changes to match the tRNA's, then it would seem that selection, rather than drift, is causing the codon usage to track the tRNA's. This problem of codon usage may well be the battleground on which neutrality receives its severest test.

It is not enough to argue that the neutral theory is compatible with the observations; it must also be shown that selection is incompatible. This is the weakest part of the book. Kimura's arguments against selection are the same arguments that have failed to convince anyone for the past 15 years. The main problem is that Kimura's standard model of selection assumes that a species has an infinite reservoir of unique advantageous mutants that have been slowly leaking into the population by mutation for the past few hundred million years in the face of a static environment. However, if selection is operating in response to a constantly changing environment, then even the most naïve of models yields evolutionary rates that are independent of both the population size and the mutation rate. This is because mutations to advantageous alleles do recur in large populations. Kimura, of course, knows this. Had he taken models of natural selection more seriously, he might have shaken population genetics out of the silly notion that these mechanisms of molecular evolution can be distinguished by facile arguments. As it is, his treatment will undoubtedly perpetuate an already undistinguished literature.

Although the book tries to present a summary of the relevant data from molecular biology, there are some very telling omissions. Conspicuously missing are essentially all the studies examining the evolution of protein function. No mention is made, for example, of the fascinating work of George Somero or Dennis Powers on the adaptations of enzymes to temperature and pressure in fish, or of any of the large number of papers on hemoglobin adaptations. As for the neutral theory itself, Kimura gives a very complete description of the mathematical theory as developed by himself and others at Mishima but gives very little space to the contributions of W. J. Ewens, J. F. C. Kingman, G. Watterson, F. Stewart, and others who have in many ways pushed the theory to its most sophisticated level.

Throughout one gets the sense that Kimura is using the book as a vehicle to establish for himself a niche in the history of science. He carefully tells us about his original conception of the neutral theory in 1967 and his announcement of the theory to the Genetic Club of Fukuoka in November 1967, thus attempting to establish clear priority for the idea. He spends an entire chapter, entitled "The overdevelopment of the synthetic theory and the proposal of the neutral theory," belittling the contributions of many of the participants of the synthesis. For example, he writes, "Dobzhansky's main contribution to the science of population genetics . . . is his finding with A. H. Sturtevant that chromosome polymorphisms involving inversion are abundant in some species of *Drosophila*" and "Despite the various attempts to glorify the synthetic theory of evolution, actually very little progress was made at this time." Such judgments may or may not be valid, but one is unaccustomed to hearing them from a scientist who is setting the stage for the historic importance of his own theory.

The neutral theory is a great achievement. It provides a simple (and elegant) explanation for a large number of the observations of molecular evolution. By presenting the theory from such a strong position of advocacy, Kimura does little to help the scientific community judge its merit. His aggressive stance toward those who have published criticisms is particularly distasteful because it is still unclear that the neutral theory is in better accord with the facts than are theories based on the action of natural selection.

JOHN H. GILLESPIE
Department of Genetics,
University of California, Davis 95616

Sex Determination

Evolution of Sex Determining Mechanisms. JAMES J. BULL. Benjamin/Cummings Advanced Book Program, Menlo Park, Calif., 1983. xx, 316 pp., illus. $19.95. Evolution Series.

The near ubiquity of separate sexes in vertebrates, especially the mammals and birds, with which humans are most familiar, predisposes even biologists to assume that sex determination is a rather uniform process among higher animals; the question of sex determination in higher plants escapes attention. Bull's book provides a recent summary of what is known about sex determination in animals and plants and reminds us of the great diversity of mechanisms that have actually been observed.

The book is divided into two parts, the longer first section being concerned with sex determination as such and the shorter second part dealing with the evolution of sex chromosomes. In the first part, Bull is concerned not with the origin of sex or with the evolution of parthenogenesis but instead explores the conditions under which a change from one of these mechanisms to another might occur, a subject on which he has made numerous contributions. Using his "combinatorialist perspective," he places the known mechanisms among those that are theoretically possible, a perspective reminiscent of the method of multiple working hypotheses advocated by T. C. Chamberlin and useful in encouraging an open mind and broadening inquiry.

A survey of the literature confirms that male heterogamety and female heterogamety are two of the most common forms of sex determination in higher animals. In some taxonomic groups, such as birds and mammals, one or the other of these seems uniformly to occur; in other groups, such as salamandrid salamanders and chironomid midges, individual species vary. Bull develops the argument that transition between male and female heterogamety occurs through intermediate stages with multiple sex factors. Under a variety of plausible conditions, paths of equilibria connect the extremes of male and female heterogamety. The mathematical development of this hypothesis is not presented, but references and a discussion of the assumptions and conditions for the analysis are provided. The absence of detailed mathematical treatment permits the ideas to follow more readily for a larger group of readers. Two of the three appendixes to chapters, however, do provide more detailed treatments that have not been published elsewhere, one for sex ratio evolution under systems of paternal genome loss, the other for evolution of genes with sex-specific fitnesses as a function of linkage to sex factors.

Similar treatments are provided for other possible transitions: to haplo-diploidy (arrhenotoky), in which males hatch from unfertilized and females from fertilized eggs; to paternal genome loss, in which males arise from fertilized eggs but transmit only the maternal genome. In these systems, a male transmits to progeny only its mother's genome, which doubles the genetic identity of mothers with their grandchildren. Arrhenotoky has an additional advantage: a single female can produce sons by laying unfertilized eggs; with their sperm, she can found a colony with both sexes present. This advantage is absent when the paternal genome is lost.

