

lems in primatology is that of collecting and presenting data from different habitats in ways that allow meaningful comparisons. The present book is an excellent start on this problem in one part of the field. I hope it will be used not only as a model for future baboon studies but as a model primer to be copied for other species in other habitats, which present different problems.

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THE GENETICS OF HUMAN POPULATIONS.

By L. L. Cavalli-Sforza and W. F. Bodmer. xvi + 965 pp., figures, tables, problems, bibliography, indices. W. H. Freeman, San Francisco. 1971. \$27.50 (cloth).

In recent years such rapid advances have been made in the application of population genetics theory to human variation that a great need has arisen for a major work covering the field. Previously human examples may have been sporadically introduced into texts covering the population genetics of all organisms or population genetics was included, almost as an afterthought, in works on all aspects of human genetics. With this book human population genetics seems to have finally come of age as a distinct science as opposed to biochemical, clinical, or other fields within genetics. Although expectedly it does emphasize the authors' own work and specialties, the book is comprehensive without being a completely exhaustive treatment of the subject; and anyone working on almost any problem in human population genetics can find the appropriate model and formulas in it. The rapid developments in the field would seem to imply quick obsolescence, but despite this possibility and future competitors, I think this book will remain a major source for some time.

There are some innovations in format, which I am sure will have their detractors, but given the major aims of the authors I think the innovations are very useful. First, within the nine chapters each topic is introduced with an italicized statement,

which is then expanded upon in a paragraph of two. This is sometimes a statement of fact, sometimes a theory, or just a brief outline of a particular problem. For reference, these statements do make it easier to find any particular topic, but frequently they seem more dogmatic than warranted by the evidence. However, they do stimulate critical thinking on the reader's part. Second, the mathematical proofs and more complex equations are put in appendices at the end of each chapter. This makes the reading of each chapter more even and stresses the applications of the mathematics to real data without interruptions by long proofs of the reasons why this particular equation fits. For too long population genetics has consisted of elegant mathematical models or theorems whose applications to natural populations are frequently either trivial or non-existent. However, biological science is now attaining the same position with regard to mathematical analysis as the physical sciences. The mathematicians can treat the models of physical phenomena as an axiom system and derive theorems or conclusions about it, but at the same time the physicists can just use the formulas without having to derive or prove them.

Although many of the formulas of population genetics are quite simple, e.g., $\dot{q} = \mu/s$, they do form the basic theoretical model for the understanding of genetic variation; and the major thrust of this book is to illustrate the utility of the formulas for the analysis of data. This emphasis is changing population genetics from a branch of mathematics into a science; and, as the authors point out, the main part of the book requires not mathematical expertise but only a knowledge of elementary algebra. The book is dedicated to R. A. Fisher, but, without trying to diminish his contribution, I think its approach owes more to Haldane. Haldane developed many of the theoretical formulas of population genetics, but in so many of his papers he began with a problem of genetic variation which actually existed in some species. His theory was an attempt to explain the problem, and frequently his papers ended with more questions than answers. Similarly, Cavalli-Sforza and Bodmer analyze much of human genetic

variation with models which are known to be simplifications of the real situation; and these raise many questions whose answers cannot be given at present. But it is only by examining the fit between the models and the data that progress will be made. By such an approach the authors have pointed out many of the problems in the field and in this way have anticipated future advances.

So many topics are covered that space does not permit any more than a very general outline of the organization and contents. Although it is primarily concerned with genetic differences among populations, the book necessarily begins with a chapter on the genetic process which includes the biochemical and cytological aspects of gene transfer and the Mendelian rules. Then, in the next three chapters the deterministic theory of genetic change in a single population is presented; first, the concepts of breeding population, gene frequency, and Hardy-Weinberg equilibrium and then the two causes of gene change, mutation and natural selection. The treatment of gene frequency change is very exhaustive, and there is even a simple model of overlapping generations in the appendix. The chapter on mutation includes both a consideration of mutation with reference to the genetic code and protein synthesis and the older use based on phenotypic observations. In addition, there is an analysis of the various ways mutation can be balanced by selection.

