Book Reviews

Causes of Genetic Variation

The Genetic Basis of Evolutionary Change. R. C. LEWONTIN. Columbia University Press, New York, 1974. xvi, 346 pp., illus. Cloth, $12.50; paper, $4.50. Columbia Biological Series, No. 25.

Even in these days of inflation, a book deserves notice whose cover proclaims that it "will surely become one of the landmarks in twentieth-century science." When the book has been written by Richard Lewontin, it deserves the closest attention.

There is no doubt that Lewontin has had an unusual impact upon his subject. His discovery, with Harris and Hubby, of widespread genetic polymorphism among the enzymes of fruit flies and men has set off an explosion of interest in the causes of genetic variation. Because of his reputation for incisive argument, the book has been eagerly awaited. Because of his stature, it must now be subject to the strongest critical scrutiny. There is a danger that some will suppose it to have been handed down from the mountain.

Although not of Mosaic proportions, it is nevertheless a remarkable book, reviewing with skill and perception the latest news about enzyme polymorphisms, analyzing with clarity the consequent disturbance in the currents of evolutionary theory, and setting a standard of exposition to which others may aspire. It will, no doubt, be necessary fare for future generations of undergraduates, and it will certainly benefit their intellectual nutrition.

However, although a remarkable book, it is not uniformly a good one; it is sometimes facile, sometimes pretentious, and sometimes logically inconsistent. It is also parochial. The last deficiency is perhaps the worst, denying the book a generality that so easily it might have attained, and leading on occasion to serious distortions.

If the present review now dwells upon the failings of a work that is well written, intelligent, and sometimes brilliant, it is because the failings are made more insidious by the quality of the virtues that accompany them. As the bard said, in one of his less poetic moments, "Lilies that fester smell far worse than weeds."

Lewontin, in common with others who entertain, has a fondness for dilemmas and paradoxes. He builds increasingly complex patterns of confusion and contradiction and then, suddenly, introduces the clarifying experiment or concept. The dramatic effect of these interludes is strengthened when the initial confusion is made to seem more confusing and the final solution is made to seem more complete. Occasionally one suspects that the cause of drama has triumphed over the cause of exactitude. For example, when he is discussing the problem of estimating the amount of genetic polymorphism ("the struggle to measure variation"), Lewontin is rigorously critical of preelectrophoretic attempts at a solution but he is somewhat less critical of the results of electrophoresis itself. He does not mention the evidence, scrappy but nevertheless compelling, that structural proteins such as keratins, collagens, and crystallins are much less polymorphic than soluble enzymes and serum proteins. It is evidence that threatens the generality of his electrophoretic surveys.

In the matter of the long-standing debate between "neutralists" and "selectionists," Lewontin does not so much sit on the fence as pirouette on it, sometimes with such velocity that his arguments disappear into their own assumptions. He takes Kimura and Ohta to task because they regard as evidence for neutrality the observation that evolutionary substitutions between chemically similar amino acids are more common than those between dissimiliar ones. Yet, only a few pages later, he states that the differing rates of substitution found in different proteins "should cause disquiet to those who believe that most amino acid substitutions in evolution are adaptive." Apparently, constraints upon proteins are relevant to the argument but constraints upon amino acids are not!

Criticizing the work on *Cepaea* and the human blood groups, Lewontin says firmly that it is not enough to have demonstrated selection, it is necessary to show *balancing* selection. Yet later, discussing enzyme polymorphism, he states, "If alleles are segregating at intermediate frequencies and any selection at all can be demonstrated to operate on them, it would be difficult to avoid the conclusion that they are held by some form of balancing selection."

In a footnote he makes clear the distinction between heterosis and heterozygous advantage, but three pages later he apparently confuses negative heterosis (for fitness in the offspring of interspecific crosses) and heterozygous disadvantage.

Lapses like these can be forgiven; after all, even the mighty may nod. However, there is a more serious matter. It is Lewontin's neglect of the ecological content of population genetics, and it leads him into some astonishing omissions. The section of the book that deals with correlations between genotype frequencies and environmental variables completely ignores a large part of the available data (including, for example, the relevant work on melanic moths, butterflies, grasshoppers, the whole of the plant kingdom—excepting a brief criticism of the recent work on enzymes in *Avena*—and man himself). The section on frequency-dependent selection does not mention the best-established example (frequency-dependent selection by predators on mimetic and other polymorphisms), and the section on linkage disequilibrium does not mention *Papilio, Primula*, and *Cepaea*, the only cases in which the causes of the disequilibrium can even remotely be surmised.

In a brief discussion of the ecological evidence for natural selection Lewontin writes, "The case of *Cepaea* is regarded as a paradigm by selectionists, but other polymorphisms have not so far yielded to a persistent attack." This extraordinary statement apparently dismisses the studies on *Adalia, Arianta, Biston* (and other melanic moths), *Lotus, Panaxia, Papilio, Primula, Trifolium*, glucose-6-phosphate dehydrogenase in man, and many others. All these studies have produced good evidence of selection, yet none is mentioned. Whether the omissions are due to accident or design, Lewontin has surely distorted the balance of his subject. The distortion is

serious because it may discourage others from using the ecological methods that have proved to be the most successful in detecting natural selection, and it is doubly serious now that the more general mathematical methods, such as Lewontin and Krakauer's use of the theoretical variance of f, are thought to be of dubious validity.

