# Is the Wright way right?[1]

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Sewall Wright and Evolutionary Biology. By W.B. Provine. 1986. University of Chicago Press. 545 pp. $30.00.

We have all heard introductions of lecture speakers who start by saying, "Dr. Zilch is someone who needs no introduction," and proceed to introduce the speaker at length. We all think we know the major aspects of Wright's work. Do we? Provine's book is not a substitute for Wright's treatise (which, as Provine suggests, may best be read in reverse order) or his later work, but it is intellectual history of the first water. Although I am not an avid reader of biographies, I do not recall any which come even close in quality. A superb book.

No, one doesn't learn what Wright had for dinner in 1921. There is basic personal information, but after all what makes a person like Wright interesting is his intellectual contribution. That is the focus of the book, and an author requires biological as well as historical understanding in order to be able to treat such material competently. This Provine has, although his comments on current matters are sometimes less than perfectly informed. He notes that his extensive conversations with Wright, apparently (and surprisingly) an innovative method for historians, prevented various plausible errors which would have occurred on the basis of the written documentation only.

I won't summarize the book except to note that it treats Wright's work, in a fully integrated manner, and his intellectual interactions with others, especially Fisher and Dobzhansky, about equally. (It's D.M.S. Watson, Will.) One item not mentioned here or elsewhere by Provine: For years Dobzhansky had two framed dimes, with cards saying how they were won as wagers, on the north wall of his office at Columbia. One was stated to be from Wright for there being a selective basis for the inversion polymorphism in *Drosophila pseudoobscura*. Dobzhansky is portrayed by Provine as rather a bumbling mediocrity with respect to theory. While I don't treasure his memory (he made me one of his many non-persons after I had the temerity to disagree with him), he wasn't stupid or noncreative. He was merely non-mathematical. As one may see in the case of Darwin, development of theory doesn't always require mathematical equipment.

Provine has two major reinterpretations of Wright's work. One is that Wright indeed gave a greater role to selection after the early 1940s than he had earlier, because of the accumulating field evidence for its importance. Neither Wright nor I (nor many others) had noticed this change, and it means that one can't read all his work as penecontemporaneous, as is commonly done.

The other reinterpretation is a bombshell in the adaptive landscape. "It should give pause to consider that for over fifty years the majority of evolutionary biologists have believed Wright's 1932 diagrams of adaptive landscape to be the most heuristically valuable diagrams in all of evolutionary biology, yet to discover that the surface as he conceived it is unintelligible" (p. 316.) Such an indictment requires adequate documentation, which Provine gives.

There are two points, in addition to some people's (including Simpson's) confusion of Simpson's phenotypic landscape with Wright's genotypic ones. (Another useful kind, with a phenotype x environment base, is given by Dodson [1975] and Dodson and Hallam [1977], and Wright mentioned to Provine the obvious polygenic

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depiction of Simpson's landscape.) The first is that Wright has used, and more or less interchanged, two formally and conceptually incommensurable bases for a landscape: (1) genotypes within a population and (2) mean gene frequencies of populations. Only the former conceptualizes gene interaction. The second point is that Wright's first kind of surface isn't a surface at all because it is composed of isolated points which aren't unambiguously ordered. Provine says that Wright agreed with his assessment in 1985.

I don't agree with either point, although Provine does adequately show that Wright could have been clearer in his presentations. A minor problem is Provine's getting mired by a strictly frequentist interpretation of probability, which causes so many problems (and not just in genetics) that I wonder why it is still so prevalent.

Yes, genotypes are discrete, and yes, more than one ordering is possible. But lots of orderings make no sense, while a (relatively) few do. If any allelic substitution from genotype G gives a lower fitness than G has, G is at an adaptive peak. And so on. Ordering is by a multidimensional network (strictly, set of networks), where the nodes are genotypes and the internodes are single-gene substitutions. In a diallelic haploid situation only one ordering is even possible. A stronger criticism might be as to what, precisely, the various axes represent (in a well-formed diagram they are merely the set of allelic states at a locus), but this doesn't affect the imagery of peaks.

As to the supposed incommensurability of the two landscapes, Wright (1963, fig. 4) shows how they can be combined. The genotypes provide discrete peaks and valleys as before. Then let each genotype now represent a homozygous population. (Heterozygosity merely requires additional mental effort.) The quasicontinuous surface of intermediate frequencies connecting the genotypes provides the familiar saddles, peaks, and valleys. I don't think this is at all esoteric, and I think it is a useful and basically correct, if nonrigorous, representation.

As Wright has pointed out, and Provine notes, there is excellent evidence for pervasive epistasis, despite the usually null (and equally compatible) results from isozymes. If a trait has its phenotype determined by even a totally additive set of genes (and environments), then in the very common case of an intermediate optimum there will <u>necessarily</u> be strong epistasis on the fitness scale. It is the latter that Wright's theory uses. But this situation doesn't in itself provide a block to selection, because a shift of the optimum (a vertical movement or wave in the landscape itself) doesn't create a saddle between the old and new optima. Mass selection suffices here. I think this aspect is important and, as far as I know, is not treated in this context by Wright, although he does consider environmental change in a secondary way and random variation in selection coefficients as a way of escaping local optima. He has a real need for drift to move populations to regions where higher optima are accessible only when relevant aspects of the (total) environment are insufficiently variable. The epistasis creating inaccessibility of peaks must therefore be from causes other than the presence of intermediate phenotypic optima. I don't doubt that such epistasis is real and central, but a demonstration is less easy than it appears and will presumably come from a better understanding of the control of the realizable paths of development, another major interest of Wright's.

I had not realized that Wright's shifting-balance theory (individual selection, drift and random variation in selection, interdemic selection) was based on the optimal conditions for artificial selection rather than primarily on a consideration of the natural world. It is thus surprising that the theory corresponds as well as it does with reality, that the world is often enough constructed so as to give such optimal evolution. This origin may also explain Wright's inattention, and that of his followers, to variation of the biotic and physical environment in time and space, and thus the omission of ecology from the New Synthesis until much later.

Provine thinks that Wright's interdemic selection doesn't deserve that name because it amounts to the wave of advance of an advantageous genotype. I used to think so too, but now I agree with Wright. Yes, the process reduces to individual selection when looked at from one perspective. So does all group selection if one pushes it hard enough; how hard one has to push (what criteria of groupiness must be ignored) varies among cases. But Wright's mechanism works only because there is a whole population with the advantageous genotype: if its individuals were scattered homogeneously throughout the distributional range the genotype would be broken up and selection would have nothing to work on. Similarly, a permanent zone of absence or low abundance of the species, wide relative to dispersal, is difficult or impossible to cross because the mechanism depends on the absolutely greater expected productivity (not merely greater per individual, except in founding new populations) of the expanding high-peak population. I wonder how important this constraint really is: such barriers are common in many species, but a high enough frequency of founding of new populations might often permit their crossing. So how much is a beautiful theory diminished by ugly fact?

Wright is arguably the most significant evolutionary biologist since Darwin. Despite my disagreements, Provine's book is worthy of him.

## Literature cited

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