THE "SEWALL WRIGHT EFFECT"

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THE current state of understanding of the Theory of Natural Selection, and the degree of appreciation which it now enjoys as a presumptive agency of evolutionary change, constitute in effect a reversal of the opinions held by the majority of geneticists during the early years of the century. This reversal followed, we believe inevitably, from the better understanding afforded by the Mendelian system of the genetic structure of natural populations, and of selection within them. It is natural enough that progress in such understanding has not always been easy, and that workers with different preconceptions have not always given equal weight to the same circumstances. The widest disparity, however, which has so far developed in the field of Population Genetics is that which separates those who accept from those who reject the theory of "drift" or "non-adaptive radiation," as it has been called by its author, Professor Sewall Wright of Chicago.

In a recent paper,[1] we criticised this theory of Sewall Wright. It claims that the subdivision of a population into small isolated or semi-isolated colonies has had important evolutionary effects ; and this through the agency of random fluctuation of gene ratios, due to random reproduction in a small population.

We have long felt that there are grave objections to this view, to several of which we referred, though briefly, as it was to one of them only that our new data were directly relevant. This one, however, is completely fatal to the theory in question, namely that it is not only small isolated populations, but also large populations, that experience fluctuations in gene ratio. If this is the case, whatever other results isolation into small communities may have, any effects which flow from fluctuating variability in the gene ratios will not be confined to such subdivided species, but will be experienced also by species having continuous populations.

This fact, fatal to "The Sewall Wright Effect," appeared in our own researches from the discovery that the year-to-year changes in the gene ratio in a wild population were considerably greater than could be reasonably ascribed to random sampling, in a population of the size in question. We presumed that random sampling fluctuations must always be present, but that other causes must be acting

Heredity, 4: 117-119, (1950).

too, with an intensity, which, even in a population of no more than 1000, seems to be greater than the effects of random sampling. But it is only the random sampling fluctuation which is accentuated by the small size of an isolated population ; other causes, like selective survival varying from year to year, will influence large populations equally. Indeed we pointed to other researches, notably those of Dobzhansky, demonstrating such fluctuations in large populations.

This central criticism seems to have escaped Wright's attention, so that in a recent article in *Evolution* [2] he has attributed to us opinions entirely contrary to those which we hold and clearly express in our paper. Thus on p. 291 he says : "They hold that fluctuations of gene frequencies of evolutionary significance must be supposed to be due wholly to variations in selection (which they accept) or to accidents of sampling. This antithesis is to be rejected."

This passage constitutes a direct mis-statement of our published views. There is nothing in our article even to suggest the antithesis which Wright ascribes to us. Not only do we presume throughout that accidents of sampling produce their calculable effects in causing fluctuations in gene ratios, but we take some care to evaluate them. An earlier and slightly different statement by Wright to the same effect occurs on p. 281 : "Thus Fisher and Ford insist on an either-or antithesis according to which one must either hold that the fluctuations of *all* gene frequencies that are of any evolutionary significance are due to accidents of random sampling (ascribed to us), or that they are *all* due to differences in selection, which they adopt."

Nothing could be further from our actual criticism of the particular contribution to evolutionary theory which is due to Sewall Wright. He tells us that he now attaches importance to accidents of gene sampling only as one of many factors, and (p. 281) that he has always done so. This latter statement is, however, hard to reconcile with his earlier writings. Thus in the *Statistical Theory of Evolution*,[3] he says of "non-adaptive radiation" (p. 208) : "In short, this seems from statistical considerations to be the only mechanism which offers an adequate basis for a continuous and progressive evolutionary process." He ends the same paper with the sentence : "In particular, a state of sub-division of a sexually reproducing population into small, incompletely isolated groups provides the most favourable condition, not merely for branching of the species, but also for its evolution as a single group."

Sub-division into small isolated or semi-isolated populations is clearly favourable to evolutionary progress through the variety of environmental conditions to which the colonies are exposed. Moreover, so long as it could be believed that large fluctuations in gene ratios occur only in small isolated colonies by reason of fluctuations of random survival, then it *might* have been true that such fluctuations themselves favoured evolutionary change in a way that would not be allowed in a continuous distribution of the species. If now it is admitted that large populations with continuous distributions also show year-to-year fluctuations of comparable or greater magnitude in their gene ratios, due to variable selection, the situation is entirely altered. In these circumstances, the claim for ascribing a special evolutionary advantage to small isolated communities due to fluctuations in gene ratios, had better be dropped.

Wright, and others who have supported his views, have repeatedly attempted to produce examples illustrating the spread of non-adaptive qualities. Yet the extreme difficulty of deciding what characters are of neutral survival value should be apparent : still more, the difficulty of deciding whether the total effects of the genes, or genetic situations, responsible for them are so. The fate of such speculations is well illustrated by advancing knowledge respecting the chromosome inversions found in wild populations of *Drosophila pseudo-obscura* quoted by Wright[4] p. 178, and by Sturtevant and Dobzhansky[5] as selectively neutral. Yet more recent work shows the very reverse,[6, 7, 8] and that these chromosome inversions are in fact subject to a delicate balance of selective intensity.

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