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On size and extinction: a random walk model predicts the body size of lowest risk for mammals

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ABSTRACT

Question: Is the relationship between extinction risk and size in terrestrial mammals described by a peaked function or a monotonic function?

Mathematical method: We develop a population viability analysis model where species take random walks at generational time steps. The model works like the classic gambler's ruin problem where risky combinations of variance in growth rate, population density, and generation length are eliminated from an evolutionary game.

Key assumptions: Our model ignores speciation. It assumes that the population growth rate at evolutionary time scales is zero. It assumes an unbiased random walk. Chronological time is adjusted for generation length, so that longer-lived species make fewer 'gambles' in the same period of time.

Conclusions: Particular combinations of variance in growth rate and average population density yield an extinction function that predicts a size of lowest relative extinction risk for terrestrial mammals. This size is close to the mode of continental body size distributions (at about 0.1 kg). Generation length is a fundamental evolutionary time scale.

Keywords: allometry, Damuth rule, generation time, mammal body size distribution, optimal size, population variability, probability of extinction.

INTRODUCTION

Mammals vary tremendously in size, from shrews to elephants, but the most common size is near 0.1 kg, the modal size for continental body size distributions (Brown *et al.*, 1993; Blackburn and Gaston, 1998; Kozlowski and Gawelczyk, 2002). The modal value is highly consistent across continents (Smith *et al.*, 2004), which has led some researchers to consider the possibility that the modal size is somehow advantageous or optimal. For instance, Brown *et al.* (1993) developed a model suggesting that the modal size is optimal with respect to allocating metabolized energy to offspring. Other lines of evidence also support the notion that the most typical (modal) size represents some evolutionary or ecological optimum. The island rule for

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mammals suggests that species colonizing insular habitats from continents tend to converge on a particular and consistent size roughly near the observed continental mode [although the island rule mass is a bit larger at ~0.2–0.45 kg (Lomolino, 1985, 2005)]. Further evidence from insular faunas comes from Marquet and Taper's (1998) hypothesis that extinction risk may be lowest at the modal size. To evaluate this empirically, they reasoned that the size of lowest extinction risk would have an advantage when colonizing islands. Limitations of space and hence resources on the smallest islands should favour the least extinction-prone species. Data on the maximum and minimum size of mammals on islands support this hypothesis, as the smallest islands consistently have a few species of modal-sized mammals. Moreover, the size of the smallest mammal gets smaller and the maximum size gets larger as island area increases (Brown, 1995; Marquet and Taper, 1998). Their results demonstrate that when more area is available, progressively more extinction-prone species at both large and small sizes farther from the mode are able to successfully colonize and persist. However, extinction risk is also often hypothesized (or assumed) to be a monotonic (rather than peaked) function of size, with larger species at greater risk (Brown, 1995; Blackburn and Gaston, 1998; Brook and Bowman, 2005; Clauset and Erwin, 2008) because of the larger space requirements and lower population densities of larger species (Kelt, 1997). Although the largest sizes may indeed be at high relative extinction risk, explanations are still needed for why richness peaks at an intermediate size and how extinction contributes to the statistical properties of the body size distribution.

We evaluate the role of extinction risk in explaining the modal size of mammals by testing the hypothesis that the most typical size of about 0.1 kg is the size of lowest relative extinction risk. Our approach is described by analogy to a gambler's ruin problem where species are like gamblers attempting to stay in a game that eventually ends in ruin (extinction). In the model developed below, the mammal body size distribution represents a collection of bet-hedging strategies that have managed to stay in an evolutionary game. Today we are left with a collection of winning strategies; unstable ones have been, and will continue to be, eliminated (Ginzburg and Colyvan, 2004, p. 112). The most successful strategies are found at the modal size. This scenario emerges from a random walk model that we borrow from population viability analysis (PVA) and modify using body size allometries for population density and generation time (see below). Population viability analysis is a portion of population dynamics theory that uses random walks to predict quasi-extinction probabilities (Ginzburg *et al.*, 1982; Levinton and Ginzburg, 1984; Lande and Orzack, 1988; Morris and Doak, 2002; Lande *et al.*, 2003). In short, we take a conventional PVA equation, simplify it so that it becomes a species viability equation for mammals at evolutionary time scales, and constrain the parameters with body size allometries.

