

MORTALITY AMONGST PLANTS AND ITS BEARING ON NATURAL SELECTION

THE interest for the theory of natural selection of the researches on the mortality of seedlings reported by Dr. E. J. Salisbury (NATURE, May 31) is so great, as is, in all its aspects, the development of a quantitative ecological technique, that it seems important not to allow the interpretation of the new observational material to be prejudiced by the use of an argument which contains a concealed fallacy. This argument could not be more briefly stated than in Dr. Salisbury's words, "The mortality and therefore the operation of natural selection is almost entirely confined to the juvenile stages of development".

It may be recalled that this same argument was used by Wallace as a reason for rejecting the application of the theory of sexual selection to butterflies ("Darwinism", p. 296) : "In butterflies the weeding out by natural selection takes place to an enormous extent in the egg, larva, and pupa states ; and perhaps not more than one in a hundred of the eggs laid produces a perfect insect which lives to breed. Here, then, the impotence of female selection, if it exists, must be complete." Wallace, however, did not apply this argument to a second case to which evidently it is equally applicable, for he has no hesitation in advocating the development of *protective* coloration by the natural selection of adult butterflies (*ibid.*, p. 207).

I believe the most useful step in examining the nature of this fallacy is to realise that, when mortality is heavy, immature forms of different ages are not of equal value, in the purely objective sense that they will not be equally represented in the ancestry of future generations. Knowing the rates of death and reproduction at all ages, it is possible to calculate the reproductive value, in this sense, at each age, and the course of this function for ages prior to the commencement of reproduction, is, in a stationary population, easily seen to be inversely proportional to the number living at each age. If, therefore, starting from the

seed, we have three stages of development, *A*, *B*, and *C*, to which 1 in 10, 1 in 100, and 1 in 1000 seeds actually attain, single individuals at these stages will be worth, in respect of their probable contribution to future generations, just 10, 100, and 1000 times respectively as much as the newly shed seed is worth. The selective elimination of certain individuals at stage *C* is for this reason as effective in modifying the genetic constitution of the species as the selective elimination of 10 times as many individuals at stage *B*, or of 100 times as many at stage *A*, or of 1000 seeds in their initial condition.

The concept of reproductive value seems to provide a powerful method of resolving many of the paradoxes which have arisen in Darwinian discussions. It is easy by its means to show in what circumstances, and for what reasons, such widespread assumptions as that the death-rate is a more important selective agency than the birth-rate; or that selection is most intense at times when the death-rate is highest may be in fact very far from true. The prospect of determining the vital statistics of wild populations, with sufficient accuracy to establish the relative values of different stages of development, is one of the most attractive features of the quantitative method in these fields.

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