Oecologia
https://doi.org/10.1007/s00442-019-04527-5

HIGHLIGHTED STUDENT RESEARCH

Big brains reduce extinction risk in Carnivora

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Received: 28 February 2018 / Accepted: 3 October 2019
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Abstract
Why are some mammals more vulnerable to extinction than others? Past studies have explored many life history traits as correlates of extinction, but have not been successful at developing a unified understanding of why some species become extinct while other species persist despite living at the same time, under similar conditions, and facing equivalent challenges. I propose that the lens of wildlife behavior may bring into focus a more comprehensive view of why some species have gone extinct while others persist. The fossil record has recorded extinction events over carnivoran history; unfortunately, behavior is not well recorded in the fossil record. As a proxy for behavior, I examine relative encephalization (RE), brain size after controlling for body mass and phylogeny, as it has been found to be biologically relevant in understanding a wide variety of animal behavioral traits. I focus on the data-rich order Carnivora for which there are comprehensive data on brain size and extinction between 40 and 0.012 million years ago. I use Cox proportional-hazards models to assess the role that RE and body size have played on extinction risk for 224 species in the order Carnivora that existed between 40 and 0.012 million years ago. I show generally that carnivoran species with reduced RE had higher relative risks of extinction. Additionally, I find an interaction between RE and body size such that RE had the largest effects on relative extinction risk in the smallest-bodied species. These results suggest that RE is important for understanding extinction risk in Carnivora over geologic time frames.

Keywords Evolution · Brain size · Relative encephalization · Behavior · Extinction risk · Carnivora

Introduction

Modern extinction rates are on the scale of the largest major extinction events of the prior 540 million years (Dirzo and Raven 2003; Barnosky et al. 2011) and increases in worldwide anthropogenic disturbance pose a continued threat to wildlife (Leadley 2010). Despite the ubiquitous increase in environmental perturbations, species are not equally vulnerable to extinction—even species that are closely taxonomically related, morphologically similar, or that face similar environmental perturbations do not respond the same in terms of extinction vulnerability. This begs the question of why some species move closer to extinction while others thrive in the face of environmental perturbations.

In living taxa, extinction vulnerability can be studied in the form of endangerment status, however, there are challenges in assigning endangerment status. In terms of understanding traits linked to relative extinction vulnerability, an alternative can be examining species that have gone extinct. Using species preserved in the paleontological record provides the perfect natural experiment to compare the traits of species that went extinct at any given point in history to those that persisted through that same point in time. Here I use the same approach (i.e., survival models) that statisticians in the medical field use when assessing why some people are at greater relative risk of morbidity than others (i.e.,

Communicated by Jörg U. Ganzhorn.

Past research has found many biologically significant relationships between brain size and behavior; previous results, however, have not explored the impact of brain size on the ultimate measure of species "success," i.e., extinction vulnerability. Results presented here expand a measure of behavioral capacity to understanding extinction across a deep time horizon. This manuscript shines a light on why some species are more extinction prone than others.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00442-019-04527-5) contains supplementary material, which is available to authorized users.

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from smoking) to assess traits that are linked to carnivoran extinction across the prior 40–0.012 million years.

In mammals, physical and life history traits (e.g., age at first reproduction and number of offspring) have provided important insights into extinction resistance (Cardillo et al. 2005; Davidson et al. 2009), but there is still unaccounted variation. With the goal of identifying variables that might help reduce this variation, wildlife behavior has often been under-researched (Festa-Bianchet and Apollonio 2003) and may hold insights into how individuals respond to factors that can push species to extinction (Curio 1996; Shumway 1999; Holway and Suarez 1999). I set out to assess the underexplored role of carnivoran behavior in extinction vulnerability over paleontological time scales. Because behaviors are not well recorded in the fossil record, I use relative encephalization as a metric of behavioral flexibility writ large.