The model predicts that the size of lowest risk for mammals is near both the modal size in continental distributions and the convergent size for insular populations. We show that extinction risk is a peaked, rather than monotonic, function of size as risk is minimized at an intermediate size near 0.1 kg. We conclude that a random walk model from population dynamics describes the macro-ecological process that links size-specific extinction risk to the modal size for mammals. The gambler's ruin analogy, explained in the next section, is useful for linking the evolution of life-history strategies to the observed distribution of mammal body sizes.

THE ESSENCE OF THE ARGUMENT

The basic features of a species' life-history and ecological attributes may be seen as successful combinations of traits that have, among other things, played a role in preventing the species from becoming extinct. The body size distribution represents a set of successful combinations because the traits indicative of a particular strategy (lifespan, maximum growth rate, etc.) are allometric functions of size (Damuth, 1981; Peters, 1983; Calder, 1984; Charnov, 2001; Savage *et al.*, 2004). We take population density, generation time, and variation in population growth rate as three features of a species' evolved strategies that have kept it in the game and are closely correlated with body size. In our model, species randomly walk towards eventual extinction, and the number of steps taken during a long interval of time is determined by average generation length.

To make the random walk process more intuitive, consider an analogy with the classic gambler's ruin problem in which species make bets that increase or decrease their capital (population density) until they either win the game or run out of money and become ruined (extinct) (see Feller, 1968, pp. 342–349; Thomas *et al.*, 1980). Generation time is analogous to bet frequency because each generation the species takes a step either toward or away from extinction and in a given period of time fast generation species take more steps than those with slower life histories (see below). Variation in growth rate is analogous to the size of the bet placed each generation. If this variance is high, then a species stands to gain or lose more capital (density) per gamble (generation) than if variance is low. Certain combinations of capital, bet size, and frequency are more likely to stay in an evolutionary game than are others. Because the key parameters depend on body size, the collection of winning combinations is observed as the extant body size distribution. Of course, the analogy between gamblers around a roulette wheel and the evolutionary dynamics governing body size is not perfect. Real gamblers can drastically change their strategies from hand to hand, whereas body size constrains the adjustments that animals can make from one generation to the next. The gamblers ruin problem is introduced to give the following equations a more intuitive feel.

POPULATION VARIABILITY AS A FUNCTION OF BODY SIZE

A mathematical expression for the gambler's ruin model is derived in Appendix A. The probability of extinction, P_{ext}, is given by:

$$P_{\text{ext}}(T \mid \log_e N, \sigma^2) = 2\Phi\left(\frac{\log_e N}{\sigma\sqrt{T}}\right). \tag{1}$$

This equation says that the probability of extinction, P_{ext}, during some interval of chronological time, T, is a function of the natural log of abundance, N, and the standard deviation of population growth rate, σ. The function Φ is a standard normal distribution (Appendix A). Equation (1) assumes that the long-term growth rate is zero, which is appropriate for studies of species extinction at macro-evolutionary time scales. Chronological time is scaled to the ½ power, because we assume an idealized random walk (white noise); other values for the exponent could be used to explore the effects of correlated or biased random walks (Inchausti and Halley, 2001, 2003). Chronological time, T, is used to denote a target interval over which probability of extinction is calculated. In cases of PVA analysis we might, for example, be interested in the mean time it takes a population to cross some specific threshold density below which extinction is highly probable (Ludwig, 1999).

We modify the standard PVA equation so that it computes species viability over evolutionary time. Because generation time increases as a function of body size [¼ power allometry (Millar and Zammuto, 1983)], small species wager more often or take more 'steps' in a random walk through chronological time than do large species. For this reason, we adjust the evolutionary clock by normalizing chronological time, T, in equation (1) to units of generation length τ (Ginzburg and Damuth, 2008):

$$P_{\mathbf{ext}}(\tau \mid \log_e N, \sigma^2) = 2\Phi\left(\frac{\log_e N\sqrt{\tau}}{\sigma}\right) = C. \tag{2}$$

