



Research

Cite this article: Abelson ES. 2016 Brain size is correlated with endangerment status in mammals. *Proc. R. Soc. B* **283**: 20152772. <http://dx.doi.org/10.1098/rspb.2015.2772>

Received: 17 November 2015

Accepted: 26 January 2016

Subject Areas:

environmental science, behaviour, ecology

Keywords:

brain size, relative encephalization, extinction risk, endangerment, mammals, body size

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2015.2772> or via <http://rsob.royalsocietypublishing.org>.

Brain size is correlated with endangerment status in mammals

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Increases in relative encephalization (RE), brain size after controlling for body size, comes at a great metabolic cost and is correlated with a host of cognitive traits, from the ability to count objects to higher rates of innovation. Despite many studies examining the implications and trade-offs accompanying increased RE, the relationship between mammalian extinction risk and RE is unknown. I examine whether mammals with larger levels of RE are more or less likely to be at risk of endangerment than less-encephalized species. I find that extant species with large levels of encephalization are at greater risk of endangerment, with this effect being strongest in species with small body sizes. These results suggest that RE could be a valuable asset in estimating extinction vulnerability. Additionally, these findings suggest that the cost–benefit trade-off of RE is different in large-bodied species when compared with small-bodied species.

1. Introduction

The Earth is currently experiencing what may be one of the largest extinction events over the prior half-billion years [1]. This is largely driven by human influences including urbanization, habitat loss, and environmental pollution, and is expected to intensify in the future [2]. Many species have become extinct in the face of these challenges and continued conservation efforts are needed to protect both endangered species and those that may become so in the future.

A major goal for conservation biologists is to conserve the biological functions mammals perform and the diversity that these species represent. In the face of modern environmental changes, not all mammals are equally at risk of endangerment [3]. Many life-history and physical traits, including body size, home-range size, fecundity, and age at first reproduction have helped to elucidate differences in extinction vulnerability [4]. However, animal behaviour, increasingly recognized as important to conservation, is often not incorporated into wildlife endangerment models [5].

Brain size holds promise for helping to understand species endangerment because it is an easily measured, heritable trait [6,7] and has behavioural implications [6]. Many studies have examined relative encephalization (RE), a measure of brain size after accounting for the effects of body size and phylogeny, and have found that higher RE is correlated with longer lifespan [8], complex social intelligence [9], increased learning capabilities [7], introduction success [10], and a diet more varied in space and time [11]. These studies have found RE to be a biologically relevant measure across a broad array of taxa ranging from reptiles to primates. However, despite the diversity of studies, none have examined RE and species' extinction risk in modern mammalian taxa.

The brain is one of the most costly organs [12–14] and thus a trade-off exists between larger levels of RE and the cost of maintaining additional neural tissue. The cognitive buffer hypothesis [15,16] advances a reason why larger RE is worth the cost by positing that increased levels of RE come with increased behavioural flexibility that, in turn, help individuals cope with environmental perturbations. There are other hypotheses that address the cost–benefit trade-off (e.g. [12,17]), though whatever the mechanism, it follows that the degree to which a species benefits from increased RE levels depends on environmental conditions. For example, in a hypothetical landscape where calories are scarce though logically patterned, the costs of sophisticated cognitive problem-solving may be

outweighed by the benefit of efficiently finding the few calories available; increased RE would be an asset. However, if in a similar hypothetical landscape, calories were equally scarce but distributed completely randomly, sophisticated cognitive problem-solving could not provide a clever solution to the problem; increased RE would be a liability.

To assess the relationship between RE and extinction vulnerability in modern species, I examined the relationship between increased RE and the International Union for Conservation of Nature (IUCN) endangerment status in extant mammal species. To do this, I measured brain size using a single technique, and recorded specimen specific body size, for 1 679 specimens in 160 species across eight taxonomic orders that are present in the Americas. To contextualize these findings, I used a global dataset of brain and body size for 626 species across 15 taxonomic orders from the literature. I show that RE, body size, and the interaction between RE and body size are all significantly associated with mammalian endangerment. In both datasets, I found that increased RE results in increased endangerment risk for the majority of mammalian species. Finally, in the dataset consisting of mammals from the Americas (dominated by North American species), I found that increased body size decreases the risk of endangerment, though I found the opposite trend in the global species dataset. Broader implications of this research to conservation biology suggest that RE, with the inclusion of body size, may be a useful metric to incorporate into species' extinction vulnerability assessments.