Relative encephalization (hereafter RE; brain size after accounting for body mass and phylogeny) has been identified as an effective proxy for behavior (Sol 2009a) and it is an easily measured physical trait—this is especially important when considering extinct species where skulls and other bones may be nearly all that is known of a species. Neural tissue is one of the most metabolically expensive tissues (Niven and Laughlin 2008) and, as a result, increases in RE come at a considerable biologically relevant cost (Aiello 1997; Laughlin et al. 1998; Kotrschal et al. 2013). The cognitive buffer hypothesis (Sol 2009a) posits that maintaining increased levels of neural tissue is worth the metabolic cost because larger levels of RE afford cognitive advantages (e.g., behavioral flexibility).

Prior research has found strong relationships between RE and a myriad of behavioral abilities in vertebrates ranging from foraging innovations to novel habitat colonization (Jerison 1973; Reader and Laland 2002; Byrne and Corp 2004; Sol et al. 2005, 2008; Ratcliffe et al. 2006; Amiel et al. 2011; Maklakov et al. 2011; Kotrschal et al. 2013) and which, taken together, represent behavioral flexibility (i.e., the modification of behavioral patterns in response to changing conditions) (Sol 2009a). Further, behavioral flexibility is implicated in increased survivability (Shumway 1999; Griffin et al. 2000; Miner et al. 2005) by potentially buffering individuals from environmental perturbations (Sol 2009a). Scaling up from individual-level ramifications of increased RE to species-level implications could be insightful for understanding species extinction. If RE confers advantages to species (Schuck-Paim et al. 2008; Sol et al. 2008; Amiel et al. 2011; Kotrschal et al. 2013) via a posited increase in behavioral flexibility, or by any other mechanism, then it would follow that species with higher RE should have reduced likelihoods of extinction at any given moment in time; however, this hypothesis has not been evaluated. Using the fossil record, species' relative risk of extinction can be assessed by evaluating traits of species that went extinct versus species that persisted through the same period of time.

The fundamentals of extinction vulnerability in large-bodied mammalian species can be different than in small-bodied species (Cardillo et al. 2005; Davidson et al. 2009). Cardillo et al. find that as body size increases there is a shift in the factors that are responsible for driving species to extinction and this suggests the possibility that the role of relative encephalization might be different in large- vs small-bodied species.

I examine the relationship between RE, body size and relative risk of extinction in carnivorans that originated over the past 40 million years with the most recent extinctions being 12,000 years ago. I specifically address the following questions: (1) can RE play a role in understanding carnivoran relative extinction risk? The order Carnivora has been selected because it is a taxon that has the best data to address this question. (2) Is body mass influencing effects of RE on relative extinction risk such that there is an interaction between the effects of body mass and RE on relative extinction risk? This would be the case if, for example, the role of RE on extinction vulnerability is different for large- vs. small-bodied species.

Materials and methods

This study focuses on 289 species in the order Carnivora, including 183 species in the suborder Caniformia and 106 in the suborder Feliformia, for which there is brain and body size data—these data were measured, compiled, and reported by Finarelli and Flynn (2009). Relative encephalization was calculated using the full suite of 289 species (details below). A survival analysis was then conducted to assess the role that RE and body size play in species extinction vulnerability (details below). Of the 289 species with brain and body size, 65 did not have temporal range (origination and extinction time) data which is required for the survival analysis. As a result, a subset of 224 species were used in the survival analysis. Species in this analysis are listed in table S2, contained in the supporting information document that accompanies this manuscript.

First and last appearance data

Species' temporal range data (FAE: first appearance event and LAE: last appearance event) were obtained from the Paleobiology Database (The Paleobiology Database 2012) found at http://www.paleodb.org from the "age range and collections" page. First and last appearances were recorded as age range extremes for each species. In cases where species-specific FAE and LAE were not available at the species level, FAE/LAE were collected at the genus level.

