Part III

BIOLOGY: THE NON-PROPOSITIONAL SIDE

Are Pictures Really Necessary? The Case of Sewell Wright's "Adaptive Landscapes"

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Biologists are remarkably visual people. Yet, the classics of logical empiricism never raised the general question of scientific illustration. Moreover, one suspects that the silence was, if anything, actively hostile. People did not talk about biological illustration, because they did not judge it to be part of "real science". This enterprise produces statements or propositions, ideally embedded in a formal system. It may be *about* the real world, but it is not in any sense *of* the real world, in being a copy or mirror image. Philosophers recognized that regretfully human weakness demanded the visual. But it was judged at best a prop. (See, for instance, Braithwaite 1953, Hempel 1965, and Bunge 1967; although see also Achinstein 1968. The best discussion of scientific illustration that I know is Rudwick 1976.)

As one who belongs to that growing school of philosophical naturalists, who think that one's philosophy must be informed and in accord with the methodological dictates of science, and that therefore one must be true to the real nature of science — not an idealized preconception — I am made most uncomfortable by this tension between the reality and the theory. At the very least, so major an item as biological illustration demands philosophical attention, whatever one's ultimate conclusion. Here, indeed, I shall look at but one example; although I hope that its great importance in the history of science will justify such selectivity. From among the many candidates, I chose the adaptive landscapes of the great population geneticist Sewell Wright. And the question I ask is: What was/is their status and role within evolutionary biology? (Although I differ from Provine 1986 in my assessment of the virtues of Wright's picture, my debt to him should be apparent on every page.)

1. Adaptive landscapes.

Sewell Wright's first job after leaving graduate school (Harvard) was with the US Department of Agriculture. In 1926 he was appointed to the faculty at Chicago, and it was about this time that he wrote his major paper in evolutionary theory (Wright 1931). Much of the text of this paper is given over to complex mathematics — at least by biological standards, especially by biological standards of the day. Wright concerns himself primarily with the fate of genes in populations, under given conditions of selection, mutation, and so forth, and he is interested in the consequences of popu-

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lation sizes being genuinely finite and thus subject to random factors in breeding (errors of sampling). He is able to show that if population numbers are large enough, and the forces are strong enough, then selection and like factors determine the fates of genes. For instance, a favoured gene or gene combination will establish itself in a population. However, what Wright is able to show also is that if population numbers are small (judged against the other factors), then genes will "drift" either to total elimination or total fixatio— despite counter-forces of selection and the like. Chance becomes a real phenomenon for change.

To illustrate the mathematical points, Wright gave graphs showing possible effects, and these together with the formal conclusions were used to launch Wright's own particular theory of evolutionary change: the "shifting balance" theory. [fig.1] Wright argued that very small populations would suffer from significant drift and rapidly go extinct. However, conversely, large populations under fairly uniform selective pressures would not truly be candidates for any significant change, good or bad — or at least that they could incorporate only *very* slow and stately change. For significant change, within realistic timespans, one needs a more dynamic mechanism. This is provided by the breaking of a species into sub-populations, of a size-order where drift could be effective — but not of a size so small that drift could be too effective! Every now and then such a sub-population would, by chance, come up with a highly adaptive gene complex, and then this combination could take over the species, either by direct selective elimination of rivals or by interbreeding.

Wright's theory transcends his formalisms. It is based on them but is not identical, being more inclusive (more falsifiable, in Popper's terminology). There is nothing in the formalisms about species subdividing, about new adaptive complexes being hit upon, about insufficient time for selection in large groups, and so on. This is added. Significantly, Wright and Fisher agreed on the mathematics, but because Fisher added different non-formal elements, he came up with a very different theory of change. (Most importantly, Fisher 1930 believed that selection in large groups *did* hold the key to evolution.)

Wright's paper, a long paper, appeared in the journal *Genetics*. The next year (1932) he had a wonderful opportunity to promote his theory, because he was asked (by E M East, his doctoral supervisor) to participate in a forum (with Fisher and with the third great theorist, J B S Haldane) at the Sixth International Congress of Genetics, at Cornell. Normally, Wright was as given to long mathematical demonstrations in lectures as he was in print, but here he was forced to keep his presentation very short — and urged to keep it simple. To do this, he dropped the mathematics entirely, presented his shifting balance theory in words (as he had done in his long paper) and backed up his thinking with a new metaphor, which he presented pictorially: the *adaptive landscape*.

Wright wrote, and illustrated, as follows:

> If the entire field of possible gene combinations be graded with respect to adaptive value under a particular set of conditions, what would be its nature? Figure 1 [Fig. 2] shows the combinations in the cases of 2 to 5 paired allelomorphs. In the last case, each of the 32 homozygous combinations is at one remove from 5 others, at two removes from 10, etc. It would require 5 dimensions to represent these relations symmetrically; a sixth dimension is needed to represent level of adaptive value. The 32 combinations here compare with 10^{1000} in a species with 1000 loci each represented by 10 allelomorphs, and the 5 dimensions required for adequate representation compare with 9000. The two dimensions of figure 2 are a very inadequate representation of such a field. The contour lines are intended to represent the scale of adaptive value.

