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CHANCE AND NATURAL SELECTION*

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   Among the liveliest disputes in evolutionary biology today are disputes con-
cerning the role of chance in evolution—more specifically, disputes concerning
the relative evolutionary importance of natural selection vs. so-called "random
drift". The following discussion is an attempt to sort out some of the broad issues
involved in those disputes. In the first half of this paper, I try to explain the
differences between evolution by natural selection and evolution by random drift.
On some common construals of "natural selection", those two modes of evo-
lution are completely indistinguishable. Even on a proper construal of "natural
selection", it is difficult to distinguish between the "improbable results of natural
selection" and evolution by random drift.
   In the second half of this paper, I discuss the variety of positions taken by
evolutionists with respect to the evolutionary importance of random drift vs.
natural selection. I will then consider the variety of issues in question in terms
of a conceptual distinction often used to describe the rise of probabilistic think-
ing in the sciences. I will argue, in particular, that what is going on here is not,
as might appear at first sight, just another dispute about the desirability of "sto-
chastic" vs. "deterministic" theories. Modern evolutionists do not argue so much
about *whether* evolution is stochastic, but about *how* stochastic it is.

1. Introduction. Charles Darwin's account of organic form appealed to chance in a way that did not settle well with his critics. As Darwin unhappily reported the opinion of the great scientist-philosopher, John Herschel, "I have heard, by a round-about channel, that Herschel says my book 'is the law of higgledy-piggledy.' What exactly this means I do not know, but it is evidently very contemptuous" (Darwin to Lyell, Dec. 12, 1859, in F. Darwin 1887, Vol. 2, p. 37). In time, though, Darwin was praised rather than scorned for his appeal to chance. For instance, looking back at the turn of the century, another great scientist-philosopher, C. S. Peirce, assessed Darwin's contribution in this regard more favorably:

> The Origin of Species was published toward the end of the year 1859. The preceding years since 1846 had been one of the most productive seasons—or if extended so as to cover the great book we are considering, the most productive period of equal length in the entire history of science from its beginnings until now. [For] the idea that chance begets order . . . was at that time put into its clearest light. (Peirce 1893, p. 183)

Since the turn of the century, however, and especially since the thirties, evolutionists have *further* appealed to chance in ways that Darwin himself might contemptuously have regarded as higgledy-piggledy views of nature. Indeed, proponents of one such appeal have coined the term "non-Darwinian evolution" to distance their views from his. Actually, the new appeals to chance have been matters of considerable dispute. And today those disputes are among the liveliest in the already lively field of evolutionary biology.

The following discussion is an attempt to sort out some of the broad issues involved in these disputes. The most general question at issue concerns the relative evolutionary importance of "random drift" vs. natural selection. But what does that mean? In the first half of this paper (Sections 2–3), I will try to make sense of that question. That will involve explaining the sense in which evolution by random drift is, properly speaking, an "alternative" to evolution by natural selection. Darwin did not conceive of chance as anything like an alternative to natural selection, but rather as "complimentary" to natural selection. Modern evolutionists, on the other hand, recognize alternative as well as complimentary roles of chance and natural selection. And yet, on some common construals of "natural selection", it is difficult (if not impossible) even to *distinguish* evolution by random drift from evolution by natural selection. Thus, in order to construe evolution by random drift and evolution by natural selection as proper alternatives, the concept of natural selection itself must first be properly interpreted. Unfortunately, though, even on a proper interpretation of "natural selection", it is difficult to distinguish between

what I call the "improbable results of natural selection" and evolution by random drift.

In the second half of this paper (Section 4–5), I discuss the variety of positions taken by evolutionists with respect to the evolutionary importance of random drift vs. natural selection. I will then consider the variety of issues in question in terms of a conceptual distinction often used to describe the rise of probabilistic thinking in the sciences. I will argue, in particular, that what is going on here is not, as might appear at first sight, just another dispute about the desirability of "stochastic" vs. "deterministic" theories. Modern evolutionists do not argue so much about *whether* evolution is stochastic, but about *how* stochastic it is.

2. Chance in Darwinian Evolutionary Theory. Darwin usually invoked "chance" (or "accident") in the context of discussions about how variations, the materials of evolution, arise. His notion of "chance variation" was especially important for the purpose of distinguishing his own theory of evolution from the older "use and disuse" theory (Hodge and Kohn forthcoming). So a brief discussion of the differences between those theories might be helpful. The paradigm application of the theory of use and disuse is the account of the evolution of giraffes from shorter-necked, four-footed grazers. As the account goes, the ancestors of giraffes found themselves in an environment in which they had little upon which to graze, other than leaves of trees. They stretched their necks to reach more and more leaves, and were physically modified in the process. Their offspring inherited the modification—i.e., having longer necks as juveniles than their parents had as juveniles. The offspring also stretched to reach more and more leaves, lengthening their necks even beyond the length inherited. The third generation inherited the further modification. And so on, until all the descendants of the original group were quite long-necked. The important point here concerns how the variations that aid the survival of their possessors first arose—namely, in response to the survival needs of their possessors. That is, the chance of such a variation occurring was increased by the very fact that the organism needed it to survive.

On the Darwinian account, we are asked to consider what would have happened if, among the shorter-necked ancestors, some slightly longer-necked offspring happened "by chance" to be born. Those who happened to have the slightly longer necks would be able to reach slightly more food, and hence would slightly outsurvive and outreproduce the others. Assuming that neck length was inheritable, then, a slightly greater proportion of the next generation than of the previous generation would be longer-necked. This process alone would result in an ever-increasing frequency of the slightly longer-necked individuals. But now consider what would happen if, among those slightly longer-necked organisms, some

slightly even longer-necked offspring happened by chance to be born. These in turn would slightly outsurvive and outreproduce the others. Thus, the proportions of longer- and longer-necked individuals would increase from generation to generation, until the present proportions were reached.

The important point for now concerns how, according to the Darwinian account, the variations that aid the survival and reproduction of their possessors first arise. They do not, as on the use-and-disuse account, arise in response to the survival and reproductive needs of their possessors. On the other hand, whether or not they further increase in frequency does depend on whether they serve those needs. But the probability of a particular variation occurring in an individual is not increased by the fact that that variation would promote the survival and reproduction of that individual. In that sense, it is a matter of "chance" that an organism would be born with a variation that promotes its survival and reproduction, though, again, not a matter of chance that that variation further increases in frequency in subsequent generations. As Darwin thus distinguished his account from the use-and-disuse account, the latter explains the evolution of adaptation in a way "analogous to a blacksmith having children with strong arms", while the former relies on "the other principle of those children which *chance* produced with strong arms, outliving the weaker ones" (Darwin 1839, passage 42). As Darwin elsewhere more eloquently explained the notion of chance variation,

> [Evolution by natural selection] absolutely depends on what we in our ignorance call spontaneous or accidental variability. Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental. Yet the shape of each has been determined . . . by events and circumstances, all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up through the power of selection. . . . (Darwin 1887, Vol. 2, p. 236)

There are several, more general notions of chance in terms of which one might try to understand the notion of chance variation. There is, for instance, the natural theological notion of chance vs. intelligently intended occurrences. There is also the old Aristotelian notion of chance as coincidence. Or we might invoke the Laplacean notion of chance, not in order to say anything about the event in question itself, but just as an admission of ignorance concerning the causal chain of events that resulted in that event. It seems to me possible to make a case for construing chance variation in each of these ways—Darwin sometimes seems to have fa-

vored one, and then at other times another more general meaning. Sometimes he spoke of chance variations in contrast with benevolently intended, useful variations. Sometimes he meant that it was a matter of coincidence that a useful variation should arise. And sometimes he seems only to have wanted to leave entirely open the question of how variations arise—thus making clear that his theory of evolution did not rely on the use and disuse account of that process. All three interpretations are suggested, for instance, by the quotation above! (See also Ghiselin 1969, Schweber 1982, and Sheynin 1980 with regard to these more general concepts of chance variation.) But perhaps the most important thing to consider is what is distinguishably Darwinian about the notion of chance variation. And that is, I think, best brought out simply in contrast to the use and disuse theories of evolution, from which Darwin wanted to distance himself.

