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Body size is the history of life: growth confronting landscapes of death

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ABSTRACT

Question: How can we best understand adult body sizes (M_a) both in the present and in the past?

Methods: Maximization of an individual's Darwinian fitness (R_0) for an individual production (growth) function $dM/dT = A \cdot M^{0.67}$ and external sources of death (Z) in the setting of M_a.

Conclusions: The body size at maturity (M_a) favoured by natural selection is always of the form $M_a^{1/3} \propto [A/Z_a]$. This equation is central to understanding the distribution and fluxes of M_a in space and time because it links adult size to the externally imposed mortality rate (Z) combined with the growth function.

Keywords: body size, fossil record, macroecology, macroevolution, mortality-external source.

Body size dominates the study of ecology and paleontology simply because so many biological rates and times are body size dependent, and because body sizes are the central character of fossil assemblages. Fluxes in body size are perhaps the most prominent feature in the history of life; mammals were small at first, then the dinosaurs disappeared, then mammals became larger. Nothing in the history of life makes sense without considering what sets body sizes.

Adult body sizes (M_a) are simply the result of growing for time α, but that's only one-third of the story. If $dM_a/dT = A \cdot M^{0.67}$, $M_a^{1/3} = (A/3) \cdot \alpha$ (where α is time since $M = 0$), predicting M_a requires that we also know A, the height of the production/growth curve. So, the growth function $dM/dT = A \cdot M^{0.67}$ and time α are two-thirds of the answer of what sets M_a. The final essential piece is externally imposed mortality, here called Z. Unless Z is small, natural selection will not set α large. The survival to age α is $e^{-\int_0^\alpha z(x)dx}$, and it is always a fitness cost to setting α larger, hence M_a larger. The balance between the benefits of greater production of offspring (which are simply diverted personal growth: $dM/dT = A \cdot M^{0.67}$) and the mortality cost of growing larger ($e^{-\int_0^\alpha z(x)dx}$) defines the adult body size (M_a) favoured by natural selection. If we assume that selection takes place in non-growing populations, with

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the net reproductive rate (R_0) the appropriate fitness measure, the favoured (ESS, equilibrium) M_α is quite simple (Charnov, 1991):

$$M_\alpha^{1/3} = C\left(\frac{A}{Z_\alpha}\right) \tag{1}$$

[where C may vary somewhat depending on some other life-history details such as determinate vs. indeterminate growth, etc. (Charnov and Gillooly 2004)]. Z_α is the mortality rate around age α, and A is the height of the individual's production/growth function.

   The evolution of adult body size is a problem in life-history evolution, and equation (1) is the most general form of the answer because it ties together personal production (A) in the face of the risk of death (Z, specifically Z_α) to give the M_α. Numerous datasets support versions of this rule for mammals, fish, and reptiles (Charnov, 1991, 1993; Charnov *et al.*, 2001, 2007; Charnov and Gillooly, 2004; Charnov and Zuo, 2011).

   I suggest that equation (1) is the central key to understanding distributions and fluxes in body size at all times and places. Here are some specific suggestions, followed by one summary/main hypothesis:

   Call the local collection of Z's the 'landscape of death', comprised of and caused by those that eat you and those that eat what you eat – your biological community of predators and competitors. A is determined by factors such as food quality, body temperature, the oxygen content of the environment, or perhaps population density, since A is the height of an individual's growth curve.

   Equation (1) is, of course, an ESS-type answer, the equilibrium under normalizing natural selection. Assuming this requires that natural selection on body size occurs so rapidly that species are expected to be mostly at optimal M_α, given by equation (1) all the time. This may seem a strong assumption, but the widespread success of ESS-type models in behavioural ecology supports the assumption. For example, sex allocation theory, the 'type-specimen' for ESS arguments, has been very successful in quantitatively predicting phenotypes (Charnov, 1982; West, 2009). In fact, selection acts no more strongly on sex allocation than it does on body size (as a life-history character), and often acts more weakly on sex allocation than on body size. Thus, changes in A or in Z (the landscape of death), perhaps due to events such as, for example, large-scale invasions of new environments, are expected to be closely tracked, with optimal M_α's being quickly established or restored. It is hard to know if the community-level dynamics that drive A, or that more likely drive the landscape of death (Z), could in themselves cause fluxes or cycles in Z or A, resulting in large-scale fluxes in M_α's.

   The main hypothesis is as follows: Events such as mass extinction could disrupt the distribution of M_α independent of A and Z. Otherwise, fluxes in M_α's will always be driven by A *and* by Z, the landscape of death, as combined in equation (1). Surprisingly, A and Z enter equation (1) as equal partners in setting M_α. Adult body sizes will increase if A increases, or if Z decreases. If both change in the same direction, expected changes in M_α will depend on which changes more, A or Z. If, for example, A goes down in low-temperature environments, the expected adult body sizes depend upon whether the community-generated Z's go down more, or less, or perhaps don't change at all. I suspect that Z may change/flux on much shorter time-scales than does A. Imagine the following picture, a square with A plotted along the y-axis, and Z along the *x*-axis; by equation (1), lines of equal body size are just rays from the origin because M_α is a constant for each

A/Z value. Onto this [*Z*, *A*] square we can plot habitats/environments/biological communities/events in the history of life; the associated (predicted) adult sizes simply depend upon the part of the square occupied by the habitat, community, etc.

Did the original mammals remain small because of a wall of death (high *Z*'s) generated by numerous predatory, small-bodied dinosaurs (including immatures)? And then only after these predators' mass demise did the landscape of death reflect small enough *Z*'s to (quickly) favour large M_a's? Could the largest body sizes be increasing through time because, at the edge of the M_a in the community, the species periodically/occasionally escape their containing *Z*'s? Could the large-scale movement of taxa due to, say, colliding continents reset the *A*'s, and more likely the *Z*'s, for entire communities; that is, could bouts of extinction be followed by the rapid evolution of all new M_a's? Could the invasion of new habitats, such as land itself, give rise to temporary escape from *Z*'s, thus favouring large body sizes until the predators/competitors catch up? The consequences of special types of invasions, such as island invasions, may be tricky; *Z* might go down (one's predators are left behind), but *A* might also go down if increased population density (or novel food) compromises individual growth rates. In many situations, we will be unable to determine which changed more, *A* or *Z*. Cases where we can know will be the most useful for testing the theory, the hydrogen atoms of equation (1).

The history of life on Earth is a story of the fluxes of distributions of body sizes. With the exception of perturbations due to mass extinctions (and perhaps mass invasions), body size(s) follow equation (1), which considers growth rates and death rates together. This hypothesis provides a whole new window into predicting adult body sizes. We should look through it.

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