Carnivore extinction in the Late Quaternary

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# Abstract

# Introduction

Drastic megafaunal extinction during the Late Quaternary (~115ka – 500 ya) has been mainly attributed to human activity (Flannery, 1990; Surovell et al., 2016). Many large-bodied land vertebrates that had never encountered humans before were more likely to go extinct even under weak hunting pressures (Brook & Bowman, 2004). 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.(Sandom et al., 2014). 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 (Barnosky & Lindsey, 2010; Stewart et al., 2021). A model proposing both human activity and climate change has also been put forward (Koch & Barnosky, 2006). 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 (Johnson, 2002). 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 (Cardillo et al., 2005).

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)(Fernández-Sepúlveda & Martín, 2022).

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 114 terrestrial carnivoran species above XX kg (excluding pinnipeds) available in the Ecoregister (http://ecoregister.org). Four variables of interest were obtained by averaging the observed values per species for 934 observations over 195 sites from all continents - body mass, home range, basal metabolic rate (BMR), diet. All sites were dated from Xya to Xya (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>

Furthermore, we obtained the first principal component (PC) derived from a principal component analyses (PCA) based on the following variables obtained from Noonan et al. (2015): social class, natal den, hibernaculum, predation, food storage, residence, fossorial propensity, primary, secondary, occupant, and burrowing class (for detailed description of these variables see Noonan et al. (2015)). The so obtained PC is related to burrowing behaviour and fossoriality as indicated by the highest positively loaded variables - fossorial propensity (0.68) and burrowing class (0.53). We chose only the first PC explaining ~53% of the variance, as there was a steep decline in explained variance into the subsequent principal components (PC2 – 23% proportion of variance explained, PC3 - 12%, and PC4 – 5%).

Due to high collinearity 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 min-max normalised 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 |  |  | (Michaud et al., 2022) | 28 |
| EQ | Index | Derived using CEQ formula |  |  | (Chambers et al., 2021) | 49 |
| PC | PC score | See methods for details |  |  | (Noonan et al., 2015) | 46 |
| BMR | ml O2 hr-1 |  |  |  | Ecoregister | 0 |
| Litter size | number | Number of offspring per litter |  |  | (Noonan et al., 2015) |  |
| 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 |  |  | (Gálvez-López & Casinos, 2022) | 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 (~19% in our case) (White et al., 2011). 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 (Little, 1988)). 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) (Buuren & Groothuis-Oudshoorn, 2011; Rubin, 1987). Imputation was run over 100 iterations using the package mice (Buuren & Groothuis-Oudshoorn, 2011). 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.

## Phylogeny

We used the phylogeny provided by PHYLACINE (version 1.2.1) comprising 1000 trees of 111 of the 114 carnivoran species in our sample (Faurby et al., 2018). The 3 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*, and *Felis lybica* as sister to *Felis silvestris*.

## Statistical analysis

All statistical analyses were performed in R 4.2.1 (R Core Team, 2021) 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 (Paradis & Schliep, 2019) | 5.6.2 | Phylogenetic analyses |
| BAMMtools (Rabosky et al., 2014) | 2.1.10 | Tree manipulation |
| caper (Orme, 2012) | 1.01 | Estimation on D phylogenetic signal |
| dplyr (Wickham, 2020) | 1.0.10 | Various data manipulation |
| easystats (Lüdecke, 2022) | 0.5.2 | Descriptive statistics and plotting |
| ggplot2 (Wickham, 2016) | 3.3.6 | Plotting |
| ggtree (Yu et al., 2017) | 3.4.4 | Phylogenetic tree visualisations |
| lattice (Sarkar et al., 2015) | 0.20.45 | Plotting |
| lavaan (Rosseel et al., 2017) | 0.6.12 | Structural Equation Modelling |
| mice (Buuren & Groothuis-Oudshoorn, 2011) | 3.14.0 | Multiple imputation |
| MCMCglmm (Hadfield, 2010) | 2.34 | MCMCglmm |
| mulTree (Guillerme & Healy, 2014) | 1.3.7 | Incorporating multiple trees in MCMCglmm |
| naniar (Tierney et al., 2019) | 0.6 | Analyses of missing data |
| phylolm (Ho et al., 2016) | 2.6.2 | Phylogenetic logistic regressions |
| phytools (Revell, 2012) | 1.2.0 | Various phylogenetic data manipulation |
| psych (Revelle, 2015) | 2.2.9 | Descriptive statistics and plotting |
| semTools (Jorgensen et al., 2016) | 0.5.6 | Plotting SEM |
| vegan (Oksanen et al., 2013) | 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

The linear discriminate analysis was able to predict extinction status with 1 linear discriminant. Three variables had high negative loading: basal metabolic rate controlled for body mass (-1.78), diurnal activity pattern (-1.71) and body mass (-1.21). The highest positively loaded variable was semiarboreal locomotor mode (1.01).

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.

# Discussion

Cold climate is associated with increased BMR after correcting for body mass (Avaria-Llautureo et al., 2019; Careau et al., 2007) 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 (Wroe et al., 2004). Accordingly, a study by Johnson (2002) 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 (Abelson, 2016; Dembitzer et al., 2022) we did not find any support for this hypothesis in Carnivora. Additionally big brain size was suggested to reduce extinction risk specifically in Carnivora (Abelson, 2019), 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.

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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).