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CANADIAN JOURNAL OF PHILOSOPHY
Supplementary Volume 14

Is the Theory of Natural Selection a Statistical Theory?

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I

In *The Structure of Biological Science* (Rosenberg [1985]) I argued that the theory of natural selection is a statistical theory for reasons much like those which makes thermodynamics a statistical theory. In particular, the theory claims that fitness differences are large enough and the life span of species long enough for increases in average fitness always to appear in the *long run*; and this claim, I held, is of the same form as the statistical version of the second law of thermodynamics.

For the latter law also makes a claim about the *long run*, and its statistical character is due to this claim: thermodynamic systems must in the long run approach an equilibrium level of organization that maximizes entropy. Over finite times, given local boundary conditions, an isolated mechanical system, like the molecules in a container of gas, may sometimes interact so as to move the entropy of the system further from, instead of closer to the equilbrium level. But given *enough* interacting bodies, and *enough* time, the system will always eventually move in the direction prescribed by the law. Thus, we can attach much higher probabilities to the prediction that non-equilibrium systems will reflect greater entropy in future periods

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than we can to predictions that they will move in the opposite direction. And as we increase the amount of time and the number of bodies interacting, the strength of the probability we can attach to the prediction becomes greater and greater.

The same kind of probabilistic claims that the second law of thermodynamics makes about the direction of entropy-change, is made by evolutionary theory about the direction of fitness-changes. Evolution need not and does not move in a straight line towards equilibrium levels of populations for various species and their subpopulations. The theory asserts that over the long run, evolution must move in the direction of equilibrium, and that the length of time it takes to get there is a probabilistic function of fitness-differences and population sizes.

I now think that this account of the statistical character of the theory is at least quite incomplete. It is certainly misleading. To begin with, the analogy to the statistical character of thermodynamics is not very illuminating, because the statistical character of the second law is itself not well understood. Although the law makes a probabilistic claim, it is supposed some how to be reducible to and reflect fully deterministic behavior in accordance with Newtonian mechanics among the constituents of thermodynamic systems. Yet this reduction has never been satisfactorily effected in the general case. So, there is no explanation of how thermodynamic probabilities emerge from mechanical certainties. Nor is it clear what kind of probability the theory trades in: does it make a claim about epistemic probabilities, probabilistic propensities, long run relative frequences, or is there some other interpretation of probability that is most suitable to expressing its claims?

In the absence of solutions to these problems, the parallel between the statistical character of evolutionary theory and thermodynamics is not very fully enlightening. So, in what follows I will dispense with the analogy to thermodynamics and approach the problem of expressing the relation of probability to evolution directly.

First some preliminary distinctions. The question of whether evolutionary phenomena are statistical or not, is a different one from the question whether *our best theory* of these phenomena is unavoidably statistical. For our best theory, present or future, may turn out to be statistical because the deterministic facts about evolution are

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beyond our cognitive and computational powers to apprehend in useful terms. If this is the case, then the best theory we can frame about evolution will turn out to be a *useful instrument,* but not a complete account of evolution itself.

Thus we need to address separately the questions of (1) whether the process of evolution is deterministic or probabilistic, and (2) whether the theory of natural selection, as currently understood, is deterministic or probabilistic. Addressing either question requires us to identify the evolutionary features or 'state-descriptions' with respect to which we make claims of determinism or probabilism. For, as Nagel pointed out long ago ([1961], 285ff), a theory, like quantum mechanics for example, can be deterministic with respect to one set of state-descriptions, e.g. the quantum mechanical ones, and indeterministic or probabilistic with respect to another set, e.g. the classical or Newtonian ones.

This requirement confronts us with a difficulty, for it is by no means clear what the appropriate state-descriptions are, with respect to which we should pose the questions of whether either the process of evolution itself or the theory of natural selection is deterministic or not. I suppose that the philosophically least controversial assumption about the appropriate state-description for our purposes is that the states to be systematized by evolutionary theory are proportions of population within and between species, and I will operate on this assumption hereafter.

Then there is the question of what interpretation to attach to the probability operators that are ubiquitous in evolutionary discussions. Are they epistemic, or long-run relative frequency claims? Or do they reflect some sort of objective propensities? By examining the role of probability we can hope to shed light on this question. But two sorts of interpretations seem to be ruled out straight away.