Species that did not have either an age range for the species or the genus were not included in the study. Out of the 224 species in the study, 68 had genus-level data. Of the 224 species, 95 are extinct and the remaining 129 are extant. A breakdown of species' extinction status by species- vs. genus-level data is presented in the supporting information (table S1). To ensure that results were robust given two different levels of age range data, analyses were run in four discrete ways: (1) analysis of all species using species-level FAE/LAE if available and genus-level FAE/LAE if species-level data are not available. (2) Analysis using species-level FAE/LAE when available and bootstrap FAE/LAE based on genus-level FAE/LAE for each species where only genus-level information is available. (3) Analysis including only species that have species-level FAE/LAE information. (4) Analysis identical to method (1) above with the exception of controlling for phylogeny by employing a stratified Cox proportional hazard model (CPHM) where stratum is the taxonomic family. Details on the utility of the CPHM can be found in the section below titled "Cox proportional hazard model usage, model inputs and phylogenetic corrections." Results from the four methods described above were substantively the same—I present results from method one in the main manuscript text with a detailed description of the approach and results from methods two through four in the Online Resource 1 (section b, "alternate analyses").

Table S2, available in the Online Resource 1, contains the species included in this study, calculated relative encephalization (RE), first appearance event (FAE; in millions of years), last appearance event (LAE; in millions of years) and an indicator of which species have genus-level FAE/LAE.

Cox proportional hazard model usage, model inputs and phylogenetic corrections

To calculate the effect that RE and body mass have on extinction risk, I used a Cox proportional-hazards regression model (CPHM) for survival (Kumar and Klefsjö 1994). The paleontological record poses a number of unique challenges including shifting baselines in RE and body mass over time. For example, if five species went extinct 10 million years ago, it would not be productive to compare the traits of those five species to all other species that have existed across the prior 40 million years. Similarly, it would be uninformative to compare all extinct species to all living species. This is because environmental conditions, trait variability and evolutionary states have changed dramatically over the prior 40 million years. Factors leading to carnivoran species extinction 5 million years ago are likely quite different than factors leading to extinction 35 million years ago. A survival model approach only compares the traits (i.e., RE and body size) of those taxa that went extinct at any given time period against those species that persisted through that same unique time period.

The Cox proportional-hazards model is well suited to these data in two important ways:

1. The CPHM permits the inclusion of both extinct and living species (i.e., right censoring). At any given extinction event, there are three types of species: species that went extinct during that event, species that persisted through that event but would later go extinct in a subsequent event, and species that persisted through that event and remain extant. The CPHM, as a type of survival model, groups species in the third category (extant species) with species in the second, i.e., extant species are right censored (Cox 2018). The survival model never assesses species that are alive today against other species that are alive today. Rather, extant species are only considered as survivors of previous extinction events. That is, for any given extinction event, the traits of species that went extinct are compared against those that persisted through that extinction event, whether they continue to persist or subsequently went extinct themselves.
2. The CPHM uses species cohorts based on discrete extinction events and therefore is not sensitive to background changes over time in species' body mass, RE or absolute risk. The CPHM assesses the importance of predictor variables in the context of each species' extinction from the dataset relative to only the other species alive at that time of extinction. This is critical because Finarelli and Flynn demonstrated that across evolutionary history of caniform carnivorans, encephalization has not only increased in terms of the maximum values of brain size (corrected for body mass) but also in terms of the variance (Finarelli and Flynn 2007).

The change across time in maximum brain size and brain size variance poses a serious difficulty in examining extinction across the 40 million years of data included here. That is, at any extinction event, RE for any given species relative to other species alive at only that same time period could be very different than when compared to species alive at any other point in time. For example, the most encephalized species that went extinct 30 million years ago is only of average encephalization when compared to species alive today. The CPHM is designed for cases such as these; it assesses relative risk only for species that lived through, or went extinct at, each extinction event. Because the CPHM assesses relative risk only it is therefore not sensitive to the fluctuations in absolute risk of extinction over time. Relative risk is the ratio of any given species' extinction risk compared to the risk of a species with average RE and body size at any given

point in time (i.e., at a given extinction event rather than across all recorded extinction events).

