Response to Comment on "The Illusion of Invariant Quantities in Life Histories"

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Savage *et al.* describe two different kinds of invariant. The kind they claim to have the greatest biological importance allows the invariant quantities to vary widely, even randomly, between different species. We do not agree that such quantities reveal any deep constraints on evolution.

The purpose of our study (*1*) was to show that the usual technique of identifying invariants does not work. This technique involves regressing logged variables against each other and looking for a slope of 1 and, as a bonus, observing a high R^2 (*2*).

Savage *et al.* (*3*) distinguish between two types of invariant. In type A invariance, two variables, *X* and *Y*, such as weaning weight and adult weight, have a ratio *X/Y* that does not vary systematically, e.g., as a function of adult weight. Such invariance is easy to discover. Simply find two variables, one of which is some random fraction of the other, and divide the two. Note that for type A, "invariance" does not mean invariable: The ratio may be extremely different for different species. Savage *et al.* observe that our analysis assumed that the data satisfied type A invariance. This is certainly true, and we do not find it remarkable that a variable such as weaning weight might be a random multiple of adult body weight and do not think that this fact tells us anything deep about the world. It is also clear that the log-log regression analyses are appropriate for identifying type A invariants.

In type B invariance, the ratio of the two variables is tightly constrained and, as noted by Savage *et al.*, it does not change. We would find this kind of invariance interesting because it would reveal what Savage *et al.* refer to as "fundamental and pervasive constraints." Other readers have also found this type of invariance to be the interesting type: Maynard Smith, for example, wrote of one invariant: "*M/b* is approximately constant (≈0.2) for species as different as the tree sparrow and wandering albatross" (*4*). The purpose of our paper was to show that the log-log regression analyses cannot identify this type of invariance. This is easily demonstrated by constructing data that no one would consider invariant and showing that the log-log regression analyses return a slope of 1 and perhaps also a high R^2 value. So statements such as the following in the figure legend from Charnov's monograph [(*2*), p. 65] are non sequiturs: "$\log_e M$ versus $\log_e k$ for 17 stocks in the fish family Scombridae (tuna and mackerel). The slope of unity means that *M/k* is a constant equal to 1.7."

Demonstrating that the ratio *X/Y* may be highly variable even though a regression of $\log Y$ against $\log X$ has a slope of unity and a high R^2 is straightforward. It is factually incorrect to say that our arguments depend on a combination of boundedness and the assumption of a uniform distribution. Anyone with a statistical package that can generate random numbers from different distributions can readily confirm this. The particular formula we derived depend on the assumption of a uniform distribution, but the point we were making does not. Note 9 in Savage *et al.* (*3*) should be read in this light. It should also be noted that type B invariance is a subset of type A. We consider it to be the interesting subset and believe the importance widely attached to invariance is predicated on its being of type B.

Regarding the other points made in (*3*), we are surprised by the inclusion of figure 1 and associated discussion. In our final paragraph in (*1*), we clearly stated that differences among taxa in dimensionless, but not necessarily "invariant," quantities are interesting. Indeed, we specifically discussed the data shown in figure 1 in (*3*) in this context, considering the ratio of age to maturity and adult life span. We reemphasize the need to distinguish between the dimensionless approach and the assumption of invariance.

With regard to figure 2 in (*3*) and the associated discussion, as mentioned above, the uniform distribution plays no central role in our argument. As stated in our original study (*1*), "the uniformity of the data is not relevant to the question of invariance because nonuniform distributions can be highly variable, whereas a uniform distribution may have tight bounds." Finally, the Savage *et al.* critique of our analysis of clutch size and annual mortality does not grasp the nature of our analysis. The purpose of our calculations was to show that the observed relationship follows immediately from a model in which nothing of biological interest is occurring. It does.

We certainly do not claim that life history theory implies that invariants show no variation. According to Charnov (*2*), "…the invariance holds only in a statistical or probabilistic sense. Most life history variables estimated for field populations are noisy…How constant is constant enough to be considered invariant is worthy of much thought…" It is difficult to construe this as referring to anything other than type B invariance.

References

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3. V. M. Savage *et al.*, *Science* **312**, 198 (2006); www.sciencemag.org/cgi/content/full/312/5771/198b.
4. J. Maynard Smith, *Q. Rev. Biol.* **68**, 557 (1993).

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