First there is the notion that evolutionary phenomena might be probabilistic for reasons having to do with the indeterministic character of the fundamental physical processes on which evolutionary phenomena supervene. The world is certainly indeterministic in its fundamental laws of working, and since fundamental microphysical processes are hooked up to macroprocesses in ways that convey their micro-indeterminism to the macro-world (for example in Gieger counters), phenomena at every level of organization and aggregation

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are 'infected' with quantum mechanical indeterminism. The only sort of probability that seems to me to make sense of quantum mechanical indeterminism is that according to which probabilities are unanalyzable propensities or dispositions of events to bring about other events. Accordingly, some evolutionary events must have these probabilistic propensities to result in evolutionarily significant consequences, just because they are built up out of or hooked up to quantum events. But this admission settles no problem of interest to evolutionary biologists. For the probabilities involved are so small, and the asymtotic approach to determinism of everything above the level of the chemical bond so close, that quantum mechanical probability could never explain the probabilistic character, if any, of either evolutionary phenomena or evolutionary theory.

Second, I take it that if the *only* probabilities at work in evolutionary theory are epistemic, then this is no reason to suppose that evolutionary phenomena are in themselves indeterministic or probabilistic. Epistemic probabilities are 'subjective.' They are relations between events and ourselves, or more exactly between them and our beliefs, our evidence. If there are no epistemic agents, there are no epistemic probabilities. Since evolution can and does take place in the absence of epistemic agents, the process could not involve any such probabilities. Another somewhat tendentious way of saying this is that if evolutionary processes are probabilistic, the sort of probability in question must be 'real,' 'objective,' and not 'subjective.' On the other hand, even if epistemic probabilities are no part of the process of evolution, they may still figure in our best theory of evolution. But if they are, we shall have to seriously rethink the nature of that theory and its relation to the world.

II Drift

Evolutionary biologists seem to identify the source of unpredictability in evolution with the phenomenon or drift. For example, Strickberger (1968) writes as follows: mutation, selection and migration 'act in a directional fashion to change gene frequenceis progressively from one value to another... whether going towards fixation or equilibrium, the constancy of these forces enables them to be

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described as *directional*' (736: emphasis in original). Strickberger continues: 'In addition to these directional forces, however, there are also changes which are not tied to the gene frequences involved. Because of this, such forces cause gene-frequency changes that can go in one direction or another, from generation to generation, *without any predictible constancy*. One of the most important of such *nondirectional* forces arises from variable sampling of the gene pool each generation and is known as *random drift*' (first emphasis added).

According to Strickberger, genetic drift results when the effective population size (roughly the number of parents in a population) is small enough for gene frequences to vary as a result of 'Sampling error.' In this context 'sampling error' has a misleading connotation, since it suggests investigator-intervention that might mistakenly select for experimentation or some further treatment a non-representative sample from a population. 'Sampling error' is to be understood here in terms no more anthropomorphic than the meaning of 'selection' in evolutionary theory. It is 'nature' that picks a subset of the population for further treatment; if its selection is not representative of the whole population, the results may be different from what they otherwise would be. And as all experimenters know, the smaller the sample, the higher the probability that it will be unrepresentative.

Only a subset of the members of each generation of a population reproduce. This subset constitutes the 'sample.' Reproduction constitutes the 'treatment.' The smaller the sample is, the less likely it is to be representative, and the more likely it is that there will be 'sampling error.' As long as the effective population size is very large, in the absence of selective forces successive generations will deviate only a little in gene frequency. If standard deviation from previous generations is measured as σ:

$$\sigma = \sqrt{pq/2N}$$

then if N is large, the frequencies of two alleles, p and q, will remain close to their starting frequences approximately 68 % of the time. But when N is small, the frequencies will fluctuate widely and will frequently go to fixation for one of the two alleles, and extinction for the other. If a species is composed of a large number of small

