( Gibson Johnson) we used only EQ and not brain volume, and for the same reason BMR was transformed to ‘residual BMR’ after a phylogenetic regression (pgls) on body size, and only the residuals were used in further analyses. A correlation table of all variables can be found in the supplement (Table XXX).

All continuous variables were natural-log transformed and scaled before imputation. Abundance was Yeo-Johnson transformed due to many 0 values.

The resulting dataset contained 25 variables in total. Detailed description of all variables used, including sources, distribution (along with distribution of the imputed datasets) is available in Table X.

Table X – data sources and detailed description of variables, including histograms of the distribution of the original dataset, and density plots of the 20 imputed datasets (red lines) and the observed original data (blue line). NM = number of missing species (out of 114)

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Variable | Units | Description | Distribution | Imputation | Source | NM |
|  |  |  |  |  |  |  |
| Body mass | kg | Body mass |  |  | Ecoregister | 10 |
| Home Range | km2 | ? |  |  | Ecoregister | 45 |
| Brain | mm3 | Endocranial volume |  |  | (*11*) | 28 |
| EQ | Index | Derived using CEQ formula |  |  | (*12*) | 49 |
| PC | PC score | See methods for details |  |  | (*13*) | 46 |
| BMR | ml O2 hr-1 |  |  |  | Ecoregister | 0 |
| Litter size | number | Number of offspring per litter |  |  | (*13*) |  |
| Shannon index of diet | Index |  |  |  |  | 46 |
| Simpson index of diet | Index |  |  |  |  | 46 |
| Abundance | Frequency of camera trap observation | See methods for details |  |  |  | 34 |
| Longevity | years | Maximal longevity |  |  | Heldstab | 49 |
|  |  |  |  |  |  |  |
| **CATEGORICAL** |  |  |  |  |  |  |
| Extinct or Extant | 0 – extinct, 1 - extant |  |  |  | Ecoregister | 0 |
| Locomotor mode | 6 categoris | A – arboreal  R – semiarboreal  SA – semiaquatic  SC – scansorial  SF – semifossorial  T - terrestrial |  |  | (*14*) | 0 |
| Diet | 6 Categories | Based on k-means clustering of scat data |  |  | Ecoregister | 46 |

## Missingness and Multiple imputation

We imputed 20 datasets following a recommendation for imputation of as many datasets as the percentage of missing data in the original dataset (~20% in our case) (*15*). The variable with the highest number of missingness was longevity (43% or 49 missing values). We analysed the phylogenetic signal in the missingness using the D statistic and additionally, the overall pattern of missingness was shown to not be missing completely at random (MCAR) (Little’s MCAR test = 1190, df=1022, p<0.001 (*16*)). All continuous variables (natural log transformed and min-max normalised) were imputed using Predictive Mean Matching with distance aided selection of donors (PMM with midas touch algorithm), all categorical variables with two levels were imputed using logistic regression, and all categorical variables with more than two levels were imputed using Polytomous logistic regression (Polyreg) (*17, 18*). Imputation was run over 100 iterations using the package mice (*18*). Detailed description of the missingness pattern and imputation analyses can be found in the Supplementary material. The distribution of the 20 imputed datasets is shown in Table X.

Test results were pooled using the median of all p-values (20 imputed sets, 100 random trees), as this was shown to be a reliable estimate for significance testing on categorical variables (*19, 20*).

## Phylogeny

We used the phylogeny provided by PHYLACINE (version 1.2.1) (*21*) comprising 1000 trees of 123 of the 128 carnivoran species in our sample. The 5 missing species were manually added to all 1000 trees as follows: *Martes caurina* as sister species to *Martes americana*, *Conepatus robustus* as sister to both *Conepatus chinga* *and Conepatus leuconotus*, *Felis lybica* as sister to *Felis silvestris*, *Canis mosbachensis* as sister to *Canis lupus* and *Ursus deningeri* as sister to *Ursus spelaeus*.

## Statistical analysis

All statistical analyses were performed in R 4.2.1 (*22*) using RStudio 2022.12.0 Build 353. All packages used are listed in TABLE X. All phylogenetic analyses were conducted on the 20 imputed datasets and were run across all 1000 trees.

