Book Reviews

Adaptation and Natural Selection

It is a curious trait of biologists that, when they are presented with a straightforward mechanism capable of explaining a very broad spectrum of natural events, they at first display an almost religious enthusiasm for its beauty and simplicity, but then soon begin to suspect that they have been had and that life must be really more complicated. Biologists are of two minds. They want biological phenomena to be explicable in terms of simple physiochemical events, but at the same time nothing would please them more than to learn that biological phenomena represent a new level of organization requiring some new fundamental laws not entirely to be framed in terms of constituent elements. In biology the war between reductionism and emergentism has been fought as a real issue. It is characteristic that a leading practitioner of mechanistic biology, J. S. Haldane, could nevertheless say that "if a meeting place between biology and physics be someday found and one of the two be swallowed up, that one will not be biology."

No aspect of the study of living organisms has been more preoccupied with the search for higher complexities than has the study of evolution, despite the remarkable success of a purely mechanistic theory of evolutionary change. In the hands of Fisher, Wright, and J. B. S. Haldane, the combination of the principle of natural selection with Mendelian genetics has produced an exact mathematical theory of evolution based on the changes in the frequency of genes in populations. In fact, if anything is wrong with the principle of natural selection as a scientific theory, it is that its power of explanation is rather too great. Yet, despite that power, evolutionists are ever on the lookout for a new principle that will explain, at a higher level of complexity, facts that seem, with a minimum of ingenuity, perfectly within the scope of the principle of Darwinian selection. **Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought** (Princeton University Press, Princeton, N.J., 1966. 300 pp., $6.50), by George C. Williams, is a beautifully written and excellently reasoned essay in defense of Darwinian selection as a sufficient theory to explain evolution without the necessity of group selection, population adaptation, or progress. Williams is especially concerned by such concepts as "adaptation" in the sense that they are intended to bring into evolution anything beyond the simple differential reproduction of genotypes in a population. Thus, he makes it a rule that adaptation "is a special and onerous concept that should be used only when necessary. When it must be recognized, it should be attributed to no higher level of organization than is demanded by the evidence." He then goes on to demolish case after case of group adaptation.

The argument with which Williams is trying to deal runs along the following lines. The neo-Darwinian theory of evolution by natural selection states that those genotypes will increase in frequency in a population whose carriers have a greater probability of survival or reproduction than other members of the population. But there are obviously characteristics that have been developed in the course of evolution that do not fit this specification. For example, if a bird gives a warning cry or makes a conspicuous display of plumage at the approach of an enemy, all the individuals in the population will be benefited by the warning, but there is no special differential benefit in fitness to the altruist who has given the warning. On the contrary, the very act of giving a warning cry or making a display will call the bird to the attention of the enemy and in this way may prejudice the survival of the foolish Samaritan. Since any genes causing such behavior will not be increased in the population by differential fitness and, indeed, may be decreased, we cannot explain the evolution of such characters by Darwinian selection. Rather we must suppose that genes harmful to the individual but beneficial to the collection of individuals have been selected by a group process, variously called *group selection* or *intra-deme selection*.

Williams' reply to this argument, and indeed the whole basis of his book, is that people who argue in this way have taken too narrow a view of Darwinism, and that this error has led to a search for selection on a population level, when selection on individuals would be quite sufficient. As Williams quite correctly points out, neo-Darwinism does not stipulate that individuals with greater potential for survival will have their genotypes increase in frequency. What it does state is that genotypes will increase in a population if the carriers of those genotypes have some mechanism for passing on more than their just share of genes to future generations. That is, the principle of natural selection is simply a tautology. In this way altruism, displayed toward close relatives, can result in an increase in the frequency of the genes for altruism even if the altruistic individual is himself destroyed in the process. As a first order of approximation it can be shown that if r is the genetic correlation between an altruist and his beneficiary, and if the altruist lowers his own Darwinian fitness by a proportion a, to confer a benefit b, the genes for altruism will increase in the population provided that a is less than r times b. As Williams points out, all cases of altruism can be seen as a spilling over of maternal care onto more distantly related or unrelated animals.

By a similar method it is possible to explain all apparent cases of group selection, provided a little ingenuity is used. Since neo-Darwinian explanations are sufficient, Williams argues, the principle of parsimony forces us to rely on them. The burden of proof is on those who wish to show the insufficiency of individual selection in the origin of adaptations.

In general, of course, Williams is right. Science must satisfy itself with simple sufficient explanations of phenomena and, in the absence of any other method, must cut out excess complexity from its theoretic structure by a judicious use of William of Occam's famous blade. But the fact remains that some adaptations really may be the result of selection among populations rather than among individuals. This is especially true for species that make their living by colonization and rapid occupation of new habitats, only to be supplanted rapidly by a more stable community. I am suggesting that weedy species, because of their high rate of deme extinction, may undergo a reasonable amount of evolution at the population level, even though individual selection may be a sufficient explanation of their adaptations. Nature does not always operate by the simplest mechanism, and the principle of parsimony is only a methodological convention, not a fundamental revelation of the structure of the universe.