3. Chance in Modern Evolutionary Theory: Distinctions. *3.1* The dispute concerning the relative evolutionary importance of natural selection vs. random drift raises genuinely new issues concerning the role of chance in evolution. What is *not* at issue is the role of chance in evolution as Darwin conceived it (except insofar as he *too narrowly* conceived it). Modern evolutionists assume, that is, that variations are indeed "random" in the sense intended by Darwin. As one contemporary evolutionist puts it, "Mutation is random in [the sense] that *the chance that a specific mutation will occur is not affected by how useful that mutation would be*" (Futuyma 1979, p. 249).

But while Darwin considered the *origin* of variations a matter of chance, he did not consider the possibility that their evolutionary *fates* might also be a matter of chance. In particular, he attributed their evolutionary fates to natural selection in or against their favor. Natural selection took over where chance variation left off: those organisms that were by chance better equipped to survive and reproduce actually outsurvived and outreproduced the organisms that were by chance less well equipped, and thus advantageous variations increased in frequency from generation to generation. In Darwin's scheme, in other words, chance and natural selection were "consecutive" rather than "alternative" stages of the evolutionary process. With the introduction of the concept of random drift, however, came the notion that the fate of a chance variation might itself be a matter of chance—i.e., the concept that chance and natural selection might be alternative rather than just consecutive stages of the evolutionary process.

But what does it mean to attribute the evolutionary fate of a variation to natural selection vs. random drift? The distinction will be easier to make if we confine our discussion to the fates of *genetic* variations. It will be useful, in other words, to think of evolutionary changes as changes

in the gene and genotype frequencies of populations. (The Appendix consists of a review of genetic terminology that some readers might find useful at this point.) Thus, the kinds of evolutionary changes that I will be talking about are changes of the following sort. Of the alleles (genes) at a particular genetic locus of members of one generation of a particular population, 50% are of type A and 50% are of type a. Of the genotypes with respect to that locus, 25% are of the type AA, 50% are of the type Aa, and 25% are of the type aa. Of the alleles at that locus of members of a *later* generation of that population, 80% are of type A and 20% are of type a. And of the genotypes with respect to that locus of members of the later generation, 70% are of the type AA, 20% are of the type Aa, and 10% are of the type aa.

Though definitions of "evolution" in terms of such gene- and genotype-frequency changes are common (e.g., Wilson and Bossert 1971, p. 20), I recognize that we actually include more than just that kind of change under the term "evolution" (see Brandon 1978). This restriction, however, simplifies the following discussion enormously.

3.2 I will rely, for the time being, on your intuitions about what it means to attribute gene- and genotype-frequency changes to natural selection. What does it mean to attribute the same to random drift? Since as early as 1932 (Dubinin and Romaschoff 1932; see also Dobzhansky 1937, p. 129), a popular approach to the exposition of random drift has been via a classic means of modelling chance processes—namely, the blind drawing of beads from an urn. The beads in this case are alleles—the different alleles are different colors, but they are otherwise indistinguishable by the blindfolded sampling agent. One urn of beads represents one generation of alleles—a finite number, characterized by particular allele frequencies. The next generation of alleles is determined by a blind drawing of beads from an urn. This second generation of alleles fills a new urn, blind drawings from which determine the frequencies of alleles in the third generation. And so on. The frequencies of alleles may differ from urn to urn—generation to generation—as a result of the fact that frequencies of otherwise indistinguishable beads sampled by blind drawings may not be representative of the frequencies in the urns from which the samples were drawn. The probability of drawing a representative sample from a population of a given finite size is easy to calculate—the smaller the population, the smaller that probability.

Such blind sampling could take at least two forms in nature. The first form is what might be called "indiscriminate parent sampling". By "parent sampling" I mean *the process of determining which organisms of one generation will be parents of the next, and how many offspring each parent will have.* This sort of sampling might be "indiscriminate" in the

sense that any physical differences between the organisms of one generation might be irrelevant to differences in their offspring contributions. A forest fire, for instance, might so sample parents—killing some, sparing some—without regard to physical differences between them. Such sampling is indiscriminate in the same sense in which the usual model of blind drawing of beads from an urn is indiscriminate—that is, any physical differences (e.g., color) between the entities in question are irrelevant to whether or not they are sampled.

If a population is so maintained at a particular finite size—i.e., by sampling parents indiscriminately—its gene and genotype frequencies will "drift" from generation to generation. The reason is that the genotype frequencies of the parents, weighted according to their reproductive success, may by chance not be representative of the genotype frequencies of the parents' generation. There is no form of discrimination to ensure that the genotype frequencies *are* representative. To the extent that a parent sample is unrepresentative, and to the extent that the gene and genotype frequencies of the next generation reflect the appropriately weighted gene and genotype frequencies of their parents, the next generation's gene and genotype frequencies may diverge from those of the previous generation—i.e., an evolutionary change may occur.

Blind sampling in nature might also take the form of "indiscriminate gamete sampling". (This paragraph and the next can be skipped without much loss.) By "gamete sampling" I mean *the process of determining which of the two genetically different types of gametes produced by a heterozygotic parent is actually contributed to each of its offspring*. This sort of sampling might be indiscriminate in the sense that any physical difference between the two types of gametes produced by a heterozygote might be irrelevant to whether one or the other is actually contributed to any particular offspring. According to Mendel's Law (see the Appendix), there is no physical basis for a bias in the proportions of the two genetically different types of gametes *produced* by a heterozygote. What we are now considering is that there is also no physical basis for a bias in the proportions of gametes that are actually *contributed* to a heterozygote's offspring.

If a population is so maintained at a particular finite size—i.e., by sampling the gametes of heterozygotes indiscriminately—the gene and genotype frequencies of the population will drift from generation to generation. For the gene frequencies of the gametes that are contributed to a generation of offspring may by chance not be representative of the gene frequencies of the parents' generation. Again, there is no form of discrimination to ensure that they *are* representative. Thus, indiscriminate gamete sampling, either together with indiscriminate parent sampling, or alone, can result in an evolutionary change, a so-called "random drift" of gene and genotype frequencies.

Some authors construe random drift entirely in terms of indiscriminate parent sampling (e.g., Sheppard 1967, pp. 126–127). More often, random drift is construed entirely in terms of indiscriminate gamete sampling (e.g., Wilson and Bossert 1971, p. 83). But these two processes are importantly similar agents of change—both involving elements of randomness, and "randomness" in the same sense in both cases. According to this sense of "randomness", sampling from a population is random when each member of the population has the same chance of being sampled. This is a common notion of random sampling—e.g., according to a philosophical introduction to probability theory, a sampling procedure gives random samples if:

1. Each member of the population has an equal probability of being selected as the first member of the sample.
2. Each member of the population, excluding those selected as previous members of the sample, has an equal chance of being selected as the nth member of the sample (Skyrms 1966, pp. 146–147; see also Hacking 1965, pp. 118–132).

