Countdown to 150

Invisible Trade-offs: Van Noordwijk and de Jong and Life-History Evolution

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

When I started my PhD in 2000, I was a part of a cohort of graduate students delighted with the prospect that evolutionary biology could be used to predict and explain patterns of traits observed in nature. We were surrounded by a wealth of wonderful theory at varying levels of abstraction from reality, and our goal was to apply this theory to data from the specific systems that we studied.

Making predictions about traits in evolutionary biology invariably involves discussions of trade-offs. Everything eventually comes back to survival and fertility, and if there is nothing to hold back survival (or fertility), you can predict nothing more interesting than that survival (or fertility) should be maximized. Consequently, almost every graduate student in my cohort was looking for a trade-off. Not one of us could find one. It was frustrating; we thought Darwinian demons were unlikely. We knew that, somewhere, allocation decisions must have a cost; but in systems ranging from birds to plants, none of us had any success in quantifying anything that looked like one fitness component going up while another came down. In my system, plants that grew better also survived better and often produced more seeds.

And then one of us stumbled across van Noordwijk and de Jong's 1986 paper in *The American Naturalist*. There are many reasons to treasure this paper—for example, it contains my favorite definition of life-history theory: "an elaborate answer to the simple question of why having more offspring is not always selected for" (p. 137)—but it also contains a possible solution to the problem that my cohort had been wrestling with.

Van Noordwijk and de Jong bring up what they refer to as the "trivial but very real" fact that there is heterogeneity across individuals: some individuals have access to more resources than others do. This might result from luck alone, but the authors suggest that it could also be genetically based. Using an elegantly simple model, they demonstrate why this fact might conceal trade-offs. One wonderfully intuitive figure (reproduced here as fig. 1) captures a really important idea: trade-offs will be unobservable if variance in acquisition of resources swamps variation in allocation of resources.

In late 1984, Gerdien de Jong was an assistant professor at Utrecht University. A postdoc, Arie van Noordwijk, walked into her office to bounce around ideas about some puzzling results from his research. He was finding that trade-offs in *Daphnia* seemed to be altered by the amount of food in the test tubes they were raised in. They chatted, they both thought some more, and de Jong wrote down the math that evening. As she told me by e-mail, "The paper wrote itself."

The logic starts from the basic premise that resources not allocated to survival (S) will go to reproduction (R). The innovation is that the fraction of resources allocated to each demographic rate (B), but also the absolute amount of resources available (A), are assumed to vary across individuals (indicated by the lines with different values of A and B in fig. 1*a*). From this basis, van Noordwijk and de Jong precisely define when survival and reproduction are expected to positively covary (fig. 1*b*) and when they should negatively covary (fig. 1*c*) as a function of the variance in allocation (B) and acquisition (A).

As well as the startlingly powerful visualization of a subtle idea (in a figure whose existence van Noordwijk told me was suggested by an anonymous reviewer!), this paper also provides a relatively simple yardstick for applying the key concept to natural systems. Although "units" of resource are notoriously hard to pin down, van Noord-

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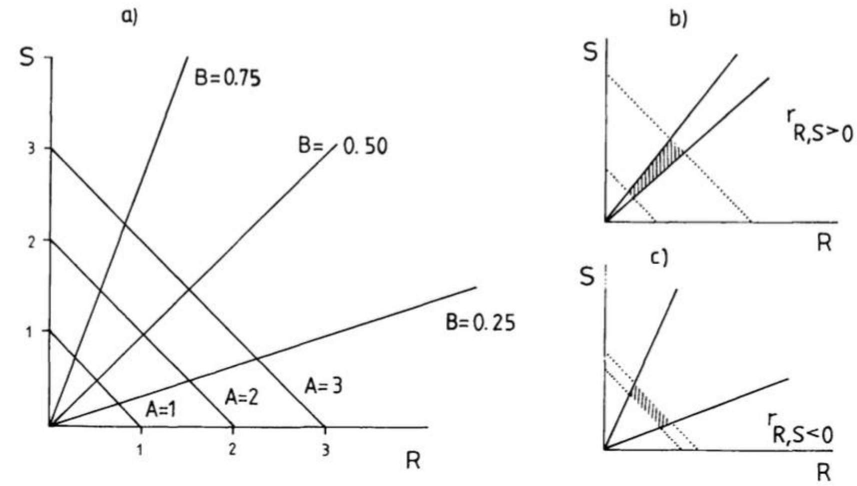

FIG. 1.—An illustration of the model: *a*, the components *A* for the total investment and *B* for the allocation between life history traits *R* and *S*; *b*, the variation in *A* is large and the variation in *B* is small, such that *R* is positively correlated with *S* (observations lie in the hatched area); *c*, the opposite case.