2. Results

(a) Dataset 1 (Americas)

Results from the general estimating equations (GEE) model presented in table 1 show that, at the species level, increasing RE (while holding body size steady) increases the risk of endangerment and increasing body size (while holding RE steady) decreases the risk of endangerment. The negative interaction effect demonstrates that there is a transition from the largest-bodied species, where RE has little influence on endangerment status, to the smallest-bodied species, where larger RE is strongly correlated with an increase in risk of being endangered.

(b) Dataset 2 (global)

Results from the GEE model presented in table 2 show a similar pattern for the effect of RE on endangerment, though differ in the effect of body size. As with dataset 1, increasing levels of RE lead to increased risk of being endangered. The negative interaction term between RE and body size demonstrates that the effect of RE on endangerment status varies significantly depending on body size. However, results for the effect of body size on endangerment differ between the two datasets. In dataset 2, the positive coefficient for body size indicates that as body size increases, the risk of endangerment also increases.

3. Discussion

As RE increases, the predicted risk of species' endangerment also increases. This is mediated by body size, due to the interaction effect between body size and RE, such that increases in RE are accompanied by the greatest increase in predicted risk of endangerment in smaller-bodied species (figures 1 and 2).

Table 1. Coefficients and *p*-values for general estimating equations (GEE) analysis of the relationship between RE and body size on endangerment status. These results are from the analysis of the species in dataset 1 (Americas) using the taxonomically adjusted brain residuals (TABR) method for generating RE.

species from dataset 1 (Americas)	coefficient	standard error (s.e.)	<i>p</i> -value
RE	10.99	4.92	0.025
Body length (log ₁₀ , mm)	−0.94	0.17	<0.0001
RE: Body length (log ₁₀ , mm) interaction	−3.86	1.93	0.046

Table 2. Coefficients and *p*-values from general estimating equations (GEE) analysis of the relationship between RE and body size on endangerment status. These results are from the analysis of the species in dataset 2 (global) using the taxonomically adjusted brain residuals (TABR) method for generating RE.

species from dataset 2 (global)	coefficient	s.e.	<i>p</i> -value
RE	5.38	1.55	<0.001
Body length (log ₁₀ , mm)	0.49	0.09	<0.0001
RE: Body length (log ₁₀ , mm) interaction	−1.43	0.40	<0.001

As such, the species at greatest risk of endangerment are small-bodied species with large levels of RE, suggesting that the costs associated with large levels of RE outweigh the benefits in small-bodied species. While increases in RE and the interaction effect (between body size and RE) had similar effects on risk in both dataset 1 (Americas) and dataset 2 (global), the effect of body size alone showed a different trend. Results from dataset 1 show that body size is negatively correlated with endangerment risk, whereas results from dataset 2 (global) show that body size is positively correlated with endangerment risk. These contrasting results for the effect of body size on endangerment are consistent with other analyses done at either global [18] or regional [19] scale and are discussed in more detail below.

(a) Relative encephalization and risk of endangerment

The costs of large levels of RE have been well discussed in the literature and include metabolic cost [13,20], decreased reproductive output [7], cost of additional neuronal connections [14,21], and reductions in the size of other expensive tissues [22]. In addition, a number of studies have demonstrated counterbalances to the costs associated with larger RE, including greater lifespan [8] and increased introduction success [10,23]. Perhaps more importantly, studies have found a number of behaviours that correlate with larger RE, such as increased behavioural flexibility [15], social cognition [7], allomaternal care [24], and tool use [9]. The costs and benefits of varying levels