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One possibility is that a particular combination gives maximum adaptation and that the adaptiveness of the other combinations falls off more or less regularly according to the number of removes. A species whose individuals are clustered about some combination other than the highest would move up the steepest gradient toward the peak, having reached which it would remain unchanged except for the rare occurrence of new favorable mutations.

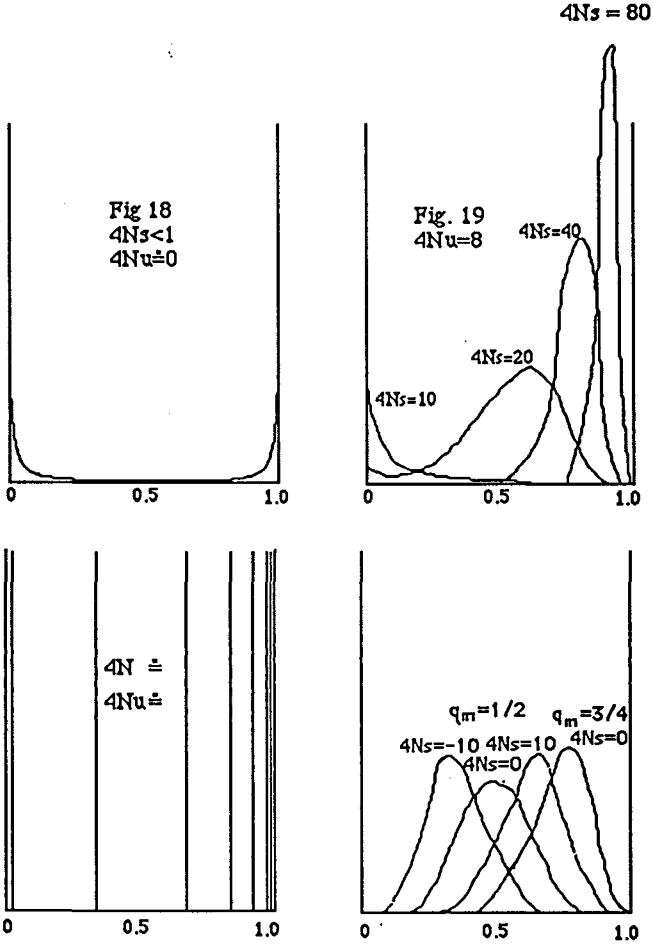

Figure 1. "Figures 18 to 21.–Distributions of gene frequencies in relation to size of population, selection, mutation and state of subdivision. Figure 18. Small population, random fixation or loss of genes ($y=Cq^{-1}(1-q)^{-1}$. Figure 19. Intermediate size of population, random variation of gene frequencies about modal values due to opposing mutation and selection ($y=Ce^{4Nsq}q^{4Nu-1}(1-q)^{4Nu-1}$. Figure 20. Large population, gene frequencies in equilibrium between mutation and selection ($q=1-u/s$, etc.). Figure 21. Subdivisions of large population, random variation of gene frequencies about modal values due to immigration and selection. ($y=Ce^{4Nsq}q^{4Nmq_m-1}(1-q)^{4Nm(1-q_m)-1}$."

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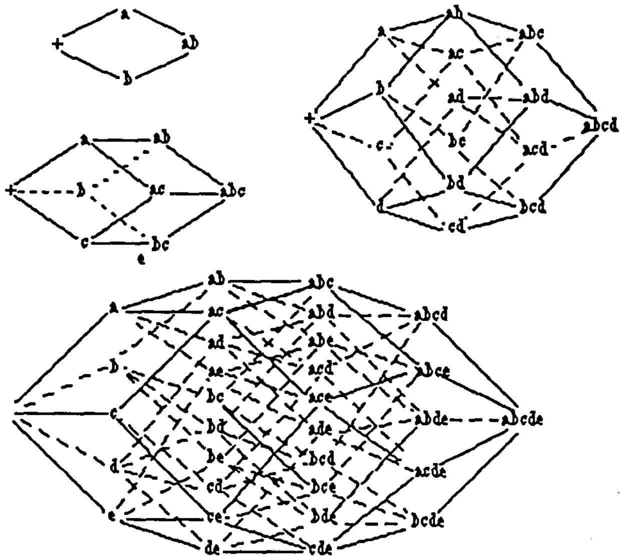

Figure 2. The combinations of from 2 to 5 paired allelomorphs.

