Does Body Size Optimization Result in Skewed Body Size Distribution on a Logarithmic Scale?

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Kozlowski and Weiner (1997) challenged the idea that interspecific allometries reflect unitary functional relationships between parameters that are shared by all of the species within a set. They suggested that these allometries might also be produced as a by-product of underlying intraspecific processes. In the course of their argument, Kozlowski and Weiner developed a model for the optimal adult body size and found a striking result, which is that optimizing body size produces a distribution of sizes within a taxon that is skewed to the right, even when examined on a logarithmic scale. In this note, we point out that while this result was based on a limited range of parameters, it is actually a very general outcome of optimizing body size in their model.

Kozlowski and Weiner's (1997) new model is based on the assumptions that assimilation and respiration are allometric functions of body size, aw^b and ηw^β, respectively; that the production rate, $P(w)$, is the difference between assimilation and respiration, that is, $P(w) = aw^b - \eta w^\beta$; that the mortality rate, $m(w)$, can be described by $m(wx) = -\gamma w^\lambda$; and that the optimal adult body size can be found as a solution of

$$\frac{dP(w)}{dw} E(w) + \frac{dE(w)}{dw} P(w) = 1, \quad (1)$$

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where $E(w)$ is the reciprocal of the mortality rate, $m(w)$. They selected 100 values for the parameters a, b, η, β, γ, and λ at random from a normal distribution, with a fixed mean and coefficient of variation (CV), and solved equation (1) to obtain the optimum body size. The resulting body size distribution of species within a taxon was skewed to the right even when body size was logarithmically transformed (Kozlowski and Weiner 1997).

Because they were not trying to explain the distribution of body sizes, they used only one set of arbitrarily chosen mean parameter values (table 1), and they did not try to mimic those suggestive of any specific taxonomic group. How robust is their result? To test for this, we repeated Kozlowski and Weiner's (1997) simulations for a broad range of means of their parameters (table 1). For any fixed mean and CV we chose parameters independently from normal distributions. In some cases, this procedure generates parameter values that prevent equation (1) from being solved, for example, $b > \beta$. We have overcome this problem in two ways: we have forced the model to yield exactly 100 optimal sizes by using more than 100 random choices—results referred to as A—and we have omitted any parameter combination in which the condition

$$1 > \beta > b > \lambda + .5 \quad (2)$$

was not satisfied (results B). It can be easily shown analytically that equation (2) is sufficient for a unique solution of equation (1). As it is usually assumed (Schmidt-Nielsen 1984) that β is close to .75 and b is close to .67, and as the exponent for mortality is much lower than those for assimilation and respiration, this seems to be a reasonable restriction of the model.
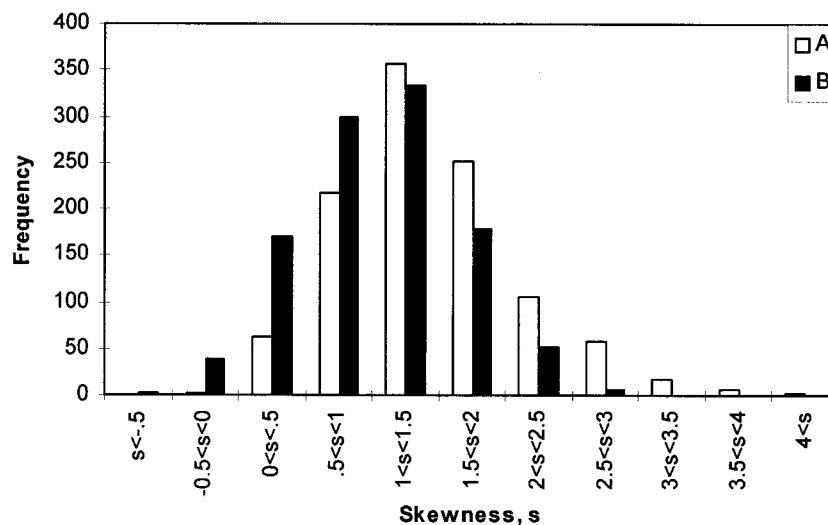
The simulation results (fig. 1) clearly indicate that most of the distributions are positively skewed, which is consistent with Kozlowski and Weiner's (1997) results. However, there are cases in which the skewness is close to zero or even negative. Out of 1,080 cases, 1,001 of the cases produced a statistically significantly positive skewness in set A and 880 in B. None of the cases in set A were statistically significantly negatively skewed, while three were negatively skewed in set B. The tendency for fewer

Table 1: Parameter values used in Kozlowski and Weiner's (1997) paper and in this study

Parameters	Kozlowski and Weiner				This study			Coefficient of variation
	Mean	Coefficient of variation			Mean			
		Case 1	Case 2	Case 3	Lowest	Largest	Step	
a	.050	20	10	20	.05	2.05	.4	20
b	.670	5	2.5	5	.67	.67	...	5
η	.015	20	10	20	.015	1.015	.2	20
β	.750	5	2.5	5	.75	.75	...	5
γ	.0015	50	50	20	.0015	.0815	.02	50
λ	−.100	10	10	2.5	−.100001	−.000001	.02	10

Fig. 1: Distribution of skewnesses obtained in this study. A = model forced to yield exactly 100 optimal sizes. B used only parameters satisfying condition (2).

of the distributions to be positively skewed in B is because condition (2) does not allow the model to produce extremely large (and biologically probably not realistic) optimum body sizes. Thus, the distribution of body sizes published by Kozlowski and Weiner (1997) is a typical, but not a general, one for their model.

The distribution of body sizes within a taxon is often (May 1978; Blackburn and Gaston 1994; Purvis and Harvey 1997), but not always (Dixon et al. 1995; Novotný and Kindlmann 1996), skewed to the right when body size is logarithmically transformed. Our results support the possibility that Kozlowski and Weiner's (1997) model can be applied to the real world. Here we focused only on a sensitivity analysis of four out of the six life-history parameters in the Kozlowski and Weiner's (1997) model and used the same values as Kozlowski and Weiner (1997) did for b and β; testing all of them would require an unrealistic number of simulations. In the future it would be inter-

esting to test the influence of the remaining two parameters and also the effect of nonnormal distributions.

An alternative hypothesis for these types of size-diversity curves associates theory with some size-related feature of its food (Dixon et al. 1995). If the latter is true, then the body size distribution of such taxa should strongly depend on that of the organisms on which they feed. The same will be predicted by Kozlowski and Weiner's (1997) model, if the assimilation and respiratory rates of the predator are dependent on the size of the prey.

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