Equation (2) can be set to a constant level of extinction risk, C, in term of N, τ, and σ. Chronological time, T, is dropped from the model because we assume that we start the 'clock' at the same time for all mammal species, thereby assuming that all of the players (species) are present when the game begins. This is equivalent to ignoring speciation and assuming that all the mammal species under consideration (extinct and extant) appeared before the interval T began. This assumption does not affect our results if species longevity does not depend on body size. The longevity of a taxon is independent of its age (Van Valen, 1973) and size may increase with time (Cope's rule), but the specific dependence of longevity on size is unclear (but see Liow *et al.*, 2008). The argument that speciation may be more frequent at the modal size or that extinction probability is greater for large species (Brown and Nicoletto, 1991; McKinney, 1997) suggests that some dependence may exist but at evolutionary time scales the effect is likely to be rather weak. The model could easily be adjusted to explore the effects of any hypothesized dependence of longevity on body size by changing the value of the random walk exponent (see Appendices). As a consequence of removing T from the expression, the predictions we make are in terms of relative risk rather than the specific quantitative risk calculations typical of PVA studies. While deriving exact extinction probabilities would be desirable on the one hand, on the other the advantage of this simplification is that we have simple analytical expressions with no free parameters that do not require computer simulation to solve. This advantage allows us to calculate a measure of relative extinction risk solely in terms of body size (not possible with a more complicated expression).

The variables that determine population density (capital) and the generation length (bet frequency) are both allometric functions of body size and these can be substituted into equation (2) yielding an expression for σ that depends only on size. The allometries for population density and generation time are: $N = 47.75M^{-0.77}$ and $\tau = 1.74M^{0.27}$, where M is body size in kilograms. The allometry for N is the well-known Damuth rule (Damuth, 1981, data from Damuth, 1993) and the expression for τ comes from Millar and Zammuto (1983). Substituting these into equation (2) and re-arranging gives a proportionality relating σ to body mass:

$$\sigma \propto (5.1 - \log_e M)M^{0.135}, \tag{3}$$

which can be used to calculate isoclines for constant levels of extinction risk. This works because equation (3) is arrived at by setting the numerator and denominator equal in the argument of the function described by equation (2), so any given combination of parameters would necessarily give the same extinction risk. This function (equation 3) describes the surface of an extinction landscape with the peak of each isocline representing the size of lowest risk. At this size, randomly chosen steps in mass-sigma space have the lowest chance of increasing relative extinction risk. The size at the isocline peak also represents where the greatest range in population variability (bet size) can exist for any given combination of density and generation length. Data for mammals plotted on this surface indicate the space they actually occupy. Values for non-extinct mammals should be roughly bounded by this space and should tend to aggregate towards values of low relative extinction risk.

METHODS

The predictions of equations (2) and (3) are evaluated with data on population growth rates compiled by Hajagos (2005) from the online Global Population Dynamics Database (GPDD; see http://cpbnts1.bio.ic.ac.uk/gpdd/). Numerous records are available in the GPDD, but because of our interest in the standard deviation of growth rate, only time series of 15 or more years were included. Computation follows that of Pimm (1991), who was the first to compile measures of population variability from population dynamics data (Pimm's study led to the development of the GPDD). Many of the time series contain gaps and for these we required a minimum of 14 individual rates of increase for inclusion in the final data set. Time series sampled more often than annually were also excluded. In total, 669 time series for mammal populations met the criteria (Hajagos, 2005). Values for different populations of the same species were averaged together, resulting in a total sample of 140 estimations of σ. A variety of sources for body size were used for the original compilation of data by Hajagos, but missing values were taken from Smith *et al.* (2003).

The rate of increase r at time t was calculated as:

$$r_t = \log_e\left(\frac{N_{t+1}}{N_t}\right). \tag{4}$$

The standard deviation in r_t is given by:

$$\sigma_r = \sqrt{\frac{\Sigma(\bar{r} - r_i)^2}{n-1}}, \tag{5}$$

where i is an index of each calculable r_t in a time series, $\bar{r}$ is the average r for the series and n is the number of r in the set (Hajagos, 2005). It should be noted that the distribution of body sizes of the populations available for study in the GPDD that met our criteria is not exactly proportional to the typical continental body size distribution. The GPDD sample we use has a mode that is similar to actual continental distributions of mammal sizes but has an overabundance of populations at large sizes (Fig. 1). Nonetheless, the data set used here provides a reasonable sample upon which to examine the model presented above.

