RANDOM DRIFT AND THE OMNISCIENT VIEWPOINT

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Alexander Rosenberg (1994) claims that the omniscient viewpoint of the evolutionary process would have no need for the concept of random drift. However, his argument fails to take into account all of the processes which are considered to be instances of random drift. A consideration of these processes shows that random drift is not eliminable even given a position of omniscience. Furthermore, Rosenberg must take these processes into account in order to support his claims that evolution is deterministic and that evolutionary biology is an instrumental science.

1. Introduction. Darwin's theory of natural selection, although lambasted as the "law of higgledy-piggledy" during its own time, is often presented by late 20th century biologists and philosophers as a deterministic theory. This deterministic interpretation of Darwin's views stems in part from Darwin's assertion that by "chance" he meant only to acknowledge "our ignorance of the cause of each particular variation" (Darwin 1964, 131). A second reason Darwin's theory is viewed as deterministic is that it lacks the concept of random drift, commonly held to be the most important source of stochasticity within evolutionary theory. Random drift is a process in which organisms are sampled by chance, irrespective of their physical traits. This contrasts with natural selection, a process whereby organisms are sampled on the basis of their physical traits. However, Alexander Rosenberg claims that the prescence of random drift in evolutionary explanations is an "admission of ignorance" (1994, 82). In applying this Darwinian concept of chance to random drift, Rosenberg thus extends the deterministic interpretation of Darwinian evolutionary theory to encompass current evolutionary theory.

Rosenberg's claim is particularly interesting when viewed in the context of his overall argument for the instrumentalism of biology. If evolution is deterministic, with the stochasticity of random drift only an admission of our ignorance of the actual deterministic processes, then an omniscient being would have no need for the concept of random drift. Thus our (inevitably non-omniscient and stochastic) version of evolutionary theory may be instrumentally useful, but it should not be interpreted realistically.

However, is Rosenberg justified in claiming that an omniscient account of evolution would have no need for the concept of random drift? I argue that he is not—that any evolutionary theory, omniscient or otherwise, must take into account random drift. I begin by examining Rosenberg's arguments for the claim that random drift is eliminable from an omniscient viewpoint, and show that the concept of random drift upon which they rest is an impoverished one. I then provide

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three reasons why random drift is not eliminable from an omniscient account of evolution. Finally, I suggest that not only has Rosenberg yet to prove that evolution is deterministic, but also that he cannot use random drift as evidence for the instrumentalism of biology.

2. Rosenberg's Argument. Rosenberg (1994) constructs a fictional situation in which poachers have removed the longest-necked members from a small giraffe population and transported them to zoos, where they fail to reproduce. For several generations afterward, the short-necked giraffes predominate in the population. Biologists are left with the task of determining why the population shifted towards short-necked giraffes in spite of the fact that the long-necked giraffes are fitter than the short-necked giraffes in this environment. Since the biologists do not know about the poachers, the explanation they would provide is a non-omniscient one. Furthermore, Rosenberg argues, their explanation would invoke random drift, since to do otherwise would be a "disconfirmation of the theory of natural selection" (1994, 71).

However, since we know the reason for the increase in short-necked giraffes, we are in a position to provide an explanation from the omniscient viewpoint. Would we attribute the change in the giraffe population to random drift? Rosenberg's answer is no; rather, "we, who know the facts . . . will say that for a short time the environment changed, making long-necks maladaptive and therefore shifting gene frequencies through selection" (1994, 73). Rosenberg thus reinterprets a case of random drift as a case of selection by switching from a non-omniscient viewpoint to an omniscient one. Random drift is eliminated from the explanation, eliminating the element of stochasticity along with it (assuming, of course, that natural selection is itself non-stochastic). Generalizing from this particular example, Rosenberg concludes that, "from a position of omniscience, there is no need for the notion of drift" (1994, 73). Elaborating, he suggests that "a deterministic theory in which drift plays no role" would either be "so generic in its claims as to have little predictive content" or extremely "detailed in its enumeration of selective forces" (1994, 83).

According to Rosenberg, because we are non-omniscient, finite creatures, the "detailed" theory is "beyond our powers to discover and express" and is "hopelessly unwieldy" (1994, 83). Since the omniscient account is beyond our reach, Rosenberg argues, we do have a need for probabilities and the concept of random drift in our evolutionary theory, but solely for reasons of utility. In other words, Rosenberg claims, biology is an instrumental science.

Rosenberg's claim that random drift is just a way of referring to selective forces of which we (as non-omniscient beings) are unaware may strike some as extreme selectionism. However, it is important to note that this claim places Rosenberg squarely in the tradition of such prominent biologists as Ernst Mayr and Arthur J. Cain. For example, Mayr asserts that only after all attempts to explain biological processes through natural selection have failed, is a biologist "justified in designating the unexplained residue tentatively as a product of chance" (1983, 326). Even more strongly, Cain asserts that the real basis for every random drift hypothesis is that "[t]he investigator finds that he, personally, cannot see any [evidence of selection], and concludes that, therefore, there is none" (1951, 424). The reason some biologists have come to hold these selectionist views is that the accepted explanations for a number of phenomena, such as the frequencies of chromosome shapes on *Drosophila*, changed from random drift to natural selection (Gigerenzer et al. 1989, 156–157). It would seem, however, that while Rosenberg shares the selectionist views of these biologists, he offers additional reasons for adopting them. It is to these reasons, and the conception of random drift that lies beneath them, that we now turn.