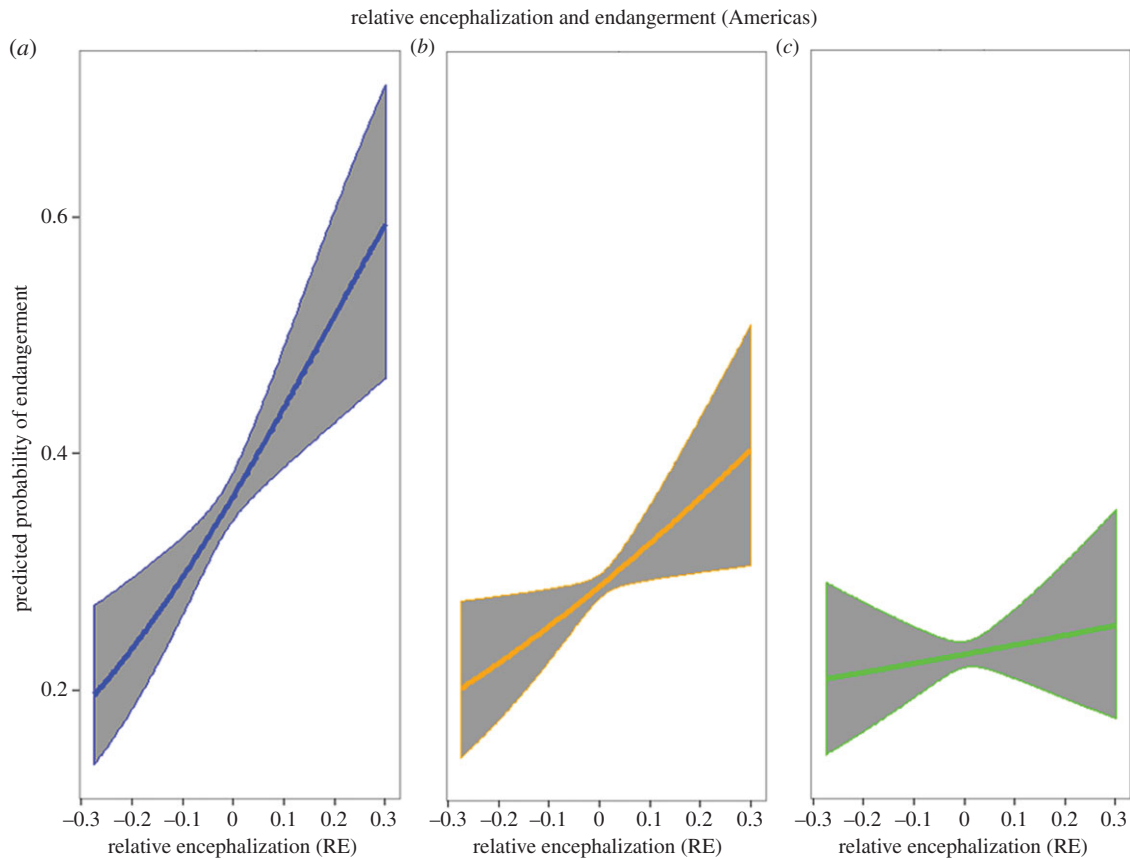


Figure 1. Predicted probability of endangerment by RE for (a) small-, (b) mid- and (c) large-bodied species (Americas model). This figure shows three main results: (i) increased RE is accompanied by increased predicted probability of endangerment. (ii) The magnitude of the effect of RE on predicted probability of endangerment depends on body size. (iii) Species with larger body sizes are at the *lowest* predicted probability of being endangered. Each subfigure depicts the relationship between RE and modelled predicted probability of endangerment holding body size (length) constant. Subfigures *a*, *b*, and *c* show body size, respectively, at the 25th (109 mm), 50th (253 mm), and 75th (538 mm) percentiles of body size. (Online version in colour.)

of RE suggest that there is a balance to be struck. Simply put, neural tissue is expensive; to support larger levels of RE there must either be greater caloric input, reduction in somatic tissue, or a decrease in energy expenditure [7]. The cognitive buffer hypothesis suggests that the counterbalance to increased neural tissue costs is that increased neural tissue helps buffer individuals from environmental perturbations by enhancing behavioural adaptations in the face of environmental changes [15].