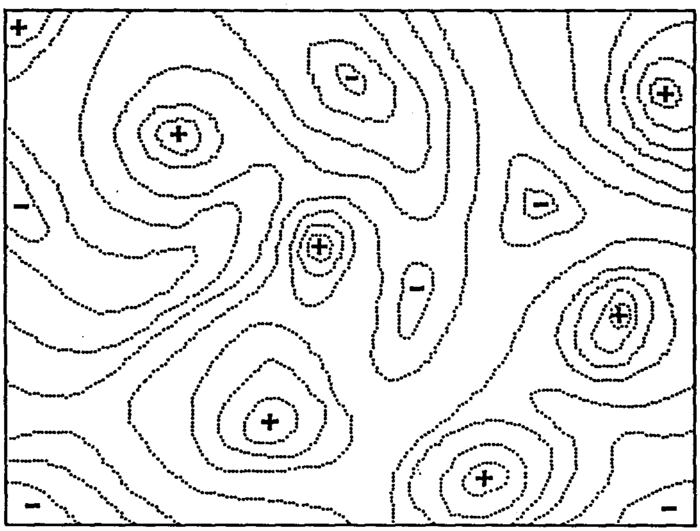

Figure 3. Diagrammatic representation of the field of gene combinations in two dimensions instead of many thousands. Dotted lines represent contours with respect to adaptiveness.

But even in the two factor case (figure 1) [fig 2] it is possible that there may be two peaks, and the chance that this may be the case greatly increases with each additional locus. With something like 10^{1000} possibilities (figure 2) [fig 3] it may be taken as certain that there will be an enormous number of widely separated harmonious

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combinations. The chance that a random combination is as adaptive as those characteristic of the species may be as low as 10^{-100} and still leave room for 10^{800} separate peaks, each surrounded by 10^{100} more or less similar combinations. In a rugged field of this character, selection will easily carry the species to the nearest peak, but there may be innumerable other peaks which are surrounded by "valleys." The problem of evolution as I see it is that of a mechanism by which the species may continually find its way from lower to higher peaks in such a field. In order that this may occur, there must be some trial and error mechanism on a grand scale by which the species may explore the region surrounding the small portion of the field which it occupies. To evolve, the species must not be under strict control of natural selection. Is there such a trial and error mechanism? (Wright 1932, 162-4)

Next Wright presented (without the mathematical backing) versions of the graphs of gene distribution that had been given in the large paper. [fig 4] He showed visually how drift and other phenomena can occur, given the right specified conditions. Then, using the landscape metaphor, Wright showed how the various options might or might not lead to change, and — as before — he opted for a position that involved a break into small groups, drift, and then reasonably rapid adaptive change in one direction. [fig 5]

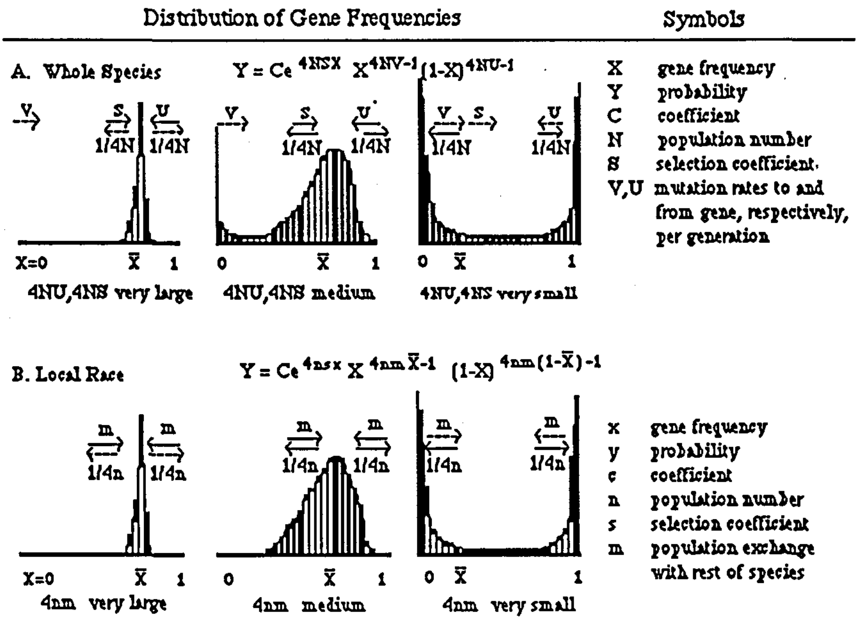

Figure 4: Random variability of a gene frequency under various specified conditions.

