

The newest candidate is variation in DNA, as shown by the following quotation from Jukes: "Changes in the third base of codons for amino acids will in most cases not produce a change in the amino acid assignment, so that in such cases they are, therefore, selectively neutral." This assertion not only manifests the fallacy of omniscience, it also ignores a good deal of evidence that natural selection can act directly on the composition of nucleic acids.

By rigorously following the "neutralist" argument, Kimura and Ohta have maneuvered themselves into the entertaining position of having to postulate that the majority of the changes during evolution have been mildly deleterious. The concept of evolution taking place against a background of progressive deterioration is one whose implications remain to be explored. Does it predict, for example, that life could not indefinitely survive in a perfectly constant environment? We must await the answers with impatience.

If, in this book, the arguments for neutrality leave something to be desired, so alas do the arguments for selection. Ayala, for example, claims that the relative uniformity of the numbers of alleles and their frequencies among widely separated natural populations of *Drosophila willistoni* are incompatible with neutrality. However, they might well be the result of a recent "bottleneck" in numbers followed by a rapid expansion of range. Similarly, his finding that alleles at the *Lap-5* and *Est-5* loci come to equilibrium in experimental populations does not demonstrate that they are directly subject to selection. It might be due to their being in a state of linkage disequilibrium with selectively important alleles at other loci. This disequilibrium could also be the consequence of a recent constriction in numbers. Explanations in terms of bottlenecks may not be the correct ones, but at least they should be considered.

The conclusions of Allard and Kahler are subject to similar reservations. Several polymorphic loci of the wild oat *Avena barbata* show parallel variations that are correlated with changes of habitat from xeric to mesic. This, however, does not necessarily mean that the loci themselves are subject to selection. Another plausible hypothesis is that there are two distinct genetic entities (semispecies) with different ecological preferences, hybridizing in some habitats. Although *Avena*

is largely self-fertilizing, hybridization is common within the genus, and attributions to particular species are often difficult. Allard and Kahler do not discuss these difficulties.

In another paper, Gatlin reports her studies on the "information density" of DNA. She defines a component that measures the degree to which the probability of occurrence of a base depends upon the nature of the adjacent bases. She makes the interesting observation that the value of this component appears to have increased during the evolution of vertebrates. On the basis of her findings, she claims to have discovered a new evolutionary principle, that natural selection acts to improve the informational efficiency of the "source" (DNA). If she is merely proposing that selection acts directly on the DNA, and can improve its efficiency, then her principle is not new. If, however, she is going further, as she seems to be, and claiming that selection acts directly on the characteristic of informational efficiency, then her claim is premature. There are several parameters ($\bar{W}$ for example) that are increased as a result of natural selection, but on which it does not act directly. They are consequences rather than causes.

Reichert adapts Gatlin's methods to the study of proteins, and in the course of his discussion wins this year's Lewontin Prize for the best throwaway remark: "The molecular biological format provides a testable basis for significance, and may even lead us, quite incidentally, to the meaning of meaning."

This indeed would be a desirable destination, but on the way we are faced with the more prosaic matter of attempting to decide whether or not natural selection has been the dominating factor in molecular evolution. How are we to proceed? The two most critical essays in the book, by Stebbins and Lewontin and by Bodmer and Cavalli-Sforza, make it clear that juggling with numbers will not solve the problem. Our present estimates of evolutionary rates, mutation rates, genetic loads, effective population sizes, and numbers of genes are all so inexact that by a suitable choice of values we can favor either case. Clearly these estimates must be refined, but there are other approaches. The most obvious, and in my opinion the most likely to be productive, is to study the properties of the molecules themselves, to discover if contemporary variants of

enzymes differ in their biochemical activities, and to find out if the differences are detectable by natural selection. The task is not easy, but the first steps have been taken. A fascinating example is provided here by MacIntyre, who reports an inquiry into the differences between the homologous enzymes of closely related species, using the techniques of subunit hybridization. The results of this study leave little doubt that the differences have important biochemical effects. They provide little comfort for supporters of the neutralist view.

It is surprising that none of the contributors has clearly made the most obvious point about molecular evolution. While the arguments for neutrality are inadequate, and the direct evidence for selection is inconclusive, the selectionist hypothesis remains the most economical one. A large part of biological research during the past century has been involved in establishing the primary role of natural selection. It would be illogical to change course, in the face of all the evidence, because of a temporary ignorance.

In whatever way the debate may eventually be resolved, at the present we must content ourselves with the fare that is offered by this book. It contains some good meaty pieces of reading and much entertainment, both intentional and unintentional. It can be recommended to believers and cynics alike, but while digesting it they are cautioned to remember the prescient words of Goethe: "The web of this world is woven of Necessity and Chance. Woe to him who has accustomed himself to finding something capricious in what is necessary, and to ascribe something like reason to what is capricious."

BRYAN CLARKE

Genetics Department,
University of Nottingham,
Nottingham, England

A Sampling of Ecology

Growth by Intussusception. Ecological Essays in Honor of G. Evelyn Hutchinson. E. S. DEEVEY, Ed. Connecticut Academy of Arts and Sciences, New Haven, 1972 (available from Archon Books, Hamden, Conn.). 442 pp. + plates. Paper, \$25. *Transactions of the Academy*, vol. 44, Dec. 1972.