Table X Packages used in the analyses and data processing.

|  |  |  |
| --- | --- | --- |
| **Package name** | **Version** | **Use** |
| ape (*23*) | 5.6.2 | Phylogenetic analyses |
| BAMMtools (*24*) | 2.1.10 | Tree manipulation |
| caper (*25*) | 1.01 | Estimation on D phylogenetic signal |
| dplyr (*26*) | 1.0.10 | Various data manipulation |
| easystats (*27*) | 0.5.2 | Descriptive statistics and plotting |
| ggplot2 (*28*) | 3.3.6 | Plotting |
| ggtree (*29*) | 3.4.4 | Phylogenetic tree visualisations |
| lattice (*30*) | 0.20.45 | Plotting |
| lavaan (*31*) | 0.6.12 | Structural Equation Modelling |
| mice (*18*) | 3.14.0 | Multiple imputation |
| MCMCglmm (*32*) | 2.34 | MCMCglmm |
| mulTree (*33*) | 1.3.7 | Incorporating multiple trees in MCMCglmm |
| naniar (*34*) | 0.6 | Analyses of missing data |
| phylolm (*35*) | 2.6.2 | Phylogenetic logistic regressions |
| phytools (*36*) | 1.2.0 | Various phylogenetic data manipulation |
| psych (*37*) | 2.2.9 | Descriptive statistics and plotting |
| semTools (*38*) | 0.5.6 | Plotting SEM |
| vegan (*39*) | 2.6.4 | Calculating of Shannon and Simpson index |

## Analyses

Initially we performed liner discriminant analyses in order to identify the orthogonal variables in our dataset, which we tested in a separate model. Additionally, we tested **5** models, as follows:

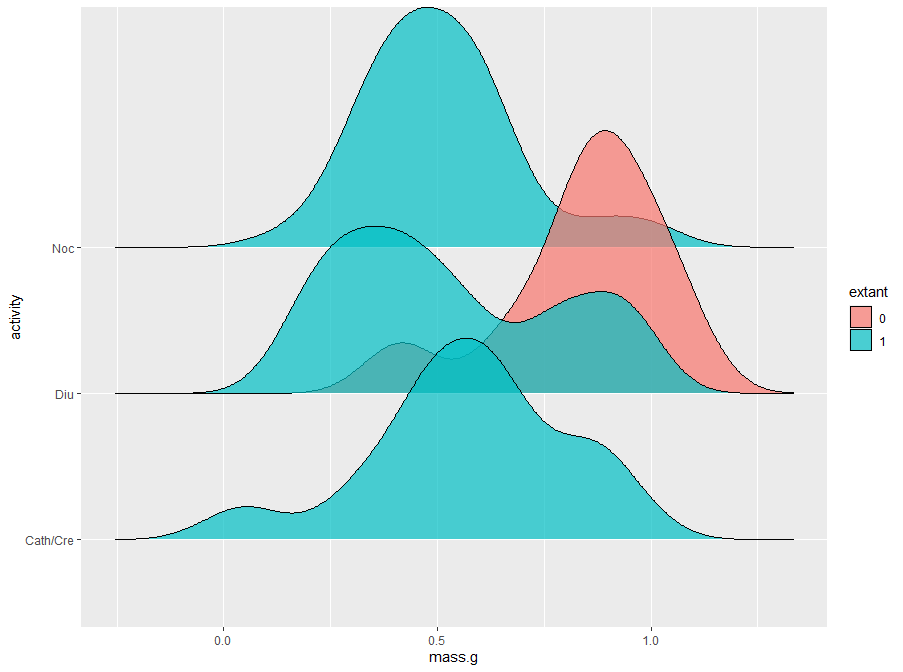
Brain size: EQ

Social: Social complexity + Group size + PC

Reproductive: Longevity + Gestation length (days) + Interbirth interval (days) + Weaning age (days) + **Litter size**

Diet: Diet category + diet diversity (Shannon or Simpson index)

Spatial: **Home range (km2)** + Abundance + **Locomotor type** + Biogeographic area (**Afrotropic**, Australasia, Indomalaya, Neotropic, Nearctic, Palearctic)

**In each model extinction status was used as dependent categorical variable.** We ran a custom function incorporating phylogenetic logistic regressions using phylolm on each model on all 20 imputed datasets and 100 randomly selected trees from the 1000 available. The results were pooled and averaged, and the resulting p-values and estimates were plotted.

