

17th January, 1949

My dear Henry,

Thanks for your note. I saw Wright's article in Evolution and feel as you do that controversy is a nuisance and a very unprofitable one, though occasionally one has to intervene to prevent others from being misled.

To show the state of my own opinion I enclose a draft statement, which is exceedingly rough, but which you might like to see in case we are tempted to send a note to Evolution. It is quite clear that Wright himself will not be affected by any argument. When my book on Natural Selection came out, his review of it, if I remember right, took me to task for ignoring the important effects which Wright had demonstrated, and in the following year he plagiarized and has since constantly referred to ~~it~~ as his own, some of the mathematical treatment of selection in relation to gene ratios. It is obvious from his last paper that he feels the weakness of the position he had taken up and now wishes it to be thought that he alone takes a comprehensive view of selection problems, while we, on the contrary, tend to over-emphasise special factors. This from Wright who has contributed one idea only, suggests a shifting of ground.

Yours sincerely,

In a recent paper (Heredity ) we criticised the view widely ascribed to Sewall Wright, that the subdivision of a population into small isolated colonies has had important evolutionary effects; 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 theory, to several of which we referred, though only briefly as it was to one of them only that our new data <sup>are</sup> 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 effects 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 fact 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 presume that random sampling fluctuations must always be present, but that other causes must be acting 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 affect 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; consequently he has evidently <sup>favoured</sup> ~~favoured~~ and given publicity to a view of our opinions very wide of the mark. In his summary, for example, he says (p281)

"They hold that fluctuations of gene frequencies of evolutionary significant <sup>as supposed to be due wholly</sup> must be ~~due~~ either to variations in selection (which they accept) or to accidents of sampling. This antithesis is to be rejected."

There is actually nothing in our paper even to suggest the antithesis which Wright ascribes to us, we presume throughout that accidents of sampling produce their calculable effects (the extent of which we give some <sup>care to</sup> ~~care to~~ calculating), in causing fluctuations in the gene ratios. An earlier and slightly different statement by Wright on 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 evolutionally 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 ascribable to Sewall Wright. It is true he now tells us that he attaches importance to it only as one of many factors. This is all to the good. Still, if it has been from the first based on a misapprehension, and has been accepted in spite of its obvious difficulties on false ground, it is as well to admit it when the misapprehension is demonstrated and the grounds for its acceptance <sup>are shown</sup> ~~are~~ to be false. So long as it could be believed that large fluctuations in gene ratios occurred only in small isolated colonies by reason of the fluctuations of random survival, then it might have been true that such fluctuations favoured evolutionary advance in a way that would

not be allowed by <sup>a</sup>the continuous distribution of the species.

If now it is admitted that the large populations with continuous distribution also show year-to-year fluctuations <sup>of considerable or greater magnitude</sup> in their gene ratios, due to variable selection, then the claim for ascribing a special evolutionary advantage for small isolated communities had better be dropped.