The action of selection is related to the concepts of balanced and transient polymorphisms, which seem to be the two possible mechanisms in terms of deterministic theory for the maintenance of so much genetic variability in human populations. The hemoglobin and G6PD deficiency polymorphisms are used as illustrations. By an original analysis of the massive hemoglobin data from West Africa which compares the frequencies of the genotypes in each population to those expected in a Hardy-Weinberg equilibrium, they postulate that the hemoglobin C allele is replacing the S allele and thus that this locus is partially a transient polymorphism. Their analysis assumes that individuals with only hemoglobin C are homozygous for this allele, but they could be hetero-

zygous for both hemoglobin C and β thalassemia. This accounts for the very high estimate of the fitness of C homozygotes. Their estimates of fitness also do not take into account differences in fertility, and SC females are known to have a very difficult time in pregnancy. The authors point out that the hemoglobin C distribution in West Africa has the general shape one would expect from the origin and diffusion of an advantageous mutant. This may be true to some extent but hemoglobin C has diffused much farther into Southern Europe than one would expect and to the west of Ghana it is practically non-existent. Thus, I am still more convinced of my own analysis and its conclusion that hemoglobin S is replacing C.

The authors also argue that in malarious regions the G6PD locus is a transient polymorphism with the deficient allele replacing the normal one. However, both the African deficient allele and the Mediterranean one are extremely dispersed geographically and ethnically and are found in frequencies of 10–30% in most populations with malaria. If the deficient alleles were replacing the normal one, surely more populations would have frequencies close to or greater than 50%. The very high frequency in Kurdistan Jews is given as evidence for the transient polymorphism hypothesis, but it seems unlikely that this population had the deficient allele and malaria many years before any others. There are also other explanations for their frequency, which seem more likely since surrounding populations have very low frequencies of the deficient allele. Admittedly, with the discovery of the hemoglobin S and malaria association, balanced polymorphism was so enthusiastically received by geneticists and anthropologists that it has been overworked as an explanation. But when the geographical distributions and the time involved for change are considered, I don't think a good case can be made for either the hemoglobin or G6PD locus being a transient polymorphism.

On the other hand, in their chapter on the ABO and other blood groups, Cavalli-Sforza and Bodmer state that heterozygotes must have a greater fitness for the blood group polymorphism to be stable. The ABO blood groups are commonly consid-

ered to be a balanced polymorphism, but they could just as well be balanced by frequency dependent selection, where the heterozygote has the lowest fitness. The blood groups seems to be related to infectious diseases, and parasites adapt to their hosts by becoming antigenically similar, which would seem a possible mechanism for giving rare antigenic types an increased fitness. Cavalli-Sforza and Bodmer also cite Lederberg that some viruses acquire part of their coat and hence some antigens from the host cell they have infected, and this would also lead to increased fitness of rare genotypes. In any case, their discussions of these polymorphisms are comprehensive and provocative, although some of their conclusions may be wrong.

The next set of chapters, on genetic demography, inbreeding, and population structure, introduce other parameters into the simple deterministic models of gene change in a single population. The principles of population demography are outlined, and the effect of the age structure and age specific mortality on fitness is shown with reference to human disease. In the chapter on inbreeding the concept of genetic load is presented in detail, although most would agree when the authors question its utility. It is now being increasingly recognized that the concepts of gene flow and gene drift can be encompassed under the more general concept of population structure. There are many recent attempts to develop matrix models of the relationships among several isolates. The authors discuss their own work for the most part, but these models are so similar that one model including features of many of these beginning attempts will be the eventual outcome. The chapter also contains a detailed description of stochastic gene frequency change and several models of the balance of linear systematic pressures such as selection and migration and gene drift. With the development of models by geneticists which reflect population structure, anthropological knowledge is becoming more relevant to population genetics. Obviously, the economy, social organization, and political structure of a group determine their population structure to a great extent. The authors have only a brief description of

"technological" differences among human populations, but any explanation of modern genetic variability will have to infer the population structure of the group in the past, and this will be done primarily on anthropological knowledge and theory.

