A Second Installment

Evolution and the Genetics of Populations. Vol. 2, The Theory of Gene Frequencies. SEWALL WRIGHT. University of Chicago Press, Chicago, 1969. viii + 512 pp., illus. $15.

This volume is the second in a three-volume treatise by one of the masters in the field of population genetics, and can reasonably be treated as a considered summary of nearly 60 years of work in that subject. With this in view, the book must be judged by the highest standards, and anything said below must be read with this in mind.

A major difficulty in assessing the book is that the final discussion and verdict on a number of points have been left to the third volume of the treatise, yet to appear. It follows that there must be an air of incompleteness about this review which would not exist if volume 3, to which one looks forward eagerly, were simultaneously available. Indeed, one hopes for an eventual review of all three volumes treated as an organic whole.

What is the writer's aim? The dust jacket claims that "this encyclopedic treatise is a summary of vast work done by Wright and his followers in the field of population genetics, a field created in large part by Wright himself." Perusal of the book indicates that the points of view it puts forward are in the main those of Wright himself, and are not always counterbalanced by the opposing points of view of other workers on some important and contentious issues. It may therefore be properly assumed that the dust jacket means just what it says, and that one of the author's aims is to give very much his own views on the subject (which he is surely entitled to do). Further, it appears to be an aim of the author to present in many places the full historical development of any argument, rather than merely the current theory. The reviewer found this approach illuminating, but believes it might overwhelm the novice who wishes to use the book to learn the subject from scratch. Clearly this book is not aimed at such a novice.

Now to discuss the contents. The early chapters give the most complete treatment known to this reviewer of the classical results on the effects on gene frequency of selection, mutation, immigration, and so on, all of which are treated in a variety of situations (one locus, many loci, many alleles, sex-linked loci, and so on). Further, several topics not often found in textbooks, for example the mathematical theory of meiotic drive, are also included. For the "one-locus" case, all this is admirable and indeed definitive. For the "many-locus" case, it is well known (and here recognized by Wright) that a proper treatment requires consideration of gamete frequencies rather than gene frequencies. However, much of the analysis is in terms of gene frequencies rather than gamete frequencies, under the assumption that, with loose linkage and small selective differences, this gives a sufficiently accurate picture of what is happening. Although this assumption may be reasonable for a small number of loci, it is by no means certain that it continues to hold for many loci, and recent work does cast some doubt on this assumption's holding in such cases. The reviewer therefore feels that the gene frequency approach, together with the adaptive topography theory deriving from it, should be handled with some caution, and is a little hesitant about the bias toward this approach prevalent throughout the book. This point will be returned to later in this review.

A substantial portion of the middle section of the book is taken up with an examination of various consequences of inbreeding in a wide range of circumstances. Again, this is an extraordinarily complete treatment, definitive and lucid, suffering perhaps only slightly in the last respect because of the extensive use of path coefficients, a method with which no other worker has approached Wright's facility of operation. Here the concept of effective population size (to be used often later) is first introduced, together with a most interesting chapter on population structure, the theory of which is relevant to Wright's theory of evolution by the joint effects of selection and drift in semi-isolated subpopulations.

Drift requires finite populations and a stochastic treatment, and this is taken up in the next two chapters. In the first of these the author stresses most heavily the historical development mentioned earlier in this review, and modern results, although not of course omitted, tend to be submerged. The second of these chapters considers many alleles and many loci: here the treatment is less of a historical nature since indeed most results are comparatively new. The two main questions covered in it concern the number of selectively neutral and self-sterility alleles maintained in a finite population. Each receives a full discussion, the main omission being the effects of population subdivision on the results reached. These effects are indeed of minor magnitude, but one feels that this very fact is relevant to the question of the importance of population subdivision.

The final two chapters are of a different nature, and discuss questions of correlation between relatives, estimation of heritability, and so on, using the techniques of the analysis of variance and path coefficients. This is again a most complete treatment, having comparatively few points of contact with the rest of the book, and one suspects that a more complete fusion will occur in volume 3.

The final chapter presents a summary of, rather than, as the title suggests, overall conclusions derived from, the main results reached. Again one suspects that the real conclusions will emerge in volume 3, and this final chapter concisely and clearly summarizes the results upon which these conclusions must lean heavily.

There are several, perhaps minor, points which deserve comment. First, while Fisher's so-called Fundamental Theorem of Natural Selection is known for two and more loci to be untrue, the theorem is of considerable interest, not only historically, and has points of contact with the adaptive topography theory so fully treated. It is therefore surprising to find only a brief mention of this theorem tucked away in a chapter on frequency-dependent selection. Second, although the reviewer agrees with the rather bald statement (on p. 36) that "[the principle of genetic load] does not, of course, apply at all to equilibrium due to a favorable heterotic effect of the heterozygous mutant," he feels that some discussion on this point would have been desirable, since much recent work in population genetics, not least by Wright's followers, revolves around this point. Finally, the reviewer completely disagrees with the equally bald statement (on p. 105) that Moran's attacks on the concepts of adaptive topographies are "based on a misunderstanding of the concept." On the contrary, recent work shows Moran's comments to be justified and all too true, in that many examples now exist of populations which do *not* move towards "peaks" in their adaptive topography. (It is of course an entirely different matter to ask how often such behavior may be expected to occur in real life).