RESULTS

The results indicate that extinction risk is minimized near the modal size. Equi-risk lines are plotted in Fig. 2. The lines can be interpreted as contours describing a surface where each isocline is a change in the relative risk of extinction in size-sigma space. The bulk of species are contained within contours of low relative extinction risk and there are few at high-risk

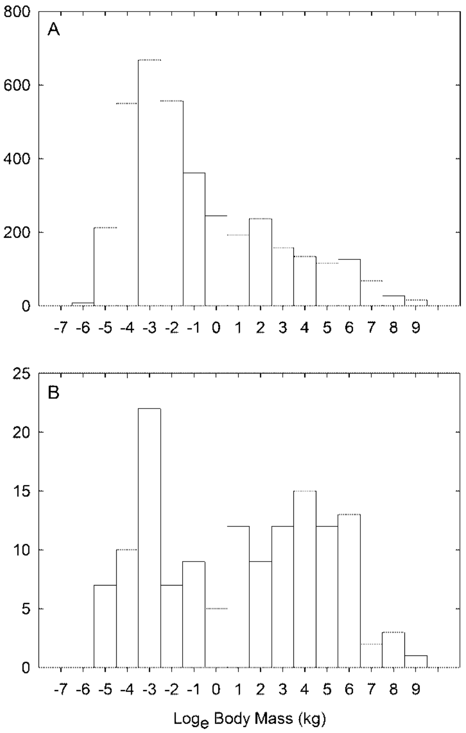

Fig. 1. Histograms of body size. (A) The body size distribution for all continental mammals (data from Smith *et al.*, 2003). (B) The body size distribution for the mammal species from the GPDD that met the criteria for inclusion in this study. The figure illustrates that the body size distribution for the species in our study is not exactly proportional to the continental distribution. This explains the apparent over-abundance of fairly large sized species in Fig. 2.

values. Furthermore, Fig. 3 plots the number of species contained within each interval of extinction risk in Fig. 2, demonstrating that most species have relatively low-risk strategies; 92% of the species are in the lowest three intervals. The body size where extinction risk is minimized is approximately 0.1 kg (local maximum where $d\sigma/dM = 0$), near the empirically observed modal size. We investigate the sensitivity of this prediction to model parameters in Appendix B. The size of 0.1 kg represents the 'maximum' on the extinction landscape where the widest range of values can exist at low levels of relative extinction risk and hence predicts the mammal size that should be most common (modal).

DISCUSSION

The model presented here demonstrates that extinction risk does indeed peak at an intermediate size, consistent with the prediction of Marquet and Taper (1998). Moreover, a constrained random walk/diffusion process appears to be useful for understanding the mechanisms generating the statistical properties of mammalian body size distributions (Stanley, 1973; McShea, 1994; Alroy, 1998), particularly its mode. However, note that most studies of

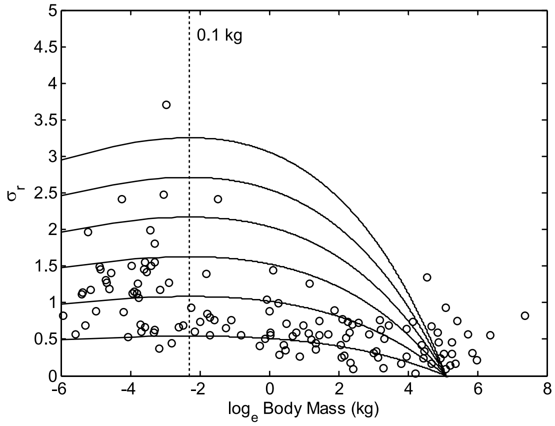

Fig. 2. Equi-risk contours on a plot of the standard deviation of growth rate versus log transformed body size (kg). Each data point is a species average. The lines are constant values of extinction risk based on equation (3) (see text). The exact location for the peak of the function is indicated by the dotted line. It represents where extinction risk is minimized, 0.10 kg, and occurs where the space on this size-sigma landscape is greatest.