Why then, despite the support for increased levels of RE benefiting a species with increased cognition, does RE correlate with increased levels of endangerment in this study? The answer may lie in the complex relationship between the trade-offs that accompany larger RE. In order for increased cognition associated with enlarged RE to be worth the cost, the environment must be one in which the benefits outweigh the cost of increased RE. Extant mammals are facing substantial environmental disturbances resulting in extinction rates not seen in the past 65 Myr [1]. The overarching drivers of extinction likely stem from large-scale, human-caused landscape alterations, including pollution, hunting, urbanization, introduction of invasive species, and climate change [25]. The cognitive buffer hypothesis provides a tractable framework for why larger RE can protect species against environmental variability. However, current large-scale and persistent environmental alterations may work to shift the cost–benefit trade-off accompanying larger RE.

Modern anthropogenic disturbance may serve to select against large RE, undercutting the benefits proposed by the cognitive buffer hypothesis, in several ways. Increases in RE, and related increases in metabolic burden, are advantageous

only if species face environmental disturbance or stochasticity that can be overcome cognitively. For example, environmental pollution may often be a problem without cognitive solutions. Additionally, increased RE may be accompanied by life-history traits that increase the risk of endangerment [26]. In the context of larger RE benefiting species introduced to novel landscapes as demonstrated by Sol *et al.* [10], the results presented here may suggest a difference between a mammalian introduction event, similar to an acute landscape-level disturbance, and long-term persistent disturbance.

(b) Body size and endangerment

Larger-bodied mammals have generally been found to be at greater risk of endangerment [4,18] (figure 2). Effects of body size on endangerment, however, have been shown to be dependent on the region and historical context [19]. Results presented here are consistent with previously delineated differences in body size effect stemming from global versus regional analyses. I found that the largest-bodied species in dataset 1 (Americas) were the *least* at risk of endangerment, whereas those from dataset 2 (global) were at the *greatest* risk of endangerment. This likely represents a case of endangerment filtering [19]; species in North America have gone through a period where large-bodied species had suffered large population losses. These species are now either extirpated or protected with rebounding populations and, thus, are not considered endangered.

Ultimately, I found that the effect of RE on extinction is mediated by body size. This relationship suggests that the

