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Multiple Causes of High Extinction Risk in Large Mammal Species

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Many large animal species have a 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 3 kilograms. 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 ± 1.43 g), on average, than nonthreatened species (139 ± 1.13 g) [3]. Futhermore, 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 data sets for sizable groups of species spanning a wide range of body sizes. Here, we investigate the association between size and risk with the use of a data set including nearly 4000 species of nonmarine mammals, a group spanning eight orders of magnitude in body mass, from the 2-g least woolly bat to the 4000-kg African elephant.

We used multiple linear regression on phylogenetically independent contrasts [10] to test associations between extinction risk and a range of predictor variables. As our measure of extinction risk, we followed previous studies in the use of classifications based on criterion A of the IUCN Red List [3], converted to a numerical index from 0 to 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 [10] for justification].

Extinction risk shows a positive association with adult body mass [$t = 3.86$, degrees of freedom (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(body mass) and moved the window along the body-mass axis at increments of 0.5 units (Fig. 1). For all predictors, slopes of extinction risk varied substantially along the body-mass axis, confirming the significant body-mass interactions in the regression models. In all cases, there was a sharp increase in slope toward 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 3 kg; for gestation length and geographic range size, it occurs above 20 kg. The slope of extinction risk against human population density increases steadily at smaller body sizes, then drops sharply at around 3 kg, although the steepest positive slope is nevertheless found in the largest body-mass interval (Fig. 1).

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Dividing mammal species into small-bodied and large-bodied subgroups at a cutoff of 3 kg, we used multiple regression with model simplification to find the sets of predictors, selected from a wide range of variables (table S1), that independently contribute to extinction risk in each subgroup (Table 2). For species smaller than the cutoff body mass, the minimum adequate regression model includes no intrinsic biological traits, only environmental factors determined by the size and the location of species' geographic ranges (size and median latitude of geographic range and 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 3 kg; 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 that goes beyond a simple scaling of risk-promoting factors with body size. Intrinsic factors predict extinction risk only in species weighing more than 3 kg; 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 about 6.5 kg (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 impacts on natural environments continue to increase, declines toward extinction will be more rapid, on average, in large species compared with small species with similar biological characteristics or that are exposed to similar amounts of human impact. This can be illustrated with the use of our model predicting extinction risk from the level of external threat (Table 1 and table S2). 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 300 kg compared with only 0.38 for a species of 300 g. 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

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 table S2. HPD, mean human population density; ETI, external threat index (10). Dagger indicates $P \leq 0.1$; single asterisk, $P \leq 0.05$; double asterisks, $P \leq 0.01$; triple asterisks, $P \leq 0.001$. Blank entries indicate terms that were not measured or not significant in a particular model.

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). Dagger, $P \leq 0.1$; single asterisk, $P \leq 0.05$; double asterisks, $P \leq 0.01$; triple asterisks, $P \leq 0.001$. Blank entries indicate terms that were not measured or not significant in a particular model.

Predictors	Small species (<3 kg) (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***				
HPD	−0.084	−2.1*			1.65	5.36***
HPD^2	0.03	3.48***			−0.081	−3.81***
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**

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 and 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 that 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, analy-

ses 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 preemptive approach to conservation planning.

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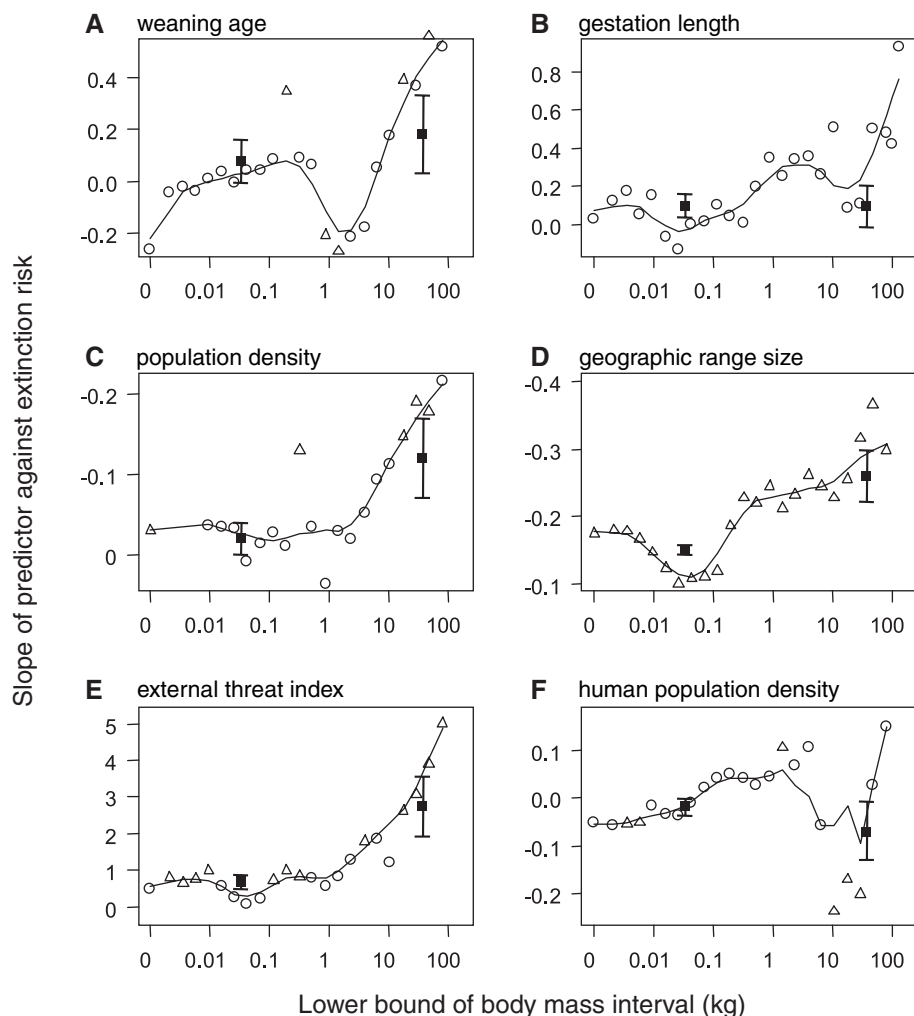
Fig. 1. (A to F) Slopes of key predictors against extinction risk at different body masses. Each point is located at the lower bound of a body-mass interval of width 2ln(g). Triangles indicate slopes significantly greater or less than zero ($P \leq 0.05$); circles, slopes not significantly different from zero. Lines are Lowess smoothers fitted through the points with span of 0.3. Solid squares indicate slopes (±1 SE) of the predictor against extinction risk for small (<3 kg) and large (≥3 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.