NOTE: SEVERAL COMMENTS ARE APPENDED TO THIS PAPER

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The three-quarter-power scaling of extinction risk in Late Pleistocene mammals, and a new theory of the size selectivity of extinction

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ABSTRACT

Questions: What is the pattern of body mass versus extinction risk in the Late Pleistocene extinctions of mammals, both qualitatively and quantitatively? Are there patterns that relate extinction risk to the well-known allometries of body mass with population density or population growth rate?

Theory: A simple theory to predict both qualitative pattern and quantitative parameters of the size-selectivity of extinction. First, I assume that external pressures (e.g. human impact and climate change) increased the overall risk of extinction in the Late Pleistocene in a way that does not depend on body size. Then, I assume that this overall risk is modified by a species' biological traits and that these traits are related allometrically to the species' body mass. Specifically, the traits are population density, N, which scales as body mass to the power of -0.75 (Damuth, 1981), and population growth rate, r, which scales as body mass to the power of -0.25 (Fenchel, 1974). I assume that extinction probability is the reciprocal of either N or r. This leads to an allometric relationship between extinction risk and body size. I assume that the external pressures during the Late Pleistocene did not change the shape (e.g. slope) of that relationship, making it possible to tease out some of its important features.

Prediction: The probability of extinction, P, is a logistic function of log-transformed body mass with slope 0.75 or 0.25. Or, equivalently, the odds of extinction, $P/(1 - P)$, scale as body mass to the power of 0.75 and 0.25, respectively.

Test data: A comprehensive database of body masses of all mammalian species from four continents, containing all species on those continents that became extinct in the Late Pleistocene and all those that survived it (Smith *et al.*, 2003).

Methods: Ordinary logistic regression and logistic regression with mixed effects (the latter to account for the non-independence of data that is inherent in comparative species analyses). I analysed the full data set with and without bats or pinnipeds, as well as a truncated data set containing only species whose mass is/was 5 kg or greater. I also analysed continent-specific subsets of species.

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Results: For both full and truncated data sets on a worldwide scale, the probability of extinction follows a logistic curve whose slope is close to, and statistically indistinguishable from, 0.75, the value that assumes that extinction probability depends on population density. The continent-specific subsets of species, however, deviate from the worldwide pattern.

Conclusions: The Late Pleistocene extinctions, although strongly biased towards large-bodied species, are biased no more than expected from the −0.75-power population-density scaling.

Keywords: allometric scaling, body mass, extinction pattern, logistic regression.

‘Но природа, увы, скорей
разделяет, чем смешивает. И уменьшает чаще,
чем увеличивает; вспомни размер зверей
в плейстоценовой чаще’

‘But Nature, alas, rather
divides than mixes. And diminishes more often
than boosts; remember the size of beasts
in the Pleistocene wilds’

Joseph Brodsky, ***An Elegy***
(translation by L.V.P.)

INTRODUCTION

Near the end of the Pleistocene, mammalian faunas experienced dramatic changes (Koch and Barnosky, 2006). Typical of these was the disappearance of many large-bodied species such as the mastodon, several species of mammoth, and the woolly rhinoceros. Whole continents were hit hard. Australia, then the home of many marsupial giants, was deprived of all terrestrial species weighing more than 50 kg (Lyons *et al.*, 2004). Despite two centuries of research (Grayson, 1984), debate continues as to why these extinctions were so strikingly size-selective.

Among modern hypotheses of the Late Pleistocene extinctions, the most popular are human impact (Martin, 1967; Alroy, 1999) and climate change (Graham and Lundelius, 1984; Wroe *et al.*, 2006), or a combination of the two (Barnosky *et al.*, 2004). Recent evidence of an extraterrestrial impact 12,900 years ago (i.e. around the time of the megafaunal extinction in North America) suggests a third cause (Firestone *et al.*, 2007). Most previous analyses have focused on the chronologies of events to evaluate the hypotheses (Johnson, 2002). Yet, these efforts have not produced a convincing solution to the size-selectivity problem (Koch and Barnosky, 2006). Lyons *et al.* (2004) and Brook and Bowman (2004) suggest that improving the quantification of the pattern of size selectivity might help.

In this paper, I investigate the pattern of size selectivity in connection with N (population density) and r (maximum per capita population growth rate). I will also relate the results to two well-known macroecological coefficients that scale N and r to body size.

Whether an improved quantitative pattern helps to solve the mysteries of Late Pleistocene extinctions, just describing these patterns on their own should provide sufficient interest.

STRATEGY

During the Late Pleistocene, mammal species became extinct more rapidly than usual. In addition, however, the larger a species' body size, the greater was its extinction risk; that is, extinction was somewhat selective. We need to separate any factors that increased the overall risk during the Late Pleistocene from those that determined the relative risk. It is the latter problem that is the focus of this study.

My null hypothesis is that external pressures, such as climate change or human impact, would increase extinction risk roughly in the same proportion for all species independently of body size (for the precise meaning of what is meant by 'increasing extinction risk independently of body size', see equation 10 on p. 16). Then I assume that there is an underlying relationship between a species' body mass and its extinction probability, which is determined by allometric relationships between body mass and population density N, and between body mass and population growth rate r. N scales as body mass to the power of -0.75 (Damuth, 1981) and r scales as body mass to the power of -0.25 (Fenchel, 1974). Because species with low densities, N, and slow population growth rates, r, are more prone to extinction than those with higher N or larger r, I assume that extinction probability is the reciprocal of either N or r.

What we actually observe in the Late Pleistocene is the usual background extinction probability raised to a higher level because of external pressures. Since I assume that these pressures had no effect on the shape (e.g. slope) of the relationship between extinction probability and body size, it should be possible to tease out some of the important features of the relationship. These assumptions form the starting point from which I deduce the pattern of size selectivity of extinction.

Both ecological theory and nature conservation practice suggest that small population size, narrow geographic range, and low population growth rate may put species at risk (Rosenzweig, 1975, 2001; Pimm, 1991). Large population size buffers against demographic stochasticity, while wide geographic range buffers against environmental stochasticity, so long as conspecific populations weakly correlate over space (Lawton, 1994). High growth rates, in turn, allow species to recover faster from population crashes.

These theoretical ideas are being translated into conservation strategies. A consistent decline in population size and/or geographic range is considered to be among the main reasons for placing a species on the Red List of threatened species (Rodrigues *et al.*, 2006). Annual fecundity is an important component of population growth rate. And mammals with low annual fecundity tend to be the species on the Red List (Polishchuk, 2002).

Many of the traits and processes not explicitly considered above are closely correlated with those that are. Litter size and time to maturity, which affect extinction in mammals (Cardillo *et al.*, 2006), contribute to population growth rate. Genetic deterioration correlates inversely with population size (Lynch *et al.*, 1995; Popadin *et al.*, 2007). Nevertheless, I have not included some complex processes that may contribute to extinction, such as metapopulation dynamics (Hanski, 1998), because it is hard to include them in a simple theory. If the theory does a good job despite their omission, we will have evidence that these complex processes may be less important than we now suspect.

Next, I make the simplifying assumption that any of the potentially significant characters – population density N (taken as a measure of population size), geographic range A, or population growth rate r – is the single predominant contributor to extinction probability P. And I examine the consequences of this assumption.

The simplest, yet plausible, relationship between these characters and P is

$$P = 1/(1 + \varepsilon Z) \tag{1}$$

where Z stands for N, A or r. Equation (1) implies that extinction probability is inversely related to these traits, as it should. The 1 in the denominator ensures that when N, A or r approaches 0, P tends to 1. This requirement is obvious for N and A, but perhaps less so for r. But note that when r approaches 0, its variance, σ_r^2, remains strictly positive, so that eventually $\sigma_r^2 > 2r$, which makes extinction almost certain (May, 1974). Finally, ε, an arbitrary positive constant, provides some flexibility because otherwise one has to assume that, for example, at $Z = 1$, $P = 0.5$, which is too restrictive.

Now let Z (i.e. N, A or r) be an allometric, i.e. a power function of body mass,

$$Z = \eta W^{-\beta} \tag{2}$$

where $-\beta$ is the scaling exponent written with a minus sign for convenience, and η is a positive constant. This relation is well justified for N (Damuth, 1981, 1987) and r (Fenchel, 1974), although less so for A (Madin and Lyons, 2005). Substituting equation (2) into equation (1) gives the following chain of equations:

$$\begin{aligned} P &= 1/(1 + \theta W^{-\beta}) \\ &= 1/(1 + \theta \exp(-\beta \ln W)) \\ &= \exp(\alpha + \beta \ln W)/(1 + \exp(\alpha + \beta \ln W)) \end{aligned} \tag{3}$$

where $\theta = \varepsilon\eta$ and $\alpha = -\ln\theta$. The last equation can be readily recognized as a logistic function (Hosmer and Lemeshow, 2000), which means that an allometric relationship of some of the key extinction-related characters to body mass (equation 2) requires the structure of a logistic function for the relationship of extinction probability to log body mass (equation 3). Note that logarithmic transformation of body mass is almost always used in comparative-species studies (typically, to reduce the right-skewness of a body-size distribution).

The logistic function plays a prominent part in metapopulation dynamics, where it is used to parameterize the probability of a patch being occupied (ter Braak *et al.*, 1998). Outside ecology, it is commonly used in medical and social research; an early and famous example is the study of the risk of coronary heart disease at Framingham (Truett *et al.*, 1967). The logistic function, on the other hand, has not often been employed to assess extinction probabilities among species; only a few studies have used it to date (Lessa and Fariña, 1996; Lessa *et al.*, 1997; Polishchuk, 2002; Brook and Bowman, 2004).

Most often, the logistic function has been applied on purely phenomenological grounds. In the context of species extinction, however, its use is theoretically justified, first, by the causal link between extinction probability and population density or growth rate and, second, by the allometry of these traits.

The logistic function suggests an allometry for extinction risk, too. Using the standard logit transformation, I rearranged equation (3) to

$$\ln(P/(1 - P)) = \alpha + \beta \ln W \tag{4}$$

which implies $P/(1 - P)$ scaling as a power function of body mass

$$P/(1 - P) = \gamma W^{\beta} \tag{5}$$

where $\gamma = \exp(\alpha) = \theta^{-1}$. That is, the allometry of an extinction-related character such as N or r (equation 2), through a logistic function for extinction probability P (equation 3), leads to the allometry of $P/(1 - P)$ (equation 5). In the context of a logistic function, $P/(1 - P)$ is called 'odds'; here, therefore, it is the odds of extinction. It follows that the allometry of population density (or growth rate) implies the allometry of extinction odds. The two allometries share a common scaling exponent β (cf. equations 2 and 5) – except for its sign.