All analyses were conducted in R version 3.5.3 (R Core Team and R Foundation for Statistical Computing 2019). The data included in the CPHM were checked for, and passed, the proportional-hazards assumption of the model (i.e., constant relative hazard) using the cox.zph function in the Survival package version 2.43-3 (Therneau and Lumley 2018).

Model inputs Three types of data were used in the CPHM to analyze the effects of body mass and RE on relative risk of extinction during any given extinction event. The three data types include (1) survival data, (2) body mass and (3) relative encephalization—each is described below:

1. *Survival data* Survival data for each species consists of the time of first appearance, time of extinction and, if the species is extant or extinct.
2. *Body mass* Body mass was collected from Finarelli and Flynn 2009. Body size was logged ($\log_{10}$) and mean centered.
3. *Relative encephalization* RE is calculated as brain size that has been size corrected for the allometric effects of body size using a phylogenetically informed regression (specifically, the residuals from a phylogenetic generalized least squares regression of brain size on body size) (Revell 2009, 2012). RE was calculated from the full set of 289 species with brain volume and body mass data available from Finarelli and Flynn 2009. While the full set of 289 species was used to calculate RE, 65 of these species did not have origination and extinction times. Therefore, only a subset of 224 species was used in the survival analysis. A single phylogeny is not available for the included species, which range across a global spatial-scale and a 40-million-year temporal scale. Because of this, a phylogeny was generated using the taxonomic hierarchy with species nested within genera within families (Crozier et al. 2005; Ricotta et al. 2012) using the as.phylo function in the ape package for R (Paradis et al. 2018). All branch lengths were set to 1 using the compute.brlen function (also in the ape package for R) (Paradis et al. 2018).

Predictor variables for this model include RE, body mass and their interaction. Body mass was included in the model because, after methods to remove the allometric effect of body mass, a small but significant correlation between RE and body size remained (correlation 0.134, p value 0.02). Additionally, to allow for differential effects of RE on extinction risk based on body size, I include the interaction term in the model (this accounts for the possibility that RE is playing a different role in small-bodied taxa than it is in large-bodied taxa).

RE was calculated using a phylogenetic generalized least squares model with the phyl.resid function (Revell 2012) in the phytools package version 0.6-60 (Revell 2018), which generates phylogenetic size-corrected brain size by accounting for body size (an allometric relationship) and phylogenetic relationships. This method is described in detail in Revell (2009) and follows methodologies presented by Felsenstein (1985 and Garland et al. (1992). This procedure is important because species brain and body sizes are likely not independent due to a shared ancestry (Felsenstein 1985). The method employed in phyl.resid first generates a covariance matrix based on phylogenetic relationships. It then uses this covariance matrix in a generalized least squares regression and computes the residuals (the difference between the observed value for brain volume and the predicted value for brain volume) (Revell 2009).

Risk of extinction between 40 and 0.012 million years ago based on body size and encephalization

Historical risk of extinction, over the prior 40–0.012 million years, for any species in this study can be calculated using Cox proportional-hazards model coefficients, encephalization and body size. This extinction risk is an instantaneous risk (probability of extinction) at any given moment in time. To contextualize the magnitude of extinction vulnerability based on encephalization level, one can calculate the risk of extinction for two species of the same body size with different levels of encephalization and then determine the degree to which one species is more vulnerable to extinction than another. To calculate the risk of extinction, I use the coefficients from the Cox proportional-hazards model, mean-centered log of body mass and relative encephalization values [i.e., log risk = (RE × RE coefficient) + (body mass × body mass coefficient) + (interaction coefficient × (RE × body mass)]. Because survival models yield log risk, log risk can then be exponentiated and then one species extinction risk can be divided by another to calculate the relative increase/decrease in risk.