Figure 1: From van Noordwijk and de Jong (1986).

wijk and de Jong contend that if whatever is being measured has a broadly monotonic relationship with energy, then positive correlations will suggest dominance of acquisition and negative correlations dominance of allocation. In practice, when the number of traits exceeds two, identifying whether allocation or acquisition is dominating can rapidly become complicated, but the insight remains profound.

Van Noordwijk and de Jong were not the first to introduce this idea. Bruce Riska (1986, "Some Models for Development, Growth, and Morphometric Correlation," *Evolution* 40:1303–1311) and J. W. James ("Genetic Covariances under the Partition of Resources Model," appendix 1 in A. K. Sheridan and J. S. F. Barker, 1974, "Two-Trait Selection and the Genetic Correlation. II. Changes in the Genetic Correlation during Two-Trait Selection," *Australian Journal of Biological Sciences* 27:89–101) had offered similar concepts. However, van Noordwijk and de Jong's lucid description, both verbal and mathematical, has made this paper justly influential. Empirically supported and heavily cited, it has provided us with a key explanation for failures to find trade-offs but also underscored the importance of using controlled conditions in attempts to demonstrate the existence of trade-offs. The issue that led me originally to this paper—that is, quantifying trade-offs in natural populations—remains a knotty one. Quantitative genetics approaches initially seemed like a hopeful avenue. Since purifying selection should minimize genetic heterogeneity, moving beyond the "phenotypic gambit" (J. D. Hadfield, A. Nutall, D. Osorio, and I. P. F. Owens, 2007, "Testing the Phenotypic Gambit: Phenotypic, Genetic and Environmental Correlations of Colour," *Journal of Evolutionary Biology* 20:549–557) to focus on the underlying genetics seemed likely to contribute to pinning down allocation decisions. However, this promise has remained largely unrealized, barring a few exceptions (J. K. Conner, 2012, "Quantitative Genetic Approaches to Evolutionary Constraint: How Useful?" *Evolution* 66:3313–3320).

Overall, although decades of research in evolutionary ecology have thrown up an array of evidence for trade-offs (from the nearly ubiquitous seed-size/seed-number tradeoff in plants, to evidence for antagonistic pleiotropy in a number of systems), trade-offs are arguably less ubiquitous than anticipated by basic life-history theory. Various lines of research suggest that negative relationships are probably lost in the noise of multiple allocation decisions involving multiple labile traits and complex associated signaling pathways. Indeed, most of the mechanisms that give rise to trade-offs remain a mystery, despite the fact that characterizing trade-offs is likely to be essential to elucidating the determinants of variation in natural systems. Here again, van Noordwijk and de Jong's insights are essential, highlighting the importance of careful control of resource heterogeneity in this body of research (e.g., in H. F. Nijhout and D. J. Emlen, 1998, "Competition among Body Parts in the Development and Evolution of Insect Morphology," *Proceedings of the National Academy of Sciences* 95:3685–3689).

It can be argued that much of ecology and evolution comes down to trying to describe the processes that push distributions of traits around. Thinking clearly about the drivers of this variation can be rather counterintuitive, but van Noordwijk and de Jong provided us with a wonderfully clear template for starting to do so.

Acknowledgments

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In *The American Naturalist*

van Noordwijk, A. J., and G. de Jong. 1986. Acquisition and allocation of resources: their influence on variation in life history tactics. American Naturalist 128:137–142.

"Among the wood-cuts the antelopes, elands, spring-bock, hartebeest and their allies, are well rendered. . . . The American reader will find that some of the characteristic ruminants of his country are well drawn, as in the Rocky Mountain sheep [illustrated] and the musk ox." From the review of "Recent Literature: Brehm's *Animal Life*" in (*The American Naturalist*, 1878, 12:682–685).