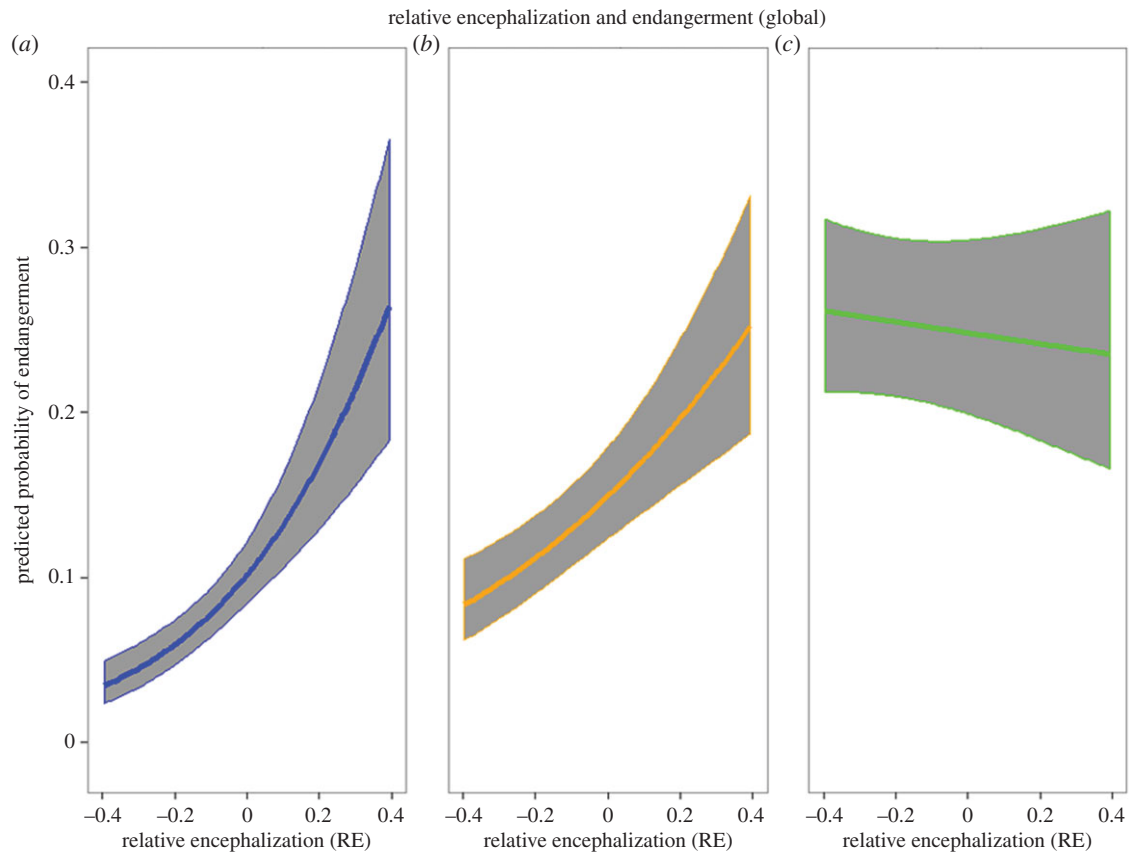


Figure 2. Predicted probability of endangerment by RE for (a) small-, (b) mid-, and (c) large-bodied species (global model). This figure shows three main results: (i) increased RE is accompanied by increased predicted probability of endangerment; the same trend shown in figure 1. (ii) The effect of RE on predicted probability of endangerment depends on body size, also the same effect shown in figure 1. (iii) Contrary to figure 1, species with larger body sizes are at the *highest* predicted probability of being endangered. Each subfigure depicts the relationship between RE and modelled predicted probability of endangerment holding body size (mass) constant. Subfigures a, b, and c show body size, respectively, at the 25th (0.05 kg), 50th (0.39 kg), and 75th (7.37 kg) percentiles of body size. (Online version in colour.)

metabolic trade-offs associated with larger RE may differ substantially between large- and small-bodied mammals, though it is also possible that RE correlates with other variables unique to large- and small-bodied animals. Further research is needed to help elucidate the interplay between costs and benefits of larger RE, the mechanistic relationship between RE and behavioural flexibility, and correlations between RE and other determinants of endangerment risk.

(c) Conclusions

Larger levels of RE are positively correlated with risk of endangerment, especially in small-bodied taxa. Many prior studies have examined correlates of greater encephalization and this finding builds on those by examining the relationship between RE and an important measure of species success, resistance to extinction. Mammalian species are facing accelerated extinction rates [1] and part of the process of protecting species is to understand the causes and correlates of extinction. Out of the known mammalian species alive today, approximately 25% of them are under some form of endangerment [3]. Perhaps more surprising is the approximately 15% of species which are data deficient, meaning that there is not currently enough known about them to assign a risk category [3].

RE, which is relatively fast and simple to measure, might help shed light on the intrinsic endangerment risk of species, especially those that we have little other information on. Behaviours are often considered to be highly important in conservation though they are often not incorporated into conservation programmes [5]. The degree to which RE, serving

as a proxy for behavioural traits, is correlated to conservation status makes it a potentially beneficial tool in understanding future extinction risk and aiding in conservation planning.

4. Material and methods

(a) Brain and body measures

Brain sizes for dataset 1 (Americas) were measured directly by determining endocranial capacity, the space inside the cranium [27]. All species included in this dataset were terrestrial mammals from the Americas. In total, 1 679 museum specimen skulls belonging to 160 species were measured at the Smithsonian National Museum of Natural History and the Museum of Vertebrate Zoology. To put the findings from dataset 1 in a global context, I gathered brain and body size of 626 non-primate mammals from the literature [24,28], to form dataset 2 (global). Endangerment status for each species was based on IUCN classifications [3]. See the electronic supplementary material for substantiation that non-inclusion of primates does not bias results, dataset 1 species list, discussion of why the two datasets were not combined into one, detailed skull measuring methods, and IUCN classification.

(b) Relative encephalization calculation

Across species, log brain size increases following a linear allometric scaling relationship with log body size. RE, in its simplest form, represents the residuals from a regression of $\log_{10}$ brain volume on $\log_{10}$ body mass. This measurement reflects the degree to which a species has a larger, or smaller, brain than would be expected by body mass alone and has been shown to be a biologically relevant measure [15].