Finally (figure 4F) [fig 5], let us consider the case of a large species which is subdivided into many small local races, each breeding largely within itself but occasionally crossbreeding. The field of gene combinations occupied by each of these local races shifts continually in a nonadaptive fashion (except in so far as there are local differences in the conditions of selection). The rate of movement may be enormously greater than in the preceding case since the condition for such movement is that the reciprocal of the population number be of the order of the proportion of crossbreeding instead of the mutation rate. With many local races, each spreading over a considerable field and moving relatively rapidly in the more general field about the controlling peak, the chances are good that one at least will come under the influence of another peak. If a higher peak this race will expand in numbers and by crossbreeding with the others will pull the whole species toward the new position. The average adaptedness of the species thus advances under intergroup selection, an enormously more effective process than intragroup selection. The conclusion is that subdivision of a species into local races provides the most effective mechanism for trial and error in the field of gene combinations.(Wright 1932, 168)

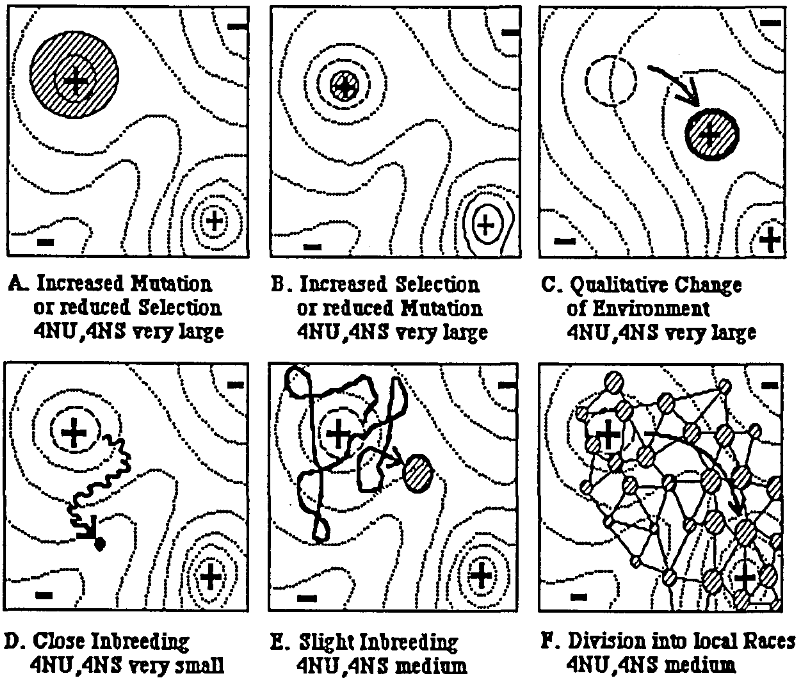

Figure 5. Field of gene combinations occupied by a population within the general field of possible combinations. Type of history under specified conditions indicated by relation to initial field (heavy broken contour) and arrow.

2. How important were the illustrations?

Let us start with the basic historical facts. Wright's talk was a great success. People grasped what he had to say and they responded warmly to his claims — at least, this seems to have been true of his American audience. Moreover, word seems to have got out, and Wright was flooded with reprint requests. Most important was the fact that among Wright's listeners at Cornell were active and ambitious young evolutionists, simply desperate for a good theory around which to structure their empirical research.

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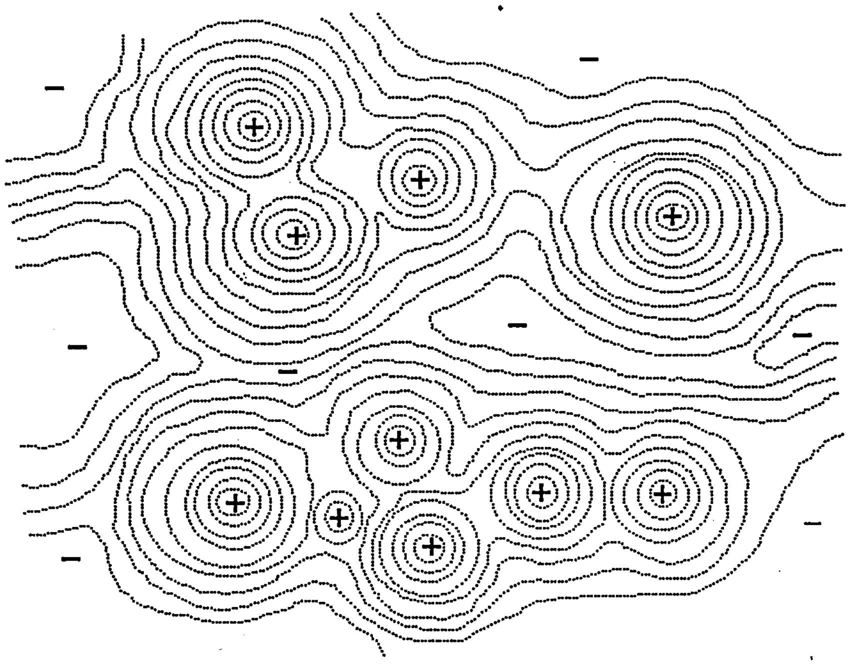

Figure 6. The "adaptive peaks" and "adaptive valleys" in the field of gene combinations. The contour lines symbolize the adaptive value (Darwinian fitness)of the genotypes. (After Wright.)