Now, on the basis of logistic function, the goal of this study can be refined: it is to determine the slope β of the probability of extinction or, equivalently, the scaling exponent β in the allometry of extinction odds, and thereby to quantify the pattern of size selectivity. A logistic function can be fitted to the data through the logistic regression, which is a standard tool to process binary (0/1) data (Hosmer and Lemeshow, 2000). Logistic regression approximates the mean of a set of 0s and 1s at any given value of the argument. This mean equals the proportion of 1s. So logistic regression gives the probability of an event coded as 1 (e.g. extinction) conditional on the value of its argument (e.g. body mass). Indeed, in the present study, species that became extinct in the Late Pleistocene are coded as 1 and those that survived into the Holocene are coded as 0. So the resulting probability is the probability of extinction in the Late Pleistocene at a given body mass.

Because the scaling exponent for population density is −0.75 (Damuth, 1981, 1987; Silva and Downing, 1995; Dobson *et al.*, 2003), β in equation (5) is expected to be +0.75. Alternatively, because the scaling exponent for maximum per capita population growth rate is −0.25 (Fenchel, 1974), β in equation (5) is expected to be +0.25. The scaling exponent for geographic range size is less certain (Madin and Lyons, 2005), so β cannot be predicted from A. This leaves us with two possible values for β, either 0.75 or 0.25, dependent on which character, population density or growth rate, primarily affects size selectivity. If neither is correct, the idea that the size selectivity is determined by allometric laws (Brook and Bowman, 2005) would not be easy to defend.

We can anticipate another result that would undermine the allometry theory. Mammals whose mass is/was 5 kg or more are more likely to have been targeted by ancient hunters (Brook and Bowman, 2004). If human hunting strongly affected the size selectivity of extinction in Late Pleistocene mammals, the basic assumption that size selectivity is intrinsically determined would no longer be valid. Consequently, the scaling exponent in the allometry of the odds (equation 5) would be unrelated to the exponent in the allometry of the extinction-related traits (equation 2). In that case, equations (3) and (5) can still be used to describe the probability and the size selectivity of extinction, but without reference to any fundamental allometry underlying them.

MATERIALS AND METHODS

Data

I used a database containing the mammal species' body masses of four continents: Africa, Australia, North America, and South America (Smith *et al.*, 2003). It includes the extant species, those that became extinct in the Late Pleistocene, and those that became extinct within the last 300 years [i.e. 'historically extinct' (Smith *et al.*, 2003)]. The complete set includes 2534 unique species (those present on more than one continent are accounted for only once) and is available at www.evolutionary-ecology.com/data/2416data.txt.

I constructed subsets of the data for analysis:

i. The basic data set comprises 2123 unique species. It does not include bats (Chiroptera) or pinnipeds (Odobenidae, Otariidae, and Phocidae), which are commonly excluded in comparative-species analyses (e.g. Alroy, 1999; Lyons *et al.*, 2004).
ii. The extended (or complete) data set comprises all 2534 unique species including bats and pinnipeds.
iii. A truncated data set (476 species) extracted from the basic set and containing only species whose mass is/was 5 kg or greater.
iv. A truncated data set (504 species) extracted from the extended set and containing only species whose mass is/was 5 kg or greater.
v. Four continent-specific subsets of species extracted from the basic set.
vi. Four continent-specific subsets of species extracted from the extended set.

I analysed (v) and (vi) to examine variation in the scaling exponent β at the continent scale.

One species, *Gazella dorcas* from Africa, was recorded twice and I deleted the extra record. I also excluded 21 species from the Australian data set (see below). Seventeen are marked 'introduced' in the database, and four others are non-indigenous [*Canis lupus*, *Vulpes vulpes*, *Lepus capensis*, *Rattus exulans* (see Sattler and Creighton, 2002; Johnson and Wroe, 2003)]. Of these 21 species, eight are native to one or two of the other three continents, are kept in those continents' sets, and consequently remain in the complete data set. I made no other changes to the original data set.

I excluded the introduced species because logistic regression must be calculated on the basis of a closed set of species that comprised the pre-extinction fauna (the one that existed just before the Late Pleistocene extinction event). Part of them became extinct during the extinction event and the other part survived it. Clearly, the introduced species do not belong to the pre-extinction fauna.

Relatively few species have become extinct within the last 300 years: 25 and 27 species in the basic and the extended data sets, respectively. How shall these 27 species be treated?

I assume, after Lyons *et al.* (2004), that (almost) all species that survived the extinction event are either extant or historically extinct. Hence, the historically extinct species are considered on equal terms with the extant species: both groups were part of the pre-extinction fauna and survived the extinction event. The average Eocene-Pleistocene mammalian species lived for 2.62 million years (Alroy, 2000). This is much longer than the time elapsed since the Late Pleistocene extinction event, which occurred at 12–15 ka (thousand years ago) in Africa, North and South America, and about 50 ka in Australia (Smith *et al.*, 2003; Lyons *et al.*, 2004) [for Australia this is possibly an upper estimate (see Trueman *et al.*, 2005)]. Consequently, apart from the most recent, historical extinctions, which are fully accounted for, only 0.6% of species that survived the extinction event could have gone extinct after it and are unseen today; this figure rises to 1.9% for Australia by itself. Given that the total number of mammalian species does not change over the Holocene, the same low percentages of extant species could have originated after the extinction event; hence, few extant species would not be found among the immediate survivors of the event.

In the end, we are left with two groups of species – those that went extinct during the extinction event (coded as 1) and those that survived it (extant plus historically extinct; coded as 0). I used these binary codes to compute logistic-regression models for extinction probability in relation to log body mass.

Statistics

I computed ordinary logistic regressions using function glm in the R statistical software (R Development Core Team, 2005).

Ordinary logistic regressions can be compromised by the effect of shared ancestry, resulting in characteristics of individual species being typically more similar within groups of relatively close relatives than among such groups. This effect violates the assumption of data independence inherent in conventional regression analyses (Harvey and Pagel, 1991). It has to do with not only such obviously heritable traits as body mass but also with extinction rates, because extinctions are non-randomly distributed across the tree of life (Purvis *et al.*, 2000). In such a case, one must account for non-independence of data (Kunin, 2008).

The standard way to solve this problem is the method of phylogenetically independent contrasts (Felsenstein, 1985). However, this method assumes a linear relationship between the characters of interest and the normal distribution of errors, whereas a logistic relationship is non-linear and its error distribution is binomial (Quader *et al.*, 2004). So, to control for the effect of non-independence of data, I employed another method, logistic regression with mixed effects (Pinheiro and Bates, 2004). I implemented this method of regression in all three possible ways: a model with random intercept; a model with random slope; and a model with both random intercept and random slope. (By intercept and slope of a logistic-regression model, I mean the corresponding parameters of its linearized form, equation 4.) I clustered species data by orders.

I computed mixed-effects logistic regressions using R software (R Development Core Team, 2005), function glmmPQL from the MASS library (Venables and Ripley, 2002; J. Fox, personal communication). For Australia, in two cases corresponding to the basic data set (Table 1) and in one case corresponding to the extended data set (Table 2), an R-algorithm failed to converge or else gave a slope that goes to infinity. In these cases, I computed mixed-effects regressions using SAS software (SAS Institute, Inc., 2004), macro glimmix.

I tested the regressions for significance using a Wald test for ordinary regressions as implemented in the R-function glm and a *t*-test for mixed-effects regressions as implemented in the R-function glmmPQL or in the SAS macro glimmix, as appropriate.

Besides slope and intercept, another characteristic of a logistic function is the odds ratio, which shows how much the extinction odds increase when the independent variable, here $\log_e$ body mass, increases by 1 or, equivalently, when body mass increases by a factor of e (= 2.718). The odds ratio is a measure of size selectivity: the stronger the selectivity, the faster the odds increase with increasing mass. From equation (5), we see that the odds ratio equals e^{β}. Since comparative-species studies often use the decimal logarithm, I also report the odds ratio corresponding to a 10-fold increase in mass; it is 10^{β}. The slope and the odds ratio are given with a 95% confidence interval (CI), which is $\beta \pm 1.96$ S.E. for the slope, and for the odds ratio either $e^{\beta \pm 1.96 \text{ S.E.}}$ or $10^{\beta \pm 1.96 \text{ S.E.}}$, depending on whether the odds ratio is calculated as e^{β} or 10^{β}; S.E. is the standard error of β (Hosmer and Lemeshow, 2000). Body mass is expressed in kilograms.

RESULTS

Basic data set (bats and pinnipeds excluded)

The parameters of a logistic-regression model for extinction probability are given in Table 1 (first row). The model does a good job of approximating the data, as illustrated by

Table 1. Parameters of ordinary and mixed-effects logistic regressions for the basic data set (bats and pinnipeds excluded)

Model	Slope (S.E.)	95% CI for slope	Odds ratio	95% CI for odds ratio	Intercept (S.E.)
	Four-continent data set ($n = 2123$, $n_0 = 1916$, $n_1 = 207$)				
Ordinary logistic regression	0.76 (0.04)	0.67–0.85	2.14	1.96–2.34	−3.71 (0.19)
Mixed effects, random intercept	0.83 (0.08)	0.67–0.98	2.28	1.96–2.66	−3.83 (0.38)
Mixed effects, random slope	0.82 (0.10)	0.62–1.03	2.28	1.86–2.79	−3.87 (0.25)
Mixed effects, random intercept and slope	1.01 (0.19)	0.64–1.38	2.75	1.90–3.98	−4.57 (0.47)
	Africa ($n = 603$, $n_0 = 590$, $n_1 = 13$)				
Ordinary logistic regression	0.86 (0.18)	0.51–1.21	2.36	1.66–3.36	−6.58 (1.01)
Mixed effects, random intercept	0.81 (0.10)	0.62–1.01	2.25	1.86–2.73	−6.94 (0.64)
Mixed effects, random slope	0.86 (0.09)	0.68–1.03	2.36	1.98–2.81	−6.58 (0.50)
Mixed effects, random intercept and slope	0.81 (0.10)	0.62–1.01	2.26	1.86–2.74	−6.93 (0.64)
	Australia ($n = 250$, $n_0 = 205$, $n_1 = 45$)				
Ordinary logistic regression	1.84 (0.33)	1.19–2.50	6.31	3.28–12.17	−5.89 (1.08)
Mixed effects, random intercept	2.45 (0.35)	1.77–3.14	11.60	5.85–23.00	−6.74 (1.19)
Mixed effects, random slope*	2.54 (0.68)	1.20–3.87	12.63	3.33–47.90	−7.82 (0.97)
Mixed effects, random intercept and slope*	2.16 (0.65)	0.89–3.43	8.66	2.43–30.82	−6.85 (1.58)
	North America ($n = 550$, $n_0 = 472$, $n_1 = 78$)				
Ordinary logistic regression	0.62 (0.06)	0.50–0.73	1.85	1.65–2.07	−2.46 (0.22)
Mixed effects, random intercept	0.62 (0.07)	0.48–0.75	1.85	1.62–2.12	−2.46 (0.26)
Mixed effects, random slope	0.62 (0.07)	0.48–0.75	1.85	1.62–2.12	−2.46 (0.26)
Mixed effects, random intercept and slope	0.62 (0.07)	0.48–0.75	1.85	1.62–2.12	−2.46 (0.26)
	South America ($n = 774$, $n_0 = 698$, $n_1 = 76$)				
Ordinary logistic regression	1.23 (0.14)	0.96–1.50	3.42	2.61–4.49	−5.14 (0.56)
Mixed effects, random intercept	1.23 (0.22)	0.80–1.67	3.43	2.22–5.29	−5.14 (0.90)
Mixed effects, random slope	1.23 (0.22)	0.80–1.67	3.42	2.22–5.29	−5.14 (0.90)
Mixed effects, random intercept and slope	1.23 (0.22)	0.80–1.67	3.42	2.22–5.29	−5.14 (0.90)