Discussions of random drift, pedagogical or otherwise, generally do not include discussions of the concepts of "randomness" and "chance". Rather, evolutionists have, in general, simply relied on what is an *exemplary* model of random sampling in the literature of probability, statistics, and philosophy—i.e., the blind drawing of beads from an urn. Evolutionists are not, in general, inclined to defend any particular interpretation of "randomness". It is enough, for their purposes, to say of any process in nature that is sufficiently similar to their bead-drawing model of random drift, that evolution in this case is as much a matter of "random sampling" and "chance" as are the exemplary cases of random sampling upon which probabilists, statisticians, and philosophers rely.

In what follows, in comparing random drift to natural selection, I will be discussing only random drift via indiscriminate parent sampling, not via indiscriminate gamete sampling. So, in effect, I will be contrasting natural selection of parents and indiscriminate parent sampling. I could also contrast natural selection of gametes with indiscriminate gamete sampling, but that will not be necessary in order to make the kinds of points that I want to make.

3.3 Natural selection is not random sampling in the sense of "random" just discussed. Natural *selection* is, as its name suggests, a discriminate form of sampling—a sampling process that discriminates, in particular, on the basis of *fitness* differences. The general issue involved in the disputes concerning the relative evolutionary importance of random drift vs. natural selection, then, boils down to the question of the relative evolu-

tionary importance of *sampling without regard to fitness differences vs. sampling with regard to fitness differences*. But I cannot unpack this issue without first discussing briefly the notion of fitness. For according to the most common conception of fitness, the distinction between random drift and natural selection of the fittest dissolves, and along with it dissolves the issue of the relative evolutionary importance of the two supposedly different sorts of processes.

According to the most common definition of "fitness", the fitness of an organism is a measure of its actual reproductive success. I. M. Lerner's definition of "fitness" is typical in this regard—according to Lerner, "the organisms who have more offspring are fitter in the Darwinian sense" (Lerner 1958, p. 10; see also Waddington 1968, p. 19; Mettler and Gregg 1969, p. 93; Crow and Kimura 1970, p. 5; Dobzhansky 1970, pp. 101–102; Wilson 1975, p. 585; Grant 1977, p. 66). Along the same lines, the fitness of a genotype is the actual average offspring contribution of organisms of that type. For instance, to say that organisms of type *AA* are fitter than organisms of type *aa* is to say that organisms of the first type actually leave a higher average number of offspring.

But if fitness is so construed, then it is not clear what the supposed distinction between natural selection of the fittest (i.e., sampling on the basis of fitness differences), and sampling without regard to fitness differences, amounts to. How could parent sampling be *anything other* than fitness discriminating, when the organisms that leave the most offspring are by definition the fittest? On this conception of fitness, *all* parent sampling processes are fitness discriminating.

Consider, for instance, the proposed bead-drawing models of selection that are based on this notion of fitness—those models are indistinguishable from the bead-drawing models of random drift. Consider, in particular, the bead game called "Selection", described by Manfred Eigen and Ruth Schuster in their otherwise thoughtful book, *Laws of the Game* (Eigen and Schuster 1981, pp. 49–65). The game requires a checkerboard, the playing squares of which are identified by coordinates, and are occupied by colored beads, one bead per square. To begin, the beads that cover the board are of at least two colors—in whatever initial frequencies desired. The roll of two dice (each of which has the appropriate number of sides) picks out a square on the board. A bead of whatever color occupies that square is used to replace whatever color is on the square picked out by the next roll of the dice. This is followed by another color-determining roll, followed by another color-replacing roll. And so on, until eventually one color fills the entire board.

This is supposed to represent selection of the fittest color, where the fittest color is, as Eigen and Schuster put it, "the one that turns out to be the winner" (1981, p. 55). This is also, of course, just indiscriminate

sampling. Indeed, Eigen and Schuster say of their model that "We are faced with the paradox that the selective process produces a winner in every game though competitors do not differ from each other at all" (1981, p. 55). Unfortunately, Eigen and Schuster are not just calling this game "Selection", they actually intend to explicate the concept of Darwinian selection in terms of the game. But if this is a proper explication of selection, then the problem of the relative evolutionary importance of random drift vs. natural selection is a pseudo-problem—there is no difference between them.

There is, however, another conception of fitness that keeps the issue alive. To motivate this conception briefly, consider the example of two genetically identical twins, one of whom is struck by lightning and killed, the other of whom is spared. As a result, say, the former leaves no offspring, while the latter goes on to be a parent. We balk at the consequences according to our conception of fitness. That is, we hesitate to attribute zero fitness to the former twin and relatively high fitness to his genetically identical, but seemingly luckier brother.

One way of accommodating these intuitions is to identify the fitness of an organism not with the actual number of offspring it contributes, but with the *number of offspring that it is physically disposed to contribute* (Brandon 1978, Mills and Beatty 1979, Sober 1980, Burian 1983). Along the same lines, we can talk about the fitness of a genotype in terms of the average number of offspring that possessors of that genotype are physically disposed to contribute.

On this conception of fitness, the two physically identical twins, who must be physically disposed to contribute the same number of offspring, are equally fit. Hence we can say of the lightning that killed one and spared the other, that it did not sample the twins on the basis of their fitnesses—it was not an agent of natural selection. It was clearly an indiscriminate sampling agent—indiscriminate, that is, with regard to physical fitness differences between the organisms sampled.

3.4 That is perhaps as much about fitness as we really need to discuss in order to make meaningful the issue concerning the relative evolutionary importance of random drift vs. natural selection. But I am afraid that, as much as I would like the distinction between natural selection and random drift to be a clear-cut one, it is not as clear-cut as the preceding discussion suggests. (Elliott Sober and Kenneth Waters helped me considerably with the following discussion.) In order to complicate matters somewhat, let me elaborate a bit upon the notion of "fitness".

First, it is important to recognize that the fitness of an organism is the number of offspring it is physically disposed to contribute *in a particularly specified environment*. For instance, the number of offspring that a

dark-colored moth is disposed to contribute is greater in a dark environ-ment in which it is effectively camouflaged from its predators, than in a light environment in which it is more conspicuous. So all attributions of levels of fitness must be relative to particularly specified environments.

The specification of the environment, in turn, involves specifying a range of circumstances, each weighted according to the likelihood of its occurrence, or according to the likelihood of the organism(s) in question experiencing it. So one changes the environment, so to speak, by chang-ing either the quality or the weighting of the component environmental circumstances. The ability of the dark moth to survive and reproduce in a uniformly dark environment is presumably different from its ability in a three-fourths dark environment, and that is presumably different from its ability in a half-dark environment, and so on.

The environmental circumstances relative to which fitness values are ascribed to members of a population are, ideally, all the environmental circumstances relevant to determining differences between the reproduc-tive successes of those organisms. Some of these factors discriminate be-tween the organisms on the basis of fitness differences between them. For instance, the combination of a dark background and color-sensitive birds favors the reproductive success of dark moths over light moths, *because of the difference in their color*. Some other factors among the specified environmental circumstances may be responsible for differences in reproductive success, but *not* in connection with any fitness differences between the organisms in question. Forest fires, for instance, might kill and spare moths without regard to any fitness differences between them. Not only the former factors, but also the latter belong in the environ-mental specifications relative to which fitness values are ascribed. Dark moths may be able to leave more offspring than light moths in environ-ments in which the background is dark and the major predators are color sensitive, and in which forest fires are rare. But dark and light moths may have roughly the same offspring-contribution dispositions in an environ-ment in which forest fires are very frequent, even if the background is otherwise dark and the major predators are color sensitive. Similarly, the dark and light moths might have roughly equal fitnesses in an environ-ment in which their predators are color *in*sensitive.