One of these people was the Russian-born Theodosius Dobzhansky, then working in Morgan's lab at Cal Tech. In his own words, "he simply fell in love with Wright", or at least with the ideas (Provine 1986, 328). Thus, when in 1936 Dobzhansky was invited to give the Jessup lectures at Columbia, Wright's shifting balance theory had pride of place, and in the published version next year — *Genetics and the Origin of Species* — Wrightian adaptive landscapes get (early) praise. It is not to much to say that the metaphor pervades the whole book.

> Every organism may be conceived as possessing a certain combination of organs or traits, and of genes which condition the development of these traits. Different organisms possess some genes in common with others and some genes which are different. The number of conceivable combination of genes present in different organisms is, of course, immense. The actually existing combinations amount to only an infinitesimal fraction of the potentially possible, or at least conceivable, ones. All these combinations may be thought of as forming a multi-dimensional space within which every existing or possible organism may be said to have its place.
>
> The existing and the possible combinations may now be graded with respect to their fitness to survive in the environments that exist in the world. Some of the conceivable combinations, indeed a vast majority of them, are discordant and unfit for survival in any environment. Others are suitable for occupation of certain habitats and ecological niches. Related gene combinations are, on the whole, similar in adaptive value. The field of gene combinations may, then, be visualized most simply in a form of a topo-

> graphical map, in which the "contours" symbolize the adaptive values of various combinations (Fig. 1). [fig 6] Groups of related combinations of genes, which make the organisms that possess them able to occupy certain ecological niches, are then, represented by the "adaptive peaks" situated in different parts of the field (plus signs in Fig.1). The unfavorable combinations of genes which make their carriers unfit to live in any existing environment are represented by the "adaptive valleys" which lie between the peaks (minus signs in Fig. 1). (Dobzhansky 1951, 8-9)

Dobzhansky's book had immense influence. It has fair claim to having been the most important work in evolutionary theory since the *Origin*. And with the influence has gone the Wrightian landscape — reproduced again and again, in work after work (not the least of which were Wright's own writings, which were using the original illustrations right down to the 1980s). In America, all of the major evolutionists and most of the minor evolutionists used the notion of a landscape, and although the British were not so keen on Wright's actual theory, the metaphor itself found its way across the Atlantic.

Most interestingly, those evolutionists who could not use Wright's landscapes directly adapted them to their own ends. As a paleontologist, G G Simpson(1944) could not work at the genetic level, nor could he think in terms of individual populations of a species. So he hypothesized landscapes of phenetic or morphological difference, and he supposed taxa of higher categories working their ways across the landscapes, down valleys and up peaks. Wright, incidentally, approved of this extension. [figs 7,8 and 9, taken from the later Simpson 1953]

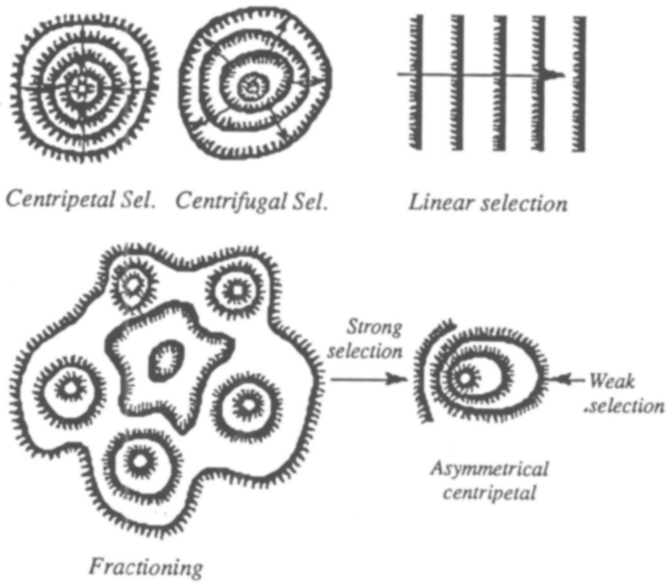

Figure 7. Selection Landscapes. Contours analogous to those of topographic maps, with hachures placed on downhill side. Direction of selection is uphill, and intensity is proportional to slope.