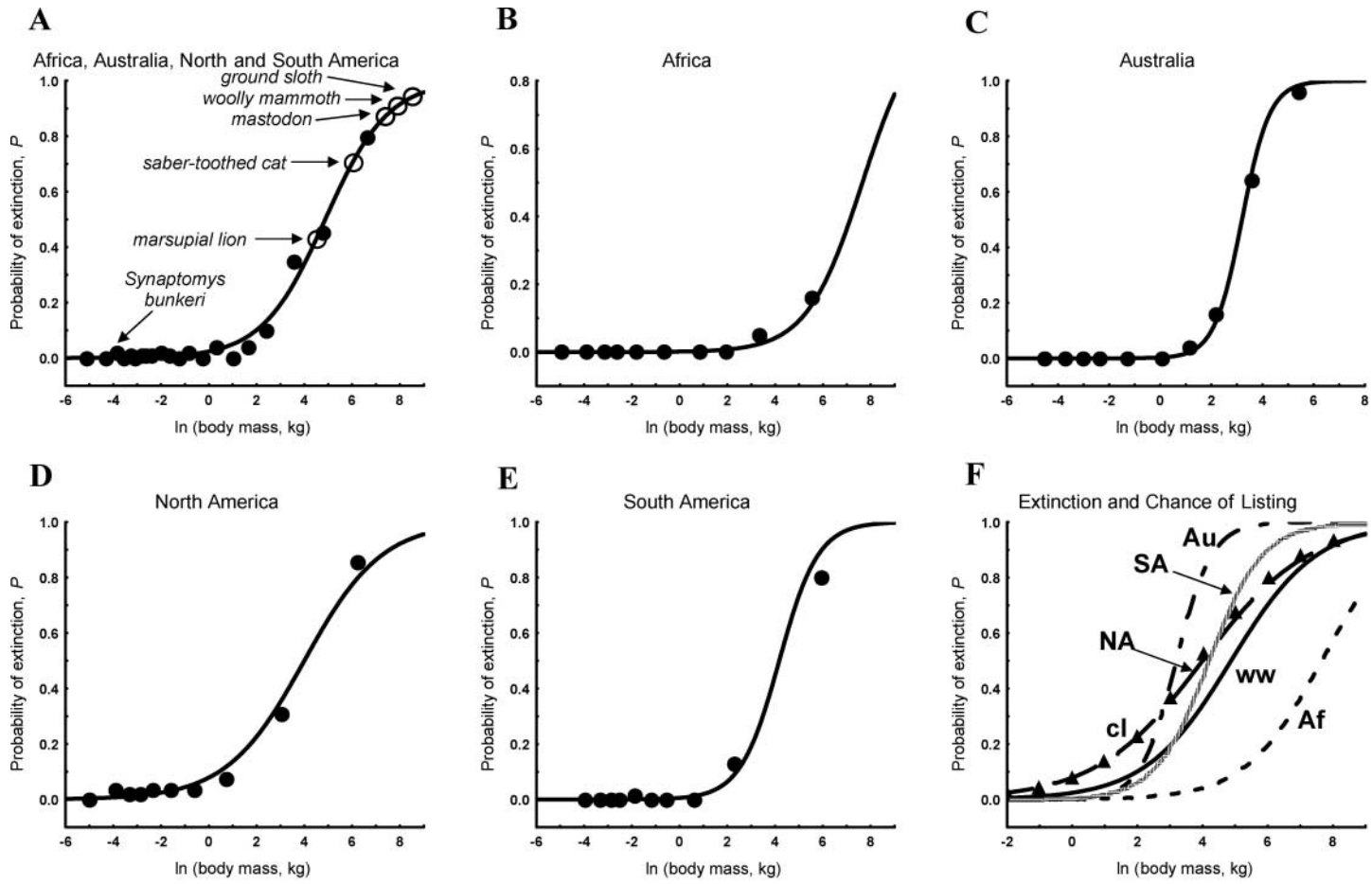
Note: Slope and intercept are parameters β and α, respectively, in the linearized form of logistic equation (equation 4 in the text). S.E, standard error; CI, confidence interval. Odds ratio and 95% CI for odds ratio are given for an e-fold increase in body mass. n_0 and n_1 are the number of species surviving into the Holocene and extinct in the Late Pleistocene, respectively; $n = n_0 + n_1$. Since some continents, in particular North America and South America, share common species, the four-continent data set contains fewer species than the sum total for the continents. All regressions are statistically significant with $P < 0.001$, except for two Australian models labelled with (*) for which $P = 0.010$ (model with random slope) and $P = 0.021$ (model with random intercept and random slope).

Table 2. Parameters of ordinary and mixed-effects logistic regressions for the extended data set (bats and pinnipeds included)

Model	Slope (S.E.)	95% CI for slope	Odds ratio	95% CI for odds ratio	Intercept (S.E.)
	Four-continent data set ($n = 2534$, $n_0 = 2327$, $n_1 = 207$)				
Ordinary logistic regression	0.72 (0.04)	0.64–0.80	2.06	1.90–2.23	−3.72 (0.18)
Mixed effects, random intercept	0.77 (0.06)	0.64–0.89	2.16	1.91–2.44	−3.78 (0.35)
Mixed effects, random slope	0.80 (0.10)	0.60–1.00	2.23	1.83–2.73	−3.82 (0.22)
Mixed effects, random intercept and slope	1.04 (0.20)	0.65–1.43	2.83	1.91–4.19	−4.76 (0.50)
	Africa ($n = 735$, $n_0 = 722$, $n_1 = 13$)				
Ordinary logistic regression	0.86 (0.18)	0.51–1.21	2.36	1.66–3.36	−6.59 (1.00)
Mixed effects, random intercept	0.79 (0.09)	0.61–0.97	2.19	1.83–2.63	−7.10 (0.65)
Mixed effects, random slope	0.84 (0.09)	0.68–1.01	2.33	1.97–2.75	−6.67 (0.47)
Mixed effects, random intercept and slope	0.78 (0.09)	0.60–0.96	2.19	1.83–2.62	−7.09 (0.65)
	Australia ($n = 316$, $n_0 = 271$, $n_1 = 45$)				
Ordinary logistic regression	0.95 (0.14)	0.67–1.22	2.58	1.96–3.39	−3.69 (0.53)
Mixed effects, random intercept	2.47 (0.28)	1.92–3.01	11.81	6.84–20.39	−11.04 (2.90)
Mixed effects, random slope	2.14 (0.61)	0.96–3.33	8.53	2.60–27.95	−7.79 (0.85)
Mixed effects, random intercept and slope*	1.81 (0.64)	0.56–3.07	6.13	1.75–21.44	−6.88 (1.55)
	North America ($n = 715$, $n_0 = 637$, $n_1 = 78$)				
Ordinary logistic regression	0.57 (0.05)	0.47–0.67	1.77	1.60–1.95	−2.60 (0.21)
Mixed effects, random intercept	0.57 (0.06)	0.44–0.69	1.77	1.56–2.00	−2.55 (0.31)
Mixed effects, random slope	0.60 (0.08)	0.43–0.76	1.82	1.54–2.14	−2.57 (0.23)
Mixed effects, random intercept and slope	0.61 (0.09)	0.43–0.79	1.84	1.53–2.20	−2.64 (0.24)
	South America ($n = 930$, $n_0 = 854$, $n_1 = 76$)				
Ordinary logistic regression	1.20 (0.13)	0.94–1.47	3.33	2.56–4.34	−5.17 (0.56)
Mixed effects, random intercept	1.20 (0.19)	0.82–1.59	3.33	2.28–4.88	−5.17 (0.82)
Mixed effects, random slope	1.20 (0.19)	0.82–1.58	3.33	2.28–4.88	−5.17 (0.82)
Mixed effects, random intercept and slope	1.20 (0.19)	0.82–1.58	3.33	2.27–4.88	−5.17 (0.82)

Note: All regressions are statistically significant with $P < 0.001$, except for one Australian model labelled with (*) for which $P = 0.025$. See Table 1 footnote for explanation of symbols.

comparison of the fitted probabilities and the actual proportions of extinct species (Fig. 1A). The extinction probability increases with body mass, as expected. It is perhaps less obvious that, while a great majority of extinct species (some of which are shown in Fig. 1A) are predictably large-bodied, extinctions did in fact occur over a range of more than five orders of magnitude in body mass, although with a greatly varying probability.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Africa, Australia, North and South America
ground sloth
woolly mammoth
mastodon
saber-toothed cat
marsupial lion
Synaptomys bunkeri
Probability of extinction, P
ln (body mass, kg)
B
Africa
C
Australia
D
North America
E
South America
F
Extinction and Chance of Listing
Au
SA
NA
ww
cl
Af

The smallest extinct species is the North American lemming *Synaptomys bunkeri* (Rodentia, Arvicolinae), whose mass was only 0.02 kg and extinction probability 0.0012 (Fig. 1A).

The parameters α and β presented in Table 1 produce the following allometric equation for the odds of extinction:

$$P/(1-P) = 0.024\ W^{0.76} \tag{6}$$

with the exponent quite similar to 0.75, the value predicted from the allometry of population density, but quite different from 0.25, the value predicted from the allometry of population growth rate. The result excludes population growth rate as the underlying mechanism because that would have returned 0.25 as the exponent.

Equation (6) quantifies the large-mammal extinction bias of the Late Pleistocene. Extinction odds increase by a factor of 2.14 when mass becomes e times larger (Table 1) and by a factor of 5.77 (95% CI: 4.72 to 7.05) when mass is 10 times larger.