At any rate, relative to an environmental specification in terms of weighted environmental circumstances, there is a *range* of numbers of offspring that an organism is more or less disposed to contribute. For instance, in an environment made up of 60% dark-colored trees and 40% light-colored trees, a dark moth has a chance of visiting more or less than 60% dark trees, and more or less than 40% light trees. Given its physical structure, it may leave somewhat more offspring if it lands on more dark trees and somewhat fewer if it lands on fewer dark trees.

So for an organism in a particularly specified environment, there is a range of possible offspring contributions. And for each number within the range, there is a greater or lesser ability on the part of the organism to leave that number. Accordingly, we can talk about fitness *distributions* relative to specified environments. For instance, relative to a particularly specified environment, an organism might have a fitness distribution like the one in Diagram 1. Here the x-axis represents the range of offspring contributions, and the y-axis represents the strength of the organism's ability to leave the corresponding number on the x-axis.
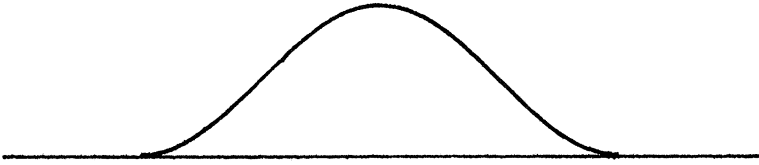
DIAGRAM 1

Somewhat alternatively, we can view this distribution as a probability distribution of offspring contributions, where the x-axis again represents the range of offspring contributions, and the y-axis the probability that the organism will contribute the corresponding number on the x-axis. The probabilities should, however, be interpreted as strengths of the organism's *physical ability* to contribute various numbers of offspring, in line with a *propensity* interpretation of probability (Brandon 1978, Mills and Beatty 1979). We can also construct a fitness distribution for a genotype. The range of this distribution would consist of the union of the ranges of possible offspring contributions of the individual members of the genotype. The height of the distribution at any point along the extended range would represent the group's average probability of leaving that many offspring.

Now the last thing I want to do in connection with this very general discussion of random drift, natural selection, and fitness, is to consider a possible scenario that requires that we give a bit more thought to the distinction between natural selection of the fittest and the indiscriminate sampling sources of random drift. How distinguishable are they, after all? Imagine again the case of the light and dark moths and their color-sensitive predators. Imagine too that they inhabit a forest in which 40% of the trees have light-colored bark and 60% have dark-colored bark. In this environment, we would say that the dark-colored moths are fitter, since the forest provides more camouflage for them than for the light moths. The fitness distributions of finite numbers of the two types might thus differ in the way shown in Diagram 2.
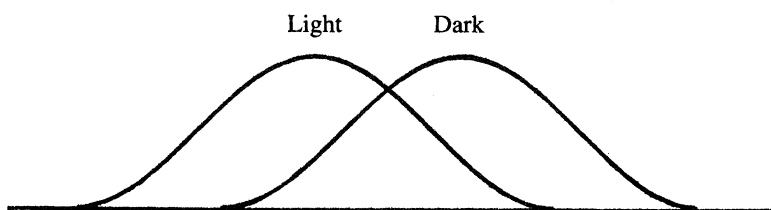
Light   Dark

DIAGRAM 2

But suppose that in one particular generation, we find, among remains of the moths killed by predators, a greater proportion of dark moths than was characteristic of the population as a whole, and a smaller proportion of light moths than was characteristic of the population. Say the actual average offspring contributions of the two types of moths in the previous generation differed as in Diagram 3. And finally, let us say that we find the remains so distributed in the areas of dark and light trees that we have reason to believe that the dark moths were perched on light trees when attacked, and the light moths on dark trees. In other words, the dark moths chanced to land on light trees more frequently than on dark trees, even though the frequency of dark trees was greater.

x_d x_l
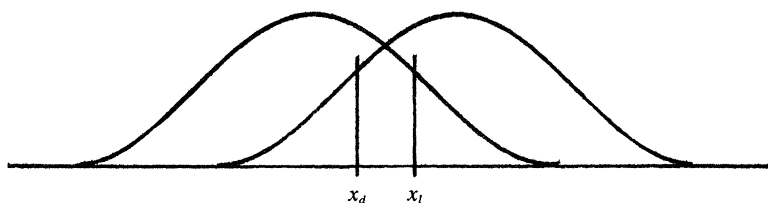
x_d = Actual average number of offspring of dark moths in E
x_l = Actual average number of offspring of light moths in E

DIAGRAM 3

That's the scenario. The question it raises is this. Is the change in frequency of genes and genotypes in question a matter of natural selection, or a matter of random drift? That is, is the change in question the result of sampling discriminately or indiscriminately with regard to fitness differences? It is not easy to maintain that the sampling was entirely indiscriminate with regard to differences in survival and reproductive ability. At least it is difficult to maintain that the death by predation of *conspicuously* dark moths in this environment is indiscriminate sampling, whereas the death of *conspicuously* light moths in the same environment is selection. On the other hand, it is also difficult to maintain that selection alone

is the basis of the change. At least, it is difficult to maintain that the fittest were selected.

The problem here, I think, is that it is difficult to distinguish between random drift on the one hand, and the *improbable results of natural selection* on the other hand. Wherever there are fitness *distributions* associated with different types of organisms, there will be *ranges* of outcomes of natural selection—some of the outcomes within those ranges will be more probable than others, but all of the outcomes within the ranges are possible outcomes of natural selection. And yet some outcomes within a fitness distribution (the outer-lying outcomes of a bell-shaped fitness distribution, for instance), are in a sense "less representative" of the offspring-contribution abilities of the organisms in question. Consider a coin-tossing analogy. "Fifty heads : fifty tails" and "ninety heads : ten tails" are both possible outcomes of one hundred flips of a fair coin, where by "fair coin" I mean a coin equally disposed to land heads up and tails up. And yet "ninety heads : ten tails" is in a sense less representative of the fairness of the coin. So too in the case of the light and dark moths just discussed, the actual average offspring contributions shown in Diagram 3 are possible results of natural selection, but not very "representative" of the fitnesses of the light and dark moths. To the extent that those outcomes are *less* representative of the physical abilities of those organisms to survive and reproduce in the environment in question, any evolutionary change that results will be *more* a matter of random drift. In other words, it seems that we must say of some evolutionary changes that they are to some extent, or in some sense, a matter of natural selection *and* to some extent, or in some sense, a matter of random drift. And the reason (one of the reasons) we must say this is that it is conceptually difficult to distinguish natural selection from random drift, especially where *improbable results of natural selection* are concerned.

Even given these difficulties of conceptual analysis, though, the new conception of the role of chance in evolution *clearly* goes beyond Darwin's conceptions, and raises questions that did not arise for him. In Darwin's scheme of things, recall, chance events and natural selection were consecutive rather than alternative stages of the evolutionary process. There was no question as to which was more important at a particular stage. But now that we have the concept of random drift taking over where random variation leaves off, we are faced with just such a question. That is, given chance variations, are further changes in the frequencies of those variations more a matter of chance or more a matter of natural selection?

