Natural selection like it is[1]

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Natural Selection in the Wild. By J.A. Endler. 1986. Princeton: Princeton University Press. 336 pp. $40.00 hardbound, $13.95 paperbound.

It perennially astonishes me that people think there is little evidence for the actual operation of natural selection. Intelligent people. Reasonably well-informed people. I don't mean the general importance of adaptation, doubts of which also astonish me (although I reviewed diverse mechanisms of nonadaptive evolution as early as 1960), but real, specific occurrences of natural selection.

I suppose much of the problem is that there has been no good review of the subject. Books by Johnson (1976), Sheppard (1975), Ford (1975), and others are useful but consider rather few cases, so the casual reader might (and, I infer, often does) conclude that there aren't any more to discuss. I have been collecting evidence on the subject for many years with an eye to providing a balanced overview some fine day. Endler has scooped me, in part, for which we can all give hin thanks.

The book should become an instant classic. At both the theoretical and empirical levels the author knows what he is doing and provides a (usually) clear path through some rather dense thickets of several kinds. The scope of the book is rather narrow but its focus is probably improved thereby.

The empirical part of the book begins with a detailed and critical treatment of how selection in natural populations is detected so that it can be measured. Endler classifies the subject into ten "methods." These lead into a discussion of how false positives and false negatives for individual cases can occur, again with many categories. With this background he gives a table of several hundred cases he accepts. (I am doubtful about a few of those he includes, for reasons such as possible change with age in the character studied, and he would probably be more skeptical than I am about some others. I have no idea, for instance, why he omits all cases of selection on chromosomal inversions in the Diptera. We each also have records of cases the other has overlooked.) They are from many groups of (multicelled) animals and plants; cases also exist among bacteria and, if I recall correctly from my differently organized file, among protists and perhaps fungi. A wide variety of traits and most of the possible kinds of individual selection are represented.

Endler then uses these results to examine the distribution of the strength of selection. In the 1960s I started a program to examine selection on randomly chosen characters and organisms (random with respect to expectations, not feasibility) but found that this brute-force approach to estimating the distribution was impractical. Because of literature bias the distribution from published cases can't be taken at face value, and the set of values not significantly different from 0 undoubtedly incorporates a hidden or virtual distribution of relatively low values. Nevertheless Endler is able to show that strong natural selection, even in the range of that practiced in artificial selection, is common. "The frequent statement that selection is usually weak in natural populations is without merit."

Endler omits a lot deliberately. Most importantly, he excludes all cases other than those of individual selection. In fact, extraordinarily, he even <u>defines</u> natural selection to exclude all other levels. But it's the same process with

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different materials, and close study of other levels can illuminate the nature of selection on individuals. (He also doesn't consider the frequent discordance of our criteria of individuality with each other; it often isn't clear just where to draw boundaries among individuals. What then is individual selection?)

Local interspecific competition is a form of selection which can usefully be regarded as occurring at both the individual and group levels. An individual dies or multiplies because of its own properties in relation to its particular environment, yet these properties are (mostly) not uniquely its own but characterize a larger and unified group (population, species, etc.) to which it belongs. Selection among clones provides an intermediate case. Similarly, differential mortality among species in a community, caused by their own species-level properties (susceptibility to heat, predation, etc.), is also selection which has properties of both levels. Maximum reductionism applied to situations like these loses part of what is actually happening.

Endler oddly defines natural selection to include both the selection itself and the population's genetic response to it. Note that there can be even one-locus selection with no response, as in balanced polymorphism, and (as Endler notes) also a response in the absence of any heritability at all, with transmitted or otherwise correlated environments. More importantly, though, Endler's definition denigrates the importance of the phenotype. Mayr once said (orally) that he had been "brainwashed by Dobzhansky" into thinking that the phenotype was just a barrier on the way to the genotype, rather than the main focus of evolution itself. To treat evolution as merely a change in gene frequencies is to lose sight of most of evolution, both causally and phenomenologically. Mayr more or less recovered; I hope others will too.

No specific cases are discussed in any detail in this book; there is no natural history, although Endler does realize its importance.

The book contains the clearest discussion I know of the various indices, statistics, and relevant theory for measuring natural selection on one or more characters. (For users of Smith's test for comparing variances, p. 172, see the correct formulas in Evolutionary Theory 4: 202 [1980] and 7: 194 [1985.]) Endler also gives an interesting classification of views on the importance of selection. His more abstract discussions seem to me less successful, but to defend this assertion would be a discourse in itself.

One point, though, needs mention, and that is Endler's cavalier dismissal of the problem of "genetic" load, with a nod to Bruce Wallace. I was perhaps the first to show how the problem of load can be ameliorated (Van Valen, 1963a, where I also extended it to genome-wide heterosis and called the problem "Haldane's dilemma"), but this isn't the same as eliminating it. Take my study of selection in the extinct horse Merychippus primus (Van Valen, 1963b), included in Endler's tabulation. As I noted then, the amount of mortality required to account for the inferred selection was close to the total mortality in the interval used. It would not have been possible for there to have been similarly intense selection on any uncorrelated character during this interval. That is the significance of phenotypic load: the load space (another way of looking at the subject of Crow's index of opportunity for selection) determines how much selection can possibly occur. That's why Haldane developed it (he called it a "cost"), and indeed why Kimura developed his theory of neutral evolution (but see Van Valen, 1984.) There remain problems in partitioning and measuring this space and assessing interactions, although perhaps no longer in bounding it, but we shouldn't ignore it. "The situation is similar, except for the element of intent, to one that is familiar to livestock breeders. With very intensive selection for particular characters, others must be allowed to vary at random if numbers are to be maintained" (Wright, 1948, p. 285.)

You need this book.

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