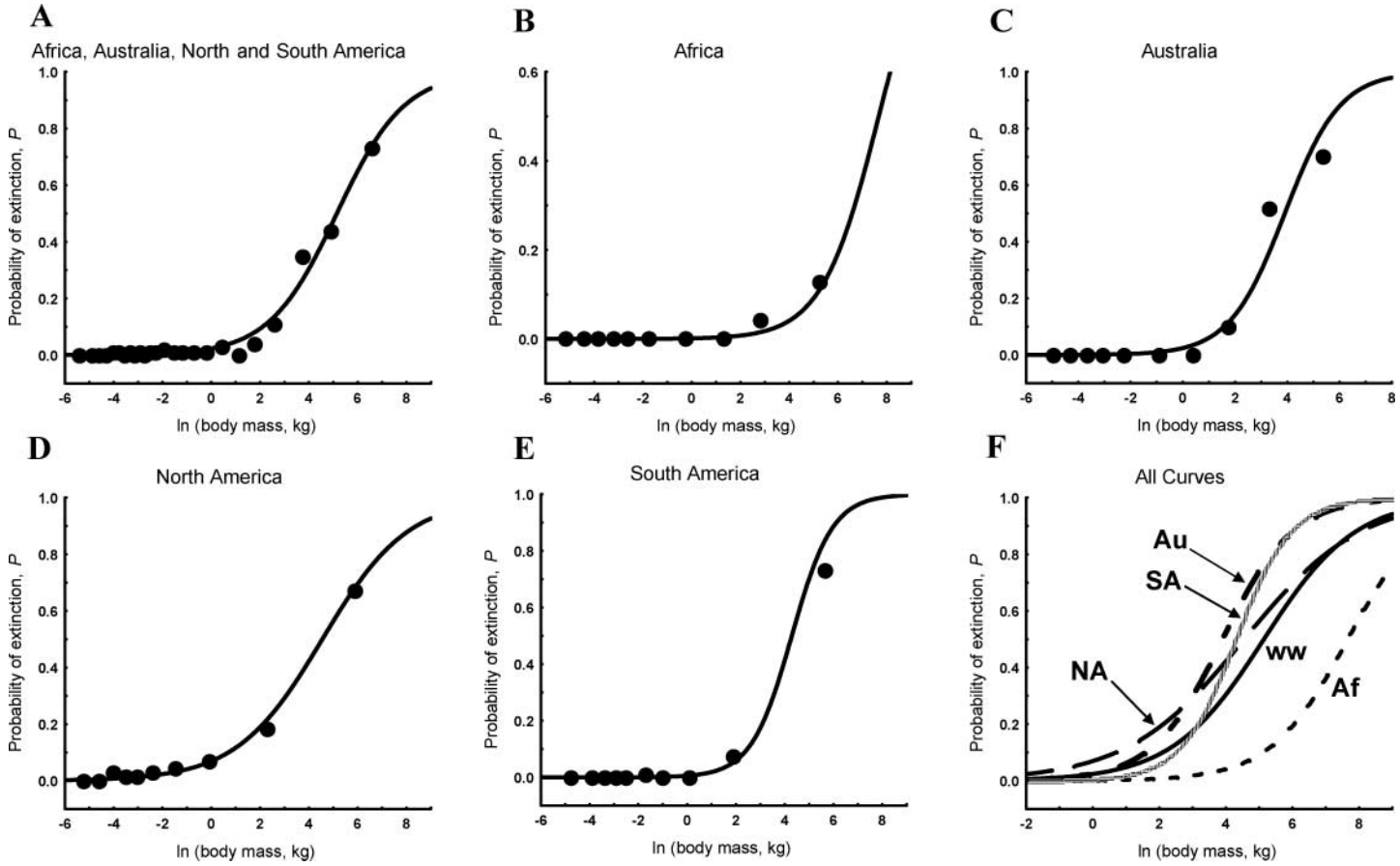
Extended data set (bats and pinnipeds included)

The allometric equation for the odds of extinction is

$$P/(1-P) = 0.024\ W^{0.72} \tag{7}$$

with the exponent, 0.72, being again close to, and not significantly different from, 0.75 (95% CI: 0.64 to 0.80; Table 2, first row; Fig. 2A). The extinction bias towards large mammals remains largely the same as for the basic set: when mass increases e-fold, extinction odds rise by a factor of 2.06 (Table 2), and when mass increases 10-fold, by a factor of 5.28 (95% CI: 4.38 to 6.36).

Fig. 1. Probability of extinction in relation to body mass for the basic data set (bats and pinnepeds excluded). (A) The curve for the four-continent data set. Featured on the curve (by open circles) are five of the most charismatic extinct mammals: ground sloth (*Megatherium americanum*), woolly mammoth (*Mammuthus primigenius*), mastodon (*Mammut americanum*), saber-toothed cat (*Smilodon fatalis*), and marsupial lion (*Thylacoleo carnifex*); the first three are spaced apart for clarity. Also shown (only by arrow) is the bog lemming *Synaptomys bunkeri*, which exemplifies an extinct, small-bodied species. (B–E) Curves for individual continents. Solid circles in (A–E) display the actual proportions of extinct species. I obtained these by arranging species of each set in increasing order of body mass, then dividing the set into 21 bins (for the four-continent data set) or 10 bins (for individual continents). The four-continent data set had 100 species per bin except for the largest-bodied group, which had 123. Africa, 60 species per bin (and 63 for the largest sizes); Australia, 25 species per bin (for all bins); North America, 55 species per bin (for all bins); South America, 77 species per bin (and 81 for the largest sizes). Although I computed logistic regressions using raw, individual-species data rather than bin proportions, nevertheless the bin proportions follow the regression lines well. (F) The four-continent data set and continent-specific curves superimposed on one graph together with chance-of-listing. Chance-of-listing, 'cl', is the probability of a living species occurring on the Red List of rare and endangered species (see text for details). *Note*: cl-values are represented by the solid triangles. Although they fall very close to the North American curve, cl-values come from a previous analysis independent of any of these regression curves. 'ww' stands for 'worldwide' (i.e. the four-continent data set); Af is Africa; Au is Australia; NA is North America; SA is South America. In (A–E), the x-axis extends over the range of body masses, W, actually present in the corresponding data set. In (F), it starts at $\ln W = -2$ to better use available space. The extinction curves represent ordinary logistic regressions (Table 1 reports the regression parameters).


A
Africa, Australia, North and South America
Probability of extinction, P
ln (body mass, kg)
B
Africa
Probability of extinction, P
ln (body mass, kg)
C
Australia
Probability of extinction, P
ln (body mass, kg)
D
North America
Probability of extinction, P
ln (body mass, kg)
E
South America
Probability of extinction, P
ln (body mass, kg)
F
All Curves
Au
SA
NA
WW
Af
Probability of extinction, P
ln (body mass, kg)

Truncated data sets ($W \geq 5$ kg)

The allometric equation for the odds of extinction of large mammals truncated from the basic data set is

$$P/(1 - P) = 0.019\ W^{0.83} \tag{8}$$

The allometric equation for the odds of extinction of large mammals truncated from the extended data set is

$$P/(1 - P) = 0.022\ W^{0.75} \tag{9}$$

The exponent of equation (8), 0.83, is not significantly different from 0.75, and that of equation (9) is equal to 0.75 (Tables 3 and 4, first rows). The odds ratios for these two analyses are therefore close to the values observed for the non-truncated data: 2.29 and 2.12 when mass increases *e*-fold for the large-mammal set truncated from the basic and the extended set respectively (Tables 3 and 4), and 6.77 (95% CI: 4.75 to 9.64) and 5.66 (95% CI: 4.07 to 7.87) when mass increases 10-fold for the large-mammal set truncated from the basic and the extended set respectively. In short, focusing on larger body sizes – that is, those potentially most affected by external factors such as human hunting – did not noticeably change the pattern of size selectivity.

Accounting for non-independence of data

The mixed-effects models maintained statistical significance ($P < 0.001$) for all data sets and types of models (Tables 1 to 4). Two of the three models for each of the non-truncated sets (those with either random intercept or random slope) and one model for the truncated sets (that with random intercept when applied to the data extracted from the extended set) yielded slopes that are in the range of 0.77 to 0.83, which is not far from 0.75. The remaining combinations of mixed-effects models and data sets produced slopes that are in the range of 0.92 to 1.14. Yet, the 95% confidence intervals of the slopes always contained 0.75, although sometimes this value lay at the end of the confidence intervals (Tables 1 to 4). In contrast to this, the alternative β-value based on the allometry of population growth rate, 0.25, lay far beyond the observed confidence intervals.

Fig. 2. Probability of extinction in relation to body mass for the extended data set (bats and pinnepeds included). (A) The curve for the four-continent data set. (B–E) Curves for individual continents. (A–E) also display the actual proportions of extinct species (solid circles) calculated similarly to the actual proportions in Fig. 1 (except that the four-continent data set was divided into 24 groups of 100 species and one of 134 for the bin with the largest sizes). The individual-continent sets were divided into 10 groups each. Africa, 73 species per bin (and 78 for the largest sizes); Australia, 31 species per bin (and 37 for the largest sizes); North America, 71 species per bin (and 76 for the largest sizes); South America, 93 species per bin (for all bins). As in Fig.1, although I did not generate the bin proportions with any regression analysis, nevertheless the bin proportions follow the regression lines well. (F) The four-continent data set and the continent-specific curves on one graph; notation as in Fig. 1F. In (A–E), the x-axis extends over the range of body masses, W, actually present in the corresponding data set. In (F), it starts at $\ln W = -2$ to better use available space. The extinction curves represent ordinary logistic regressions (Table 2 reports the regression parameters).

Table 3. Parameters of ordinary and mixed-effects logistic regressions for truncated data ($W \geq 5$ kg) based on the basic data set (bats and pinnipeds excluded)

Model	Slope (S.E.)	95% CI for slope	Odds ratio	95% CI for odds ratio	Intercept (S.E.)
		$n = 476$, $n_0 = 285$, $n_1 = 191$			
Ordinary logistic regression	0.83 (0.08)	0.68–0.98	2.29	1.97–2.68	−3.98 (0.36)
Mixed effects, random intercept	0.95 (0.10)	0.75–1.14	2.58	2.12–3.14	−4.30 (0.62)
Mixed effects, random slope	1.05 (0.15)	0.76–1.34	2.85	2.14–3.81	−4.57 (0.44)
Mixed effects, random intercept and slope	1.14 (0.22)	0.71–1.57	3.13	2.03–4.82	−4.88 (0.61)

Note: All regressions are statistically significant with $P < 0.001$. See Table 1 footnote for explanation of symbols.

Table 4. Parameters of ordinary and mixed-effects logistic regressions for truncated data ($W \geq 5$ kg) based on the extended data set (bats and pinnipeds included)

Model	Slope (S.E.)	95% CI for slope	Odds ratio	95% CI for odds ratio	Intercept (S.E.)
		$n = 504$, $n_0 = 313$, $n_1 = 191$			
Ordinary logistic regression	0.75 (0.07)	0.61–0.90	2.12	1.84–2.45	−3.82 (0.35)
Mixed effects, random intercept	0.78 (0.09)	0.60–0.96	2.18	1.82–2.62	−3.66 (0.59)
Mixed effects, random slope	0.92 (0.14)	0.64–1.20	2.51	1.90–3.33	−4.14 (0.43)
Mixed effects, random intercept and slope	1.05 (0.28)	0.50–1.60	2.87	1.66–4.96	−4.55 (0.95)

Note: All regressions are statistically significant with $P < 0.001$. See Table 1 footnote for explanation of symbols.