4. Chance in Modern Evolutionary Theory: Issues. *4.1* As I suggested earlier, there are at least two versions of this general question. At

issue in the first version is the extent of so-called selectively "neutral" mutations. The most likely candidates for this title were discovered during the molecular-biology boom of the fifties and sixties. It was discovered then that different permutations of the sequences of bases that make up DNA code for different amino acids. But it was also discovered that the sequence of bases that codes for a particular amino acid can sometimes be changed in a certain way such that the same amino acid is produced. These were called "synonymous" changes, in the information language of the field. It is certainly a plausible enough suggestion that synonymous changes have no effect on the numbers of offspring which organisms are physically disposed to contribute. Claims for neutrality have, however, also been extended to grosser phenotypic differences, from single amino-acid differences between proteins of the same functional family, to differences between blood types (Wright 1940), to differences between banding patterns on snail shells (Diver 1940). Many such changes have not, upon first thought, had any imaginable effect on the numbers of offspring that their possessors were physically disposed to contribute.

Sampling among such alternatives would be indiscriminate with regard to fitness differences, simply because there would be no such differences. As Jack King and Thomas Jukes expressed the basic idea in their classic position paper, "Natural selection is the editor, rather than the composer, of the genetic message. One thing the editor does *not* do is to remove changes which it is unable to perceive" (King and Jukes 1969, p. 788). As a result of this sort of indiscriminate sampling, the frequencies of neutral genetic alternatives may drift. In the words of the self-styled "neutralists", the "fates" of these genetic alternatives are matters of "chance" (e.g., Nei 1975, p. 165).

The neutralist theory of evolution is mathematically very sophisticated, though some of its features can be discussed informally. The theory is "stochastic" rather than "deterministic", in the sense that, given the gene and genotype frequencies of one generation, and values for all the other variables of the theory (like the size of the population), one can at best calculate the *probabilities* of possible gene and genotype frequencies in successive generations. It is not possible to predict *one specific gene or genotype frequency* for each successive generation.

Diagram 4 is an example of the sorts of calculations that the theory allows (from Roughgarden 1979, p. 62). In this case, we are talking about an infinite number of populations, each of which has a constant size of 8 individuals, and each of which starts off with gene frequencies of 0.5 A and 0.5 a—i.e., 8 A alleles and 8 a alleles. This is represented by the top distribution, a bar that signifies that 100% of the populations have 8 A genes at time $t = 0$. According to the theory, over the course of generations, the distribution of populations spreads out with respect to

　　　　　　　　JOHN BEATTY

Number of A alleles in population i
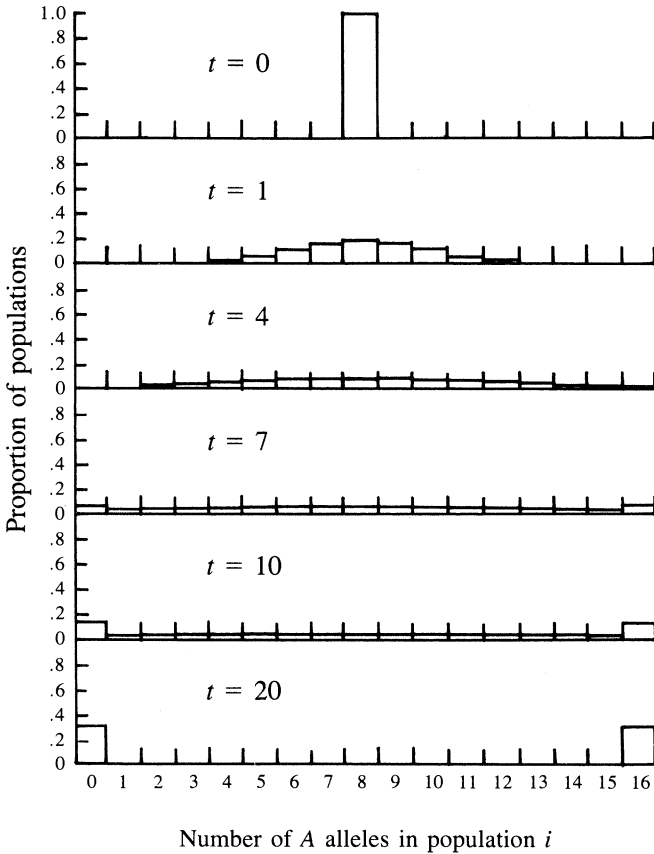
DIAGRAM 4

the frequency of A allels in each, until finally all of the populations have either no A alleles, or 100% A alleles (i.e., either 0 or 16 A alleles). We cannot predict whether or not a particular population will have, say, 50% A and 50% a alleles after one generation, but we can predict the *prob-ability* that it will be 50 : 50, in terms of the proportion of populations that will still be 50 : 50 after one generation. The probability is about 0.2. Diagram 5 is a somewhat more general way of representing what Diagram 4 represents. This is the first of such diagrams, from Sewall Wright's pioneering 1931 work on drift. According to the diagram, the frequencies of populations with all or none of a particular allele increase faster, the smaller the population size N.

That is, of course, just a glimpse of the general theory of the random

"Rate of decay" of
variability = $^1/_2$N

Proportion of populations

Allele frequency

| 0 | 0.25 | 0.5 | 0.75 | 1.0 |
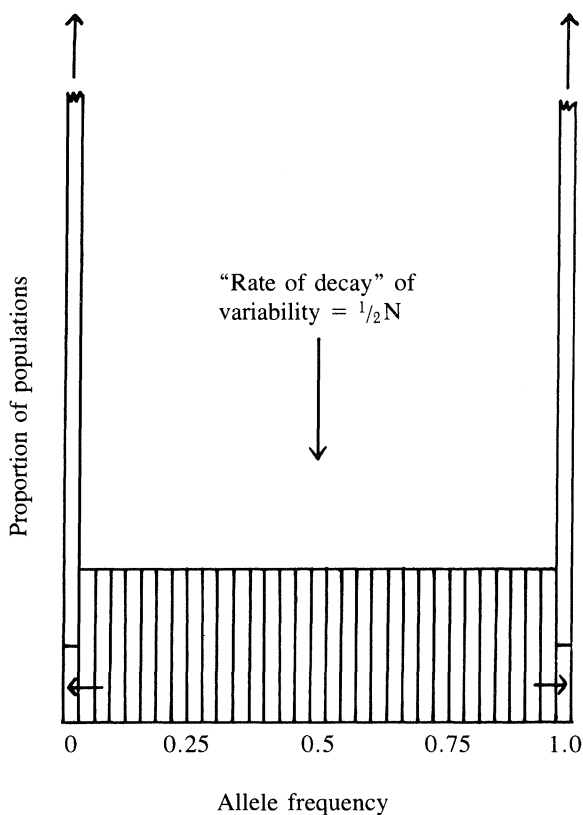
DIAGRAM 5

drift of frequencies of selectively neutral genetic alternatives. But even
that glimpse is important for our purposes. It is important, too, that we
consider the sorts of issues that divide investigators in this area. There
are more specific as well as more general issues. The more specific issues
concern whether or not a change in frequency of a *specific set of genetic
alternatives* can be ascribed to their selective neutrality and the conse-
quent random drift of their frequencies. Complementarily, one might ex-
pect that the more general issues concern whether *all or no* evolutionary
changes—or whether all of a certain kind or none of a certain kind of
evolutionary change—are due to random drift alone. It is important to
recognize, however, that even the most general issues surrounding this
version of the importance of random drift do not boil down to questions
of all or none, but to questions of *more or less*. I cannot improve on

Douglas Futuyma's assessment of this situation, so I will simply quote it. (I especially like this quotation because it is from a textbook in evolutionary biology, and communicates to students of evolution a valuable lesson concerning the nature of evolutionary theorizing, and of the nature of disputes in that field.)