Results

The results of the analysis (Fig. 1) show a significant relationship between RE ($p = 0.002$), body mass ($p < 0.0001$) and relative risk of extinction. Additionally, the interaction between body mass and RE is significant ($p = 0.005$) and indicates that the relationship between relative risk of extinction and RE varies with body mass (Fig. 1). Coefficients and standard error from the CPHM follow: RE = −2.52 (SE 0.80), body mass = 0.95 (SE 0.16), RE–body mass interaction = 2.58 (SE 0.92). That is, for small-bodied species, each additional unit of RE comes with a large predicted reduction

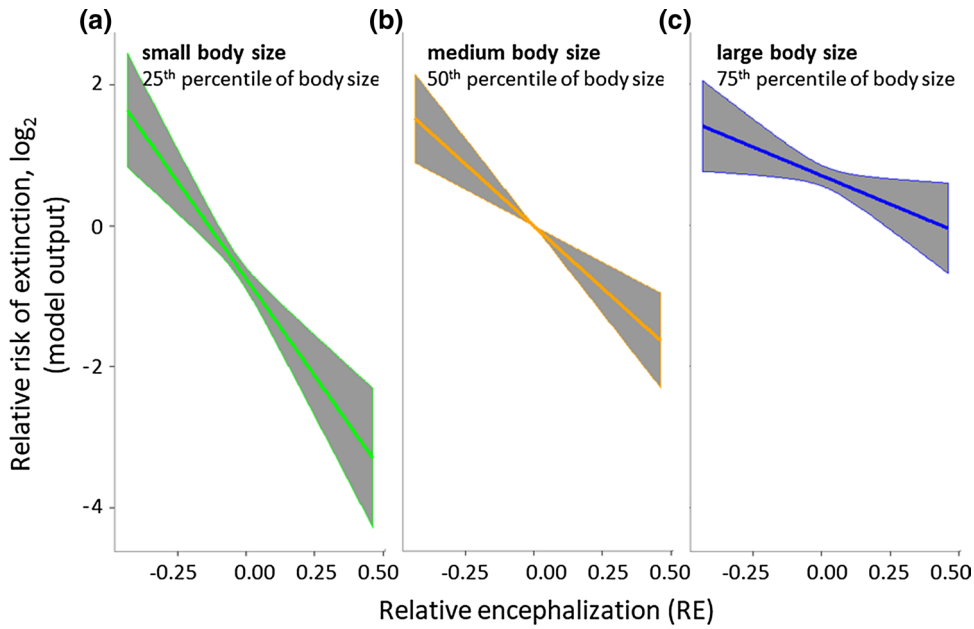

Fig. 1 Relative risk of extinction ($\log_2$) as a function of relative encephalization. This figure is generated from model output and displays the relationship between relative encephalization (RE; brain size controlling for body mass and phylogeny), body mass and the interaction between RE and body mass on relative extinction risk. Gray bands are the 80% confidence intervals around predicted relative risk. **a**–**c** Model-based relative risk for species with body masses at the 25th (2.2 kg), 50th (7.9 kg) and 75th (27.3 kg) percentiles (respectively) taken from the 224 species in the dataset. Three main effects are demonstrated: (1) there is a significant effect of RE. (2) Increased body mass results in increased relative risk of extinction. (3) A negative interaction effect is seen such that smaller-bodied species derive bigger reductions in relative risk for each unit increase in RE, and that the relationship weakens in larger-bodied species

in relative extinction risk. A unit increase in relative risk (as seen on the *Y*-axis in Fig. 1) denotes a doubling of relative risk. Because RE is on the $\log_{10}$ scale, a RE of 0.301 is 100% larger than a RE of 0. A RE equal to 0.447 is 200% larger than a RE of 0.

The model estimates indicate that as body mass increases from the smallest species to the largest, RE has a progressively diminishing effect on relative risk of extinction until, at 78 kg [the approximate size of *Ursus thibetanus* (Asian black bear)], the relationship reverses. To contextualize this finding, while body masses of the 224 species in this study range from 0.1 to 545 kg, the majority of these species, 87%, weigh less than 78 kg and have reduced relative risks of extinction with increased RE.