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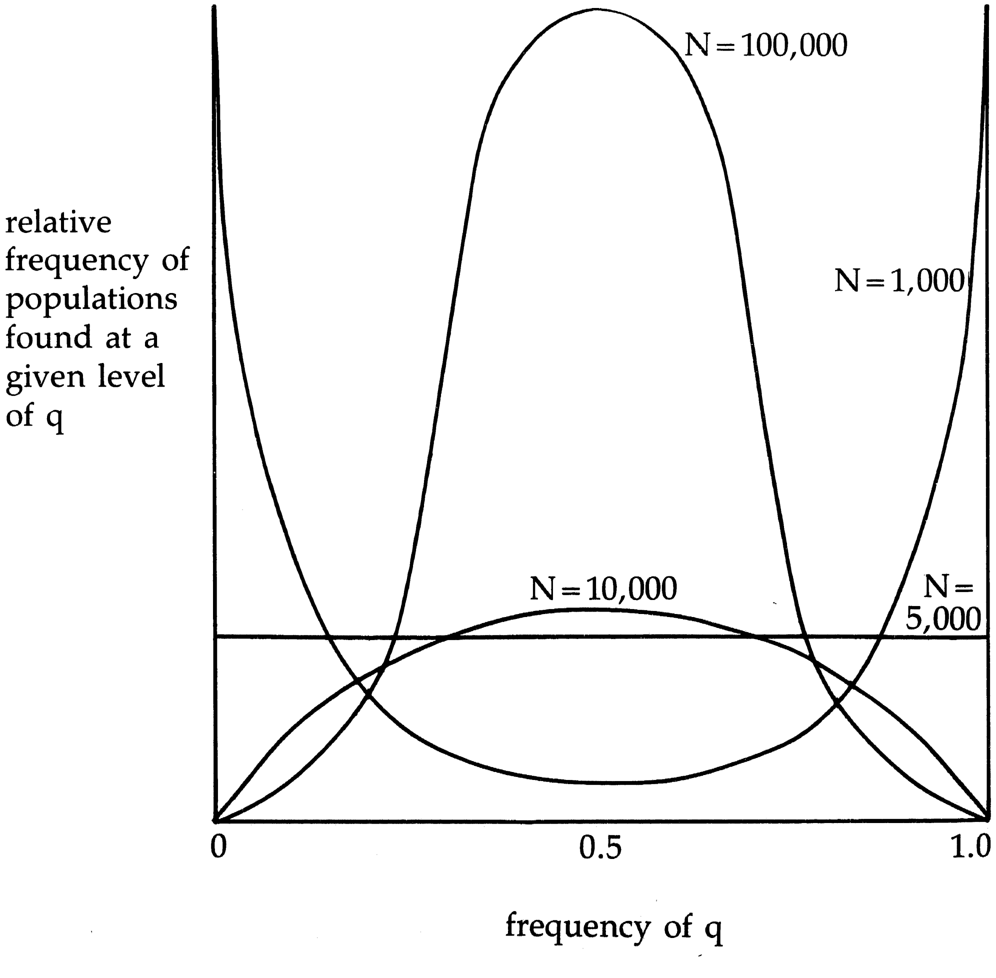
isolated subpopulations, then the result may well be 'fixation' for p among half the subpopulations and for q among the other half. Only one of the two genes will be represented in any of the subgroups. And this may happen even if the starting frequency of each allele in the whole population is 0.5. Strickberger reproduces a graph from Sewall Wright (1951) to illustrate the effects of drift, for different population sizes (N = 100,000, 10,000, 5000, 1000) when selection is zero, migration is small, and where the starting frequency for q is 0.5:



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In the largest population (N = 100,000) the frequencies of p and q remain close to 0.5. In the smallest population (N = 1,000) the proportion of populations in which both alleles are equally represented is quite small. It is clear that even when the total population of a species is very large, the number of conspecifics with which one organism can interact throughout its entire life-time may be quite small. And this possibility provides wide scope for drift. As Strickberger notes, according to Sewall Wright a good deal of change in gene frequencies over time, even in the face of selective forces, may be due entirely to the effects of random drift on a population whose 'structure' reflects such isolated sub-groups. A hundred populations of 1,000 may be equal in total numbers to a single population of 100,000, but as the graph shows, they may reflect a quite different set of gene-frequencies.

Is random genetic drift then the source of the probabilistic character of the theory of natural selection? It is certainly responsible for the probabilistic character of many of the theory's characteristic claims. But that is not enough either to say the theory is probabilistic or that drift is the source of its statistical nature. After all, the application of Newtonian mechanics to astronomy, or for that matter to any system in which measurement-errors are made, requires an appeal to statistical considerations, and produces results that are probabilistic. Given a probability distribution of the positions and momenta of the bodies in a Newtonian mechanical system, we can predict with a probability as close to 1 as we like, that probability distributions of position and momentum at any future time will be equally arbitrarily close to those the deterministic equations of Newtonian mechanics leads us to expect when appied to the original probability distribution. Yet these facts have no tendency to show that Newtonian mechanics is probabilistic. Of course if, as it turns out, position and momentum are not just epistemically indetermined, but physically indetermined, as quantum mechanics requires, then the best theory governing these variables will be indeterministic, for reasons above and beyond our inability to give more than probabilistic estimates of exact position and momentum.

Moreover, even the possibility of small errors of measurement can make a deterministic system utterly unpredictible in its behavior. In this respect, whether a theory is deterministic or not is

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independent of whether it enables us to make well-confirmed predictions about states of the system it describes. If our measurement of initial conditions must be probabilistic, because of limitations on our measuring devices, then the theory's predictions will be probabilistic at best. And at worst, the theory will make no definite predictions at all, because of magnifying interaction effects between variables we can only measure probabilistically and not accurately enough.

