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NUMERICAL ABUNDANCE AS THE CRITERION FOR SUCCESSFUL SPECIES

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In introducing his discussion of this subject, Professor A. Franklin Shull says, "Even as late as the early years of the present century, a work canvassing the status of Darwinism at that time, referred to natural selection, on page after page as involving life-and-death distinctions. Conn, some years earlier, had pointed out the needlessness of this assumption, and occasionally others shared his view. But for a long time the prevailing assumption was that a character must save a life that would otherwise be destroyed, or destroy an individual which without that character could survive, if natural selection were to work." (1936, p. 152.)

It must be noted, nevertheless, that if the Darwinism theory is being adhered to, the view cited must be retained. Darwin says that "any variation in the least degree injurious would be rigidly destroyed" (?1912, p. 70); and that "A grain in the balance may determine which individuals shall live, and which shall die—which variety or species shall increase in number, and which shall decrease, or finally become extinct." (ibid., pp. 454–5.)

Shull goes on to inquire, "What should supplant this view? To answer this question it need only be recalled that success or failure depends on numbers" (1936, p. 152). "Numbers in whatever manner attained constitute the best assurance of permanence" (ibid., p. 153). "Even a very slight percentage increase, not necessarily occuring every generation but perhaps only occasionally, should suffice eventually to enable the favored type to supplant those less favored. It is clear, therefore, that natural selection need not render life-and-death decisions in order to work. Mere differential numbers suffice. Recognition of this fact alters somewhat the criticisms that may be leveled against it, and conclusions regarding what it can accomplish" (ibid., p. 154).

It is difficult to see why any effort should be made to retain the term "natural selection" since it is probably the most unfortunate that ever afflicted biological science. At any rate the thing that Shull is talking about is not Darwinian natural selection but numerical dominance. Darwin insisted upon numbers as the criterion of success in evolution but it was always numbers attained by mitigation of destruction (?1912, p. 59), by protection from predation or from other environmental checks (ibid., p. 94). The theory should not be warped away from its original form and still be represented as the same. This gives Darwin undue credit and proponents of the new view unjust advantage from his prestige.

The present criticism is not directed particularly against Shull—he merely furnishes quotable extracts good for a take-off. "The leaving of many descendants is recognized as the criterion of success" (1936, p. 212), he continues, and repeats "success in evolution depends on numbers" (ibid., p. 217).

The objections that can be urged against this point of view are numerous and weighty. In the first place it must not be forgotten that "natural control is necessary and inevitable. No species can go on increasing in numbers indefinitely." (Moss, 1933, p. 220.) In fact, self-limitation of populations is a widespread, perhaps a universal, phenomenon (McAtee 1936). That would not be the case if numbers alone were necessary for "success."

Again, whether as a function of natural control, or not, the carrying capacity of the environment for any organism has an upper limit that apparently cannot be transgressed more than temporarily. There is in effect, therefore, regardless of its mechanism, what amounts to a direct limitation of numbers by environmental influences. Carrying capacity thus rather rigidly regulates populations and is far from leaving attainment of abundance as something to be achieved through merit of the intrinsic qualifications of an organism.

It is certainly worthy of note also that the "leaving of many descendants" is characteristic chiefly of species that manifest excessive reproductive effort a process that is almost invariably accompanied by a high percentage of failure. Call such species "successes" if you will, but face the question, Are species successful from an evolutionary or any other point of view when they must produce a thousand or more eggs, a million or more sperms for every individual brought to maturity? Under the selection principle of adaptation they must be regarded as very crudely adapted, and it is difficult to see how they can be esteemed as successful under any phase of natural selection doctrine with its fetish of "survival of the fittest."

As a theoretical consideration it may be pointed out that it is just those species with a low birth rate that would seem most likely to be moulded by the alleged perfecting influence of natural selection, for the reason that there would be less scope in their case for indiscriminate elimination of progeny. On these grounds, under the theory, the species most affected by natural selection, namely, the rare ones, would be the most successful Attainment of large numbers would hardly seem a "natural selection" phenomenon, anyway, as "natural selection" is exclusively a destructive or checking influence

One of Darwin's remarks upon the subject of numerous progeny is, "the real importance of a large number of eggs or seed is to make up for much destruction at some period of life." (?1912, p. 59.) Like many another statement, this gives natural selection on anticipatory effect which, of course, it could not have. Destruction, moreover, is not a fixed toll but is more or less in proportion to production. If this were not the case, species would never recover from descending oscillations in numbers, although they regularly do.