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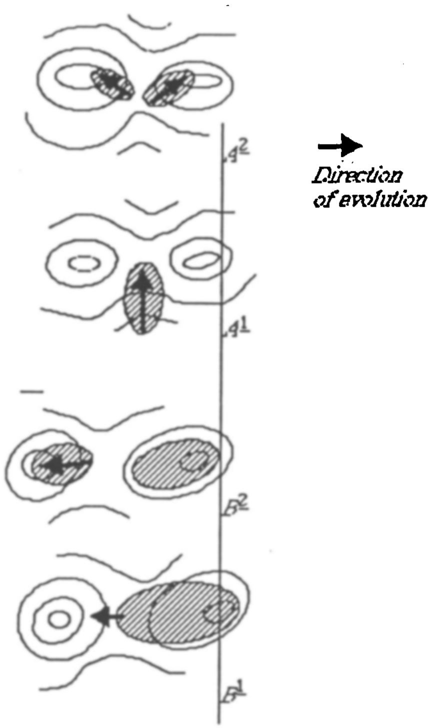

Figure 8. Two Patterns of Phyletic Dichotomy; Shown on Selection Contours Like Those of Figure 7. Shaded areas represent evolving populations. A, Dichotomy with population advancing and splitting to occupy two different adaptive peaks, both branches progressive; B, dichotomy with marginal variants of ancestral population moving away to occupy adjacent adaptive peak, ancestral group conservative, continuing on same peak, descendant branch progressive.

So much for history. Wright's idea of an adaptive landscape — where by "idea" I mean at the general level the metaphor, but at a specific level actual pictures, and usually the original pictures of Wright himself — became a commonplace in evolutionary thought. But speaking now at a philosophical level: Were the landscapes *really* part of evolutionary thought? Since Dobzhansky is generally taken as one of the founders of the "synthetic" theory of evolution, also known as "neo-Darwinism": Was Wright's metaphor in general, and his pictures in particular, *really* part of the synthetic theory of evolution, of neo-Darwinism?

The answer, of course, depends on what you mean by "*really* part of". The pictures were around in a big way, so they are clearly candidates for inclusion in a manner that for instance (to take an object entirely at random) the head of King Charles the First was not. The decision for inclusion must therefore depend on how one construes inclusion itself. Let us run through some possible senses.

At the most basic level, the pictures obviously are part of evolutionary thought. Evolutionists thought about them a great deal — and there is an end to the matter. I realize, of course, that many philosophers — all of those of the older cast of mind — will find this answer profoundly unsatisfying. They will claim that the question is not

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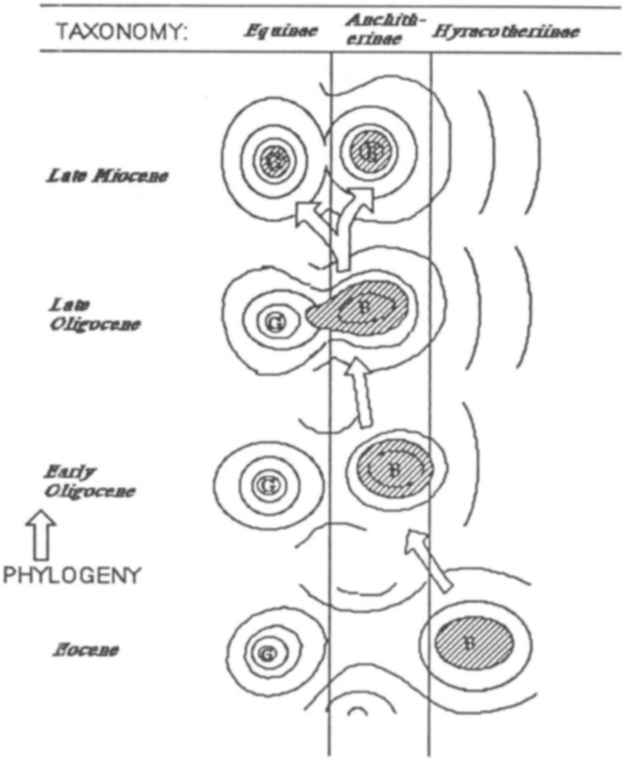

Figure 9: Major Features of Equid Phylogeny and Taxonomy Represented as the Movement of Populations on a Dynamic Selection Landscape.

whether people did think about them — we know that they did — but whether they *had to* think about them. Were the pictures an integrally necessary part of the science? Putting matters another way: The pictures were part of evolutionary thought. But, were they part of evolutionary *theory*?

In response, the argument for their necessity can easily be made a notch stronger. Not only were the pictures part of evolutionary thought, the scientists involved could *not* have done their work without the pictures. I speak now at the empirical level of psychological or intellectual ability. Wright's mathematics was simply too hard for the average evolutionist. It was certainly too hard for that very non-average evolutionist Theodosius Dobzhansky. He admitted again and again that he could not follow Wright's calculations. And he was not alone. G L Stebbins, another who heard Wright at Cornell, and later to provide the botanical arm to the synthetic theory, likewise was quite incapable of thinking mathematically.

But, they could understand the pictures! And so, as a matter of empirical fact, this was the level at which these men worked. They seized on the notion of an adaptive landscape and they experimented and theorized around it. Dobzhansky, for instance, studied natural populations of Drosophila, looking for evidence that they have drifted

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apart in a non-adaptive fashion (Lewontin *et al* 1981). As it happens, at first he did think he had evidence for his hypothesis. Then he found evidence against it. What is important is that, in both cases, in was at the picture level that he was thinking, because quite frankly he could do no other. In this sense, therefore, history supports the philosophical claim that the pictures were necessary. The science would not have been done without them.