> The answer to the question, Is enzyme polymorphism due to selection or drift? will, of course, be: Both. But this is really no answer at all. No neutralist would deny that some few enzyme polymorphisms are maintained by selection, and even the staunchest selectionist would not deny that some amino acid substitutions must have such trivial effects that they have vanishingly small effects on fitness and so fluctuate in gene frequency by drift alone. The real question is, What fraction of the variation is attributable to each factor . . .? (Futuyma 1979, p. 340)

Similarly, Masatoshi Nei, a principle figure in the neutralist disputes, characterizes the strongest neutralist position as only "a majority rule" (1975, p. 165). As he explains, even the strongest neutralist position does not *rule out* selection with regard to some sets of genetic alternatives. It asserts instead that the majority of gene-frequency changes involve selectively neutral alternatives. Motoo Kimura, perhaps the principal neutralist, has emphasized over and over again the slack in his relatively very strong position. As he recently reported, along these lines,

> . . . in one of my papers on the neutral theory (Kimura 1968), I wrote: "the recent findings of 'degeneracy' of DNA code, that is, existence of two or more base triplets coding for the same amino acid, seem to suggest that neutral mutations may not be as rare as previously considered." However, I also added a note of caution: "It is important to note that probably not all synonymous mutations are neutral, even if most of them are nearly so." Perhaps this was a pertinent statement in light of the recent finding that synonymous codons are often used in "non-random" or unequal fashion (Kimura 1981). (Kimura 1982, p. 8)

4.2 The proponents of the second version of the importance of random drift discourage dividing evolutionary changes into those due entirely to natural selection and those due to random drift with no role for selection. They encourage, instead, analysis of the evolutionary effects of natural selection and indiscriminate sampling acting *concurrently*. That is, they rather encourage dividing evolutionary changes into those due *predominantly* to natural selection, those due *predominantly* to random drift, and those in which natural selection and random drift *both* play important

roles. Consider, for instance, Wright's criticism of the evolutionary per-
spective of R. A. Fisher and E. B. Ford—that they misconstrued the
importance-of-drift problem:

> They hold that fluctuations of gene frequencies of evolutionary sig-
> nificance must be supposed to be due either wholly to variations in
> selection (which they accept) or to accidents of sampling. The an-
> tithesis is to be rejected. The fluctuations of some genes are un-
> doubtedly governed *largely* by violently shifting conditions of selec-
> tion. But for others in the same populations, accidents of sampling
> should be much *more* important and for still others *both* may play
> significant roles. It is a question of the relative values of certain coef-
> ficients (Wright 1948, p. 291, emphases added).

Wright's criticism was twofold. First, he was warning against reducing
the importance-of-drift question to an all-or-none neutralism issue—i.e.,
to an issue concerning whether all or no evolutionary changes are due to
random drift with no role for selection. This is an issue that I just claimed
was not really an issue with regard to the neutralist version of the im-
portance of drift. And Fisher and Ford also denied being concerned with
it (Fisher and Ford 1950, p. 175). But Wright was also warning against
reducing the importance-of-drift question to even a more-or-less neutral-
ism issue—i.e., to an issue concerning whether more or fewer evolu-
tionary changes are due to random drift with no role for selection. Wright
considered that the proper version of the importance of random drift rel-
ative to natural selection was one that concerned the *concurrent* relative
roles of indiscriminate and selective sampling in accounting for evolu-
tionary change with regard to each set of genetic alternatives. As Theo-
dosius Dobzhansky, following Wright, also expressed this version,

> An evolutionary change need not be due either to directed or to ran-
> dom processes [for example, either to natural selection or to indis-
> criminate sampling]; quite probably it is the result of a combination
> of both types. The theoretically desirable and rarely achieved aim of
> investigation is to quantify the respective contributions of the differ-
> ent factors of gene frequency change, as well as their interactions.
> (Dobzhansky 1970, p. 231)

As for the various ways in which selective and indiscriminate sampling
can act concurrently, several possibilities come to mind. The change in
frequencies of *A* and *a* genes, and *AA*, *Aa*, and *aa* genotypes over the
course of generations may be due predominantly to natural selection dur-
ing some generations, and to indiscriminate sampling during others. In-
discriminate and selective sampling are only loosely "concurrent" in this
case. Or the changes in frequencies of those genes and genotypes may

be due to a combination of discriminate parent sampling and indiscrim-
inate gamete sampling, or vice versa. Or the changes may be due to sam-
pling in some geographical subpopulations by entirely indiscriminate
sampling agents, like forest fires, while the rest of the population is sam-
pled selectively. Or the changes may be due to the sort of more-or-less
selective and more-or-less indiscriminate samplings that I discussed in
Section 3.4.

The general theory that describes the concurrent roles of random drift
and natural selection is, like the neutralist theory, stochastic rather than
deterministic—again in the sense that, given the gene and genotype fre-
quencies of one generation, and values for all the other variables of the
theory (including, again, size of the population, and in this case fitness
values as well), one can at best calculate the *probabilities* of possible
gene and genotype frequencies in successive generations.

The general theory includes, among many other things, variations on
the U-shaped curves that describe the effects of random drift without se-
lection. For example, Diagrams 6(a) and 6(b), again from Wright's pi-
oneering 1931 work, show the effects of the same variety of selection
pressures in small (6a), and then in large (6b) populations. As in Dia-
grams 4 and 5, we are dealing with *proportions* of populations and their
gene frequencies. So all we can predict about a population with the help
of these diagrams is the *probability* that it will have a particular combi-
nation of gene frequencies. Also, as in Diagram 4, all the populations in
question had $50 : 50$ gene frequencies at time $t = 0$. Diagrams 6(a) and

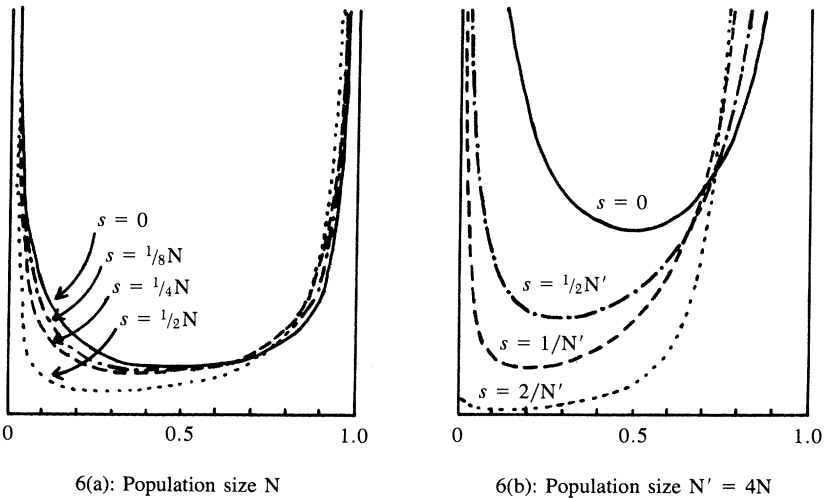6(a): Population size N   6(b): Population size N' = 4N

DIAGRAM 6

6(b) show the distributions at some much later time. When there is no selection—represented by the case where the selection coefficient, s, equals zero—the characteristic U-shaped distribution results, although it "squeezes out" more populations with intermediate gene frequencies in the case of the smaller populations. For both the large and small populations, greater selection results in a greater skewing of the curve—that is, more and more of those populations have greater and greater frequencies of the gene whose frequency is represented on the x-axis. But this shows up more clearly in the case of the larger population, where in the case of strong selection for the allele in question (i.e., where $s = 2/N$), almost all of the populations have between 70% and 100% of that allele; whereas in the case of weaker selection (i.e., where $s = 1/2N$), many more of the populations have less than 70% of the allele in question.