If "success in evolution depends on numbers," how has it happened that organic populations have evolved, almost everyone of which undergoes profound fluctuations in numbers? One enthusiastic selectionist has asserted that "for an animal species in a state of nature, a declining population involves grave hazards." (Williams, 1932, p. 306.) If this be so, why has natural selection permitted fluctuation to be a characteristic of apparently all organic populations? Why does it allow all more or less regularly to decline in numbers?

In various well-known instances, fluctuations occur regularly at intervals of a decade or less. According to the numerical criterion of success, these species are successful at the crest of the population wave, unsuccessful at the trough. That the same species can be both successful and unsuccessful, evolutionarily speaking, and that too within ten or fewer years is another of the paradoxes to which selectionists are so hospitable.

As to fluctuations, if numbers were a guarantee of "success," populous species would not lose their abundance, and if numbers were necessary to "success," species could not regain them after a "low." The fact that both phenomena are of regular occurrence is another of the many evidences that "natural selection" is not in control.

One of the Darwinian tributes to numerical abundance is: "a large stock of individuals of the same species, relatively to the numbers of its enemies, is absolutely necessary for its preservation." (?1912, p. 62.). If numbers are so vitally important, it certainly is pertinent to inquire why the strictly utilitarian principle of "natural selection" has permitted establishment of an almost universal feature of the cutting down of the numbers of all organic populations by an enormous percentage (90–99 or more) in every generation.

A fact overlooked in connection with the Darwinian edict quoted is that predation tends to be proportional to population (McAtee, 1932, 1934, 1935). Rarity, in itself, protects both by evading notice and by forcing enemies to turn their attention to more abundant sources of subsistence. The prey-predator, is just as important as the predator-prey, relationship. The enemies of cyclic species have a low immediately following that of their prey but in the transition period with prey scarce, predators not yet scarce, there is no indication of extermination; the last few of anything are hard to find.

When as in the predator-prey or parasite-host relationship, numbers of a species depend on those of one or more food or host organisms, they may fluctuate without regard to survival value of their own characteristics. More hosts, more prey, bring an increase in no way due to excellences of the dependent species. Such attainment of numerical abundance is not a result of survival of the fittest for "natural selection" of species (the dependents) cannot be based on the qualifications of other species (the supporters).

The very term numerical dominance implies the contemporaneous existence of less numerous, along with the more numerous, species. This is not only a fact of every-day observation but the fundamental phenomena of food-chains and other inter-organismal dependencies clearly demonstrate that it has always prevailed. The success of parasites and predators cannot be measured by numbers because the more numerous they are, the more they prejudice their own interests Consumers must be fewer in numbers (or less in bulk) than producers. This is a truism, an inexorable law, that has prevailed throughout the whole course of evolutionary history.

This fact alone proves that less numerous species have been just as successful as the more numerous. They have maintained existence in numbers appropriate to their ecological status and as permitted by the dominating principle of fluctuation. There have been rare, there have been common, there have been abundant, species in all states of evolution. The less common, so far as we can judge from paleontological evidence, have been no more prone to extinction that the more common. Among the latter, some Brachiopods, for instance, were so abundant that the shells of the dying formed thick beds of limestone. The same is true of certain Crinoids, while some Foraminifera have a similar relation to chalk. Some of the plants that were the basis of coal deposits must have been very abundant. All of these organisms and many more, that could be named, once were very numerous but now are totally extinct. Their history amply refutes the dictum that "success in evolution depends on numbers."

Taxonomic investigations of large groups characteristically show that the wide-ranging and common, that is dominant, species are relatively few, while those of more restricted range and populations are relatively numerous. Ecological study generally confirms the principle stated by Raunkiaer that "the least frequent species are much the more numerous." (1934, p. 397.). An evolutionary theory based on dominants, therefore, ignores a large numerical preponderance of species. As all are the product of evolution and as all are concerned in whatever evolution is now occurring, the theory cited can hardly be regarded as satisfactory.