Continent-specific analyses

Following the same protocol as for the worldwide data sets, I performed separate analyses for individual continents so as to give some idea of the variation in β under different regional circumstances (Tables 1 and 2; Figs. 1B–E and 2B–E). I analysed only the basic and extended sets and not the truncated sets (because the latter contain too few species to be further divided into continental subsets).

For three continents – Africa, North and South America – the slopes are quite similar between data sets, basic or extended, types of logistic regression, ordinary or with mixed-effects, and across different types of mixed-effects regression (Tables 1 and 2). The same is true for seven of Australia's slopes. However, the eighth slope, 0.95 (for the extended data set examined with ordinary logistic regression), seems quite a bit less than the other seven and lies below the confidence intervals of four of them.

It is even more interesting to compare the continent-specific slopes with 0.75. For Africa, the slopes did not differ significantly from 0.75 (95% CIs always include 0.75; Tables 1 and 2). For North America and South America, however, the slopes did differ from 0.75. The South American slopes are consistently >0.75 (this value lies to the left of the lower end of the 95% CIs). On the other hand, the North American slopes are <0.75 (the 0.75 value is

just within or just outside the upper end of the 95% CIs; Tables 1 and 2); Figs. 1F and 2F present these relations.

For Australia, all four models for the basic set and two models for the extended set (mixed-effects regressions with either random intercept or random slope) produced slopes that are >0.75 (based on the position of the lower end of the 95% CIs; Tables 1 and 2). The other two Australia models for the extended set (ordinary regression and mixed-effects regression with both random intercept and random slope) produced slopes that do not differ significantly from 0.75 (95% CIs both include 0.75; Table 2), although the likeliest β-values, 0.95 and 1.81, are also >0.75.

DISCUSSION

This study shows that on a worldwide scale, the probability of extinction in Late Pleistocene mammals follows a logistic curve whose slope is close to 0.75, and statistically indistinguishable from it. Equivalently, the odds of extinction scale as body mass raised to the power of 0.75. This result does not depend on whether bats and pinnipeds are included (these taxa are often believed to be too dissimilar to the bulk of mammals and thus would make the sample overly heterogeneous). The result also persisted when only large species (≥5 kg) are considered. Finally, it generally held in analyses that took non-independence of data into account.

The extinction bias towards large mammals can be characterized by the odds ratio, which indicates how fast extinction odds increase with body size. In the Late Pleistocene, the odds ratio is typified by a value of 2.12 ($= e^{0.75}$) when body mass increases e-fold, or by a value of 5.62 ($= 10^{0.75}$) when body mass increases 10-fold.

Although it has already been suggested that the cause of the preferential extinction of large mammals may lie in the nature of allometric relations (Brook and Bowman, 2005), this study is the first to show that the 0.75-power scaling of extinction odds may be intrinsically related to the −0.75-power scaling of population density. The latter scaling provides a qualitative understanding of size selectivity (large species have low densities, and low densities make species more prone to extinction). But also it explains size selectivity quantitatively: the Late Pleistocene extinctions, although strongly biased towards large-bodied species, are biased no more than expected from the −0.75-power population density scaling.

Because the scaling of population density is part of the system of fundamental allometric laws, which are not isolated from each other but inherently interrelated (Peters, 1983; Marquet *et al.*, 2005), the fact that the scaling of extinction odds can be deduced from the scaling of population density suggests that the scaling of odds may also be an allometric law. Furthermore, the scaling of density is closely associated with the energetic equivalence rule (Damuth, 1981; Nee *et al.*, 1991), which has recently been established as a general evolutionary principle (Damuth, 2007). The rule implies that energy flow through a population of a given species is approximately independent of its body size – that is, no species has an advantage in gaining trophic energy solely on the basis of size. Since an individual's metabolic rate scales as a 0.75-power of body mass (Kleiber, 1932; Winberg, 1956; Savage *et al.*, 2004), this size-invariance implies that population density scales as a −0.75-power of body mass, which is actually the case (Damuth, 1981, 1987; Silva and Downing, 1995; Dobson *et al.*, 2003). Taking a step further, I show here that a −0.75-power scaling of population density leads to a 0.75-power scaling of extinction odds. It is hard to avoid concluding that the pattern of size selectivity with a

slope of 0.75 might result from such fundamental biological principles as the energetic equivalence rule and the 0.75-power metabolic-rate scaling.

Allometric laws have always been associated with intrinsic, evolutionarily determined structures and processes. The metabolic-rate scaling, for example, may be governed by either fractal-like geometry (West *et al.*, 1997, 1999) or general connectivity (Banavar *et al.*, 1999, 2002) of the biological distribution systems [but for criticism of the current theories, see Kozłowski and Konarzewski (2004) and Makarieva *et al.* (2005)]. If the scaling of extinction odds does belong to, and even originate from, the fundamental allometric laws, one may not need to invoke external pressures such as human hunting and climate change to explain the extinction bias towards large mammals in the Late Pleistocene. External pressures may have increased extinction risk but not selectively with respect to body size.

Climate versus humans

This study does not address the long-standing question of which of the external factors – humans or climate – is the main cause of the high extinction rates of the Late Pleistocene (Barnosky *et al.*, 2004; Koch and Barnosky, 2006). Instead, it shows that population density scaling is sufficient to explain the degree of size selectivity that is actually observed. How might this be reconciled with more conventional hypotheses?

External pressures might increase extinction rates without changing the pattern of size selectivity governed by population-density scaling if they increase extinction odds by a factor of λ, $\lambda > 1$, independently of body size. This would result in:

$$P/(1-P) = \lambda\gamma_0 W^{\beta} = \gamma \mathrm{W}^{\beta} \tag{10}$$

where $\gamma_0 W^{\beta}$ corresponds to a hypothetical background (low) level of extinction risk and $\lambda\gamma_0 W^{\beta} = \gamma W^{\beta}$ to its actual (high) level observed in the Late Pleistocene (cf. equation 5). From equation (10), we see that the slope β of an extinction probability curve would be unaffected, while the whole curve would be shifted to a higher level (Fig. 3). A characteristic feature of this shift is that, although P increases with increasing γ, its relative increment turns out to be smaller for large mass (see Fig. 3). Basically, this is because probability P is bounded from above by 1, hence its large values, which are not far from 1, cannot increase many-fold, whereas its small values, which are close to zero, can. That is, increase in overall risk ought to be more detrimental to small rather than large species.

One possible scenario consistent with this condition is that climate change might have caused the loss of suitable habitats, as exemplified by the collapse of steppe-tundras in Eurasia between the Late Pleistocene and the Holocene (Zherikhin, 1994; Nogués-Bravo *et al.*, 2008). This, in turn, might have led to severe food shortages, which incur greater risk for small mammals because they are less tolerant to starvation (Lindstedt and Boyce, 1985; Blackburn and Hawkins, 2004).

Could this scenario occur if human impact was a primary factor responsible for the overall level of risk? Humans preferentially hunted large and perhaps middle-sized mammals (Byers and Ugan, 2005), and are, therefore, unlikely to have consistently increased their pressure in the direction of small body size; this is just the opposite of what is commonly believed, after all. However, one cannot exclude the possibility that humans could have operated in parallel with climate, so that the former increased extinction probability in large species while the latter did so in small ones.

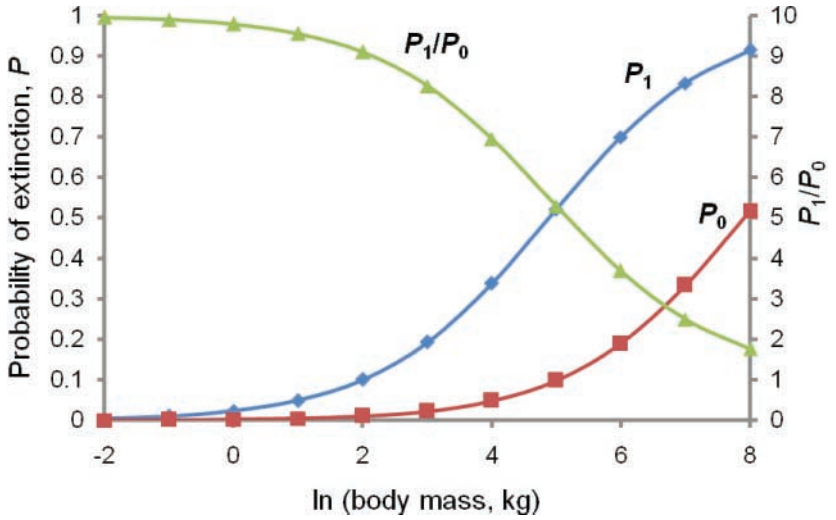


Fig. 3. A numerical example showing the relative increase in the probability of extinction P with regard to body mass W when parameter γ from equation (5) varies but scaling exponent β remains unchanged. $P_1 = \exp(-3.71 + 0.76 \ln W)/(1 + \exp(-3.71 + 0.76 \ln W))$, which is the actual equation for extinction probability (Table 1, first row). $P_0 = \exp(-6.01 + 0.76 \ln W)/(1 + \exp(-6.01 + 0.76 \ln W))$, which corresponds to a 10-fold decrease of γ ($\gamma = 0.024$ for the former equation vs. $\gamma_0 = 0.0024$ for the latter). The shift from P_0 to P_1 is meant to show a shift from a hypothetical background (low) level of extinction probability to its actual (high) level observed in the Late Pleistocene. The graph demonstrates that the ratio P_1/P_0 declines with increasing body mass.

So either climate alone or both climate and humans acting simultaneously could have raised extinction probabilities without changing the pattern of size selectivity dictated by population-density scaling. The present findings, therefore, seem consistent with a role for climate or climate in combination with humans as drivers of the overall level of risk.

Within versus between continents

The scaling of extinction odds, as well as the scaling of population density underlying it, has a global, macroecological character. Macroecological patterns observed on large spatial scales may not always be maintained on smaller scales. This pertains to population-density scaling (Blackburn and Gaston, 1997) and, most probably, to extinction-odds scaling. The reason is that on a large scale, external forces might cancel each other out, making it possible for the global pattern of extinction odds to emerge. With regard to extinction, external forces might include climate, humans, and any factor other than population-density scaling. But on a small scale, external forces are likely to be out of balance, pushing the slope of an extinction curve away from 0.75. The −0.75-power density scaling might even cease to exist. One would, therefore, expect the small-scale slope to differ from 0.75, and also expect the deviation to be larger where external forces are stronger and less balanced. This is in line with the situation in Africa where climate variability was relatively limited at the end of the Late Pleistocene (Scholz *et al.*, 2007); indeed, the deviation from 0.75 in Africa is the smallest of the four continents in this data set (Tables 1 and 2).