There again you have only a glimpse of a theory, but hopefully a glimpse that will be of some use. Again, somewhat aside from the theory, there are more or less specific and more or less general issues that divide investigators in this area. Specific issues with regard to this version of the importance of drift are those that concern the relative, concurrent importances of selective and indiscriminate sampling in accounting for changes in frequency of a *specific* set of genetic or genotypic frequencies (e.g., Kerr and Wright 1954, Dobzhansky and Pavlovsky 1957, Lamotte 1959). The general issues are, as in the case of the neutralism version of the importance of random drift, *more or less* issues rather than *all or none* issues. In other words, the issues do not simply boil down to whether indiscriminate sampling has a certain relative importance in *every* evolutionary change, but whether it has a certain relative importance in *many* evolutionary changes. For instance, Wright, who comes as close as anyone to defending a general position on the relative importance of random drift, nevertheless warns, "There is no theoretical necessity for supposing that evolution has proceeded in the same way in all groups. In some it may proceed largely under direct selection pressure following change of conditions, in other cases it may be determined by random differentiation . . ., with or without selection" (Wright 1940, p. 181). And as Dobzhansky so nicely summed up this version of the importance of random drift, and the general issues associated with it,

> Since evolution as a biogenic process obviously involves an interaction of all of the [agents of evolutionary change, including natural selection and indiscriminate sampling], the problem of the relative importance of the different agents presents itself. For years this problem has been the subject of discussion. The results of this discussion so far are notoriously inconclusive. . . . One of the possible sources of the situation may be that a theory which would fit the entire living

world is in general unattainable, since the evolution of the different
groups may be guided by different agents. To a certain extent this
possibility is undoubtedly correct. In species that occur in great abun-
dance in a fairly continuous area of distribution, the population size
factor is bound to be less important than in species that are subdivided
into numerous local colonies each having a small effective breeding
population. [For] organisms whose environment is in the throes of a
cataclysmic change, natural selection and mutation pressure are more
important than [for] organisms living in a relatively constant envi-
ronment. Nevertheless, one can hardly eschew trying to sketch some
sort of a general picture of evolution. (Dobzhansky 1937, p. 186)

I have tried, so far, to distinguish two versions, and two sets of issues,
concerning the evolutionary importance of random drift. But, of course,
the distinction can be collapsed. As one investigates smaller and smaller
fitness differences, one moves from an investigation of the second version
of the importance of drift, to the first. Whether—or to the extent that—
research programs into the two versions of the importance of random drift
have maintained separate identities in spite of this sort of conceptual con-
tinuity, or whether this continuity has, at times, favored a unified pro-
gram, is something that I can only say that I would like to know more
about.

5. Chance in Nature. At any rate, given a suitable interpretation of fit-
ness and natural selection, there are two more or less distinguishable ver-
sions of the evolutionary importance of indiscriminate vs. selective sam-
pling. Now if we step back from these positions and do not concentrate
so much on the *variety* of issues involved, we see in the development of
evolutionary biology what we see in the development of so many sci-
entific disciplines in the nineteenth and twentieth centuries, namely the
rise of stochastic theories. We have already discussed, very briefly, the
respects in which evolutionary theories that encompass genetic drift are
stochastic vs. deterministic. It might also be helpful to discuss the sto-
chasticity of evolutionary theory by comparing the stochastic "version"
of evolutionary theory with the effectively deterministic version that is
presented in the opening chapters of most textbooks (prior to the intro-
duction of the stochastic version).

The deterministic version, like the stochastic version, is based on the
so-called "Hardy-Weinberg Law". According to that principle, in an in-
finitely large population in which individuals mate randomly with respect
to their geneotypes, and in which there is no selection, mutation, or mi-
gration, the gene and genotype frequencies remain at equilibrium. More
specifically, if the only alleles at a locus are A and a, and if we represent
the proportion of A genes by p and the proportion of a genes by q, the

genotypic frequencies of the population will remain in the equilibrium frequencies,

$p^2AA : 2pqAa : q^2aa.$

Now assume for the moment that population size is not a variable of the theory—that the theory only applies to populations of infinite size. In an infinite population, any "local" misrepresentations of gene and genotype frequencies due to indiscriminate sampling would balance out. So by insisting that the population be infinitely large, evolution by genetic drift is effectively ruled out.

Given this version of the Hardy-Weinberg Law, given values for p and q in one generation, and given 1) magnitudes of selection for or against the various genotypes, 2) rates of mutation with respect to the various alleles, 3) magnitudes of preferential mating between the different genotypes, and 4) magnitudes of migration of the different genotypes, we can calculate the exact gene and genotype frequencies in the succeeding generations. For instance, if the frequencies of A and a are p and q respectively, and if the relative average fitnesses of the genotypes AA, Aa, and aa are 1, 1, and 1 − s respectively, then the change in frequency of A (Δp) in one generation is,

$\Delta p = (spq^2)/(1 - sq^2).$

The theory of evolution, thus construed, would be neatly deterministic, but would be grossly incomplete with respect to the many finite populations that supposedly also undergo evolutionary change! To cover these, population size must be considered as a variable. We can then formulate the sorts of stochastic extensions of the theory that we have already discussed. Without them, the theory of evolution would be awfully incomplete.

As in the cases of thermodynamics and quantum mechanics, stochastic theories play a very important role in evolutionary biology. In spite of all the disputes concerning the evolutionary importance of random drift, no one denies that evolutionary theory should be stochastic. But just to say that evolutionary theory is stochastic, and that is that, is to overlook an important respect in which stochasticity continues to be an issue in evolutionary biology. I do not mean that the issue has been transformed into the sort of stochasticity vs. *in-principle* stochasticity issue characteristic of quantum mechanics. I have in mind yet another respect in which the stochasticity issue in evolutionary biology is far from being settled. It is kept alive by the variety of issues and disputes concerning the importance of random drift. In order to see the connection, it will be useful to consider the disputes concerning the importance of random drift in the context of other, somewhat similar disputes in evolutionary biology.

Evolutionists recognize a variety of modes of evolution—a variety of ways in which the gene and genotype frequencies of a population may be changed (basically, any of the ways in which Hardy-Weinberg equilibrium might be upset). There is evolution via the genetic mutation of one allele to another, evolution via the migration of genetically different types of organisms into or out of the population, evolution via the preferential mating of organisms with particular genotypes, and of course evolution via random drift, and evolution via natural selection. Evolutionary theory describes the separate and concurrent outcomes of these various processes, depending on the values of the relevant variables. So, for instance, evolutionary theory describes what happens in a large population when there is no migration, no mutation, and moderate selection; what happens in a small population when there is moderate migration, moderate mutation, and no selection; etc.