The title of this volume may conceivably mislead some medically oriented readers. This bit of mystification, chosen by the editor, is something

Evelyn Hutchinson might indulge in himself. Its actual reference is to the development of ecological theory, in which Hutchinson and his students have had an eminent share. Deevey's preface also warns: "To describe the contents of this volume seems to require a tedious and most un-Hutchinsonian disquisition, on the nature of modern ecology." The varied diet in this volume does more, but also less, than this. It allows one to savor, at one step removed, many of the interests that have occupied an active career. Through an afterword by S. D. Ripley, it even allows a fleeting, more personal glimpse of some early episodes in it, the African and East India expeditions, which exerted a lasting influence. A further personal touch is provided by Rebecca West's charming portrayal of an utterly unimportant, but revealing, episode from her acquaintance with Hutchinson.

The rest of the 20-odd papers are more traditional, though their range is formidable and characteristic. Perhaps most in keeping with Hutchinson's style is E. Leigh's article on the significance of the angular arrangement of leaves around the stem, which has evolutionary implications that go beyond the author's evident enjoyment of the mathematics and geometry. Other scenes from the evolutionary play have been chosen by a major fraction of the authors, among them the Browsers, M. J. Dunbar, I. McLaren, L. B. Slobodkin, and P. Wangersky. There are papers on the history of science (J. L. Brooks and E. Mills) and of a lake (M. Tsukuda). Two papers are primarily taxonomic, with that by Hartman and Goreau having important paleoecological implications. D. Zinn and S. Kahn's account of the geography and geology of Penikese Island approaches Hutchinson's geological interests, though their compass is far narrower. Curiously and unfortunately, biogeochemistry receives no emphasis in the entire volume, nor is its treatment in the recent issue of *Limnology and Oceanography* honoring Hutchinson commensurate with the importance of this field among his endeavors.

Of the essentially solitary forays, P. Klopfer's examination of the origin of human consciousness and U. Cowgill's discussion of seasons of birth and death of man in Portugal are worth singling out. The latter also provides an unconscious (I think) bit of humor with a statement about the temporal sequence

of birth rates, "Minima appear alternately around the maxima."

The rest of the papers are on aspects of ecological theory whose relations are becoming increasingly clear: diversity, species interactions, and ecosystem stability. R. Margalef, in a vast generalization, suggests that diversity in nature rarely exceeds 5 bits per element. A. Covich shows some of the advantages and difficulties of applying economic models to exploitation as practiced by organisms other than man, and F. Smith examines the conditions for ecosystem stability, using computer simulations as a tool. He concludes by returning to one of Charles Elton's rather neglected insights, that spatial heterogeneity seems a prime requirement for stability.

A number of the contributions are undoubtedly important, perhaps some I have not discussed. In sum, they do begin to suggest the variety of one's experience in becoming acquainted with G. E. Hutchinson. Still, reading most of them one longs for the felicity of his prose and the fertility of his imagination.

PETER W. FRANK

Department of Biology,
University of Oregon, Eugene

Primates in Natural Groups

The Social Behaviour of Monkeys. THELMA ROWELL. Penguin, Baltimore, 1973. 204 pp., illus. Paper, \$2.50. Penguin Science of Behaviour series.

Thelma Rowell has written a very interesting and stimulating little book about the social behavior of monkeys. Concerning herself primarily with data from the Old World monkeys, she has produced a volume which challenges some old ideas, presents some new theories, and effectively communicates the complexity of nonhuman primates and their social systems.

The brief opening chapter introduces the primates and puts their behavior and organization into perspective by comparisons with other social mammals. Rowell then presents a general account of the behavior of the wild baboons (*Papio cynocephalus*) which she studied on the Uganda side of the Ishasha River. Among the more interesting conclusions drawn from the field study (many of which contrast with those from other studies of feral

baboons) are that adult females serve as a focus of the group's social activity, and that they "lead" the group in the sense of selecting the direction for the day's march; adult males change groups frequently, and the stable core of a group is the subset of adult females; the adult males of the Ishasha troops were not arranged in dominance hierarchies; and adult males failed to defend the troop against external threat, choosing rather to lead the retreat.

The Ishasha study then serves as reference data for expanded discussions of several major areas of primate behavior and organization. These include communication, sexual behavior, infant social development, and the effects of environment on behavior. All are areas of personal research for Rowell, and the chapters are excellent. I was particularly pleased with the discussion of mating and estrus. Rowell appreciates and communicates to the reader the intricate interplay of variables which combine to produce mating behavior. One of her conclusions which I wish to underscore is that for many primate species estrus and mating can and do occur at times other than proximal to ovulation. This fact necessitates a bit of rethinking by primate researchers accustomed to equating estrous cycles and menstrual cycles.

A chapter on adult behavior includes discussions of dominance hierarchies, territory, social roles, and the ways kinship and age affect behavior. I must take issue with Rowell on the topic of dominance hierarchies. I think she is overstating her case when she suggests that a hierarchy may be a "pathological response" to stressful conditions. At present, too little is known about the formation, maintenance, and functioning of dominance hierarchies to warrant labeling them pathological. In fact, such a label could provide an excuse for the termination of research into the phenomenon of hierarchical dominance systems—an effect which Rowell would detest, I am certain.

The book is good, and I heartily recommend it. Surely one of its best points is the evaluation of old theoretical approaches and the presentation and discussion of new ones. Toward the end of the book is a statement which will please those readers who believe (as I do) in the value of longitudinal studies of groups containing individuals of known relationships. Rowell says, "I would predict that kinship