In South America, the extinction curve was steeper (slope >0.75) than the worldwide curve. Here the Great American Interchange might be the external force responsible. An excess number of large South American mammal species (beyond that determined by population-density scaling) could have gone extinct due to competition with the North American immigrants (Simpson, 1980).

In contrast, the North American curve was shallower (slope <0.75) than the worldwide curve, which may be attributed to a wholesale, presumably climate-driven reorganization of North American ecosystems (Graham and Lundelius, 1984). This reorganization might have resulted in the extinction of many large, medium, and even some small-sized species, such as the North American *Synaptomys bunkeri* (Fig. 1A).

In Australia, the situation is less clear. The Australian curve is steeper than 0.75, the steepest of the continent-specific curves. But results from the extended data set seem to exhibit considerable variation and ordinary logistic regression yielded a slope of 0.95, which does not differ significantly from 0.75 (Table 2). The Australian case requires further analysis.

Logistic regression versus binning

In this study, I applied logistic regression to describe the relationship between a binary variable, species status – extinct (denoted by 1) versus extant (denoted by 0) – and an independent variable, log transformed body mass. Although logistic regression is a tool used traditionally to deal with binary data in medical and social sciences (Hosmer and Lemeshow, 2000), it is a novelty in palaeobiology. So one might ask why I prefer it to an obvious and seemingly more transparent alternative method involving binning the data. The binning method would work as follows:

- Arrange the data in body-mass order.
- Divide the ordered data set into *n* bins.
- Calculate the proportion of species in each bin that are extinct.
- Calculate the mean body mass in each bin.
- Regress the proportions against the mean body masses.

Logistic regression has two advantages over binning. First, extinction probability varies as the reciprocal of population density. Therefore, I was able to show that extinction probability ought to be a logistic function of log body mass (see 'Strategy' section above). Second, logistic regression converts a binary variable to the probability of an extinction (i.e. the event denoted by 1). This property may seem puzzling but it has a very simple explanation. For any given value of the independent variable, logistic regression (like linear regression) approximates the mathematical expectation of the dependent variable. For a set of 0s and 1s, the mathematical expectation is just the proportion of 1s.

Meanwhile, binning has two disadvantages. First, ordering species according to their body mass is not unambiguous. Many species may have indistinguishable mean body mass (at a practical scale of resolution). Among practically equal-sized species, some may be extinct whereas others are not. If equal-sized species fall on a boundary between bins, then the number of extinct species in a given bin would depend on the arbitrary order of the equal-sized species. Second, the binning itself can be performed in many different ways,

with potentially inconsistent probability estimates. In particular, the number of bins itself is an arbitrary choice of the analyst.

Logistic regression analysis is not subject to either of the arbitrary features of binning. It is based on original, individual-species data. Given also its two inherent advantages – that these data are predicted to fit a logistic curve, and that the output of the regression is a simple, meaningful estimate of extinction probability – logistic regression is the method of choice.

Nevertheless, for illustrative purposes, I did calculate an example of binning. I arranged the species in order of body mass and divided them into bins (as specified in the legends to Figs. 1 and 2). Then I determined the proportion of extinct species in each bin and plotted the results in Figs. 1A–E and 2A–E. These figures show clearly that the bin-based proportions closely match the logistic-regression probabilities. But they might not have, in which case the logistic-regression probabilities would be preferable.

Implications for conservation

Will modern extinctions also follow the Late Pleistocene pattern of size selectivity in mammal extinctions? There is some evidence to suggest that this may be so. It comes from a related metric – the probability of a living species being under threat of extinction. This metric is termed 'chance of listing'. And 'being under threat' means being on the Red List of threatened and endangered species (see Polishchuk, 2002).

Polishchuk (2002) found a logistic-regression equation that fits the chance of listing for Russian mammals. It is based on a limited sample of 90 species and a regional Red List. The equation is:

$$P = \exp(-2.47 + 0.64 \ln W)/(1 + \exp(-2.47 + 0.64 \ln W))$$

The slope of that equation, 0.64, does not differ much from 0.75 (S.E. = 0.16; 95% CI: 0.33–0.95; Fig. 1F). We do not know yet whether a slope of 0.75 or thereabouts would fit the chance of listing in a global data set of Red Listed species.

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On the size selectivity of extinction in Late Pleistocene mammals: a mini-forum based on Polishchuk (2010: *Evol. Ecol. Res.*, 12: 1–22)

COMMENTS

Leonard Polishchuk provides a novel approach to a well-studied problem. By developing a logistic function for the relationship between body size and extinction probability, he argues that the end-Pleistocene mammal extinctions, famous for the disappearance of the planet's largest land mammals, were simply an amplification of the background extinction probability. Moreover, this probability is an intrinsic species characteristic set by the −3/4 power scaling of population density with body mass, or the well-known Damuth rule (Damuth, 1981: *Nature*, **290**: 699–700). Any external forces involved in the extinction, it follows, affected all species equally but are not responsible for the size-selective nature of the pattern. We agree with Polishchuk that allometric constraints are central to the problem of size-biased extinction. That said, we have several misgivings regarding the rationale for the model and the interpretation of its results.

The logistic regressions describe the data well (see his Figs. 1 and 2). However, the conclusion that the slopes of these regressions are set by the Damuth rule is, in our view, highly questionable. This is because the finding emerges from an arbitrary choice for the equation linking mass to extinction risk. Polishchuk selects an inverse function to describe the relationship (see his equation 1), which is described as the 'simplest, yet plausible' choice. It is important to realize that the main conclusion, that population density sets the shape of the relationship between extinction and body size, emerges directly from this choice of equation. It is not clear whether the result would be preserved if this choice were made differently. For example, an exponential form is one possible alternative that is at least as simple and plausible as the inverse form he uses. So why pick one form over another? To make the choice more convincing, one option might be to consider a wide class of equations and show that the finding of a slope near 0.75 is independent of the choice of the functional form of the relationship. While we strongly doubt the feasibility of such a demonstration, another option would be to justify equation (1) as making biological sense rather than choosing it as just simple and plausible (especially since it isn't even necessarily the simplest or most plausible). Without such justification, the main result is unconvincing as it could be this choice that generates the 0.75 rather than the actual role of population density in extinction risk. In its current form, there is no biological reasoning that links the results of the logistic regression to population density and the value of 0.75 appears coincidental.

In addition, Polishchuk assumes that conventionally studied external pressures such as climate and hunting 'had no effect on the shape (e.g. slope) of the allometric relationship between extinction probability and body size'. This assumption is made, in part, so that he can 'tease out' the important features of the relationship based on deviations in the slope, yet this component of the analysis is lacking. Exceptions to the null hypothesis don't lead to the identification of external forces. Hence, the argument is that there is some background extinction probability and whatever it is that happened at the end of the Pleistocene affected

this probability in roughly the same manner for all species, independent of mass. In terms of allometric determinants of extinction risk, this is equivalent to saying that external forces affect the intercept (normalization constant) but not the slope (exponent) of the extinction risk scaling relationship. If external pressures were important to the shape of the relationship, they would change the slope from 0.75. In the global dataset he finds a slope of ~0.75, but other values are found in some of the continent-level datasets. What should be made of this? Setting aside our concerns with the rationale for the model, these continent-level deviations could be interpreted as falsifications of the null hypothesis and demonstrate where external forces have indeed altered the shape of the relationship between extinction risk and body mass. It is noteworthy that the deviations from 0.75 occur on continents heavily hit by size-biased extinction (Australia, North and South America), where the possibility that humans changed the shape of the relationship is highest (Lyons *et al.*, 2004: *Evol. Ecol. Res.*, **6**: 339–358). We see this is as a problem for the model and are not convinced that the continental deviations simply represent small-scale sampling noise in the true underlying global pattern.

If the model were in fact an accurate depiction of the size selectivity of extinction, it should apply to the background extinction rate at any time during the Pleistocene as well. The end-Pleistocene extinction is a special event that, according to the model, amplifies the background pattern without changing its shape and hence any point in the geological record of mammals, with sufficient fossil resolution, should generate extinctions curves like those in Polishchuk's Figs. 1 and 2. The background rate at any earlier point in time, according to the model, should yield the same slope but a lower intercept for the scaling of extinction risk and body mass. Such a demonstration would lend support for Polishchuk's other claims.

The model assumes that the size selectivity of extinction is intrinsically determined. To evaluate the possibility that human hunting, as an external force, may have altered the size selectivity of extinction, Polishchuk removes species weighing less than 5 kg. His argument is that if human hunting affected the size selectivity, the truncated dataset will have a different slope from the full datasets and if no difference is found then humans as an external force do not alter the intrinsic risk set by population density. However, removing species below 5 kg doesn't actually do anything to capture the effects of human predation. Rather, the 5-kg truncation serves to remove the modality from the underlying distribution of mammal body sizes (Burger and Ginzburg, 2009: *Evol. Ecol. Res.*, **11**: 1017–1029). This well-known modality may create a problem for his model. If extinction risk is a determining factor in the shape of the body size distribution, the species of lowest risk should be the most common, but more species and more individuals occur at an intermediate size, which is not what Polishchuk's model would predict. As such, Polishchuk would have to invoke a currently unspecified external force to account for the observed patterns in mammal size distributions or argue that extinction processes play no role in the distribution of smaller mammal sizes.

In spite of our reservations, there is much in Polishchuk's paper that may be built upon. The use of logistic regression in this context is useful and it may be that a more thorough derivation of the model could be developed that would strengthen the link between the slope in the regression and the slope of the Damuth rule. However, as currently presented, we think this link is tenuous at best.

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In a recent interesting paper published in *EER*, Leonard Polishchuk took a novel approach to characterize extinction risk in mammals. He developed a simple null model that assumes the allometric scaling of population density drives a general pattern of size selectivity, with larger mammals more prone to extinction. He tested this idea with the MOM database of Late Quaternary mammals (Smith *et al.*, 2003: *Ecology*, **84**: 3402) and concluded that his analysis supported his *a priori* predictions.

