

Multiple Causes of High Extinction Risk in Large Mammal Species

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Many large animal species are at high risk of extinction. This is usually thought to result simply from the way that species traits associated with vulnerability, such as low reproductive rates, scale with body size. In a broad scale analysis of extinction risk in mammals, we find two additional patterns in the size-selectivity of extinction risk. First, impacts of both intrinsic and environmental factors increase sharply above a threshold body mass around 3kg. Second, whereas extinction risk in smaller species is driven by environmental factors, in larger species it is driven by a combination of environmental factors and intrinsic traits. Thus, the disadvantages of large size are greater than generally recognized, and future loss of large mammal biodiversity could be far more rapid than expected.

A major challenge for conservation biology is to explain why some species are more likely to be threatened with extinction than others (1). One of the traits associated most often with high extinction risk among animal species is large body size (2). In mammals, for example, declining species considered threatened with extinction are an order of magnitude heavier ($1374 \pm 1.43\text{g}$), on average, than non-threatened species ($139 \pm 1.13\text{g}$) (3). Furthermore, the size-selectivity of the current extinction crisis echoes past extinction events such as that of the late Pleistocene, which disproportionately affected larger species (4, 5). However, it is not clear which mechanisms are primarily responsible for the association between body size and extinction risk (5–9), and a thorough investigation requires large comparative datasets for sizeable groups of species spanning a wide range of body sizes. Here we investigate the association between size and risk, using a

dataset including nearly 4000 species of non-marine mammals, a group spanning eight orders of magnitude in body mass, from the 2g Least Woolly Bat to the 4000kg African Elephant.

We used multiple linear regression on phylogenetically independent contrasts to test associations between extinction risk and a range of predictor variables (10). As our measure of extinction risk we follow previous studies in using classifications based on criterion A of the IUCN Red List (3), converted to a numerical index from 0 – 5 (11–13). This corresponds to a coarse but quantitative measure of the rate of recent and ongoing decline, and excludes those threatened species listed simply on the basis of small geographic distribution or population size (3). Potential predictors of extinction risk can be grouped into three broad types: (i) environmental factors, where the size and location of a species' geographic range determines the environmental features and human impact to which it is exposed; (ii) species' ecological traits, such as population density; and (iii) species life-history traits, such as gestation length. To represent each of these types we selected six key predictors (geographic range size, human population density, an index of external threat level, population density, gestation length and weaning age; see Materials and Methods (10) for justification).

Extinction risk shows a positive association with adult body mass ($t = 3.86$, d.f. = 1530, $p = 0.0001$, controlling for geographic range size). In separate regression models, each key predictor except weaning age is also significantly associated with extinction risk (Table 1). When a term describing the interaction between body mass and the key

predictor is added to each model, a significant interaction is found in every case, except in the model for geographic range size (Table 1). In every model, the sign of the interaction term indicates that the slope of extinction risk against the key predictor becomes steeper with increasing body mass. The effects of risk-promoting factors on extinction risk, therefore, become stronger as body mass increases.

To visualize the effects of these interactions between body mass and the key predictors on extinction risk, we fitted models within a sliding window with a width of 2 units on the scale of $\ln(\text{body mass})$, moved along the body-mass axis at increments of 0.5 units (Fig. 1). For all predictors, slopes of extinction risk vary substantially along the body-mass axis, confirming the significant body-mass interactions in the regression models. In all cases, there is a sharp increase in slope towards the upper end of the body-mass scale, with steepest slopes found in or near the largest body-mass interval. For weaning age, population density and external threat, this sharp increase in slope occurs at around 3kg; for gestation length and geographic range size it occurs above 20kg. The slope of extinction risk against human population density increases steadily at smaller body sizes, then drops sharply at around 3kg, although the steepest positive slope is nevertheless found in the largest body-mass interval (Fig. 1).

Dividing mammal species into small-bodied and large-bodied subgroups at a cutoff of 3kg, we used multiple regression with model simplification to find the sets of predictors, selected from a wide range of variables, that independently contribute to extinction risk in each subgroup (Table 2; see Supporting Online Information for the full list of variables). For species smaller than the cutoff body mass, the minimum adequate regression model (MAM) includes no intrinsic biological traits, only environmental factors determined by the size and location of species' geographic ranges (the size and median latitude of geographic range, and the human population density and external threat level within the geographic range). For species larger than the cutoff body mass, intrinsic biological traits (population density, neonatal mass and litters per year), in addition to environmental factors, are independent, significant predictors of extinction risk. This basic result is robust to bracketing the small:large cutoff below and above 3kg; the sets of significant predictors vary only slightly in each case (10).