Agreement with regard to the theory as described still leaves open some very important questions—namely, questions concerning the relative evolutionary importances of the various modes of evolution *in nature*—hence, the magnitudes of the relevant variables *in nature*. It is remarkable how many modern evolutionists have been of the opinion that the work that "remains to be done" in evolutionary biology is just that of measuring these magnitudes. Timofeef-Ressovsky's 1940 assessment of the work-to-be-done is representative of this opinion, and has been echoed often since then. As Timofeef explained the situation, evolutionary theorists of the likes of R. A. Fisher, J. B. S. Haldane, Sergei Tschetverikov, and Sewall Wright had succeeded in

> . . . showing us the relative efficacy of various evolutionary factors under the different conditions possible within the populations (Wright 1932). It does not, however, tell us anything about the real conditions in nature, or the actual empirical values of the coefficients of mutation, selection, or isolation [limitation of population size]. It is the task of the immediate future to discover the order of magnitude of the coefficients in free-living populations of different plants and animals; this should form the aim and content of an empirical population genetics (Buzzati-Traverso, Jucci, and Timofeef-Ressovsky 1938). (Timofeef-Ressovsky 1940, p. 104)

And as A. J. Cain expressed the same position much more recently,

> The researches of R. A. Fisher, J. B. S. Haldane, and Sewall Wright laid the foundations of the mathematics of population genetics. . . . What they did was to provide a mathematical theory covering all possible contingencies, from which quantitative predictions of both deterministic and stochastic processes could be made. That was a great gain, but it does not tell us what of all these possibilities are

actually exemplified in the wild—what, in short, are relevant to the actual process of evolution. (Cain 1979, pp. 599–600)

So evolutionists can agree on *theory*—on what are the possible modes of evolution, and how evolution occurs given various possible magnitudes of the relevant variables—and at the same time disagree vehemently as to the actual magnitudes of these variables and thus the relative importances of these modes of evolution *in nature*. Since Darwin, evolutionists have continually haggled over such matters. Neo-Lamarckians concerned themselves for a long time with the relative evolutionary importance of an evolutionary factor that is no longer included in evolutionary theory— namely, the inheritance of acquired characters. Darwin and Moritz Wagner argued about the importance of migration relative to selection (see Sulloway 1979). In the early twentieth century, William Bateson and W. F. R. Weldon argued over the importance of mutation size and pressure relative to selection (see Provine 1971). There are even disputes as to which is the most important kind of selection. For instance, there was a long, complicated, and even bitter controversy between Dobzhansky and H. J. Muller as to the relative evolutionary importance of selection in favor of heterozygotes vs. selection in favor of homozygotes (see Lewontin 1974). Representative of this interest of evolutionary biologists in ranking the modes of evolution according to their importance is the title of a book by A. L. and A. C. Hagedoorn, published in 1921: *The Relative Value of the Processes Causing Evolution*.

These are rarely all-or-none issues. The disputants defend the importance of their favorite modes of evolution without ruling the others entirely out of the question. As Stephen Gould and Richard Lewontin characterize such issues, "In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory" (Gould and Lewontin 1979, p. 151). The neo-Lamarckians recognized selection, though their neo-Darwinian opponents did not reciprocate. Darwin did not altogether deny the evolutionary effects of migration, nor did Wagner completely rule out selection. Bateson certainly did not ignore selection, nor did Weldon ignore mutation. Dobzhansky always admitted cases of selection in favor of homozygotes, and Muller always admitted cases of selection in favor of heterozygotes.

The structure of these disputes thus has the important effect of not rendering entirely fruitless those parts of evolutionary theory that deal with the supposedly less important modes of evolution. So those parts of the theory are rarely threatened by elimination. These disputes can take place, in other words, without bringing any part of evolutionary theory into question, either for reasons of incorrectness or lack of fruitfulness.

The issues concerning the relative evolutionary importance of random

drift are very similar: What is more important in accounting for evolu-
tionary change, indiscriminate sampling in finite populations, or discrim-
inate sampling? As has been discussed, these issues are not all-or-none,
but more-or-less issues. As Gould characterizes the random drift issues,
"The question, as with so many issues in the complex sciences of natural
history, becomes one of relative frequency" (Gould 1980, p. 122). Thus,
no neutralist *denies* selection. No selectionist *denies* neutral mutations.
No one who investigates the concurrent action of natural selection and
random drift believes that either of those factors is *always* overwhelming.
The stochastic theory that describes the evolution of neutral alternatives,
and that describes the concurrent effects of different degrees of indis-
criminate sampling and natural selection, is thus not at issue.

But precisely because the actual relative magnitudes of population size
and indiscriminate sampling on the one hand, and selection pressure on
the other hand, *are* at issue, stochasticity is still an issue in evolutionary
biology. Evolutionary biologists are content to have a stochastic theory
of evolution, but are not at all in agreement concerning how important a
role to attribute to chance in accounting for actual evolutionary change.
The stochasticity issue in evolutionary biology is decidedly not *whether*
chance plays a role in evolutionary biology, but *to what extent*.

I will close with reference, once more, to the long-standing dispute
between Wright and Fisher concerning the relative evolutionary impor-
tance of random drift vs. natural selection. In his forthcoming biography
of Wright, William Provine thoughtfully analyzes the development of their
agreements and disagreements. As Provine points out, Wright and Fisher
were ultimately able, in published work and correspondence, to work out
differences concerning the mathematical theory involved. For instance,
Wright succeeded in convincing Fisher that the rate of decay of neutral
variability was $1/2N$ (Diagram 5) rather than $1/4N$ as Fisher originally
thought.

As Wright acknowledged in his review of Fisher's landmark, *The Ge-
netical Theory of Natural Selection* (Fisher 1930), "our mathematical re-
sults on the distribution of gene frequencies are now in complete agree-
ment, as far as comparable" (Wright 1930, p. 352). But as Wright also
made clear, agreement with regard to mathematical theory still left room
for considerable disagreement. And the most important source of dis-
agreement was Fisher's assumption of large population sizes in nature,
which effectively ruled out the actual importance of evolution by random
drift. Again, this issue was somewhat detachable from the mathematical
theory. As for the real disagreement, as Wright later put it, "It is a ques-
tion of the relative values of certain coefficients" (1948, p. 291). Thus,
evolutionists like Wright and Fisher could agree that small population size
and chance are important in theory, all the while disagreeing considerably

as to their importance in nature. It is in this sense that the stochasticity issues in evolutionary biology are still far from being resolved.

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APPENDIX

Recall that the hereditary material of sexual organisms comes in pairs of morphologically
similar, or homologous, chromosomes. The genes reside linearly along the chromosomes;

A

a
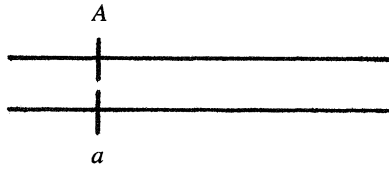
the two genes that lie opposite one another on homologous chromosomes are said to occupy the same chromosomal location, or "locus", and are said to be "alleles" with respect to that locus. In the diagram, A and a are alleles at a particular locus. The two alleles at a locus may be materially different, as in the case of A and a (as the different symbols are supposed to represent), or they may be materially identical. Different combinations of alleles may result in alternative states of the same general character, like blue eye color vs. brown eye color.

The particular combination of alleles that an organism has is called its genotype. We can speak of the genotype at a particular locus—for instance, we can speak of the Aa genotype in the case at hand—or we can speak of the entire genotype. If the two alleles at a locus are different, the organism is said to have a "heterozygotic" genotype with respect to that locus. Otherwise, it would be said to have a "homozygotic" genotype with respect to that locus.

Finally, the gametes that a sexual organism produces (i.e., the sperm/pollen or egg cells that it produces) each appropriately contain one allele from each locus. According to "Mendel's Law", there is no physical basis for a bias in the number of gametes containing one or the other allele of a heterozygotic organism. In other words, in the long run, a heterozygotic organism should produce gametes, half of which contain one allele, and the other half of which contain the other allele.