It seems clear that probabilistic measures of gene-frequencies are of the error-measurement sort. They reflect the degree of our confidence that we have avoided large 'measurement error.' So these probabilities cannot be the source of the statistical character of the theory of evolution, still less of the phenomena of it. We measure the proportion of genes in terms of relative frequences, not because these proportions are indeterministic but because the only feasible means of applying the theory of natural selection is to sample the population and infer the distribution of genes. Here there is experimenter or observer sampling error. But there is no reason, within the theory of natural selection itself, to suppose that the proportion of different genes is undetermined, or inherently probabilistic. Indeed, as I have argued elsewhere (Rosenberg [1985]), since the theory of natural selection itself makes no mention of genes but only presupposes some vehicle for hereditary transmission, indeterminism of any sort at the level of genes, including Mendelian segregation and assortment, can not be responsible for the probabilistic character, if any, of natural selection *in general* or of the theory of natural selection considered in isolation. If probabilistic methods are forced on us *only* because we have to apply the theory of natural selection to events that are probabilistic as a result of Mendelian assortment and segregation, then neither evolution as a general phenomenon, nor the theory itself is inherently probabilistic. Only its local applications turn out to be. In a biosphere with different, much simpler hereditary mechanisms, change in trait frequencies could be thoroughly deterministic.

Might random drift figure in our theories in the same way our probabilistic measures of gene-frequency do, reflecting our ignorance of initial conditions, and not an essential probabilistic element in the theory of natural selection? Could this be the right vew: is

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drift a matter of epistemic probabilities touching on the initial conditions to which we apply the theory. There are some tempting reasons to think so. First consider the minor terminological note. Strickberger identifies selection, mutation and migration as evolutionary forces, which determine the direction of evolution, by contrast with drift, which he declines to identify as another *evolutionary* force. Gene frequencies *change* under the effects of drift, but they may not be said to *evolve,* i.e. to show changes of apparently adaptational significance. Indeed, insofar as evolution means adaptational change, drift is clearly no part of it, for no one identifies the source of adaptation in drift alone. Could drift actually be a way of referring to those unknown *non-evolutionary* forces that interfere and deflect evolution from the outcomes which deterministic forces like selection, mutation, and migration, would otherwise secure? Alternatively, could drift be a way of dealing with those evolutionary forces that escape our notice because of their irregularity and subtlety? If either of these alternatives is right, then drift provides no reason to think evolution 'in the objects' is in fact probabilistic. If the second view is right then drift would be a source of indeterminism only within the theory, without reflecting any probabilities in the phenomena.

III Two alternative interpretations of drift

Suppose there is a small population of, say giraffes, whose longest necked members are most well adapted to the veldt, and are secretly removed by poachers to zoos just because they have the longest necks, there to languish, leaving no off-spring. As a result, gene frequences change in the small population. Short-necked giraffes come to predominate in the group for several generations. What are the game-preserve biologists to say? Is the change in gene-frequences a case of drift? Since the physical environment has not changed, and they know nothing of the poachers, their choice seems either to be drift or disconfirmation of the theory of natural selection. Naturally, our biologists choose drift. In so choosing, are they embracing the hypothesis that non-evolutionary forces interfered to move the population away from evolutionary equilibrium? Or are

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they adopting the idea that as yet unrecognized evolutionary forces did so, shifting the equilibrium position, and moving the population towards it? Well, if the naturalists begin a careful study of the environmental conditions of giraffes hoping thereby to explain the change in gene frequences in terms of a change in the adaptive topography, then evidently the explanation is the latter. But if so, either the naturalists do not grant that drift played a role, or else for them drift *means* simply evolution of gene frequencies in adaptive but unexpected and temporarily inexplicible directions. If so, drift-hypotheses are introduced to explain changes in gene-frequences as expressions of our ignorance of deterministic evolutionary forces, and drift does not confer any real probabilistic features on the phenomena of evolution or on the theory of natural selection. It simply reflects our ignorance.

