May 2, 1938

Dear Ford,

Many thanks for having sent me the page proof of your book on The study of heredity. I have read it with the greatest pleasure and interest, as I think you would expect. There is only one point which I should like to take up argumentatively; that comes on pp. 174-5 where you give a statement of views developed by Sewell Wright, and either the statement of the original views seems to be confused. If one thinks of the different genotypes possible in a species segregating in some hundreds of factors, it appears that these are discontinuous and may be represented spacially as the points of a lattice. I mean, for example, that, if there are two competing allelomorphs at any one locus, then in respect of this factor every genotype must be one of three types; that is, there will be two other genotypes differing from it, but alike in all other factors. Varying two factors at a time, one gets similarly a 3 x 3 lattice of 9 possible genotypes, and for n a 3^n lattice. Lethality will cut out certain combinations, and multiple allelomorphism will require a

slightly more elaborate representation having a number of dimensions to each factor, which is also adequate to deal with the different types of multiple heterozygotes which can be formed by linked factors. The point is, however, that, so far as individuals are concerned, there is only a discontinuous aggregate of lattice points, each having its own selective value. There is no continuum of possible values in which we might speak of peaks or maxima.

Such a continuous representation in multiple space occurs only when we think of the gene ratios existing in a species as a whole. A point then does not represent an individual, but a possible specification ~~in a~~ of the gene content of the species. Any such species must contain individuals of greatly differing selective value, which, if favoured by selection, will move the point representing the aggregate of gene ratios to another part of its field. If one is thinking of a special representation of possible species compositions, it is not clear on what the distinction between peaks and valleys is based. So far as I can see, natural selection is only definable in terms of the relative selective advantage of the different genotypes possible to individuals. I think Wright must be thinking of altitude as a kind of average selective value of all the individuals of the species, which is quite reasonable if the different genotypes can be assigned fixed values independent of the genetic composition of the other

individuals present in the population. If this is so, the fact that a number of different genotypes may be of equal selective value is no reason for anticipating a multiplicity of peaks. The difficulty of imagining such a multiplicity seems to increase with the number of dimensions, that is, with the number of factors the gene ratios of which need to be represented. In one dimension, as on a road, we pass over an alternate series of hills and dips, so that half of the level points are maxima. In two dimensions, in addition to peaks and bottoms we have cols, which may be regarded as lowest points on ridges or highest points on valleys, the curvature of the ground being positive in one direction and negative in another, and the peaks are only about one quarter of the level spots. In n dimensions only about one in 2^n can be expected to be surrounded by lower ground in all directions.

I make these points because I think your experience with the Melitaea colony likely to be of great importance for the problem of species formation, but that its importance may be overlooked if it is thought that it is all plain and easily understood on current views.

Tell me if you want the page proof back; it is being read with some interest in my Department. On a verbal point I should suggest the omission of the word "the", the last word of line 11, page 169, which gives the impression that the same flies were trapped rather than their descendants

Yours sincerely,