Particularly interesting to this reviewer was the summary of data on environ-

mental determination of sex. Plausible explanations are given for the advantage of environmental sex determination in the echiurid worm *Bonellia* and in mermithid nematodes that parasitize insects of different sizes. As the author acknowledges, the advantage of environmental sex determination in those turtles and crocodilians in which it is known is less clear.

While paths of equilibria may, with appropriate assumptions, connect many of the mechanisms of sex determination, the development of markedly heteromorphic sex chromosomes is a major deterrent to such shifts; in those reptile groups in which both features have been studied, environmentally determined sex is absent when heteromorphic sex chromosomes are present; the uniformity of male heterogamety in mammals and of female heterogamety in birds and the occurrence of XX/XO systems in large groups of insects, arachnids, and nematodes probably reflect the extreme sex chromosomal heteromorphism seen in those groups. Although empirical studies of the degeneration of one sex chromosome are difficult, an appropriate experimental model probably exists in the hemiclonally inherited genomes of hybridogenetic fishes (*Poeciliopsis*) and frogs (*Rana esculenta*).

The chapters on cytoplasmic sex determination, though interesting, are less convincing to me than others because the cytoplasmic factors are maternally transmitted microorganisms. Neither the assumption that infected females are as fit nor the apparent ascription of genetic fixity to the microorganisms themselves seems appropriate. I could not help wondering whether the great complexity of sex determination patterns seen in the isopod *Armadillidium* was not a result of genetic heterogeneity in the parasite as well as the host. Nevertheless, the model developed is useful in pointing up significant features of the biology of these systems, especially in *Armadillidium*, that need further exploration before a satisfactory explanation of the observations is possible.

The book is well printed and relatively free of defects. A conspicuous misprint on p. 215, substitution of "never" for "always," is easily recognized. The bibliography contains over 600 references; both subject and author index are provided. I found much to think about in this book; I recommend it to general biologists and to anyone interested in broad patterns of evolution.

THOMAS UZZELL
Academy of Natural Sciences, Philadelphia, Pennsylvania 19103

Ecology Around the World

The Ecological Century. A Personal Appraisal. E. BARTON WORTHINGTON. Clarendon (Oxford University Press), New York, 1983. xvi, 206 pp., illus. $27.50.

E. Barton Worthington is a unique example of a highly competent person born in the right place at the right time (1905). He was in school when ecology was just beginning, and he was a student in the first limnology course at Cambridge. Most of the young British scientists at that time wanted experience in the African colonies. Hence it is not surprising that, only a few weeks after completing his degree at Cambridge in 1927, Worthington was involved in a fishery survey of Lake Victoria, and later, in 1930–31 in a study of some more remote lakes of Kenya and Uganda. This represents the beginning. From here on he participated, usually as director, in a steady succession of progressively grander programs. Water was involved in some way in all the projects, and so was ecology. Worthington's conception of ecology gradually developed into an ecosystem approach, which included systems analysis, economics, sociology, and even politics. The book is based on his personal experiences, but it is not an autobiography.

Worthington considers that ecology has gone through a sequential development, which can be categorized roughly by quarter centuries. The first quarter of the 20th century was mainly one of exploration, the second quarter was descriptive except for exploratory work still going on in high and low latitudes, and the third quarter was experimental. The fourth quarter sees ecology as a well-established discipline having wide applications in human affairs. Worthington calls the entire century ecological because of the emergence of ecology as one of the essential factors in planning for the persistence of spaceship Earth and its long-evolved ecosystems.

A mere listing of Worthington's responsibilities would be impressive. From 1933 to 1937 he participated in Sir Malcolm Hailey's survey of Africa south of the Sahara, during which he gradually focused more strongly on the broad ramifications of ecology. He saw many aspects of tropical diseases and parasites, crop pests, the effects of frequent fires, the effects of wild animals and forests on flow regimes downstream, and other environmental phenomena. After these African experiences he served as the first director of the Freshwater Biological Association (FBA) Laboratory on Lake Windermere from 1937 through 1946. During the war the staff was involved in increasing human food derived from the stunted perch in the lake and from silver eels. In the later years of the war and while still director of the FBA Laboratory, Worthington became involved with the Scientific Advisory Mission of the Middle East Supply Center, the chief objective of which was to reduce the dependence of the populace on materials that had to be shipped from Europe. In 1946 he was asked to prepare a 10-year development plan for Uganda. Among other things Worthington proposed a dam just below Owen Falls near the mouth of Lake Victoria, which when completed in 1954 made the lake the largest freshwater reservoir in the world. In addition, Worthington was instrumental in the establishment of the Queen Elizabeth and Murchison Falls national parks, which were highly successful in conserving wildlife up to the demise of Idi Amin's regime.

At the completion of this project, Worthington had wanted to be in England while the FBA Laboratory was being relocated. But instead he was asked to be the scientific secretary to the East African High Commission, the function of which was to set up inter-territory research centers for Kenya, Uganda, Tanganyika Territory, and Zanzibar. This work in East Africa enhanced Worthington's appreciation of "holism" in ecology. Among many other activities, Worthington established a well-designed fisheries research laboratory at Jinja on Lake Victoria, and later established a sea fisheries laboratory in Zanzibar.

A major scientific conference was held in Johannesburg in 1949, which led to the establishment of the Conseil Scientifique pour l'Afrique, of which Worthington was made secretary-general. The chief function here was to coordinate research among all the colonies or regions—English, French, Belgian, and Portuguese—south of the Sahara. This was done by encouraging fundamental or long-term research and by organizing scientific conferences for the discussion of common problems. This "international"