

THE MEASUREMENT OF SELECTIVE INTENSITY*

* Contribution to a discussion on the present state of the theory of natural selection.

Professor R. A. FISHER, F.R.S.—*The Measurement of Selective Intensity*—Theories of Evolution are of two kinds, those that, in Professor Watson's words, "are explanations primarily of adaptation and only secondarily of the origin of species", and those which fail to account for adaptation. To the first class belongs the theory of the inheritance of acquired adaptations, commonly called Lamarckism, and the theory of the natural selection of innate adaptations. For these two theories evolution *is* progressive adaptation and consists in nothing else. The production of differences recognizable by systematists is a secondary by-product, produced incidentally in the process of becoming better adapted.

I do not know whether, at the present date, anyone is prepared to advocate a theory of the development of living organisms, which ignores the necessity of explaining adaptations, in the wide sense of that term. Such theories also are of two kinds. It has been proposed that animals evolve by reason of something which may be called an inner urge, implanted in their primordial ancestors, which causes a progressive change

of form along a predetermined course, undeterred by any difference in the death-rate or birth-rate that may be set up. It has been proposed, alternatively, that the environment, picturesquely renamed the landscape, governs the course of evolutionary change, much as the field of force determines the trajectory of a comet. One might think that these two theories between them exhausted the narrow possibilities open to inventors of theories of non-adaptive evolution, but the example of the so-called mutation theory, once popular among geneticists, shows that this is not so. The explanatory content of a theory of evolution only reaches its absolute zero with the mutation theory. Organisms evolve, that is to say, heritable changes take place in them, because they mutate—because unexplained heritable changes take place.

I submit that the omission of this group of theories to explain adaptations is, from the most elementary point of view, an intolerable one; for they fail totally to explain the functioning either of the entire organism or of any of its parts. Palaeontologists, impressed by the disappearance of some imposing creature, as they pass from one stratum to the next, have sometimes rashly surmised that this was evidence that they had become less well adapted to the current conditions. But even they will admit, if their subjects had eyes, that they were functional organs, not inoperative as optical and sensory systems; that their instincts impelled them to catch their prey, or to browse on their forage, and to carry out the necessary functions of their reproductive cycle; that their nervous systems did convey afferent and efferent impulses; and, perhaps, that their digestive systems were in good working order. This simple list implies, I suppose, some hundreds of nicely adjusted adaptations. Good work, one might say, for the primordial “urge” to have foreseen, or for the moulding finger of the “landscape” to have created.

For *rational* systems of evolution, that is for theories which make at least the most familiar facts intelligible to the reason, we must turn to those that make progressive adaptation the driving force of the process. Lamarckism was first in the field, and the reasons for its abandonment are familiar. But it is worth considering why, during the three-quarters of a century for which Darwin's views have been known, so many biologists have felt, and raised, objections to them.

I believe the explanation must be more temperamental than intellectual. Darwin's work reached a wide public. His views, or something like them, were supposedly familiar to all educated men. That being recognized, few scientific specialists, specialists at least in biology, could suppose that *they* had anything to learn from his works. Even the “Origin”, when read at all, would seem to have been read cursorily, without the

expectation of learning anything from it. It always seems more knowledgeable to expound the *latest* views, however flimsy.

Then, fireworks look much brighter against a *black* background. Biologists, exploring a vast field, for the greater part of which the public care nothing, have, I think, sometimes been tempted by the illusion that their valuable findings have a bearing, which they really lack, on evolutionary doctrine, in which, for a time, the public really were interested. That this interest has since largely evaporated must, I think, be principally due to the intellectual frivolity of the discussions on evolution during the past 40 years, which it has been customary for biologists to stage. The old arguments on which the whole subject still rests have been neither answered nor furthered, and Darwinism has been too often misrepresented merely to supply a black background against which to exhibit the brilliance of modern advances.

In places some of the black paint seems to have stuck. In his second paragraph Professor Watson says that Darwin's theory "rests on the assumption that *the* differences between individual members of a species are heritable". Should he not have said "some of the differences"? For that is sufficient for natural selection. Then the alleged "assumption" is reduced to a mere rejection of the postulate that all members of the same species are genotypically identical. I believe no one asserts this postulate; and that it is known to be untrue of all species, without exception, which have been investigated. It is a peculiarity of Darwin's theory, that it relies only on causes demonstrable independently of their evolutionary effects.

In plants at least, Turesson's results in Sweden are abundant and conclusive in showing that different ecotypes do very generally differ genetically. Agricultural experience is also wide and uniform in finding obvious differences in the adaptation of different varieties of cultivated plants to different climates. Professor Watson suggests that similar knowledge is lacking in the case of animals.

Professor Watson also seems to have real doubts of the existence of differential mortality between different genotypes in natural populations. Is he really tempted by the inconceivable assumption that the net measure of fitness, whether thought of in terms of death or reproduction, for it must involve both, is *identical* in all the environmental situations which occur, even for any two of the thousands or millions of genotypes which most species must have? Or is he only providing a cue for discussion? I will try to answer his point.

Some years ago I suggested that in polymorphic species we have natural markers maintained in equilibrium by a balance of selective agencies.

The equilibrium is stable only if the heterozygotes have an advantage over both homozygotes, but the fact of selective balance allows, in these cases, selective intensities to occur greater than can exist elsewhere, that is, unbalanced, merely by reason of the rapidity with which any species subjected to them would be transformed. The selective intensities may be measured by the known crossover frequencies against which they are balanced. I had some correspondence with Dr. Nabours of Manhattan, Kansas, who was able to organize an extensive collecting trip in Texas and Mexico with a view to ascertaining the frequencies with which different gene combinations, recognizable, on the basis of Dr. Nabours's genetic work, from the colour pattern, were found among a number of species of grouse-locust. I must admit that I believe neither Dr. Nabours nor I have published anything about it. He sent me quantities of illuminating data, and I sent him very lengthy dissertations about them. I am confident that Dr. Nabours will forgive me for mentioning the matter now, for certainly every one of the species *Acrydium arenosum*, *Paratettix texanus*, *Paratettix cucullatus*, *Apotettix eurycephalus*, for which large samples were collected, showed unmistakable evidence of differential survival among the genotypes in their wild habitats. In most cases the differential elimination was sufficiently moderate for it to have been due either to death only in the period between the formation of the zygote and the time of capture, or in the other half of the cycle between the time of capture and the formation of the next generation, when both differential mortality and differential fertility would be effective. In one case, I remember in *Acrydium arenosum*, no amount of differential fertility, even complete sterility, would suffice to explain the disparity in numbers observed, for crossing over alone would produce more than were observed. In fact, the figures could only be explained by the differential elimination down to about 40% of one genotype mahogany *My* without white line *W*, compared with its competitors. The low viability of this type in nature was further confirmed by breeding experiments in which an even lower viability was indicated in culture.

That, however, is only an extreme case out of many, and I must emphasize again that only in balanced systems are selective intensities of this order to be expected. The selective intensities effective in evolutionary change are, I believe, more likely of the order of 1% to a tenth of 1% in each generation. Breeders of *Drosophila*, if they set their hearts on it, could, I think, just manage to breed enough flies to detect differences in viability and fertility of these magnitudes. I do not know the series of writers which Professor Watson refers to as having tried to demonstrate the existence of selection without success. I would suggest, however,

that it is no evidence against the existence of the planet Pluto that he cannot be seen with even quite a good opera-glass. Negative evidence is worthless if we do not know both the magnitude of the theoretical effect to be observed and of our errors of observation.