We accept that the extinction probability for Late Quaternary mammals on most continents was strikingly size-biased. Indeed, this long observed and intriguing pattern has driven considerable research on the event (e.g. Martin, 1967: *Pleistocene Extinctions: The Search for a Cause*. New Haven, CT: Yale University Press; Alroy, 1999: pages 105–143 in *Extinctions in Near Time: Causes, Contexts and Consequences* (R.D.E. McPhee, ed.). New York: Plenum Press; Alroy, 2001: *Science*, **292**: 1893–1896; Koch and Barnosky, 2006: *Annu. Rev. Ecol. Evol. Syst.*, **37**: 215–250). Interestingly, a significant size bias even extends to lower hierarchical levels; larger species within orders were selectively eliminated, as were larger species within families (Lyons *et al.*, 2004: *Evol. Ecol. Res.*, **6**: 339–358). However, a notable exception to this pattern is the continent of Africa, where only a handful of non-selective extinctions occurred (Lyons *et al.*, 2004; Koch and Barnosky, 2006). Although Polishchuk approached this analysis differently, this result can be seen clearly in his Fig. 1B, where the probability of extinction is largely invariant with body size. Unfortunately, statistics were not provided for the regression but visual inspection suggests the slope is largely flat and distinctive from other continents considered. Even the largest size class (containing the largest mammal to become extinct in Africa, the Proboscidean *Elephas iolensis*), has an extinction probability of only ~10–15%, compared with 70–80% for mammals of that size on other continents. [As an aside, we note recent work suggests *Elephas iolensis* was extinct by 0.034 Ma (Todd, 2006: *J. Mammal. Evol.*, **13**: 1–10) and thus considerably predates the New World event.]

While we accept the premise that the Late Quaternary extinction was highly size-skewed, we find the claim made by Polishchuk that extinction risk scales as $M^{3/4}$ to be contradicted by the data and analyses in his paper. Inspection of his Table 1 clearly illustrates that the predicted slope of 0.75 is only included within the confidence intervals for a single continent, Africa. Even here, the confidence intervals are wide (i.e. 0.51 to 1.21), providing weak support at best. In all other instances, ordinary logistic regression does not yield values that include 0.75. In fact, the slopes are widely and notably divergent from 0.75 (e.g. 0.86 for Africa, 1.86 for Australia, 0.62 for North America, and 1.23 for South America) and show no discernible pattern. Adoption of other models (e.g. mixed effects, random intercepts/slopes) only slightly alters the relationship: the slope for Australia changes to 2.45 (but does not include 0.75), while the slope for North America stays the same (0.62) but the confidence intervals widen to marginally include 0.75 (0.48 to 0.75). Results for the extended dataset (his Table 2) are largely congruent, although the confidence interval for Australia does include 0.75. Polishchuk downplays the extended dataset for good reason; it is inappropriate for an extinction analysis as the fossil record for bats is woefully incomplete. Thus, it is only when all continents are combined that the slope of the relationship is indistinguishable from 0.75.

Why are the slopes so divergent? Assuming for the moment that the underlying premise made by Polishchuk is correct, we believe his test of his theory conflates several extinction dynamics that are operating simultaneously. Consider that estimates of median/average species duration of mammals range from ~1.7 to 2.5 Ma (Foote and Raup, 1996: *Paleobiology*, **22**: 121–140; Alroy, 2000: *Paleobiology*, **26**: 707–733; Vrba and DeGusta, 2004: *Phil. Trans. R. Soc. Lond. B*, **359**: 285–293); this leads to a per capita risk of 'background' extinction of 0.01 for the 20-ka time period

Table 1. Comparison of expected with actual Late Quaternary extinctions

Continent	*N* (non-volant, non-introduced species)	Number of expected background extinctions per 20 ka	Number of Late Quaternary extinctions
Africa	840	8.4	13
Eurasia	833	8.3	12
North America	615	6.1	78
South America	783	7.8	76
Australia	269	2.7	45

Note: Expected background extinctions are computed for the time period from 30 to 10 ka assuming a median duration for mammals of 2 Ma (Foote and Raup, 1996: *Paleobiology*, **22**: 121–140; Alroy, 2000: *Paleobiology*, **26**: 707–733); the MOM database includes species with last occurrences over this time frame (Smith *et al.*, 2003: *Ecology*, **84**: 3402).

represented by mammals classified as 'extinct'. Our MOM database contains 840 non-volant, non-introduced species for Africa, 615 for North America, 783 for South America, and 269 for Australia. Consequently, expected background extinctions are ~8, 6, 8, and 3, for Africa, North America, South America, and Australia, respectively (see Table 1). This is a trivial number for most continents, representing less than 10% of the total estimated Late Quaternary extinctions. Clearly, other processes were the main drivers underlying elevated extinction risk. In contrast, background rates represent well over *half* the extinctions in Africa. Interestingly, although not included in Polishchuk's considerations, Eurasia also experienced very few, non-size-selective extinctions (12 species of 833 present; see Table 1); note that the fauna of both Africa and Eurasia were well experienced with human activities by the Late Quaternary. Humans or their predecessors arrived in Eurasia as early as 2 Ma; evidence of predation on large mammals extends to 400 ka (Thieme, 1997: *Nature*, **385**: 807–810). Anatomically modern humans were active in Eurasia by 50 ka (Mellars, 2004: *Nature*, 432: 461–465). It is likely that terminal Quaternary extinctions in Africa (and Eurasia) were largely due to background processes and only minimally due to other factors.

To summarize, Africa did not experience extinction significantly greater than background in the Late Quaternary, and what extinction that occurred was not convincingly size-biased. In contrast, the other continents examined did experience elevated levels above background and furthermore, the extinctions were highly size-biased. Only for Africa do the confidence intervals even include the predicted slope of 0.75; the other continents clearly don't show a discernible pattern.

Was the striking size-biased mammalian extinction in the Late Quaternary a general pattern of mammalian evolution? In general, is Polishchuk correct that body size increases extinction risk in a predictable way? We would argue 'no' to both questions. First, we note that predicting extinction risk is not straightforward from a simple life-history parameter such as body size. For example, while large mammals have longer generation times and smaller population sizes (both factors that could clearly increase extinction risk), they also have wider geographic ranges and greater dispersal abilities, which have been demonstrated in other taxa to *lower* extinction probablity (e.g. Jablonski, 1987: *Science*, **238**: 360–363). Hence, the finding in recent studies that extinction risk is not well predicted by body size unless anthropogenic influences are involved (Finnegan *et al.*, submitted). Second, if extinction risk is

inherently size-biased, then origination rates must also demonstrate strong positive size dependence. There is no compelling evidence to support this contention. Although large animals may have smaller effective population sizes than small animals, which arguably could increase evolutionary rates, this might be countered by increased dispersal abilities and enhanced gene flow. Third, the overall prediction made by Polishchuk that extinction risk scales positively with mammalian body mass is not well supported by the fossil record. Indeed, previous extinction events over the Cenozoic are remarkable for their *non-selectivity* (Alroy, 1999). In this context, the Late Quaternary extinctions are highly unusual, not the normal steady state. Fourth, there is a large and growing literature that documents the impact of modern human harvests on other animal populations. There is a clear pattern of a highly selective bias with respect to body mass within fisheries, whaling, and other industries when humans are involved (e.g. Jennings *et al.*, 2001: *Marine Fisheries Ecology*. Oxford: Blackwell; Cardillo *et al.*, 2005: *Science*, **309**: 1239–1241; Davidson *et al.*, 2009: *Proc. Natl. Acad. Sci. USA*, **106**: 1702–1705).

We believe the data presented by Polishchuk, as well as the arguments we have made here, overwhelmingly support his alternative hypothesis: the Late Quaternary extinction of mammals was highly (and unusually) size selective and largely attributable to human activities.

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When progress seems stalled on a topic, often an effective way forward is to change the question. I think it fair to say that over the last few decades the salient issue for most people with respect to the size-selective Late Pleistocene vertebrate extinctions has been, 'Were they caused by environmental change or, alternatively, by human activity?' We seem still to be far from a consensus on this issue, and there may be no simple, or single, general answer. At the same time, there are many other things that are poorly understood about this, and other, mass extinction episodes. Leonard Polishchuk has asked a novel question about mass extinctions, using a statistically sophisticated approach that itself has even broader utility. Ultimately, the issue his paper raises, and purports to answer, is whether the size selectivity of mass extinctions (whatever might have caused the increased extinction rates in the first place) mainly reflects only the size scaling of abundance. That is, does extinction probability of a species mostly depend simply on the number of individuals? Could it possibly be that simple?

Well, probably not. We don't often get that lucky, and, as usual, there are complications. Polishchuk finds that, worldwide, extinction probability for mammals during the Late Pleistocene scaled with body size with an exponent (0.75) that is the inverse of the way that population density is observed to scale among extant animals. From this he concludes that a simple model, where extinction probability is directly proportional to the inverse of population density, could explain the size selectivity of the observed extinctions. However, datasets analysed by continent show different exponents, seemingly with no pattern, and we currently don't know how to interpret this variation. Is it just noise around the global central tendency? Or was something different happening in different places?

Note that Polishchuk's statistical approach can at best only establish that it is something that scales *like* population density (or its reciprocal) that determines extinction probability (although population density is an appealing and logical candidate). Local population density also is not exactly the same thing as total population size, which logically should be more directly relevant to total extinction.

I think his paper has considerable value in spite of these uncertainties, because in showing how the exponents of traditional allometric relationships can be related directly to those of logistic regression, it describes a clear way to go about investigating further the host of questions that arise from Polishchuk's simple model.

One limitation of that model is that it assumes that there is just one main 'intrinsic' causal influence on extinction probability, and that this factor is related to extinction in a simple way. However, rather than the distinction Polishchuk draws between 'intrinsic' (universal allometric) versus 'external' (ecological, contingent, etc.) causal factors, I think a more useful division may be simply between those evolutionary and ecological factors that are expected to vary with body mass (or to interact to modify the scaling of those that do), and factors that operate independently of body size. This underscores the plausible possibility that multiple factors scaling with body size may interact to generate the variation in the scaling of extinction probability that we see. Taking an explicitly quantitative approach, such as Polishchuk's, to the multiple scaling relationships implied, and probably using more complex models, should eventually yield considerable insights when applied to the Pleistocene – and to other mass extinctions known in the fossil record.

Another, independent, highlight of Polischuk's paper is the case he makes for the broader use of logistic regression in the biological sciences. Logistic regression should be especially useful in paleontology, because we often want to relate changes in one or more continuous variables to a binary or categorical outcome. Polishchuk's discussion of logistic regression versus 'binning' is especially pertinent and is a valuable contribution of the paper whether or not its major empirical result is confirmed by future research.

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Leonard Polishchuk is to be congratulated for seeking to provide a quantitative description of the pattern of Late Pleistocene extinction with body size. In my view, he is correct to write that, 'Most previous analyses have focused on the chronologies of events'. Such chronologies are episodic and inherently data poor.

Yet no-one expects total success from early attempts to accomplish what one sets out to do. Polishchuk is opening doors, exposing new questions, and revealing opportunities.

His first challenge is that extinction is a categorical variable. It is categorical because there is no intermediate state – a species is extant or extinct. Logistic regression of datasets with categorical variables is spreading and Polishchuk applies the method to extinction. He shows how this statistical tool can be used to measure extinction probability – a continuous variable extracted from a categorical one. Excellent, but how may we interpret such results?