Large size has often been linked to elevated extinction risk in mammals because larger species tend to exist at lower average population densities (14), the intrinsic rate of population increase declines with body mass (15), and larger species are disproportionately exploited by humans (16, 17). However, our models reveal further complexity in the association between size and extinction risk, and provide a compelling explanation for the strong size-selectivity of the current extinction crisis which goes beyond a simple scaling

of risk-promoting factors with body size. Intrinsic factors predict extinction risk only in species weighing more than 3kg; above this size, susceptibility to both intrinsic and external threats increases sharply. This may represent the approximate body mass above which extinction risk begins to be compounded by the cumulative effects of multiple threatening factors. For example, forest fragmentation elevates the sensitivity to hunting pressure of populations of medium and large-sized vertebrates (18), and larger body sizes demand larger home ranges, bringing individuals into increasing contact with people in fragmented habitats (19). Above certain critical body sizes, species become targets for increased hunting pressure: in Neotropical forests, subsistence hunter preference increases abruptly for mammal species above approximately 6.5kg (16). Those species with low population densities or slow life histories, which tend to be of larger size, are the most vulnerable to population declines caused by hunting (17).

The reason for the sharp dip in the slope of extinction risk against human population density, around the same body mass that the slopes of other predictors increase, is less intuitive. It could represent the effects of an extinction filter, whereby the most susceptible species have long since disappeared from regions of highest human population density, leaving behind a fauna consisting of species more robust to extinction (20). This scenario is supported by evidence for widespread disappearance of mammal populations from regions of high human population density (21).

Our results also suggest that as human impact on natural environments continues to increase, declines towards extinction will be more rapid, on average, in large species compared to small species with similar biological characteristics, or which are exposed to similar levels of human impact. This can be illustrated using our model predicting extinction risk from the level of external threat (Table 1; see Supporting Online Information for full model results). We predicted extinction risk for two hypothetical species that vary in body mass but are identical in other respects (we assigned both species the median values for all mammals of geographic range size and degree of exposure to external threat). From this model we obtained a predicted extinction risk index value of 1.00 for a species of 300kg compared to only 0.38 for a species of 300g. The difference in predicted risk stems solely from the difference in body size and the interaction between body size and external threat. This, together with the interactions between other risk-promoting factors and body size, suggests that the ongoing loss of the world's large mammal biodiversity could be far more rapid than currently predicted (for example, by extrapolating from current extinction risk levels (22, 23)). The likelihood of this loss being highly selective, clustered in

large-bodied groups such as ungulates and primates, means the concomitant loss of mammalian evolutionary history and ecological diversity could also be greater and more rapid than currently expected (24, 25).

A recurring question in the study of extinctions, both recent and prehistoric, has been whether species which have declined or gone extinct have been the victims of “bad genes” or simply “bad luck” (26, 27). Our results suggest the answer to this question may be different for small and large mammals. Smaller species are more likely to become threatened simply through environmental disadvantage: that is, the size and location of their geographic ranges, and the levels of human impact to which they are exposed. For larger species, intrinsic biological traits become a significant determinant of extinction risk, in addition to environmental factors: large species are thus more likely to be evolutionarily predisposed to decline. One implication this has for conservation is that it provides a possible means of reconciling opposing views over whether area-based or species-based approaches to conservation are most effective (28). Smaller species should, in general, benefit more from the conservation of important threatened areas, whereas larger species will tend to benefit most from a conservation approach that also singles out individual species for particular attention. We do not suggest that detailed ecological studies of small mammal species are unimportant; in conservation planning, there is no substitute for a thorough knowledge of each species’ unique circumstances. However, analyses of global patterns of extinction risk from large-scale comparative studies such as ours can lead to a better general understanding of the underlying causes of decline, and importantly, of the selectivity of decline among different species. This may help to identify those species likely to be most susceptible to future decline, providing the basis for a more pre-emptive approach to conservation planning.

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Supporting Online Material

www.sciencemag.org/cgi/content/full/1116030/DC1

Materials and Methods

Table S1 – S3

References and Notes

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Figure 1. Slopes of key predictors against extinction risk at different body masses. Each point is located at the lower bound of a body-mass interval of width $2 \ln(g)$. Triangles = slopes significantly greater or less than zero ($p \leq 0.05$); circles = slopes not significantly different from zero. Lines are Lowess smoothers fitted through the points with span = 0.3. Solid squares indicate slopes (± 1 se) of the predictor against extinction risk for small ($< 3\text{kg}$) and large ($\geq 3\text{kg}$) species, respectively. Dashed horizontal lines indicate slopes of zero. Note that the y axes in (c) and (d) have been inverted to improve the visual clarity of the pattern.

Table 1. Separate regressions of key predictors against extinction risk. Each test includes geographic range size as a covariate; tests for weaning age, gestation length and population density also include adult body mass as a covariate. For clarity, only results for key predictors and interaction terms are shown here; quadratic and cubic terms are shown where significant. Full model results are in supporting online information. HPD = mean human population density, ETI = External Threat Index (10). d.f. = degrees of freedom. †p≤0.1; * p≤0.05; ** p≤0.01; ***p≤0.001.