This way with drift is one some commentators would stigmatize as hopelessly 'Panglossian' (cf. Lewontin and Gould [1979]). These biologists condemn the stategy of always seeking a new adaptational explanation whenever a previous one has been placed in doubt. Treating drift as a cover for unknown adaptational forces, to be cited whenever gene-frequencies do not evolve in the evolutionarily expected direction, deprives the theory of much of its empirical content, on these views. Such opponents of 'Panglossianism' will certainly seek a notion of genetic drift that does not condemn them to this adaptational imperative. They are committed to saying that drift either is or reflects the operation of other, nonevolutionary forces. Thus, Lewontin and Gould say specifically that alleles can become fixed in a population through drift 'in spite of natural selection' (Lewontin and Gould [1979], section 5). They do claim that there are further biological forces which though not 'selective' operate in accordance with autonomous nomological generalizations at the same levels of organization as selection, for example so-called 'developmental constraints.' I have argued elsewhere (Rosenberg [1985], 242-3) that no such autonomous generalizations are to be found within biological theory. But even if there were, they would hardly make evolutionary theory probabilistic. Indeed, such constraints might channel evolution narrowly enough to preclude drift. So, we shall have to look beyond biology altogether to find the sources of drift.

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Let us return to our giraffes. Suppose the naturalists do not launch a careful study of the ecological conditions of the giraffe population, but satisfy themselves with chalking up the change in gene frequences to drift, meaning by that that some *non-evolutionary* forces intervened, ones that operate irregularly, occasionally, in a way not normally correlated wich changes in gene-frequences. We are to imagine some Rube Goldberg-like device whose appearance on the scene and whose operations are so singular that the biologist can well be excused for not accommodating it in his theory. For example, suppose that through freakish never-to-be-repeated wind conditions, the two tallest trees on which the most attractive vegetation for giraffes grows, become so twisted that they accidentally trapped the heads of most of the tallest giraffes, causing their necks to break, and leaving them ensnared. In this case, the change in gene frequences may be said to be due to drift, but drift will refer to entirely deterministic, but utterly non-evolutionary factors, which again, through our ignorance we must treat probabilistically. If the naturalists never find these freakish trees, and never see in their crooks, the ensnared skulls of the poor giraffes who were trapped in them, then their attribution of change in gene frequences to drift will also be epistemic, and again, will not reflect any indeterminism in the theory of natural selection.

We, of course, know why the gene frequences changed, and we have informed the game wardens, who have arrested the poachers. So, they have been removed, never to trouble the giraffes again. What are we, who know the facts, to say about the change in gene frequences? Surely we will not credit the change to drift. We will say that for a short time the environment changed, making long-necks maladaptive, and therefore shifting gene frequences through selection.

If we can generalize from this science fiction case, the conclusion seems to be that from a position of omniscience, there is no need for the notion of drift; that evolution simply moves faster among small populations, when their gene frequences change at all; and that the phenomena and the theory of natural selection are thoroughgoingly deterministic ones, where adaptation, mutation, and migration always operate, and are never impeded by any biological obstacle. We finite creatures, however, have need of probabilities

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when applying the theory, and have need of the notion of drift, to serve as an epistemic fig leaf – one that protects the theory from falsification by attributing deviations from expected gene frequencies to the interference of non-evolutionary forces, and protects us from charges of ignorance, by enabling us to gather together exceptional and unknown selective forces in the grab-bag of drift.

The conclusion seems to be that the phenomena are deterministic and that if the theory of natural selection is a probabilistic one, the source of this feature cannot be in the role played by drift.

IV Sober on drift

We can explore the character of this view by comparing it with Elliott Sober's arguments to the effect that '*Random genetic drift* ... is the source of the stochastic element in evolution' (1985, 110; emphasis in original. Further page references in this and the next section are to this work).

Sober's exposition of the notion of drift is much like Strickberger's. He too describes selection, mutation and migration as *directional* forces, by contrast with drift. He explains how drift depends on population size, or more exactly, effective population size, reproduces a graph very much like the one reproduced above, points out that even where the population is large, if it is divided into isolated subpopulations, alleles can drift to fixation and extinction in each subpopulation, while both are still represented in the starting ratio within the whole population.

But then Sober becomes 'ambivalent' about the evolutionary role of drift, though not ambivalent in the two ways described above. On the one hand he writes that, while selection, mutation and migration determine the direction of evolution, drift seems to determine the *magnitude* of the changes they wrought. This gives the suggestion that drift on the one hand and selection, migration and mutation on the other are two dimensions of a vector that fixes the time-path of evolution.

But one of these dimensions is deterministic, according to Sober, and the other is stochastic. Sober claims that the directional forces are deterministic: operating on gene frequencies in the absence of

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drift they enable us to predict the expected value of subsequent frequencies with very high probability (111). But if this is right, then it is difficult to see how drift could give the magnitude of evolution. Certainly it cannot be viewed as anything like one of the dimension of a vector. For consider, if drift is zero, then coefficients of selection, migration and mutation give both the direction of evolution, *and its magnitude*. Only when drift is non-zero, do these other forces give less. What is more, when drift is very large compared to the other forces, they do not even determine the direction of evolution (for there is none, there is only change). So far from being a component vector, or the dimension of one, it looks more like drift is really a countervailing force, or perhaps one that operates orthogonal to evolutionary ones.