Consider the extremes. One extreme is Polishchuk's null hypothesis: extinction probability does not vary with body size – it is flat. The other extreme is a well-defined

threshold. All species larger than this threshold become extinct; all below it survive. The graph of probabilities would display a step function, changing discontinuously from 0 to 1 as the threshold was passed.

In no case do we see either extreme in Late Pleistocene mammal extinctions. For one thing, the null hypothesis is surely wrong. The bigger they were, the more likely they fell. And, as to a step function, in two instances, Australia and South America, extinction probability does rise sharply and then tend towards flatness, but it is not a step function in either case. And in the cases of North America, Africa, and all four land masses combined, it rises moderately rather than sharply.

By assuming that population size accounts for much of the variance in the likelihood of extinction, Polishchuk is able elegantly to relate his results to a macroecologial coefficient, 0.75, the allometric coefficient that relates body size and energy consumption rate: 'The probability of extinction, *P*, is a logistic function of log-transformed body mass with slope 0.75'. Conditions of the Late Pleistocene may have tweaked size-specific *P*-values but still, they exhibited this underlying pattern of relationship to body mass. That is his claim.

To begin to be sure of that claim, one would need analyses of other time periods. Would they show the same underlying coefficient? The data to permit such analyses are not yet available [although Smith *et al.* (2010: *Evol. Ecol. Res.*, this issue) report (based on Alroy, 1999: pages 105–143 in *Extinctions in Near Time: Causes, Contexts and Consequences* (R.D.E. McPhee, ed.). New York: Plenum Press) that previous extinction events over the Cenozoic do not support the conclusion that extinction probability rises with body size].

Polishchuk requires his data set to represent 'a closed set of species'. Otherwise, any sample might poorly represent the properties of the whole. That makes perfect sense to me. But these four biogeographical provinces are four closed sets of species, not one. We do not know a mechanism that might weld them together into a single macroecological unit.

On the other hand, the speciation/extinction dynamics of the separate provinces provide a clear mechanism to do that for each province separately. That is why, personally, I am not so keen on dismissing the results obtained from the individual provinces. In fact, these results may be among the most stimulating in Polishchuk's paper.

One would expect that if the 0.75 coefficient value is general, it would appear in all four of the separate provinces. But it does not. That suggests to me that, 0.75, the allometric coefficient that relates body size and energy consumption rate, does not help much in explaining the fundamental reason that extinction probabilities rise with mammal species body size.

One would also expect the results for North America, South America, and Australia to reflect the great megafaunal extinctions correlated with the advent of *Homo sapiens* in those three continents. First, one would surely expect them all to have elevated extinction probabilities for large-size species (compared with Africa). Then, second, consider that larger logistic regression coefficients indicate a closer approach to a threshold condition such that body sizes above threshold are particularly threatened. So results yielding large coefficients would suggest a human-caused bias against larger species that was more pronounced and consequential than results yielding small coefficients.

Results do comply with the first expectation: The three that were thought to have suffered the most anthropogenic extinction do show much higher extinction probabilities than Africa. But slopes are another matter. Australia and South America have the largest slopes. But Africa's slope comes next and it actually exceeds that of North America. There is a

mismatch here that suggests we need a better understanding of the logistic regressions. Polishchuk's method is intriguing and his results beg for more investigation.

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REPLY

My attempt to better understand the size selectivity of extinction in Late Pleistocene mammals (Polishchuk, 2010: *Evol. Ecol. Res.*, **12**: 1–22) is not a dogma and is surely open to criticism. It has three major components:

1. The idea: Size selectivity may be a manifestation of allometry.
2. The tool: Logistic regression.
3. The data: A four-continent data set containing body masses of extinct and surviving species (compiled by Smith *et al.*, 2003: *Ecology*, **84**: 3403).

None of the comments objects to or doubts the appropriateness of any of these points; many explicitly appreciate at least some of them. These three points are sufficient to obtain all the major results of the paper.

Specifically, I apply logistic regression to the data and get the slope of a logistic function for the probability of extinction, P, in relation to log body mass to be about 0.75. I then transform the logistic probability of log body mass into extinction odds, $P/(1 - P)$, scaled as a power (allometric) function of body mass, with the same scaling exponent of 0.75 (see equations 3–5 in the paper). I further note that this positive exponent matches – up to sign – the negative scaling exponent for the population density–body mass relationship [Damuth's rule (Damuth, 1981: *Nature*, **290**: 699–700)] and I suggest that this coincidence reflects the fact that less numerous species are more prone to extinction. (Consider how often the IUCN Red List refers to a small population size as a reason for a species to be endangered.) It follows that the Late Pleistocene extinctions, while strongly biased towards large-bodied species, are biased no more than one would expect from the population density scaling, and that is the main conclusion of the paper. Although interpretations of these results are bound to vary, so long as criticism does not find fault with either my treatment of the data or the mathematical and statistical tools I used, it would not seem to jeopardize the results.

I am most grateful to the reviewers for their comments. I appreciate positive comments, which are particularly encouraging to me. Below, I address some critical comments because they are stimulating and helpful in guiding future work and because I believe I can clarify them.

John Damuth (2010: *Evol. Ecol. Res.*, this issue) has emphasized the benefits of using logistic regression in paleontological studies, compared with a more traditional 'binning' approach. (The corresponding section, *Logistic Regression versus Binning*, appeared in the paper at the last moment, thanks to suggestions and guidance from Michael Rosenzweig.) In effect, this approach consists of building and statistical comparison of frequency distributions

in relation to body size for extinct and surviving species; for Late Pleistocene mammals, this was first done by Lyons *et al.* (2004: *Evol. Ecol. Res.*, **6**: 339–358; their Fig. 1). In no way do I underestimate the importance of frequency distributions as the necessary first step of statistical analysis. My paper stands on the shoulders of Smith *et al.* (2003) and Lyons *et al.* (2004: *Evol. Ecol. Res.*, **6**: 339–358). However, logistic regression does provide the next step; its significance, in addition to what is said in Polishchuk (2010), is that the regression uses raw, individual-species data and thus allows one to carry out mixed-effects regression analyses to account for data non-independence. Binning that deals with aggregated data does not allow for this type of analysis.

Oskar Burger and Lev Ginzburg (2010: *Evol. Ecol. Res.*, this issue) point out that truncating the data and repeating analyses for only large species (≥ 5 kg) implies removal of the small-size modality from the species body-size distribution. They believe that 'removing species below 5 kg doesn't actually do anything to capture the effects of human predation'. In my view, however, removing the small-sized species is an important way to check the validity of the results [see (1) and (2) below] or the validity of the interpretation of the results [see (3)]. In particular, this procedure accomplishes the following:

1. It tests the sensitivity of the scaling exponent to changes in the size structure of the data.
2. It tests whether the scaling exponent is affected by the incompleteness of the fossil record [this aspect was not mentioned in Polishchuk (2010)]. The logic behind this test is as follows. The incompleteness of the fossil record occurs primarily in small body sizes, so extinct animals are more likely to be underrepresented among small species. We take large-sized animals (≥ 5 kg), add small animals (< 5 kg), and observe that the scaling exponent does not change [cf. slopes for truncated data sets in Tables 3 and 4 vs. four-continent slopes for full data sets in Tables 1 and 2 in Polishchuk (2010)]. Hence, an incomplete fossil record is unlikely to affect the results.
3. It assesses the extinction size selectivity (measured by the scaling exponent) for a portion of the body-size range that was potentially experiencing the impact of ancient hunters, under the proposition that if ancient men were responsible for size selectivity they would have pushed the slope away from 0.75. (In fact, the slope remains intact, which puts in doubt the role of humans in its determination.)

A major problem, accentuated in several comments, is that the 0.75-power extinction-risk scaling is not found at the continent scale: among the four continents studied, none shows precisely this exponent. One chiefly intrinsic reason why this may be so is that Damuth's rule is not valid for continents. We know, indeed, that on local and regional scales population-density scaling often differs from the −0.75-power pattern (Peters and Raelson, 1984: *Am. Nat.*, **124**: 498–517; Blackburn *et al.*, 1993: *J. Anim. Ecol.*, **62**: 519–528; Blackburn and Gaston, 1997: *J. Anim. Ecol.*, **66**: 233–249). Thus the rule should hold only asymptotically, on a global spatio-temporal scale. Partly this is because only global averaging would provide population densities that could be considered species' characteristic traits (local density is not a species trait because it varies over space and time for the same species). Consequently, only such densities should be involved in scaling analyses. This argument, while not necessarily incorrect, is hard to falsify however, so scientifically it does not seem viable.

The other, chiefly external, reason may be that environmental impacts push an extinction-risk scaling away from the basic value of 0.75. (This same cause might also explain why population density scaling tends to deviate from −0.75 on continents.) The corollary is that

when the continental situation is less perturbed and is closer to background, the 0.75-power extinction-risk scaling is more likely to manifest itself. It would appear that, among the continents considered in my paper (Africa, Australia, North America, and South America), the situation in Africa is most similar to such a balanced situation, probably because Africa did not experience strong climatic perturbations (Scholz *et al.*, 2007: *Proc. Natl. Acad. Sci. USA*, **104**: 16416–16421). Remarkably, Felisa Smith, Marcus Hamilton and James Brown (2010: *Evol. Ecol. Res.*, this issue) share this opinion: 'It is likely that terminal Quaternary extinctions in Africa (and Eurasia) were largely due to background processes and only minimally due to other factors', although they view the cause differently. Whatever the causes are, the balanced situation in Africa is evident in a low extinction rate on this continent [Table 1 in Smith *et al.* (this issue)]. Hence, the African scaling exponent is *expected* to be close to 0.75 – closer at least than the other continents' exponents. This is indeed the case: only for Africa do all eight exponents, including those for basic and extended data sets and for ordinary and mixed-effects regressions, not differ significantly from 0.75 [see Tables 1 and 2 in Polishchuk (2010)]. Overall, the African scaling exponents (0.86 for ordinary logistic regression and 0.78 to 0.86 for mixed-effects regressions) are closer to 0.75 than those for any of the other three continents. Another continent having a low extinction rate is Eurasia [see Table 1 in Smith *et al.* (this issue)]. I suggest, therefore, that the Eurasian scaling exponent would also be close to 0.75. This is a 'risky' (in Popper's sense) and falsifiable prediction. To test it, we need a reliable and comprehensive dataset of body masses of extinct and surviving Eurasian mammals. As far as I know, such data are not available.

I completely agree with Burger and Ginzburg (this issue) that my paper presents no theory of the size selectivity of extinction. That is why, by the way, the section where I develop the link between population density scaling, logistic function for extinction probability and extinction-odds scaling is called 'Strategy', not 'Theory'. Such theory, when it is developed, may or may not involve a logistic equation. But if it does, this would be a bonus because, first, a logistic function is parameterized using logistic regression, which is a standard tool to describe binary data (such as 'species extinct or not'); and second, logistic regression is closely associated with probability. Clearly, probability is a natural feature of extinction.

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