Species that are more closely related to each other tend to have traits that are correlated [29]; this can result in changes to the allometric exponent and inaccurate residuals [30]. Increased variance between distantly related taxa, when compared with closely related taxa, is termed the taxon-level effect [31] or grade shift. I use methods which account for these grade shifts both in generating RE and in the analyses that use the resultant RE. Using the phytools package [32], I found a strong phylogenetic signal in model residuals ($\lambda = 0.93$, $p < 0.0001$) suggesting that methods to account for phylogenetic signal are appropriate in the analysis of these data.

To generate RE that has been corrected for body size and phylogenetic signal I used two distinct methods: taxonomically adjusted brain residuals (TABR, following Sol *et al.* [10]) and phylogenetic independent contrasts (PIC, also following Sol *et al.* [10] and Blomberg *et al.* [29]). These methods yield measures of RE that are highly correlated with each other. PIC methodology, and PIC correlation with TABR RE, is presented in the electronic supplementary material.

TABR was calculated using a general linear model. The dependent variable was $\log_{10}$ transformed brain mass and the independent variables were $\log_{10}$ transformed body mass, the taxonomic order and the interaction between the $\log_{10}$ transformed body mass and the taxonomic order. Resulting residuals are the measure of RE discussed throughout this article. This method generates RE that is specific to each order and, because of this, further analysis using RE values must also be carried out using a method that accounts for phylogenetic relatedness at the taxonomic order level.

Importantly, RE generated using the TABR method produces a measure of brain size that is completely free from the effects of body size and simply represents the extent to which encephalization in a species is greater or smaller than expected based on body size. Pearson's product-moment correlation coefficient was used to assess the relationship between TABR RE and body size. I found no correlation between the two variables (sample estimate: $\text{cor} = 4.08 \times 10^{-15}$, d.f. = 632, $p = 1$).

5. General analyses

All analyses were completed using the statistical programming language R v. 2.15.2 (R Core Team & R Foundation for Statistical Computing 2012). I used GEE with binary endangerment status as the dependent variable and RE, body size, and the

interaction between RE and body size as predictor variables. Statistics presented in the main text use RE generated using the TABR method described above. The TABR method yields RE values which are comparable within-order but not between different orders; to account for this, taxonomic order was used as the clustering variable. This controls the possibility that brain structure and function may be different, and therefore incomparable, across different orders. Body size was included as a predictor variable in the final analyses because of the strong link between body size and extinction vulnerability; interpretation of the subsequent analysis is straightforward as there is no correlation between RE and body size (Pearson's product-moment correlation sample estimate: $\text{cor} = 4.08 \times 10^{-15}$, d.f. = 632, $p = 1$). The function `geeglm` was used with a binomial family, logit link, exchangeable correlation structure, and the taxonomic order as the clustering variable. Dataset 2 was edited so that results would be directly comparable between datasets 1 and 2; details can be found in the electronic supplementary material.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Author's contribution. I designed, performed the research, and wrote the manuscript.

Competing interests. I have no competing interests.

Funding. This work was supported by the National Science Foundation (www.nsf.gov) grant no. 1110332.

Acknowledgements. I thank Rodolfo Dirzo, Amelia Wolf, Mar Sobral, Lucia Jacobs, Deborah Gordon, Gretchen Daily, Elizabeth Hadly, Rachael Vannette, Erin Kurten, and Andy Lin. This work would not have been possible without the support of the National Museum of Natural History and its welcoming staff Kristofer Helgen, Robert Fisher, and Suzanne Peurach. The Museum of Vertebrate Zoology was an amazing host and I thank Christopher Conroy, Monica Albe, James Patton, and Eileen Lacey. I owe a debt of gratitude to Reuben Youngblom, Minh Chau Ho, and William Bassett, who were instrumental in data collection. Additionally, Gladys Delgadillo, Jonathan Altamirano, Andrew Dinh, Sima Bouzid, Agnes Kim, Christina Kastley, Zoe Burr, Kristen Malinak, George Michopolos, Michele Goodman, Janine Licare, Evan Corral, and Vince Voralmen for their assistance in collecting brain size measurements. I am also appreciative of the time and thoughtfulness of two anonymous reviewers.

Disclaimer. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

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