In logic, and in fact, a species, whether common or rare, is "successful" so long as it has a place in the sun. Since none forever maintains place, none is permanently successful. Evolution is not a record exclusively of "successes;" it is a story of the origin and rise, decline and extinction of all organisms, and withal is one so consistent that we can hardly suppose that there ever have been or ever will be any exceptions. If we read evolutionary history aright, there are, in the last analysis, no "successful" species, for all eventually disappear.

Darwinism is a theory of the transformation of organic forms by mass variation and "natural selection." The importance of numerical advantage is emphasized by iteration and reiteration but what has the theory to say of the less numerous and of the rare, that have undoubtedly been present at all stages of evolution? That they kept evolutionary pace with the more numerous species is demonstrated by their presence in every phylum today.

Despite the Darwinian "view of the necessity of a large stock of the same species for its preservation" (?1912, p. 62), all species could not have developed by transformation of existing abundant species, for in that case the total number of species evolved would have been relatively small instead of extremely high as is actually the case. It is not only natural to believe, but under the circumstances, it is a logical necessity to conclude, that many, probably most, species originate in small numbers. Darwin seemed to view rarity as "the precursor to extinction" (ibid., p. 94), but it would seem equally well regarded as the normal state of a new form. Willis defends this view in "Age and Area" and a distinguished geologist (R. H. Rastall) says "It may safely be assumed that any given species arises at a point, or within a very small area, and spreads outward by migration." (1929, p. 170.) On this eminently reasonable view, it must be concluded that, as a rule, species in their origin (and this is what Darwin was writing about) lacked the very thing, numbers, upon which success in evolution is said to depend.

De Vries, concurring with Willis, notes that, "all over the earth and in every systematical group of plants the rule prevails that the most wide-spread species are the oldest." (1918, p 630.) This principle of course applies to organisms only in the assurgent phases of their history but it makes numbers (before senescence) a function of the ages of organisms—quite a different thing from being the result of the "survival of the fittest."

This essay presents evidence along about a dozen different lines, all to the effect that success in evolution does not depend on numbers. Possession of great numbers is no guarantee of success, and lack of them no threat of failure. Whatever their relative average abundance, all organisms fluctuate in numbers. On the numerical criterion, all must, therefore, be classed as both successful and unsuccessful The latter label fits all in the end, for whatever their quondam prosperity, all at length becomes senescent and finally extinct.

LITERATURE CITED

Darwin, Charles. 1912?. The origin of species by means of natural selection or the preservation of favored races in the struggle for life. Reprint, 6th ed., xix+501 pp. Hurst & Co., New York, N. Y.

De Vries, Hugo. 1922. Age and area and the mutation theory. Chapt. XXI, pp. 222–227, in Willis, J. C., Age and area. A study in geographical distribution and origin of species. x+259 pp., figs. The University Press, Cambridge, England.

McAtee, W. L. 1932. Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the food habits of nearctic birds. Smiths. Misc. Coll. 87(7), 201 pp., numerous tables.

1934. Protective resemblances in insects—experiment and theory. Sci. 79(2051) April: 361–363.

1935. Rejoinder to Dunn on "The survival value of specific characters." 4 pp., privately printed, Washington, D. C.

1936. The Malthusian principle in nature. Sci. Monthly 42(5), May: 444–456.

Moss, J. Eliot. 1933. The natural control of the cabbage caterpillars, *Pieris* spp. Journ. Animal Ecol. 2(2), Nov.: 210–231.

Ra.(stall), R. H. 1929. Geology. Encyclopaedia Brittannica, 14th ed., 10: 154–173, Pls. 1–2.

Raunkiaer, Christen. 1934. The life forms of plants and statistical plant geography. 632 pp., 189 figs., many tables. The Clarendon Press, Oxford, England.

Shull, A. Franklin. 1936. Evolution. x+312 pp., 64 figs. McGraw-Hill Book Co., Inc., New York, N. Y.

Williams, Henry Smith. 1932. Survival of the fittest. xxix+321 pp., illus. R. M. McBride & Co., New York, N. Y.

Willis, J. C. 1922. Age and area. A study in geographical distribution and origin of species. x+259 pp., figs. The University Press, Cambridge, England.