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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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