Relative risk difference between two species of the same body mass but different levels of RE is as displayed in Fig. 2. To explore the model results with an example—one can imagine two imaginary carnivoran mammal species that share the same body size of 0.1 kg (the weight of the least weasel *Mustela nivalis*) but have different brain sizes (Fig. 2). In this example, the first species had a brain size that is the expected size given its body size (i.e., RE = 0 given that RE has been $\log_{10}$ transformed) and the second species had a RE that is 100% larger (i.e., RE = 0.301). The first species (0.1 kg and RE = 0) is predicted to have a relative risk of extinction equal to 0.164, while the second species (0.1 kg and RE = 0.301) has a predicted relative risk equal to 0.0175. The second species is predicted to be 89% less likely to go extinct at any given moment over the prior 40 million years than the first species. To provide context, a 100% increase in RE is only a fourth of the total spread of RE found in this dataset and so well within the biological range of interspecific brain size variation.

To illustrate the interaction effect between body size and RE, the example above can be repeated with another species pair with a larger body size. In this hypothetical example, there are two species each having weighed 75 kg, the weight of the Asian black bear *Ursus thibetanus*, with the first species having had a RE that is the size expected given its body size (i.e., RE = 0) and the second species had a RE that is 100% larger than expected given its body size (i.e., RE = 0.301). The first species (75 kg and RE = 0) is predicted to have had a relative risk of extinction equal to 2.51, while the second species (75 kg and RE equals 0.301) had a predicted relative risk equal to 2.49. In this example, the latter species is predicted to have had only a 1% reduced relative extinction risk when compared to the first species. These hypothetical examples demonstrate not only the importance of RE on relative extinction risk but also the influence of body mass on mediating the impacts of RE.

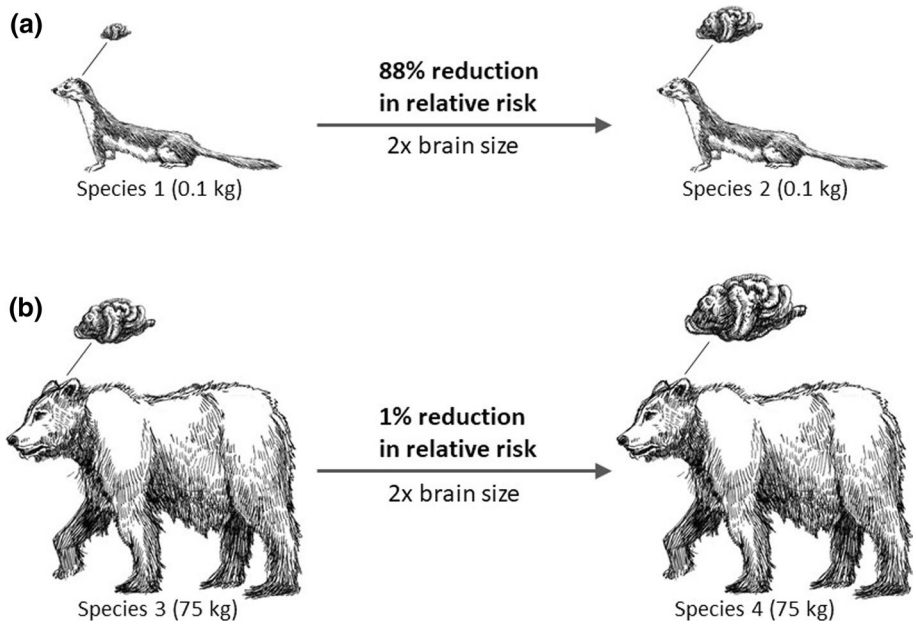

Fig. 2 Body size mediates the benefits of larger levels of relative encephalization: an example using hypothetical species. For each unit increase in relative encephalization (RE; brain size controlling for body mass and phylogeny), there is greater reduction in relative extinction risk for smaller-bodied species when compared to larger-bodied species. Species 2 (**a**) and 4 (**b**) have the same degree of increased RE relative to species 1 and 3; however, the relative risk of extinction is highly reduced in species 2 but not species 4 Artwork credit: Michael Abelson

