

FLUCTUATIONS IN ORGANIC POPULATIONS IN RELATION TO SURVIVAL OF THE FITTEST

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Fluctuations were not discussed by Darwin or by Wallace, but some of the illustrations of the struggle for existence advanced by those authors doubtless were fluctuational phenomena. It is only in comparatively recent times that marked fluctuation in numbers has come to be recognized as a general, and as probably, indeed, a universal trait of organisms. It is unnecessary to cite here the evidence for the general occurrence of fluctuations, much information and keys to the literature being available, particularly in the works of Elton (see bibliography). Fluctuational phenomena, however, come frequently to the attention of every observant naturalist. Some of them, regular in periodicity, and, therefore, known as cycles, have attracted especial attention.

Quite without regard to fluctuational phenomena, critics weighing the postulated fortuitous nature of the variations upon which natural selection is supposed to act, and the ever present changes in environmental conditions, have pointed out the great improbability that selection could be maintained sufficiently in any certain direction to account for adaptation and evolution. Those factors do, indeed, render very unlikely the chance that natural selection could produce the steady advance needed to perfect adaptations, or to cause the orthogenetic evolution that is so commonly apparent.

With the variables mentioned in control, it would surely seem that selection must be for different reasons from time to time, while the facts relating to cyclically, or other severely, fluctuating populations are convincing that selection (if the term is justifiable at all) must be for different reasons at different phases of the cycle. When in the throes of the "die-off," for instance, survival of the fittest (if there is any such thing) would spare individuals most resistant to the parasite, disease, or other agency through which the "drop" or "crash" is effected. This crisis over, the fittest would be those that could best evade enemies of varying modes of attack, or those that could breed most rapidly and produce the largest number of viable young so as to reoccupy the depleted environment. As the population again tended toward the maximum, the fittest would be those that could live on a smaller quantity of food, or breed less rapidly so as not to increase the already threatening environmental pressure. Thus in each cycle (a period of about ten years in a number of cases, less in others), selection would necessarily be for a variety of qualifications, some of them of directly opposing tendencies. Environmental changes also would affect the character of the selection and, in the case of cyclic species, the organic environment, particularly other species involved in the cycle, is constantly changing. The numbers of predators and of buffers are as inconstant as those of the basic species and their potential effects on selection, therefore, are extensively variable. Unquestionably the circumstances of cyclic oscillations indicate orthoselection as impossible.

The light thrown upon fitness by the phenomena of irregularly fluctuating populations is much the same. Description of a case in point is here quoted from Taverner (1915, p. 20). "There is a certain definite maximum of population beyond which a species cannot go. We have many evidences of this. One of the most obvious was the case of the Bluebird in the winter of 1894-5 when this common species was almost wiped out in the south. For five years the species increased rapidly to normal population and then stopped short. As far as we can see no new factor was introduced, no enemy absent during the five years of growth was present in the sixth year, the food supply and birth rate seemed constant

throughout, but the increase was definitely and positively checked during the fifth year. It is obvious that a limit to the Bluebird population had been reached."

If we consider this case as an example of natural selection, we must assume that most of the young produced during the recovery period were fit and then conclude that most of those born afterward were unfit—a manifest absurdity. The bluebird case was a violent fluctuation, but all species fluctuate more or less, some of them both decidedly and periodically. The same difficulty of harmonizing the results with the principle of natural selection applies to all, namely, that it is unreasonable to suppose that a notably larger proportion of offspring produced during the upswing are fit than of those produced during other phases of the oscillation. As a matter of fact it is the absorbing capacity or fitness of the environment that rules. When the saturation point is reached, increase of the organisms stops; they are just as fit as before but there is no room for them.

Relatively rapid increase in population after a "low" shows that stress of competition has been relieved by the fluctuation. Success then comes to species in proportion to the degree to which they are freed from the force, natural selection, that is supposed to produce all fitness.

As noted, fluctuational phenomena do not augur well for orthoselection. When, therefore, we read that "Any advantage gained in one generation tends . . . to be accentuated in each succeeding generation . . . The advantage is thus cumulative . . . Mere differential numbers suffice," (Shull, 1936, p. 154), we can only conclude that the facts as to numerical oscillations have been ignored. When the "differential numbers" are not maintained, and this is true in all cases, "advantage" can not be maintained, much less accentuated.

Under natural selection theory, the tremendous drop in numbers shown by cyclic and other severely fluctuating species should act as a purifying fire; the race should be improved rapidly and with lasting effect. Instead, it breeds up to a maximum and is swept away again in exactly the same way as its ancestors have been over and over again. There are survivors but to say they are the fittest is a travesty for there has evidently been no improvement in fitness.

The "drop" in cyclic species comes at a time when they are at the height of their numbers, when they are most successful according to selectionist doctrine, and their members presumably at the top of their fitness. Nevertheless, the mortality often approximates totality. Under such circumstances, the slogan "survival of the fittest" seems a sardonic jest.

Argument that reduction in the number of individuals in fluctuations is "an important factor in causing uniformity in a species" ignores the countereffect of wide range. The organisms survive in colonies scattered here and there, each of which may be characterized by slight local variations. From a theoretical point of view this circumstance would promote diversity rather than uniformity. Both suggestions, however, fail to take into account that regardless of fluctuations, evolution is an orthogenetic, mass phenomenon.

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