There are other omissions, particularly in a weak chapter about the genetics of speciation, but they are similar in nature to those already mentioned. It may be that Lewontin has determined to write almost entirely about electrophoretic variation, where ecological information is sparse, but if so he has failed to put his information into a balanced context, and has chosen a thoroughly misleading title.

Lewontin's final chapter deals with the effects of selective interaction and linkage. He comes to the conclusion, stated as fact and italicized for emphasis, that "selection of the chromosome as a whole is the overriding determinant of allelic frequencies." If it is correct, this conclusion is important because it suggests that studies of selection on individual loci will usually be doomed to failure. It is based on the assumptions that individual selective values are small, constant, equal, and multiplicative and that the system is in a state of equilibrium. These assumptions, however, are not watertight. It is possible, for example, that a large proportion of loci are subject to frequency-dependent selection. It is possible that selective values are grossly asymmetrical within and between the loci. Since the dynamics of complex linked systems is not understood, it is even possible that no real population is ever in a state of equilibrium. "The genome as the unit of selection" is an interesting proposition, but it should never have been stated as a fact. Such a statement is particularly hazardous when we know that detecting the direct effects of natural selection on individual loci is not only possible but has often been accomplished. It is a pity that most of these accomplishments are not recorded in Lewontin's book.

Despite its serious failings, the book remains unusually competent, unusually intelligent, and unusually well written. It is a landmark, as the cover proclaims, but it marks only the boundaries of a parish. It is not, alas, a signpost.

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Sexuality: Costs and Benefits

The Economy of Nature and the Evolution of Sex. MICHAEL T. GHISELIN. University of California Press, Berkeley, 1974. xii, 346 pp. $12.95.

There can be little doubt that evolutionary theory is undergoing something of a renaissance and that social theory based on natural selection is an important part of that renaissance. Ironically, the new movement in social theory is largely a return to Darwin and to natural selection as Darwin understood it. For reasons that are still not completely clear, after 1859 most students of social behavior fell into a pseudo-Darwinism in which social traits were imagined to serve the good of the group or of the species. This tradition—still the dominant one in the social sciences—developed despite the fact that natural selection refers to *individual* reproductive success. Indeed, on several occasions Darwin explicitly rejected the notion that traits that lower individual reproductive success can evolve because they help the group or the species to survive.

Having already contributed to the rediscovery of Darwin, Michael Ghiselin has now written a book that seeks to make substantive contributions to the current movement in social theory. Covering much the same ground as Darwin did in his *Descent of Man and Selection in Relation to Sex*, Ghiselin presents his book as a "deliberate effort to overthrow a traditional paradigm, to provide an alternative, and to develop new tools for dealing with old subjects" (p. 11). Although the book is Darwinian in its thinking, it is also mostly pre-Mendelian, and this produces one of its several ironies: far from providing a new paradigm, the book mostly rejects the genuinely new paradigm (based on Mendelian genetics) that has been emerging in the study of social behavior.

Kinship theory, sex ratio theory, theory concerning the natural selection of sex, sexual selection theory—the main topics covered by Ghiselin—all must be formulated in terms of genetics in order to be formulated properly. This requirement is clearest in the case of kinship theory, in which an animal is expected to adjust its behavior (whether altruistic or selfish) toward another individual according to its degree of relatedness to that individual. Degree of relatedness is a genetic concept: it has a precise meaning rooted in Mendelian genetics, and it cannot be expressed in nongenetical language. The importance of genetics for social theory lies not only in such novel concepts but also in the rigorous and quantitative predictions they permit. Nowhere is this better illustrated than in groups such as the Hymenoptera (ants, bees, and wasps) in which the genetic system is asymmetrical with regard to sex (females are diploid, males haploid). In such organisms, kin-directed behavior, the sex ratio, and the form sexual selection takes can all be treated in a precise, quantitative manner.

Ghiselin's book is loosely organized into nine chapters. The first serves to justify Ghiselin and his procedure. He will create a new paradigm, by working alone, resisting authority, criticizing others, employing analogical thinking, and wedding some economic ideas to classical Darwinism. Chapter 2 is a philosophical essay on group- and species-advantage thinking, and Ghiselin traces this error from the ancients in Greece to some recent sloppy thinking by community ecologists. The chapter also introduces the sort of economic concepts that will be employed, and these turn out to be commonplace in evolutionary biology: there is often in nature as in economic systems a law of diminishing returns; division of labor commonly brings gains in efficiency; salesmen and natural predators are expected to congregate where their respective prey are numerous; and so on. Chapters 3 and 4 deal with the meaning of sex and the evolution of hermaphroditism. Although poorly organized and suffering from the absence of genetical thinking, the chapters are useful introductions to some of the literature on these subjects, especially on hermaphroditism.

The next three chapters deal with sexual selection: male-male combat, female choice, and male dispersal. These chapters are uniformly weak. Parental investment and sexual selection are treated as if they were independent parameters instead of (as they have been by A. J. Bateman and G. C. Williams) as related parts of the same process. Why males are commonly eager for sex and females slow to arouse (a problem Darwin considered and failed to solve) is left unanswered. Quantitative concepts, such as variance in reproductive success, analyzed by sex, do not enter the discussion. The fascinating subject of female choice is treated in a spiritless fashion. The