But these points are minor, and one must conclude by saying that this is a most impressive book, wherein a master of the subject of population genetics has stated without equivocation his opinions on the subject. As a consequence of this unequivocal approach there are several points which one might disagree with, and which one might even claim go against the broad current of thought in the subject. But one is prepared to overlook these qualifications, since all too seldom does a great scientist summarize as well as Wright has done his own detailed and considered views on his subject.

W. J. EWENS
La Trobe University, Melbourne, Australia

Genic Polymorphism

Genetic Load. Its Biological and Conceptual Aspects. BRUCE WALLACE. Prentice-Hall, Englewood Cliffs, N.J., 1970. xii + 116 pp., illus. $5.95. Concepts of Modern Biology Series.

The development of enzyme electrophoresis brought to population genetics the first experimental theater in which its complex body of theory could be put to a general test. When the new technique revealed widespread genic polymorphism, no plausible mechanism seemed to exist for its maintenance. Heterosis, selection favoring heterozygotes, appeared too costly for any population to bear. The resolution of this paradox is important to population genetics and should be of interest to all biologists.

The book begins with an introduction to population genetics. Good use of experimental examples, always a virtue in Wallace's books, is evident. The continuous focus on cost, echoing the initial confrontation, helps make the issue clear. And the rather comfortable style of writing and the patient organization make the book easy to read. The tables are not all instantly clear, and some diagrams seem ambiguous.

Genetic Load illustrates clearly the vast amount of genetic variation that exists in nature. The role of selection is discussed, as well as the fact that the differential survival—or differential killing—of genotypes entails a cost to the population. While the computation of cost for one locus for one generation can easily be made, the proper method of combining many such costs (to calculate their overall impact on the population) was not at first clear. Wallace suggests that with the proper calculation of the total cost of selection, the vast genic polymorphism in nature *can* be reconciled with a selective mechanism. He makes the important distinction between competitive and noncompetitive selection models. As it progresses, however, the book becomes a theme and variations rather than reaching a clear resolution. The generally fallacious practice of multiplying fitnesses associated with each locus (this implies independent, separate selection, locus by locus, of individuals on the basis of their genotypes) is repeatedly resurrected and never explicitly dispatched. The continuing ambiguity is typified by the sentence (p. 106) ending ". . . the positions are filled by individuals with the highest fitness available." Fitness is the wrong word. Table 16, which begins with a misprint, is nonsense.

Papers by Sved (*American Naturalist* **102**, 283 [1968]) and by Maynard Smith (*Nature* **219**, 1114 [1968]) should have been considered; and the now customary triple reference to Sved, Reed, and Bodmer; King; and Milkman implies that they say the same thing. They don't, though they all show that previous cost estimates were far too high. Indeed, the story begun so well in *Genetic Load* is continued in the 1968 literature; but I venture to say that even most population geneticists will gain from having read this book first.

As Wallace mentions, perhaps too briefly, some people believe that genic polymorphism is maintained without cost by mutation of no adaptive significance ("neutral mutations"). Even a selective mechanism, frequency-dependent selection, can operate, in theory at least, at almost no cost, in contrast to the conclusions drawn from the examples in this book (p. 55). So alternatives to heterosis are still regarded as possible in some quarters.

Concern is expressed for certain human population problems; Wallace's remarks provide a bridgehead for further exploration of these subjects.

Genetic Load may not be the last word, and it does suffer from a lack of critical editing, but its central theme provides a most appropriate entrée into population genetics. And it looks like a good book to teach with: as usual, Wallace leaves room for thought. All in all, it's well worth the time for a broad spectrum of biologists.

ROGER MILKMAN
Department of Zoology, University of Iowa, Iowa City

A Dualism in Biology

Symmetry and Function of Biological Systems at the Macromolecular Level. Proceedings of the 11th Nobel Symposium, Södergarn, Lidingö, Sweden, Aug. 1968. ARNE ENGSTRÖM and BROR STRANDBERG, Eds. Interscience (Wiley), New York, and Almqvist and Wiksell, Stockholm, 1969. 436 pp., illus. $29.50.

Such biological macromolecules as proteins and nucleic acids are built from geometrically asymmetric units. Moreover, the biological functions of the macromolecules depend on specific asymmetric arrangements of these asymmetric units—such, for example, as the three-dimensional deployment of amino acid side chains at the active site of an enzyme. Information and dynamic function depend on asymmetry, whereas ordered (in the sense of being predictable) and symmetrical structures contain minimal information and are suitable for static or structural functions. It is not the neat symmetrical arrangement of columns and lines of type on a printed page that conveys information, but rather the asymmetric sequence of letters in the lines; similarly, the sequence of nucleotides rather than the symmetrical helical structure of DNA embodies biological information. Yet symmetries of various kinds are found throughout biology, at nearly every level from nucleic acid or protein helices to the gross shapes of organisms. These observations suggest two general questions: (i) Is there continuity in kind between the symmetries seen at the levels of the molecule, the organelle, the virus, the cell, the organism? (ii) Are these symmetrical arrangements really useful only structurally, or might they