"The science would not have been done without them"? Here the traditionalist will call a halt. The important point surely is whether the science *could* not have been done without the pictures. A philosophical analysis tries to strain out the fallibility of the individual and aim for the ideal. Moreover, the claim will probably be that the ideal, that which is in some sense preferable, would do away with the pictures. In a perfect world, the pictures could and would go.

Let me say simply that I find unconvincing the flat *a priori* dictum that the abilities of the scientists involved must necessarily (obviously?) be excluded from any adequate philosophical analysis. To the contrary, my feeling now is that the philosopher should start with the empirical necessity of the pictures and base his/her analysis on that. However, again for the sake of argument, let us grant the traditionalist the point. Still there are problems. At the least, one has to admit that the pictures were important, and may indeed now still be important, if not always in the future. And by "important" here I do not just mean "helpful". We have seen that the formalisms themselves did not express Wright's theory fully. The formalisms alone were shared by Fisher, who had an altogether different theory. The adaptive landscape idea went beyond the formalisms, expressing the notion that drift could generate variation in isolated populations, and that selection could then act to bring about rapid change. Moreover, let me point out that this, more than anything, was the *theory,* so the traditionalist cannot wriggle out of the claim that the adaptive landscape idea was (and may still be) part of Wright's basic science.

The response no doubt will be that although Wright's theory clearly did go beyond the formalism (because at that stage it was "immature"?!), the claim for the necessity of the pictures can be jettisoned. After all, in the main 1931 paper there were no pictures or even the metaphor. Everything that needed to be said, could be said and was indeed said, in words, literally.

In reply to this I will say three things. First, I simply do not know whether or not Wright had the landscape metaphor in mind when he first thought up his theory. We know that it predated publication of the 1931 paper, because it is used in an earlier letter to Fisher. Wright may have had it all along. I do know that the young Wright (and the old Wright, for that matter) was an Henri Bergson enthusiast, and something very much like the adaptive landscape metaphor occurs in *Creative Evolution* (published in 1912). It could well be that Wright was thinking seriously about landscapes even before he began his formalisms. The case for the necessity of the landscapes in the 1932 form of the theory does not depend on this, but I think the critic should tread warily before making sweeping claims about what *must* have been the case, historically.

Second, I would challenge the claim that the 1932 version of Wright's theory was simply the 1931 version, without the mathematics. The pictures do indeed add some factual claims — most importantly, that there are going to be some adaptive peaks for organisms to occupy, so long as one drifts far enough. The 1931 version really does not say much about why drift will eventually pay off. I have quoted the relevant passages and they are very vague. Indeed, Wright has already said that one small group drifting will probably go extinct. In the 1932 version, the pictures make it clear that there are all sorts of good opportunities waiting for drifters. Wright could have drawn a peak with a plain all around it, or with lots of (by definition) inhospitable sea or uncrossable rivers or chasms. But he does not, and it is certainly part of the plausibility of his theory that every peak seems to have other relatively accessible peaks in the vicinity.

Third, before it is immediately objected that one could have expressed all of Wright's new (post 1931) claims in words, let me point out that he did not. Moreover, let me point out also that (as people like Mary Hesse(1966) have pointed out generally about metaphorical thinking) there is a heuristic element to adaptive landscapes which escapes a simple list of factual claims that a scientist might make at a particular time (specifically Wright in 1932). Like all metaphors, they are "open-ended" in a way that the strictly literal is not.

In this context, consider Dobzhansky's 1937 rendering of the landscape. He has peaks clustering together in a way quite absent from Wright. Although, interestingly, he does not acknowledge the fact (that is he does not write it down in words), he is adding a distinctively new element to the theory — that adaptations are not random and that what works well in one way might have similar (although somewhat different) mechanisms also working well. The point is similar to someone noting the virtues of both gasoline and diesel motors, and noting also what a big gap there is between them and a steam engine or a jet engine.

There is therefore a forward-rolling aspect to Wright's picture. It stimulates you to push ahead with more claims. Just as in real life peaks tend to be clustered (the Alps, the Rockies), so Dobzhansky was stimulated to think of adaptive clustering. And it is certainly in this significant sense, centring on the heuristic value, that I would deny that Wright's adaptive landscape could, even in theory, be dropped without loss of content.

3. But is it good science?

We cannot conclude just yet. There is another line of argument which will tempt the traditional philosopher of science. It will be granted now that at least some science, at some level, incorporates pictures. But the complaint will now be that the *best* science does not. All science, even relatively good science, would be better were there no illustrations. Top quality science is just a formal system.