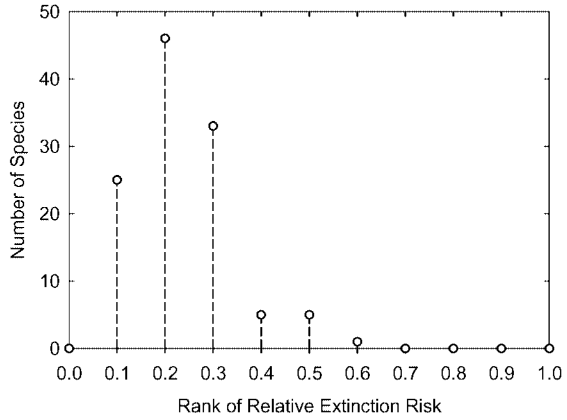

Fig. 3. The ranking of extinction risk. The abscissa represents intervals of increasing relative extinction risk arranged from 0 to 1. The number of species at each value of relative risk is the number of species between the equi-risk lines in Fig. 1. More species are concentrated at low extinction ranks. The specific values are ranks of relative risk, not actual probabilities of extinction. The data points to the right of the non-zero x-intercept in Fig. 1 are not included because they are outside of the range of the equi-risk lines.

the body size distribution that implement random walk models tend to see the modal size as a statistical artifact whereas here we have a diffusion process operating such that the mode is an advantageous size because it minimizes relative extinction risk. In a sense, this joins two very different approaches to the topic, those that have argued somewhat controversially for an ‘optimal’ body size (e.g. Brown *et al.*, 1993) and those that have studied body mass radiations as diffusion processes through evolutionary time (e.g. Stanley, 1973; Clauset and Erwin, 2008). The range of sizes that minimize extinction risk is similar to the range of sizes predicted by Brown *et al.* (1993) to maximize reproductive power. But more importantly, this range represents an especially stable size for a terrestrial mammal, as it is the size of most species, most individuals, the convergent size for insular populations, and the size of lowest extinction risk.

Extinction risk is minimized at the mode and increases in each direction towards larger and smaller sizes. While extinction risk may appear to be an increasing function of size, we suggest that it appears monotonic only because there are more species between the mode and the largest size than between the mode and the smallest size; the long tail towards larger sizes can mask the relationships between size and risk at small sizes. However, it is clearly the case that the largest species are relatively more prone to extinction as many researchers have suggested (Brown, 1995; Blackburn and Gaston, 1998; Purvis *et al.*, 2000; Brook and Bowman, 2005). The long tail towards large species also suggests that there is more 'room' on the extinction landscape for species that prioritize long generations over density than there is for the exceptionally fast gambling life histories at sizes below the mode. Indeed, while the modal size is often termed an 'intermediate' mass, it is much closer to the smallest size with several orders of magnitude of size space ($\sim 10^6$) available above the mode. With respect to extinction, the mode represents the optimal trade-off between density (capital), population variability (bet size), and generation length (frequency of bets and pace of life history). This is the size with the greatest range of variation in population growth rate and where random steps in new directions have less chance of crossing to higher levels of relative extinction risk. In a comment on Van Valen's (1973) study of extinction probability through time, Salthe (1975) makes the point that extinction should be more common when the variance of the probability of extinction is greatest. Figure 2 suggests that species near the mode will be less vulnerable to this variability, as they have more space to occupy for any given variance in growth rate and by extension are more resistant to variation in extinction probability.

The species viability model presented here helps to illuminate the role of extinction risk in the macro-evolutionary trends associated with the mammal body size distribution and perhaps body size radiations generally. However, extinction risk obviously cannot be the only process driving body size patterns of richness, as the number of species in any body size class results from the two opposing forces of extinction and speciation. As such, our model contributes to understanding one half of the picture, but more work is needed on understanding how size-specific extinction and speciation rates balance each other to determine taxon longevity and the number of species in a body size class. Along these lines, the notion of life histories as gambler's ruin problems is useful; high-risk strategies are eliminated and the low-risk strategies tend to stay in the game. It would be interesting to see if random walk processes are also related to the probability that speciation will occur at any given size as new species duplicate the strategies of their successful ancestors, change in mass, and develop different combinations of life-history traits.

