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

meaning of differential mortality by sex is neglected. Here and there bizarre statements appear—for example, "Where no biparental family exists, the female is just as well off being fertilized by one male as another" (p. 153).

The eighth chapter discusses social theory. Contentious and negative throughout, it distinguishes itself by a sustained and misguided attack on the kinship theory of W. D. Hamilton. The final chapter gives some parting thoughts on humans. We learn, for example, that "any learning that goes on during play is quite incidental" (p. 259). And the book closes by stating, "That the brain is destitute of purpose does not imply that it cannot be used" (p. 263).

Throughout the book, Ghiselin's evolutionary arguments are presented in a casual manner, bordering on the sloppy. From this book the student will learn little about the logic of evolutionary theory or about the way in which scientific evidence should be organized. This weakness can be illustrated by the treatment of three key topics that recur through the book.

1) *Kinship theory*. The best Ghiselin can say of Hamilton's kinship theory is that "something appears fallacious about many of the explanations cast in such language" (p. 137). He goes on to ask rhetorical questions. "Would we say that a sperm cell benefits from being small, since it thereby allows the existence of more individuals like it?" (Under certain conditions, yes.) "If a worker bee sacrifices herself in behalf of bees with similar DNA, should we not argue that cells that die in forming hair are doing the same thing?" (Not exactly, because cells within a body are identically related whereas bees within a hive are not.) "Where a society or an organism constitutes an integrated whole, which reproduces as a unit, such reasoning [that is, kinship theory] is both superfluous and misleading." (Quite the contrary; only a society of identically related individuals is expected to reproduce as an "integrated whole"; in all other societies, conflict and disagreement are expected—even if only one individual per society reproduces.) Ghiselin's main attack is reserved for the application of kinship theory to the social insects, a singularly unwise choice. Because in his original paper Hamilton made several mistakes in calculating degrees of relatedness for haplodiploid species, Ghiselin claims that such degrees of relatedness depend on "arbitrary decisions as to how one slices the metaphysical pie" (p. 228). This is nonsense. Hamilton's errors were corrected by himself and others, and by reference to a nonarbitrary criterion built into the original theory. Most of Ghiselin's other objections evaporate on inspection, and his entire attack is a case of substituting criticism for understanding.

2) *The meaning of sex*. Ghiselin argues (I believe correctly) that natural selection favors sexual reproduction because individuals with genetically variable offspring out-reproduce those without. But he does not mention J. Maynard Smith's observation that sexual reproduction has an immediate 50 percent selective cost (due to meiosis) in all species in which males invest little or nothing in their offspring. Understanding this cost is vital to understanding sexual reproduction. For one thing, it means that the advantage of genetic variability must be very high in almost every generation. This, in turn, implies that the correlation between what is genetically ideal in one generation and what is genetically ideal in the next must be very low. These and other implications have been developed by G. C. Williams (most recently in *Sex and Evolution*, Princeton University Press, in press).

3) *The concept of parental manipulation*. That parents might mold their offspring in the interest of themselves rather than of the offspring is an idea that is not new with Ghiselin. Like some others, he believes that this idea will explain such phenomena as sterile castes in the social insects. The problem is that offspring are expected to resist such molding, and the resulting conflict requires kinship theory for its analysis (because parent and offspring are related). An instructive example of Ghiselin's difficulties is his suggestion that sex-linked mimicry in butterflies (where females are mimetic and males cryptic) can be explained as a maternal device to reduce predation on daughters (the less frequent the mimics, the less intense the predation on them). But how would a mother force her sons to be nonmimetic? Assume that a non–sex-linked mutation for mimicry occurs in a population. Is Ghiselin imagining that the mother can make sure that this allele does not get passed on to her sons? This would be an extraordinary ability, requiring the capacity to spot a mimicry allele on whatever chromosome it appeared on and to suppress its reproduction except where it was appropriately sex-linked. These and other difficulties never surface because Ghiselin employs an imprecise, nongenetical language. Although Ghiselin mentions the hypothesis that female choice has maintained male crypticity, he dismisses it without referring to the striking fact that, in general, butterflies with visual courtship cues show sex-linked mimicry and butterflies with olfactory cues do not. This omission is especially ironic because female preference for cryptic males is the only plausible mechanism by which a female could influence the percentage of her sons who are mimetic.

One final feature of this book, its unremitting negative tone, deserves comment. Ghiselin cannot resist criticizing others. Indeed, he is as happy attacking a footnote or a sentence fragment as he is attacking an entire discipline, and his book reads like a compendium of marginal comments on the work of others. In compiling these criticisms, he is certainly no respecter of persons: the mighty and the meek, the rigorous and the befuddled, the living and the dead all must taste the terrible justice of Ghiselin's swift sword. Mayr is cut to pieces for some unwise comments on seals, Wynne-Edwards is flayed on page after page, Lorenz's musings on aggression engender several pages of criticism, Guthrie is chided for publishing a paper lacking references prior to 1937, primatologists are lined up en masse and dispatched, and the embryologist Driesch is resurrected from the turn of the century and given a good drubbing. One could go on and on. The best that can be said for this performance is that Ghiselin shows a certain fascination and talent for ferreting out the errors of others.

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Anatomy in Action

Biomechanics. An Approach to Vertebrate Biology. CARL GANS. Lippincott, Philadelphia, 1974. x, 262 pp., illus. Cloth, $12.50; paper, $5.95.

As the subtitle of this book suggests, biomechanics is less a discipline with a subject matter of its own than a style of approaching comparative and functional anatomy through the principles of elementary physics. Instead of writing yet another elementary physics textbook using biological examples, Gans