And of course Sober recognizes this. He writes: 'But the vector addition and subtraction that underwrites our understanding of how deterministic forces combine cannot be used here. If drift is a selective force, it is a force of a different color' (117). This admission severely undercuts Sober's distinction between direction and magnitude in apportioning the causal force of selection and drift. We need to take seriously his qualifications, 'drift ... says something about the *magnitude* of change, although it remains silent on its *direction'* (116, emphasis in original). Yes, drift says *something* about magnitude, but then so does selection. And drift is not always entirely *silent* about direction: given small populations it makes some outcomes more probable than others, even when selection coefficients are high.

This is what I mean by Sober's ambivalence. On the one hand drift is repeatedly described as an evolutionary force (see for instance, 116), and, since populations are finite, 'there is no doubt that chance plays a role in evolution' (112) – as opposed to merely a role in biological change. On the other hand, it cannot be summed together with other evolutionary forces, like selection, migration, mutation. Drift turns out to look more like a *nonevolutionary force*, or a way of referring to congeries of such non-evolutionary forces, ones that are responsible for *changes* in gene-frequences, but not for their *evolution*, i.e. their movement in the direction of greater adaptation to local conditions. On this view of course, drift is no part of the theory of evolution, and cannot be responsible for its statistical

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character. This is not to deny that it can be combined with a theory of evolution to explain actual diversity. But diversification may not be identical with evolution.

Of course, the other alternative is to view drift not as a cover for non-evolutionary forces that intervene to deflect evolution from its course, but as a cover for selective forces of which we are ignorant. This is an approach which makes sense of our appeal to probabilities within the theory itself as epistemic resources: they reflect our ignorance of what the proportions are, among the deterministic forces of evolution, selection, migration, mutation, that are operating. But Sober rejects this alernative. And with it, undermines his own claim that drift is the source of the stochastic element in evolution.' At most, he can retain the claim that drift is the source of the stochastic element in our *best theory* of evolution, even though evolution itself is after all deterministic. Or so I shall argue.

V Is drift a useful fiction?

According to Sober the reason we distinguish drift from selective forces is to facilitate comparisons among different populations (115), in order to frame interesting evolutionary generalizations, generalizations we would have missed, if we hadn't drawn this distinction. 'There are *biological* facts that are captured by separating drift from selection that would be rendered invisible if this distinction were not drawn' (115, emphasis added). Sober contrasts this position with what he calls the Laplacian view that the recourse to probability simply reflects our ignorance of the deterministic causes, a view he finds in a passage by Darwin:

> I have hitherto sometimes spoken as if the variations ... had been due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation. (Darwin [1859], 131)

So, despite his disavowal of drift as an evolutionary force, Sober insists there are *biological facts* that dictate the probabilistic character of evolution, and that is presumably why the theory is probabilistic,

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and not simply as a reflection of our ignorance. What are these biological facts?

Sober does not cite any directly. Instead he launches a vigorous argument in favor of autonomy of probabilistic explanation from deterministic ones. That is, he argues that even when a phenomenon is deterministic, our explanatory purposes may be better served by probabilistic explanations than by deterministic ones: 'Even with full knowledge of the details, stochastic modeling may retain its point. Besides excusing our ignorance, the probability concept is an essential one for carving out generalizations.' (This argument is preceded by an interesting digression purporting to show that probabilistic prediction and probabilistic explanation differ from one another in a significant and often unnoticed way. For the former, the latest probability assignments are always appropriate, whereas for probabilistic explanations, these may sometimes be irrelevant, and probabilities of events earlier in the causal chain leading up to the explanadum may be more suitable. I shall not challenge these claims here.)

The argument seems to be that evolutionary probabilities are, like most evolutionary notions, supervenient on nonevolutionary properties of organisms, environments, etc. This makes possible the identification of classes of events that are probablistically homogeneous, even while otherwise quite heterogeneous in their supervenience bases: that is, there is a common probability that these events will be followed by other events of a common kind. Thus, 'the concept of probability allows us to treat this wide range of populations within a single explanatory framework. This is an explanatory advantage of the probability concept that it possesses regardless of whether determinism is true' (126). Therefore, employing the concept of drift we can frame generalizations that explain the time path of gene frequencies among a wide variety of populations of differing species, at differing population levels in differing environments, in common terms.