In conclusion, the modal size is the size of lowest relative extinction risk, which is part of the explanation for why the mode is an advantageous size for terrestrial mammals. A combination of the ecological attributes generation time, population density, and population variability yield size-specific strategies that have an 'optimum' where extinction risk is lowest. This may be half of the explanation for why the mass of most mammal species and individuals is similar to the convergent mass of islands. While an organism's life history is not specifically designed to avoid extinction, the combinations of strategies that occur at the mode have the effect of increasing the odds that a species will stay in the evolutionary game.

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APPENDIX A

The probability of extinction expression used to derive equation (1) is based on a result used frequently in studies of population viability analysis (Morris and Doak, 2002). The function was derived by Ginzburg and colleagues (1982) and subsequently applied in the age-structured context by Lande and Orzack (1988):

$$P\left(T \mid \log_e\left(\frac{N_0}{N_C}\right), r, \sigma^2\right) = \Phi\left(\frac{-\log_e\left(\frac{N_0}{N_C}\right) - rT}{\sigma\sqrt{T}}\right) + e^{\left(\frac{-2r\log_e\left(\frac{N_0}{N_C}\right)}{\sigma^2}\right)}\,\Phi\left(\frac{-\log_e\left(\frac{N_0}{N_C}\right) + rT}{\sigma\sqrt{T}}\right), \text{(A1)}$$

where T is time to extinction, N_0 is initial population size, N_C is the critical population size representing the absorbing boundary condition or extinction threshold, r is mean growth rate and σ its standard deviation. It represents the mean passage time to the threshold N_C in a stochastic population. As is customary, we use a normal Gaussian function for Φ with mean of zero and variance of one (Ginzburg *et al.*, 1982; Morris and Doak, 2002):

$$\Phi(x) = \left(\frac{1}{\sqrt{2\pi}}\right) \int_{-\infty}^{x} \mathrm{e}^{\frac{-x^2}{2}}\, dx. \tag{A2}$$

The function $\Phi(x)$ is a normal distribution with x equal to the value obtained from substituting the empirically derived calculations into

$$\left(\frac{-\log_{\mathrm{e}}\left(\frac{N_0}{N_C}\right) - rT}{\sigma\sqrt{T}}\right).$$

The corresponding value for $\Phi(x)$ could be obtained numerically or more simply by using a look-up table as one might find in many introductory texts for statistics or probability theory.

However, we are interested in the case where r is 0 and N_C is set to 1 and for this reason we do not deal explicitly with the error function, $\Phi(x)$. We assume long evolutionary time scales and make the simplest possible assumption for N_C, that extinction occurs when the population size drops below one individual. As a result, the ratio N_0/N_C can be written as N, which is population density. In our model T is arbitrarily large, which in part justifies setting $r = 0$. These simplifications reduce equation (A1) to:

$$P(T \mid \log_{\mathrm{e}} N, \sigma^2) = 2\Phi\left(\frac{\log_{\mathrm{e}} N}{\sigma\sqrt{T}}\right). \tag{A3}$$

We set equation (1) in the main text equal to some constant C. To derive actual extinction probabilities for individual populations, one would have to numerically solve equation (A1) given specific parameters, but for the analysis in this paper only relative risks are calculated, as explained in the text. Equation (A3) gives us the expression for σ that holds for any given constant level of extinction risk:

$$\sigma = \left(\frac{\log_{\mathrm{e}} N\sqrt{\tau}}{\sqrt{T}}\right), \tag{A4}$$

which is further simplified by making the substitutions of allometric expressions for generation length τ and population density N. We can also write each of these allometries in a general symbolic form: $N = c_1 M^{z1}$, $\tau = c_2 M^{z2}$, where M is mass, c_1 and c_2 are the two normalization constants, and z_1 and z_2 the two exponents. Because $1/\sqrt{T}$ is some arbitrary constant A, we factor it out and write the following general equation for σ:

$$\sigma = A\,[\log_{\mathrm{e}}(c_1 M^{z_1})^*(c_2 M^{z_2})^{z_3}], \tag{A5}$$

where the exponent z_3 is usually set to ½, which is the case for an idealized random walk. We drop the constant A from any further consideration, expressing σ as proportional to the part of equation (A5) in brackets. A is some constant multiple of all estimates and is a parameter we cannot obtain in any meaningful way. For this reason, our calculations of extinction risk are for relative risk and are not to be equated directly with those obtained from standard PVA studies.