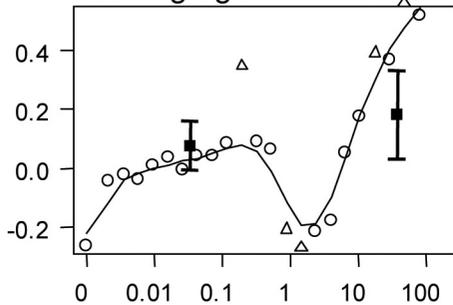
Predictors	Predictors tested without body-mass interaction			Predictors tested with body mass interaction		
	d.f.	slope	t	d.f.	slope	t
weaning age	674	0.034	0.5	673	-0.344	-2.87**
weaning age : body mass					0.074	3.8***
gestation length	748	-5.754	-3.34***	747	-1.447	-2.96**
gestation length ²		0.666	3.5***			
gestation length : body mass					0.183	4.19***
population density	570	-0.058	-3.35***	569	0.064	1.73 [†]
population density : body mass					-0.015	-3.73***
geographic range size	1625	0.311	1.61	1623	0.305	1.52
geographic range size ²		-0.043	-2.47*		-0.042	-2.36*
geographic range size ³		0.001	2.37*		0.001	2.26*
geographic range size : body mass					0.0004	0.12
HPD	1595	-0.154	-2.95**	1594	-0.075	-0.63
HPD ²		0.024	3.14**		-0.053	-1.34
HPD ³					0.008	2.06*
HPD : body mass					0.018	3.51***
ETI	1592	-0.562	-1.32	1589	-5.783	-4.45***
ETI ²		1.02	3.6***		6.256	3.48***
ETI ³					-1.941	-2.71**
ETI : body mass					0.366	5.73***

Table 2. Minimum adequate regression models of extinction risk. Results shown are models where each predictor is significant at $p \leq 0.05$ after model simplification (10). † $p \leq 0.1$; * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

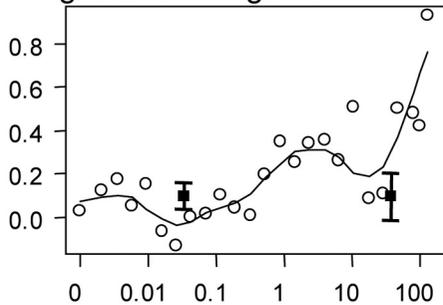
Predictors	Small species (<3kg) (d.f = 1207)		Large species (≥ 3 kg) (d.f. = 131)		All species (d.f. = 404)	
	slope	t	slope	t	slope	t
geographic range size	-0.142	-14.03***	-0.165	-3.9***	-0.516	-2.52*
geographic range size ²					0.016	2.13*
latitude	0.01	5.49***				
human population density (HPD)	-0.084	-2.1*			1.65	5.36***
HPD ²	0.03	3.48***			-0.081	-3.81***
External Threat Index (ETI)	0.629	3.71***	1.82	2.99**		
weaning age					0.3	3.46***
neonatal mass			0.401	2.09*		
litters per year			-0.618	-2.04*		
population density			-0.111	-0.27**	-0.148	-0.45***
population density ²					0.013	2.91**
geographic range size : HPD					-0.087	-4.62***
geographic range size : population density					-0.045	-3.03**

Slope of predictor against extinction risk

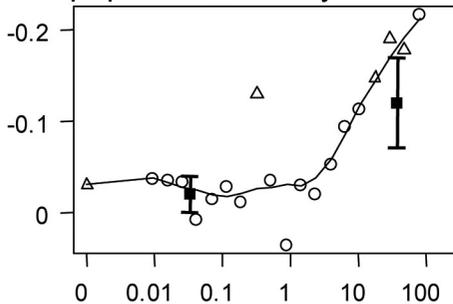
A weaning age



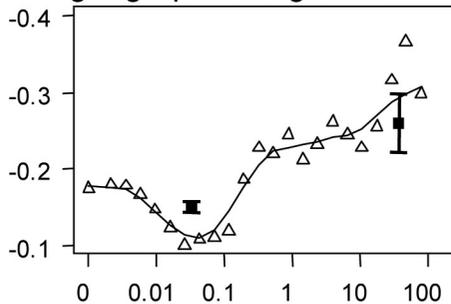
B gestation length



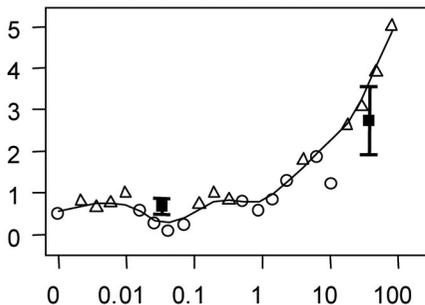
C population density



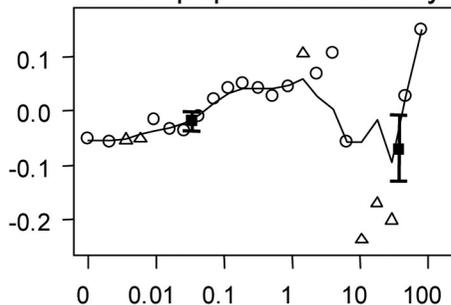
D geographic range size



E external threat index



F human population density



Lower bound of body mass interval (kg)