Occasionally Williams' argument turns against him. I think, for example, that his discussion of genetic assimilation misses the point. Certainly no one claims that genetic assimilation occurs by any means other than by Darwinian selection. It is simply that for some developmental systems organisms that give up developmental flexibility for the assurance of a particular morphology will leave more offspring and are, *ipso facto*, better adapted. Williams' argument that genetic assimilation of a previously facultative response must be a loss of adaptation smacks of the very viewpoint his book is intended to combat. It is not possible to react instantly to a change of environment and the delay may be painful or fatal, so it is sometimes better to build in the response even in the absence of the stimulus. Before the calluses come the blisters, as I discover anew each summer when I first row a boat.

Despite such reservations, however, I believe that Williams' book is excellent in its totality and that it is 95 percent correct. Most of the characteristics of organisms, including social behavior, must be the result of differential fitness at the level of individual genotypes. Only a small part of evolution, although perhaps its most intriguing aspect, has occurred as a response of groups to a higher level of differential fitness.

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Lattice Defects in Quenched Metals

At high temperatures, crystalline solids are literally riddled with holes: many lattice sites which ideally should be occupied by atoms are instead vacant. This phenomenon is in a sense the inverse of the vapor pressure of condensed matter, as if the vacuum were "evaporating" into the solid. Thus, the concentration of vacancies increases rapidly with increasing temperature, often approaching 0.1 percent near the melting point.

One of the more fruitful and interesting methods for studying lattice vacancies appeared in 1952, when J. Kauffman and J. Koehler showed that it was possible to retain most of the vacancies during very rapid cooling from a high temperature. By measuring the effects of quenched-in vacancies on various physical properties, primarily the electrical resistivity, and by observing the annealing out of the excess vacancies, information concerning the thermodynamic and dynamic properties of both isolated vacancies and associated pairs, called divacancies, can be obtained. Unfortunately, the interaction of vacancies with themselves, with impurity atoms, and with other defects often complicates the picture, so that different investigators have not always agreed on the experimental results or their interpretation.

Another aspect of the problem which has received considerable attention during the past eight years is the study of larger-scale defects produced by precipitation of the excess vacancies. Depending on the ambient conditions, the vacancies may aggregate to form voids, stacking fault tetrahedra, and various prismatic and faulted dislocation loops. All of these larger defects have been observed directly by means of transmission electron microscopy. In addition, their effects on the mechanical properties of quenched metals are readily demonstrated.

The present book, **Lattice Defects in Quenched Metals** (Academic Press, New York, 1965. 829 pp., $22), edited by R. M. J. Cotterill, M. Doyama, J. J. Jackson, and M. Meshii, consists of the papers and discussions offered at a conference devoted exclusively to defects in quenched metals. The conference was held at Argonne, Illinois, in June 1964. The book is a timely documentation of a field of investigation that is expanding. Some of the contributions give extensive surveys of experimental results, but there is little of the tutorial review that the nonspecialist would find desirable. Thus, this book is certainly not intended for the general or casual reader, but is frankly addressed to those physical scientists whose research deals with, or is affected by, lattice defects.

The overwhelming majority of the papers are concerned with face-centered cubic metals, and especially with aluminum and the noble metals. There is extensive treatment both of the experimental techniques and methods of analysis. The effects of specimen size and purity, of dislocation content, of quenching temperature and quenching rate, and of various post-quench treatments are analyzed to yield information concerning the energies and entropies of formation and of migration of single vacancies and of divacancies, as well as information on the interactions of vacancies with impurity atoms and dislocations. A wealth of electron micrographs illustrates a variety of larger defects formed by vacancy aggregation, and a number of models are proposed to account for the aggregation processes.

The problems attacked in this work involve really microscopic features of defects in metals, and it is perhaps not surprising that some questions remain unanswered and that the conference proceedings occasionally display a lack of unanimity. In some cases, such as the question of the binding energy of the divacancy in gold, one could almost say that there appears to be little uncertainty—only disagreement. This is, of course, the result of intense interest in a rather complicated problem. The really amazing thing is that we can now begin to zero in quantitatively on such elusive targets, and the detailed picture supplied by the manuscripts of this volume represents as complete an account as one could hope to find of this particular corner of solid state science.

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Earth Sciences

Textbooks on solid-earth geophysics tend to polarize between an elementary survey approach and a specialized advanced presentation. Among the former, there is a variety of available books on earthquake seismology, internal structure of the earth, and explora-