Discussion

Analyses presented here find that RE has a strong correlation with relative extinction risk in carnivorans. While prior studies have shown a relationship between brain size and behaviors that might protect individuals from death (Sol et al. 2008; González-Lagos et al. 2010; van der Bijl et al. 2015; Benson-Amram et al. 2016), I show here a direct link between RE and the ultimate measure of carnivoran species survival, relative extinction risk over the prior 40–0.012 million years. While the direct mechanism between RE and extinction risk has not been tested here, these results do show that increased RE is correlated with increased extinction resistance; this is especially true at small body sizes (i.e., smaller than 78 kg). It is unlikely that extinction resistance correlated with increased RE originates from a single identifiable causative factor, making it difficult to assess a singular mechanism by which brain size influences survival (McKinney 1997; Russell et al. 1998). However, evidence presented here suggests that fruitful avenues of future research would include examining the proximal mechanism that link RE and extinction resistance in the paleontological record.

Understanding extinction vulnerability captures the imagination, elucidates evolutionary mechanisms, and has important implications for conservation biology (Terborgh 1974; McKinney 1997). Generally speaking, there are two ways to approach understanding mechanisms important to extinction and to explore traits linked to extinction vulnerability—(1) examining extant species and, for example, identifying why some are on the precipice of extinction while other species are thriving or (2) by comparing species in the paleontological record that have gone extinct against those that persisted through their contemporary's extinction.

Examining extinction risk (endangerment status), and related traits, of currently living species is important for those interested in stemming species loss (O'Grady et al. 2004). However, one potential weakness of studies including only extant taxa is that they often rely upon endangerment status—assessing endangerment status of extant species is inherently an attempt at predicting which species are at greatest risk for extinction in the future (Cardillo et al. 2008). Methodologies for endangerment status assessments are varied and range from those arising from governmental endeavors, like the United States Endangered Species Act (U.S. Fish and Wildlife Service 1973), to those by conservation organizations including the International Union for the Conservation of Nature's Red List (IUCN 2019). These assessments are subject to a number of biases, including those of the organization carrying out the assessment (Tear et al. 1993; Wilcove and Master 2005; Green 2005; Clark et al. 2006).

Alternatively, using the paleontological record allows for a retrospective assessment comparing species that went extinct at any given point in the paleontological record to other contemporary species that did not. Because it is known which species went extinct at any given time period and which persisted, it is possible to assess traits associated directly with extinction (rather than with endangerment status as is a limitation of studies carried out on extant taxa). I used a survival model approach because it provides a framework to compare the species that went extinct at any given time only to those that lived through that particular extinction event.

I find an interaction effect such that differing levels of RE strongly influence probability of extinction at any given time point for small-bodied species. These results suggest that at the species level, excluding those greater than 78 kg (the top 13% in body size), there is an extinction resistance advantage conferred by investment in more neural tissue despite the associated increased metabolic costs. I find an effective body mass cutoff (78 kg) above which increases in RE do not predict reduced relative risk of extinction. This finding is consistent with risk factors being fundamentally different in larger-bodied species than smaller (MacFadden 1990; Cardillo et al. 2005) and does not necessarily mean that the largest-bodied species do not benefit in the same way from increased RE as small-bodied taxa. Instead, it may indicate that other factors are important in modulating the benefits of RE in large-bodied species (MacFadden 1990; Cardillo et al. 2005) (e.g., few young per year, delayed sexual maturity, lower population densities, etc.). It is possible that extinction resistance associated with larger RE plays a similar role in all species regardless of body mass, but that extinction resistance is not great enough to counter the effects of differential pressures on large-bodied taxa. Further investigation is needed to parse the advantages accompanying larger RE from the compounding extinction pressures that large-bodied carnivorans faced over the past 40–0.012 million years.