But Sober asks what if, underneath it all, evolution is really deterministic, and what if we had all the data and unlimited computational powers? Would we still require probability concepts to carve out these generalizations? If not, he concedes, our use of probabilities would not 'mark an objective feature of the world,' it would

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'merely reflect another aspect of our subjective, human perpective' (127), it would be a *useful fiction.*

Sober's response to this 'what if' question is that even if we had the powers of the Laplacian determinist, the answer would be no, probabilities would still be real. His main reason for this conclusion, however, is far too controversial to be convincing. For he argues, that even in a Laplacian world probabilities have all the ontological status that *intentional* properties have in an *extensional* world. He points out that psychological states are at most supervenient on and not reducible to neurological ones, but that for purposes of carving out generalizations about behavior, science needs to attribute these supervening intentional properties to organisms. The supervenience of the mental, Sober says, should have no tendency to convince us that there are no such things as psychological states. And he concludes, 'I suggest that it is equally implausible to think that [supervening] probabilities are unreal in a deterministic universe' (129).

Leaving aside the reaction a determined eliminative materialist would make to each of the claims about the psychological in Sober's argument, consider only the plausibility of Dennett's (1978) view that the attribution of intentional states to humans represents at best a convenient 'stance,' a useful device of ours for dealing with humans and higher animals, but certainly not an ontological commitment. To the extent this argument has merit, and I for one think it has more than 'merit' (see Rosenberg, 1986), Sober's appeal to our commitment to mental properties provides no analogical support for ontological commitment to probabilities in a deterministic world. They may turn out to be just as much of an instrumental convenience as the intentional stance is in psychology. Sober's assertion of the reality of intentionality leaves too many hostages to fortune in the philosophy of psychology to cut any ice in the philosophy of biology.

The utility of intentional notions in scientific psychology is controversial. Their utility is therefore a poor argument for their reality. The *utility* of probability in evolutionary contexts is in fact not in doubt. What is in doubt is its interpretation. Are evolutionary probabilities objective properties of events and sets of them *independent of our knowledge of them,* or are they always implicitly relativised to an epistemic background? Are they contingent on available

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beliefs of sentient creatures attempting to systematize biological processes up to the limits of their own cognitive powers?

Sober's provides a final argument for the ontological reality of evolutionary probabilities. But, ironically the argument ends up implicitly commiting him to the claim that probabilities are always relativised in this way.

Two physically identical coins are tossed one after the other. One comes up heads, the other tails. Did they have the same probabilities of coming up heads? In some circumstances, we'd say yes, in others no. Which of these assignments is correct? Sober says both are correct, and which characterization we use depends on our purposes. 'Neither science nor philosophy provides any general principle for saying whether the two coins "really" had equal or unequal chances of landing heads' (130). This is apparently because 'the probability of an event is relative to a set of propositions' (131). But propositions about what? About evidence, about people's beliefs, I shall argue.

To see this consider Sober's argument: 'looking ... at the causal chain leading up to an event, we can see that the probability of the event *evolves*. Relative to what was true at different earlier times, the event may have different probabilities as an objective matter of fact. The same relativity is found when we broaden our perspective and take account of events that do not lie on that causal chain. Other earlier events may confer probabilities on the event; and so may events that are simultaneous with or later than the one in question' (132). But this is not right. Probabilities don't change truth-values over time. *The* probability of an event on a probabilistic causal chain does not evolve, because for one thing, there is no such unique probability, as Sober has rightly argued. Rather an event has many different probabilities, each of them with respect to a different set of events on the chain (and off it). The probability with respect to an event distant in time may be lower than the probability with respect to a nearer one, but it isn't the *same* probability that has grown from small to large. More important, on the assumption of determinism here in force, the only way probabilities can vary from one is if they are *epistemic*. In whatever sense probabilities may evolve, they can only do so relative to evidence, which changes probabilities as we aquire more of it! So far from being an argument for the existence

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of probabilities as objective matters of fact in a deterministic world, these considerations show just the reverse. At least they do, if by 'objective matter of fact' Sober means, as his contrast with LaPlacianism indicates, that probabilities are not in the eye of the non-omniscient beholder.

