March 8, 1939

Dear Mr Todd,

Thanks for your interesting letter of March 7th. Both difficulties you mention arise from the same source, due to my own carelessness, for I did not distinguish as I should have the genetic variance measured in zygotes from that measured in gametes. The first is just double the second, i.e. \(2pq\alpha\), and I should now prefer to equate \(W\) to this quantity.

If you now allow your three genotypes to have observable values, \(-\alpha, 0, +\alpha\), you find

\[
\alpha = \left( \frac{h}{g + h} + \frac{f}{g + f} \right) \alpha
\]

which, as you see, even for this simple case may be greater than \(\alpha\), if there is no self fertilization.

Then your procedure evaluates the genetic variance for zygotes as \(2pq\alpha\), which identifies \(\alpha\) as the average effect, in my sense of that term. The calculations of your third page then simply verify that \(\alpha\) is the average effect on the population total of each substitution.
If an organism were to behave as a tetraploid for any length of time, which I think is very questionable, then the genetic variance in the zygotes would be $4pqad^2$. In the following section on natural selection, you will see that, since an increase in frequency $dp$ causes a total increase among zygotes of $2\times dp$, the rule that the rate of increase in zygotic fitness is equal to that its genetic variance still holds exactly.

[*7]

As regards the spatial representation, one could, for any system of measurement, choose a metric in which surfaces of equal adaptation are spheres, but it is not strictly necessary then that all directions are equally probable for mutational, or environmental, changes. Consequently a full and exact representation would be based on an ellipsoid. However, my principal concern was to get a clear idea across of the nature of the relationship you call adaptation, and the reason for expecting all undirected causes to diminish it. One need not postulate that the adaptive changes due to simultaneous alteration of two different measurements are independent, one merely has to use oblique axes when one change makes another more favourable.

Yours sincerely,

[* The *Genetical Theory of Natural Selection*, p.38] - J.M.B.