I confess that my general reaction to this line of inquiry is to query precisely whose criterion of value is being invoked here. Why is the best science non-pictorial? It seems to me that by just about any standard of excellence you might normally raise, the work of Wright and his successors like Dobzhansky rates highly. If anything, it defines the criteria rather than is measured by them. But since I have staked my position so firmly on one single case, perhaps the critic can come back on the basis of this case. Good though Wright's work may have been, there are reasons to think it might have been better without the adaptive landscape idea.

How might the critic argue? Most obviously, I suppose, by pointing out that the heuristics of the landscape are all very well, but if they lead one on false trails, their virtues are of dubious status. Take the question of other peaks surrounding any specified peak. Perhaps these exist. Perhaps they do not. One has no right to assume, as the metaphor forces on one, that they are always there. In fact, they are probably not.

In response, I would agree that perhaps Wright's picture does suggest false trails. But with respect: "So what?" No one wants to say that scientific hypotheses — exciting scientific hypotheses — always work or are always true (although sometimes philosophers have a yearning towards this last option). The point is that the theory is fertile, and with respect to something like available niches, can be tested and rejected or revised if necessary. In fact, as comments I have made already clearly imply, one can certainly redraw Wright's landscapes if one finds that niches are not readily available. And if no niches at all are available, then the whole theory must be rejected, not just the pictures.

I might add in this context that, although treatment of metaphor usually labels implications cleanly as good, bad or neutral heuristics, in real life (as our example shows) it is often not so easy to decide whether or not implications are such a very good or bad thing. Take the presumed stability of Wright's landscape. Although the possibility of change is certainly mentioned, generally — as with landscapes as opposed to water-beds — the terrain is supposed to be fairly solid. This suggests that organisms will scale ever-higher peaks, and that in short there will be progress. However, although many today — like George Williams(1966) and Stephen Jay Gould(1989) — would consider this the consequence of a negative heuristic, others are not so sure. I suspect that Wright himself endorsed progress. Certainly, the botanist G L Stebbins is a progressionist and has used Wright's ideas to make precisely such a case (Stebbins 1969). And active today someone like E O Wilson(1975) is an organic progressionist and would, no doubt, find any supporting implications of Wright's metaphor most comforting.

The critic might now argue in a slightly different way. Wright himself admits that in his diagrams he is collapsing down a huge amount of information into two dimensions (three if you consider the axis from eye to page). But is this legitimate? One is taking drift from many many dimensions and confining it to two dimensions. One of the things that Wright always prided himself on was the fact that he acknowledged the fact that genes in combination might well have very different effects from genes taken singly. What right therefore have we to assume that the many drifting genes will combine to behave like one drifting gene (or, rather, a line of such genes)?

There is an important point here — one which shows that although Wright may have been sensitive to gene interaction, critics like Ernst Mayr(1959) were not entirely off base when they accused the population geneticists of undue reductionistic thinking, in treating their subjects as beans in a bag. However, note that if there is a problem here — that the collapse of dimensions is too dramatic — it is one which affects all levels of theory and not just the illustrations. Again, therefore, I suggest that Wright's theory should simply be put to the test, and check made to see if genes do wander in the way that he suggested.

In fact, as I have intimated, a decade after Wright published, Dobzhansky and others found strong evidence that selection is far more powerful and effective than Wright and others had suspected. (I am not now referring to molecular genes which, by their very nature evolve at levels below the power of selection.) The shifting balance theory required modification. But I am not sure that such modification required/requires rejection of the very notion of an adaptive landscape. One can rework the landscape to show that factors other than drift are significant.

I conclude, therefore, that the criticisms of conservatively minded analysts are not well-taken. Wright's work was not perfect, in the sense of being absolutely true or totally without conceptual blemish. But this is a far cry from saying it was not first-rate science. Fortunately, scientific theories are like human beings — they are complex entities, with lives of their own, and the best are the best, not because they never do anything wrong, but because they do so many things right.

4. Conclusion.

What have I proved? I have certainly not proved that every scientific theory has to have pictures, or that every scientific picture is essential. By my own admission, I have been dealing with a picture or a special kind, namely one which expresses a metaphor. Nor am I claiming here that every scientific theory contains metaphors, although as a matter of fact this a claim I would be prepared to defend. I am not even claiming that every scientific metaphor gives rise, actually or potentially, to a picture. Indeed, this seems to me to be a false claim. Only in a very limited way do such important biological metaphors as natural selection or the struggle for existence give rise to pictures, and these are usually misleading.

Nevertheless, some scientific metaphors are pictorial — Wright's landscapes prove this. And those metaphors/pictures are in an important sense (any sense which is important) essential parts of the science — Wright's landscapes prove this. Moreover, the science containing these pictures can be good science — Wright's landscapes prove this also. These seem to me to be a good set of conclusions with which to end this somewhat preliminary foray into the philosophical significance of biological illustration.

I am indebted to David Hull and Ernst Mayr for typically thoughtful comments on an earlier version of this paper.

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