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.

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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.

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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 be more directly related to dynamic function?

The answer to the first question, given implicitly by several contributors to the present volume (notably by Monod in the introductory chapter), and elsewhere discussed explicitly and in depth by Bernal (*J. Mol. Biol.* **24**, 379 [1967]), is unequivocally no. We must distinguish among three ways in which symmetrical structures arise: (i) self-assembly on the basis of intrinsic atomic properties, as in crystals; (ii) self-assembly on the basis of biologically evolved recognition and binding sites (Bernal refers to this as "prescription and self-assembly"), as in enzyme aggregates, virus shells, and the like; and (iii) growth. Ambiguous, borderline cases doubtless occur, as in other biological classifications, but in general these mechanisms are clearly distinct. As Bernal points out, the symmetry of a sea star does not arise from self-assembly of the arms.

Many readers will recognize the second question as one that has received much attention in connection with the study of oligomeric regulatory enzymes. The cooperative kinetic behavior that is characteristic of this type of enzyme evidently depends on interaction between aggregated subunits. Are such symmetry elements as the molecules possess merely a necessary consequence of self-assembly of identical units, or may the symmetry itself be functionally important, as is postulated in the well-known model of Monod, Wyman, and Changeux? Several participants in this symposium deal, implicitly or explicitly, with this problem, but the answer remains in doubt.

As might be expected, those speakers who deal with structure emphasize symmetry, whereas those whose topics are more functional or dynamic deal with asymmetry. The distinction is emphasized by Malmström, who comments, in effect, that the search for order in nature may all too easily become self-directing—symmetry sometimes lies in the eye of the beholder. Because scientists search for ordering principles, "we tend to invent models involving a high degree of symmetry. This predilection may be a distinct disadvantage when we are investigating a system whose function involves an asymmetric structure." Malmström's investigation of copper-containing oxidases has shown that these molecules, previously thought to contain identical units in a highly symmetric structure, are in fact both functionally and structurally asymmetric, with at least three distinct environments for copper atoms.

Because of the general title and the wide range of topics covered in this symposium, a listing of authors and topics seems desirable. Most of the authors are sufficiently well known that their names will indicate the general approach.

An initial short section, Basic Views on Symmetry, includes a general essay on biological symmetry by Monod, an elementary mathematical treatment of helices and spirals by Coxeter, and a discussion of symmetry in nuclear, atomic, and complex structures by Weisskopf. The next section, Prediction of the Conformation of Macromolecules, includes survey articles by Scheraga, Ramachandran, and Liquori. A section on Interaction between Subunits in Polymeric Proteins contains a discussion by Rossman and colleagues of their exciting findings on the alterations in symmetry and structure of M_4 lactate dehydrogenase that follow from ligand binding, a discussion by Theorell of isozymes and subunits of liver alcohol dehydrogenase, the article by Malmström previously mentioned, an article on electron microscopy of oligomeric proteins by Valentine, an article on oxygen-hemoglobin interactions by Schuster and Ilgenfritz, and one on poly-L-glutamic acid aggregation by Schuster, Jennings, and Spach. A section on Symmetry and Cooperativity in Biological Membranes contains theoretical discussions by Kilkson and by Wyman and a theoretical-experimental treatment by Changeux of cooperativity and transitions in membranes, an article on enzymes immobilized in artificial membranes by E. Katchalski, and one on membrane crystallites in insect photoreceptors by Gemne. The section on Assembly and Structures of Viruses quite naturally bears the closest resemblance to the overall title of the symposium, since the symmetrical assemblages of the virus proteins presumably serve mainly structural, rather than dynamic, functions. Klug discusses tubular variants of the spherical papilloma viruses, Lonberg-Holm and colleagues discuss proteins of adenovirus, Höglund and colleagues write on the nucleocapsid of influenza A2 virus, Kellenberger presents a very interesting discussion of polymorphic assemblies of virus proteins, and Lundin and colleagues report on satellite tobacco necrosis virus. A section on Aspects of Macromolecular Arrangements in Muscles begins with an interesting general article by Engelhardt on biological movement, expressing doubts concerning the popular sliding-filament model for muscle movement. This is followed by a very informative discussion by Caspar and Cohen on polymorphism and protein function, with special emphasis on tropomyosin, and a brief discussion by Afzelius of filament symmetries in arrow worm muscle. The appendix consists of an admirably lucid short article by Klug on point groups and the design of aggregates, which will be helpful to readers with little background in these matters.

As is usual in such symposium proceedings, nearly everything in this book has been previously published in the original literature. Juxtaposed in one volume and, in some cases, more generally oriented than the research papers, these articles may, however, deepen the reader's insight into the dualism between symmetry and structure on the one hand and asymmetry and function on the other. Recognition of this dualism is far from new, either in biology or more generally; Caspar and Cohen cite Coleridge, and Changeux follows Nietzsche in invoking Apollo and Dionysius. As perhaps the most fundamental of the contradictory/complementary relationships of life, this dualism takes on new aspects at each stage in the advance of knowledge; it will be with us, always new but always the same, for as long as men seek to understand living systems. It is the chief merit of this volume that it brings together the contemporary views of scientists who have approached the problem in different ways, guided by quite different conceptual backgrounds.

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A Memorial in Embryology

Organization and Development of the Embryo. ROSS GRANVILLE HARRISON. Sally Wilens, Ed. Yale University Press, New Haven, Conn., 1969. xxvi + 294 pp., illus. $15. Silliman Lectures, Yale University.

This posthumous volume is based upon the outline and notes prepared by the author for the Silliman Lectures he delivered under this title at Yale Uni-