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Life history invariants: broken beyond repair?

Here's a study that *won't* be reported in the science press, but is much more important to evolutionary theory than anything else I've read this month.

Sean Nee and colleagues write in the August 19 *Science* that attempts to construct an overarching theory of animal life history evolution may be written off because of a fundamental methodological error.

The problem comes down to a simple error in interpreting log-log plots.

Here's the abstract:

> Life-history theory attempts to provide evolutionary explanations for variations in the ways in which animal species live their lives. Recent analyses have suggested that the dimensionless ratios of several key life-history parameters are the same for different species, even across distant taxa. However, we show here that previous analyses may have given a false picture and created an illusion of invariants, which do not necessarily exist; essentially, this is because life-history variables have been regressed against themselves. The following question arises from our analysis: How do we identify an invariant?

The development of the idea of "invariants" in life history is due to Eric Charnov (reviewed in Charnov 1993). The idea is that if you examine the ratio of two dimensions of life history -- for example, the ratio of maturation age to average adult life span -- that the ratio is constant across species. If this were true, then a major aim of life history theory would be to explain why these invariant ratios have the values they do. Presumably, the ratios found across animal species would reflect ecological trade-offs -- for example, bigger animals require more time to develop, and therefore must extend their adult life span proportionately longer to allow for the risks of juvenile mortality, costs of investing more in offspring, or some other constraint.

The idea of invariants is not derived from theory -- it is an argument based on empirical observations. When you plot an life history traits from different species against another trait, in many cases you find that the logarithm of one is linearly related to the logarithm of the other, with a slope very near 1.0. This would be precisely the relationship you would expect *if* the ratio between the two traits were constant.

What Nee and colleagues demonstrate is that the converse is *not* true. Although an invariant ratio does lead to a log-log slope near 1.0, a log-log slope near 1.0 may result from many relationships *other than* an invariant ratio. In particular, a *random* set of ratios will still generate a log-log slope near 1.0.

A commentary by Gerdien de Jong (subscription required) explains the paper.

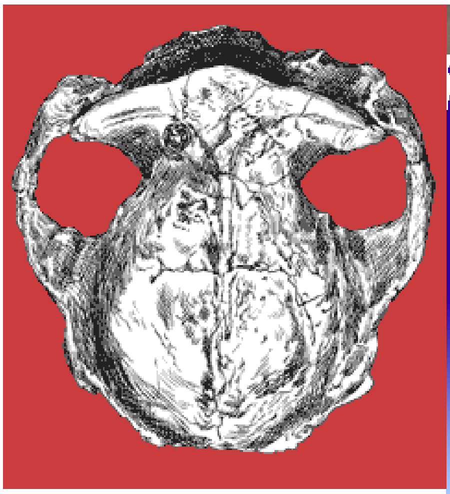
> But Nee et al. (2) describe the general rationale of how slopes of 1 at high R^2 arise in log-log plots, independent of the distributions of the traits. The culprit is a variable on the y axis that is a fraction of the x-variable: The plot is of $y = cx$, with $c < 1$. In a log-log plot of cx versus x, a slope of 1 follows automatically. A wide range on the x axis--from rabbit to whale--guarantees a high R^2. The evidence for life history invariants vanishes as the method of finding them evaporates (de Jong 2005:1194).

Why does this happen? Simply put, a short-lived species *must* have a shorter maturation age than its average life span, but not *too* much shorter. The slope of 1.0 comes from this fact alone: one variable is *constrained* to be close to the other, owing to the fact that it is some substantial *proportion* of that other variable.

Why should the correlation be high? The answer to this should be familiar to any paleontologist: it's a mouse to elephant curve. The independent variable ranges across so many orders of magnitude that the variance about the regression essentially disappears.

The essential emptiness of the theory arises here:

> The most notable invariants are typically taken to be those that hold over several orders of magnitude of variation in the value of the biological characters; we now see that it is this wide variability of the characters that inevitably makes the invariants notable (Nee et al. 2005: 1238).



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When I read through Charnov's book (*Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*), it was with an eye toward the relationship of average life span to maturation age. Personally, I found the log-log plots less than convincing, because there was too much variation hidden in them. A 0.95 correlation on a log-log plot across primates still allows individual values to vary by a lot, just because a log-log plot appears to smash the variation down so much.

This study attacks the basis of the theory much more directly:

> From the time of the introduction of invariants, many other studies and discussions have accepted their existence on the basis of these sorts of demonstrations and attempted to explain them theoretically or infer their consequences. For example, in his review of the canonical monograph on life-history invariants (1), Maynard Smith refers to the M/b data we have just discussed and says "M/b is approximately constant (0.2) for species as different as the tree sparrow and wandering albatross"(31). This is in spite of the fact that the data to which he is referring show the ratio varying between 0.1 and 0.5. Maynard Smith was not the only reviewer to accept that this ratio is constant (32), and the status of these life-history invariants is such that they have now found their way into the popular physics literature (33). In fact, in a population of constant size, the ratio M/b is, essentially, the probability of surviving from egg to breeding age and therefore is constrained to be between 0 and 1 (Nee et al. 2005: 1238).

This was certainly my perception for the primates. There was a strong claim that the values of interest were invariants, *despite the fact that the data themselves show fairly wide variation in the actual ratios*.

What is the solution to this problem for life history theory? Nee et al. suggest comparisons with other dimensionless values; de Jong suggests a direct examination of fitness relations in different species. The latter approach seems the most likely for hominoids, although this essentially amounts to a species-specific examination in each case.

What I wonder is whether other kinds of relations -- ones we may be more familiar with -- may prove to be manifestations of the same error. I'm going to be looking through some papers in the next few days with that in mind.

References:

Charnov E. 1993. Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology. Oxford University Press, Oxford.

de Jong G. 2005. Is invariance across animal species just an illusion? Science 309:1193-1195. Full text (subscription required)

Nee S, Colegrave N, West SA, Grafen A. 2005. The illusion of invariant quantities in life histories. Science 309:1236-1239. Full text (subscription required)

Posted at 00:50 on 08/19/2005 | *permanent link*

John Hawks
Department of Anthropology
University of Wisconsin—Madison