APPENDIX B

A simple analytical exploration of the extinction risk equation was conducted to further clarify how the model works and to relate the individual parameters to their impact on the model's predictions. The general equation for the size of lowest relative extinction risk is found by differentiating equation (A5) and solving for the local maximum, which yields:

$$M_{\text{opt}} = \left(\frac{e^{\left(\frac{z_1}{z_2 z_3}\right)}}{c_1} \right)^{1/z_1}. \qquad \text{(B1a)}$$

The predicted value of M_{opt}, the size of lowest relative extinction risk, depends on the allometric exponents: z_1, which relates body size to population density; z_2, which relates body size to generation time; and z_3, the random walk exponent. The parameter c_1 is the intercept or normalization constant of the Damuth allometry. The normalization constant from the generation time allometry c_2 cancels out of the expression, implying that lifetime or age at maturity could be used in its place as long as one is comfortable assuming that biological times generally scale similarly as ¼ powers (Brown *et al.*, 2004).

An understanding for the sensitivity of the predicted M_{opt} to each parameter in equation (B1a) is determined by examining the partial derivatives. Calculating the partial derivatives is easier if we write equation (B1a) in the equivalent form:

$$M_{\text{opt}} = \mathrm{e}^{\left(\frac{-1}{z_2 z_3} - \frac{\log_e(c_1)}{z_1}\right)}. \qquad \text{(B1b)}$$

Taking the derivatives, we get:

$$\frac{\partial \log_e M_{\text{opt}}}{\partial c_1} = -\frac{1}{z_1 c_1}, \qquad \text{(B2)}$$

$$\frac{\partial \log_e M_{\text{opt}}}{\partial z_1} = \frac{\log(c_1)}{z_1^2}, \qquad \text{(B3)}$$

$$\frac{\partial \log_e M_{\text{opt}}}{\partial z_2} = \frac{1}{z_2^2 z_3}, \qquad \text{(B4)}$$

$$\frac{\partial \log_e M_{\text{opt}}}{\partial z_3} = \frac{1}{z_2 z_3^2}. \qquad \text{(B5)}$$

The exponents relating body size to generation time z_2 and the random walk parameter z_3 have relatively large effects on the predicted size of least risk, as they influence the natural log of M_{opt} as $1/z_2^2$ and $1/z_3^2$ respectively, whereas the normalization constant from the Damuth allometry, c_1, has a relatively minor effect. The sensitivity of M_{opt} to the random walk parameter z_3 is interesting in that subtle biases in the ideal random walk lead to large differences in predicted optimal sizes. The value of z_3 could be changed to investigate how body size dependence of taxon longevity, if found, would alter the predicted size of lowest risk (recall that the value of ½ for z_3 used here assumes no significant trend between longevity and size). Equation (B2) shows the fairly minimal dependence of M_{opt} on estimates of c_1, the normalization constant in the Damuth allometry.

To investigate the dependence of the predicted size on the units of the Damuth allometry, we look at the values that would yield an acceptable estimate. The range of masses that could be considered to encompass the typical mammal size lie between a low of 20 g and a maximum of 400 g (one could argue for a range of perhaps 15 to 450 g, but this is slightly more conservative). This range is based on the empirically observed modes on each continent (Smith *et al.*, 2004) and empirical observations on insular fauna (Marquet and Taper, 1998; Lomolino, 2005). Using the results of the sensitivity analysis we can find the range of values for c_1 that produce approximately this range of body sizes. The empirical value of c_1 used above is 48, based on the data in Damuth (1993), but this value can vary by an order of magnitude between 15 and 145 and still predict the range of acceptable sizes. In short, the dependence of the estimated size of minimal risk is not sensitive to the value for c_1.