The final four chapters are on quantitative inheritance, human evolution, the sex ratio, and the inevitable finale of eugenics and genetic engineering. The analysis of quantitative inheritance in man is perhaps the most significant area which will require efforts by both human geneticists and physical anthropologists. The outline of the basic concepts of polygenic inheritance is detailed and lucid, and there are several applications to modern human variation. Quantitative models will also form the theoretical basis of interpretations of the fossil record. There is some quantification in the chapter on human evolution but it is minimal. The brief outline of human prehistory and evolution will disappoint the experts in the fossil evidence since it is mostly a rehash of LeGros Clark with a dash of Coon. Some new evidence and theoretical analysis has occurred since these works appeared.

Much of the rest of the chapter on human evolution is concerned with phylogenetic analysis or the construction of tree diagrams as models of human evolution based on genetic or anthropometric similarities. This is now one of the current vogues in evolutionary analysis, and Cavalli-Sforza has been one of the pioneers. Despite its popularity I am not convinced that it is a realistic model of human evolution. The majority of human population history has not been comparable to a branching process despite its appearing to be so from genealogies or the history of family names. It has been more characterized by populational equilibrium with stable populations and gene flow among them. In addition, the genetic differences which exist among the major groups of mankind are due to a greater extent to selection than to common ancestry. A phylogenetic tree based on several blood group loci is shown in the book, and it generally has the Africans and Europeans clustered together and the peoples of Asia and the South Pacific in another cluster. However, a tree based on anthropometric traits lumps the Africans and the Mela-

nesians as opposed to the Europeans and North Asians (Cavalli-Sforza and Edwards, '63). The anthropometric similarities are obviously due to natural selection, and it seems to me that there is no good reason for the same not to be so for the blood groups. The chapter on evolution also includes an outline of the new field of molecular evolution and the various formulas used to estimate the time for an amino acid substitution. Although the formulas include selection, this field generally makes the same assumptions as to the absence of any effects of selection on the process. However, the population structure and geographical dispersion of a species when combined with differential selection will surely provide a better model of species evolution than the current models which assume a species to be a single population.

In conclusion, this book is the most comprehensive treatment of human genetic variation and particularly its theoretical basis currently available. It will also probably remain one of the major works in the field for a long time and is strongly recommended for anyone interested in the genetic differences among human populations.

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CULTURE AND BIOLOGICAL MAN: EXPLORATIONS IN BEHAVIORAL ANTHROPOLOGY.
By Elliot D. Chapple. xxii + 345 pp.,
bibliography, index. Holt, Rinehart and
Winston, New York. 1970. \$8.95 (cloth).

In his preface, the author warns us that this book is intended "to show how culture (and cultural process) modifies the behavior of individuals through mechanisms which have a biological foundation."

He thus partakes of a new trend which shows increasing interest for the little explored field where biological and cultural facts overlap. After the excesses of

simplistic biologism, and, later on, the absolute reign of sociological analysis, new concepts are now being forged. Many problems that had been put aside because they involve both biology and culture, can now be taken up again.

The contribution of behavioral biology (ethnology, field studies of apes and monkeys, behavior genetics, comparative psychology) ensures better studies of the biological basis of culture. At the same time, the renewal of cultural studies in the field of communication, of information theory, of the relations of man with space, calls upon biological knowledge and urges searchers to further synthesis. This is E. D. Chapple's aim, in a book which is meant to be "an introduction to a larger field of investigation."

The relations between "culture" and "biological man" pass, according to the author, through channels of interindividual communication. The individual, who is an "interactional system in equilibrium" belongs to the biological world through which he receives his basic features. In all interaction, within diverse cultural sequences, it is culture that guides the use of these features. The book is thus divided into two parts: "Dimensions of Behavior" and "Dimensions of Culture." He shows in each part the own logics of these interdependent areas and the ways of their exchanges. Human behavior within a given culture is both their point of junction and the most revealing expression of the constraints which they impose.

This book can be read from two angles: that of the biologist and that of the cultural anthropologist.

The biological approach can be used when talking about individuals and their biological needs. Relying to a great extent on animal ethology the author deduces the bases of a human ethology yet to be written. He then presents the data concerning biological rhythms, the fundamental relations of man with time and he then connects this to man's personality. He thus tries to bring to light certain basic dimensions, hidden by the complexity of visible facts.

The biologist, who upon seeing the title expected something else feels disconcerted after reading this book. All of the field