# Results

No phylogenetic signal in Diurnality, as measured with phylo.d (D~0.73).

Lambda for BMR 0.97, p<0.0001  
Kappa for BMR 0.53, p<0.001

The phylogenetic regression models revealed no relationship between EQ, sociality and diet and extinction status. In our full reproductive model larger litter sizes were shown to be negatively associated to survival, and also larger home range and terrestrially in the spatial model. The only variable that was positively related to survival was Afrotropic biogeographic region, as attested by the lack of extinct carnivores in the Holocene in those areas.

Extant!

# Discussion

A large body of literature of correlates of extinction risk (REF). For mammals the most prominent risk factors are thought to be asdasdasd.

Cold climate is associated with increased BMR after correcting for body mass (*40, 41*) and in our sample this explains our findings to a significant extent. The relationship between extinction and higher residual BMR was mostly explained by the fact that during the Holocene we observe higher levels of extinction in the Nearctic, as compared to other biogeographic regions (Fisher’s exact test p-value 0.034).

Large body size is associated with extinction probability (“blitzkrieg” model) related to human overkill of megafauna but extinction can rarely be explained with single factor models (*42*). Accordingly, a study by Johnson (*8*) focusing on Late Quaternary megafauna extinction, did not find support for the “blitzkrieg” model (i.e. body size was not associated with extinction risk). Notably, the analyses were based not on species, but on a family level. This study also found evidence for life history and ecology variables related to activity pattern and reproduction to be predictive of extinction, suggesting diurnality and low reproductive rates to be associated with higher extinction probability. Although we confirm that diurnality is associated with higher probability for extinction, we did not find a positive relationship between reproductive rate and survival, but contrastingly, a negative relationship between litter size and survival. This could be explained by the high degree of altriciality in non-pinniped carnivores, resulting in increased parental demands which might increase the propensity for a litter falling prey to humans.

Even though brain size is related to vulnerability and extinction probability across mammals (*43, 44*) we did not find any support for this hypothesis in Carnivora. Additionally big brain size was suggested to reduce extinction risk specifically in Carnivora (*45*), but unlike the current study, the sample used by Abelson included carnivoran species spanning from the late Eocene to the Holocene (40 to 0.012 mya). Our findings suggest that increase in relative brain size does not buffer extinction, and any supposed advantages provided by a larger than expected brain do not contribute to decreasing extinction propensity.

Reproductive

Social

Extant!

Shows that these kind of predictions are robust – as there has been a natural experiment with carn extinction and the results are clear. BMR is a strong predictor of risk

Experts, conservation biologists, managers and policymakers should take this into consideration. (cause!) FACT!

Cite the people that need to pay attention!!!!!

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Supplement

Table XXX Phylogenetic signal in the missingness pattern (D statistic)

|  |  |  |  |
| --- | --- | --- | --- |
| **Variable** | **D** | **Prob random (D ≠ 1)** | **Prob Brownian (D ≠ 0)** |
| Body mass | 0.2903328 | 0 | 0.236 |
| Brain size | 0.932837 | 0.267 | 0 |
| Home range | 1.047108 | 0.685 | 0 |
| PC | 0.6307042 | 0 | 0.001 |
| Litter size | 0.7311753 | 0.01 | 0 |
| Shannon | 0.8283136 | 0.044 | 0 |
| Simpson | 0.8282997 | 0.045 | 0 |
| Abundance | 0.9189907 | 0.231 | 0 |
| Longevity | 0.932138 | 0.253 | 0 |
| Diet Category | 0.8314431 | 0.052 | 0 |

The D statistic for all variables except for body mass is significantly different from 0 (0 indicating strong phylogenetic signal) and for body mass, PC and litter size it is also significantly different from 1 (random), assuming an alpha level of 0.01. This suggests, that there is no strong phylogenetic signal in the missingness pattern, except for body mass, where D is significantly < 1 but also not significantly different from the Brownian expectation (D = 0).