Where does this leave us? Sober argues that random drift is what makes evolution stochastic, and that the stochastic character of evolution is an objective fact about it, even if the world is deterministic. We have seen, however, that there is some reason to deny that drift is an evolutionary force at all, and this is something that Sober himself grants, or at any rate is ambivalent on. There are at least two ways to accommodate drift to evolution, either as a placeholder for selective forces which we cannot identify, or as a place holder for non-selective forces. Sober cannot accept the first of these alternatives, for it turns drift into a convenient (indeed Panglossian) fiction, a way of dealing with our ignorance, instead of an independent source of stochastic effects in evolution. He cannot accept the second because it too would deprive drift of its role as such a source within evolution.

So Sober must argue that there are biological facts which the concept of drift captures for evolutionary theory. But we have seen that in an important respect, if there are such facts they are all (in part) *about us,* for they reflect our ignorance, and our needs in applying evolutionary theory.

VI Is evolution stochastic? Is the theory of evolution stochastic?

This brings us back to the view of drift as a place holder. If it is a place holder for unknown evolutionary forces, then it will be at most the source of the stochastic element in evolutionary *theory,* as opposed to evolution itself. And if it is a placeholder for non-evolutionary forces, then it cannot be the source of the probabilistic character of evolutionary theory, for it is not part of this theory at all. As between these two alternatives, the second seems to make more sense of the actual claims of biologists about drift. After all, they invariably contrast it with selection. Of course, this behavior of biologists can always be accommodated to the first interpretation,

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but doing so brings with it the accusation of Panglossianism, and certainly increases the insulation of the theory of natural selection from potential disconfirmation. As a price to pay for explaining the statistical character of the theory this seems too high. On the other hand, viewing drift as a place-holder for nonevolutionary forces that obstruct the effects of selection, not only has no such drawbacks, but is consonant with what we find in other areas of science. Thus, no one rejects the inverse square law of gravitational attraction just because feathers fall more slowly and with far more variable acceleration from occasion to occasion than billiard balls do. This reason is that air resistance, wind, humidity, and other variables, which prevent us from making anything more than a probabilistic prediction of the time it takes a feather to drop a certain distance, are no part of the inverse square law of gravitational attraction. *Mutatis mutandis* for drift and evolution.

But if this view is correct, then it appears to be reasonable to conclude that like mechanical phenomena, evolutionary phenomena are after all deterministic, or at least as deterministic as underlying quantum indeterminism will allow. But the theory is probabilistic. More exactly, the theory as we actually employ it is. Drift is a phenomenon on which the theory is not *silent*. To simply treat it as part of what is in effect a *ceteris paribus*, or *imparibus* clause seems as unrepresentative of biological thinking as treating it as a place holder for unknown selective forces.

In effect, the inclusion of drift in the theory of natural selection is on the one hand an admission of ignorance, and on the other an admirable and often successful attempt to improve its powers more accurately to predict and more fully to explain observed biological facts like those of diversity, as opposed to evolution. Instead of assuming a dignified silence in the face of marked changes that seem to reflect no apparent selective forces, the theory points to epistemic probabilities that lead us sometimes to expect such outcomes.

There is of course a deterministic theory of natural selection, in which drift plays no role, but it is either so generic in its claims as to have little predictive content, or so detailed in its enumeration of selective forces – including for example, the presence of poachers on game-preserves – as to be hopelessly unwieldy, and beyond our cognitive powers to discover and express.

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The relation of the generic version of the theory to the actual version we employ is rather like that of the deterministic or phenomenological version of the second law of thermodynamics to the statistical version. Except in two respects: the phenomenological or deterministic second law is false and useful, while the deterministic theory of natural selection is true and useless. The useful theory of natural selection embodies drift, and so is inevitably probabilistic. And it too may differ crucially from the statistical version of the second law of thermodynamics. For the kind of probabilities it involves are epistemic, they are relative to us, or other sentient creatures who formulate probabilistic hypotheses on the basis of evidence. This makes our actual theory of natural selection more of a useful instrument than a set of propositions about the world independent of our beliefs about it. It substantiates a sort of instrumentalism about the theory of natural selection. And this *may* be a very big difference between it and the statistical second law. I say it *may* be, for I am in no position to claim that the probabilities embodied in thermodynamics are epistemic, still less that the statistical second law is just a useful instrument, as opposed to the truth about how the universe is arranged.

So, the claim of *The Structure of Biological Science* that evolutionary theory is statistical in the way that thermodynamics is, turns out to be correct, but an incomplete account of the matter, and perhaps even positively misleading. A more complete and more informative view identifies at least one source of the theory's stochastic character in the notion of 'drift.' But this view reveals that the notion of drift does not fit comfortably into the theory, and when made an integral part of it, turns the theory into a set of claims not only about evolution, but also about our beliefs. As such, the theory of natural selection biologists employ may be very different from other theories, whether deterministic or statistical.

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