At first glance, a possibly puzzling aspect of the results described here is that they appear contradictory to previous work (Abelson 2016), which found increased levels of RE were correlated with *increased* rather than *decreased* risk of endangerment in modern mammals. While this may seem paradoxical, it may reflect the changing ecological landscape that modern wildlife face compared against the landscapes faced by carnivorans between 40 and 0.012 million years ago. One mechanism for a fundamental shift in the role that RE plays in modern vs. paleontological species is linked to the drivers of accelerated modern extinction rates (Ceballos et al. 2015). It is conceivable that the effects of larger levels of RE are not benefits in a landscape where no level of cognition can overcome current environmental challenges. For example, while increased cognition may help individuals avoid a novel predator or small environmental perturbations, there may be no level of increased cognition that could overcome challenges faced by individuals in the midst of current large-scale pollution and habitat destruction.

This is in line with the cognitive buffer hypothesis (Sol 2009a). Increases in RE come with a notable cost as neural tissue is one of the most metabolically expensive tissues (Niven and Laughlin 2008). The cognitive buffer hypothesis (Sol 2009a) addresses this cost–benefit balance by positing that the hardships imposed by increased metabolic costs associated with larger RE (Aiello 1997; Laughlin et al. 1998; Kotrschal et al. 2013) come with increased behavioral flexibility, which may in turn protect individuals from the vagaries of the environment (Sol 2009a, b). During the period between 40 and 0.012 million years ago, there was only a relatively low background rate of carnivoran extinctions—these are the conditions that increased metabolic costs associated with increased levels of RE would be an asset. However, as described by Ehrlich and Blumstein in "The Great Mismatch" (Ehrlich and Blumstein 2018), modern times are quite different—traits that were, over evolutionary time scales, beneficial are now a serious liability. Restating an idea described by Nesse and Williams: there can be great mismatches between the physiological design of a species' body and novel aspects of its environment resulting in serious negative consequences (Nesse and Williams 1998). The environmental conditions accompanying the extinction event we are currently in could be providing just those conditions with regard to RE. What once was an asset (cognitive benefits outweighing the metabolic cost of a large brain) might now be a burden that makes it more difficult for species with large levels of RE to thrive. Further study could focus on delving into specifics of why larger levels of RE was an asset in Carnivora between 40 and 0.012 million years ago and larger levels of RE are currently found to be a liability in mammalian taxa broadly in species alive today. While the role of RE appears to have changed over time (i.e., between species that went extinct during the prior 40–0.012 million years and those extant species that are currently identified as endangered), this work reinforces the importance of RE as a salient characteristic related to species' extinction vulnerability over a long time horizon.

Acknowledgements I thank Rodolfo Dirzo, Lucia Jacobs, Deborah Gordon, Gretchen Daily, Amelia Wolf, Maria del Mar Sobral Bernal, Noah Simon, Reuben Youngblom, Stuart Abelson, Minh Chau N. Ho, Erin Kurten, Jonathan Payne, Rachel Vannette, Susumu Tomiya, Leonid Pekelis, Kristen Malinak, and George Michopoulos, for project discussion, manuscript review, and assistance on data processing. I thank Michael Abelson for his artwork in figure two. I also thank J. Finarelli and J. Flynn for collecting and making available brain size and body size used in this study (from their 2009 publication titled "Brain-size evolution and sociality in Carnivora") and to those who worked to make the Paleobiology Database available and an incredible resource. I am appreciative of the patient and detailed review of this manuscript by Joerg Ganzhorn along with insightful comments from three anonymous reviewers.

Author contribution statement ESA conceived, designed, and executed this study and wrote the manuscript. No other person is entitled to authorship.

Funding This study was funded by the National Science Foundation Grant #1110332.

Compliance with ethical standards

Conflict of interest The author declares that there is no conflict of interest.

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