3. Rosenberg's Random Drift. Rosenberg provides only two examples of random drift in his account, both of which prove to be problematic. The main problem with each of these purported examples of random drift is that they are arguably cases of natural selection; ironically, they are also too limited in their scope. I will discuss each example in turn, explore its implications for Rosenberg's arguments, and elaborate a fuller conception of random drift.

In the first example, discussed above, the longest-necked giraffes are removed from the general giraffe population by poachers and taken to zoos where they fail to reproduce. Over the next several generations, the short-necked giraffes come to predominate in the small population. In what sense is this a case of random drift? Rosenberg seems to be suggesting that the change in the giraffe population would be *considered* to be random drift by non-omniscient biologists because 1) the long-necked giraffes are normally fitter than the short-necked giraffes in this environment; 2) the fittest organisms, the long-necked giraffes, were not the most reproductively successful; and 3) the biologists do not know the reason why the long-necked giraffes were less successful than the short-necked giraffes. Since the generational change in the population does not *appear* to be due to the fitnesses of the giraffes in their environment, but rather due to chance, Rosenberg can claim that biologists would consider random drift as the explanation.

But in actuality (despite appearances to non-omniscient biologists), the change in the population *is* due to the differential fitnesses of the giraffes. The selective agent in this case is the poachers themselves; they have specifically picked out the longest-necked giraffes in the population for removal. This is clearly a case of artificial selection, but in essence it is no different from natural selection; the organisms were sampled on the basis of their physical traits. Since having (or not having) a short neck determined the giraffes' future reproductive success, the poacher scenario is an instance of selection, not random drift. Rosenberg admits as much when he asserts that "we, who know all the facts" will attribute the change in gene frequencies to selection (1994, 73).

Thus, Rosenberg is examining hypotheses of random drift that biologists would offer as explanations of a clear-cut case of natural selection. This is problematic in itself. The real problem, however, lies in the conclusions that he draws from the poacher example. Rosenberg asserts that the omniscient viewpoint would not need the concept of drift in this example; generalizing, he asserts that random drift is not necessary for the omniscient viewpoint at all. That the omniscient viewpoint would have no need for drift in the poacher case should not be a surprising result, however, since the example was a case of selection to begin with. If you start with a case of non-drift and conclude that, knowing all the facts, you would not have a need for the concept of drift, you haven't proven much—and certainly not enough from which to make a generalization. Rosenberg needs to consider a clear-cut case of random drift, rather than a clear-cut case of natural selection. Then, and only then, can conclusions be made about the necessity of drift from the omniscient viewpoint.

The only other specific example which Rosenberg provides of random drift is also arguably an instance of natural selection. Rosenberg suggests that biologists, in ignorance of the poachers' actions, might hypothesize that some singular conditions intervened to change the proportion of long-necked giraffes within the population. As an example of such a hypothesis, Rosenberg asks us to imagine that "through freakish, never-to-be-repeated wind conditions, the two tallest trees on which the most attractive vegetation for giraffes grow became so twisted that they accidentally trapped the heads of most of the tallest giraffes and broke their necks" (1994, 72–3). This example is arguably a case of natural selection, not random drift, since the giraffes' survival is a result of their neck lengths. For this to be a clear-cut case of random drift, long-necked and short-necked giraffes would have to be killed indiscriminately; having a long neck would not be the basis for the giraffes' failure to survive to reproduce, but an incidental, irrelevant property. There is some basis for the claim that the action of the wind in this example is random drift, since it is a singular event; however, this would not be the explanation given by most biologists. As above, Rosenberg has used an example that is more clearly natural selection than random drift, casting doubt on any conclusions concerning random drift that are drawn from it.

Moreover, even if the wind example is a case of random drift, it represents only one kind of random drift. The kind of random drift represented by the action of wind conditions in Rosenberg's example is probably best described as parent sampling (see Beatty 1984). *Indiscriminate* parent sampling occurs when organisms fail to survive to reproduce for reasons unrelated to their physical traits. Thus, for example, floods could destroy acres of artichoke plants, both large and small. Or a forest fire could indiscriminately annihilate large numbers of a squirrel population. Now in these cases, it may be that one genotype does not fare as well as another genotype; say, for example, that gray squirrels were killed in greater numbers than brown squirrels. However, the gray squirrels did not have a poorer survival rate because of their color; it just so happened, say, that more of them were in the area of the forest that caught fire. If their poorer survival had been due to their color, then we would say that they were selected against. However, since the squirrels were killed indiscriminately with respect to color, we say that the change in the squirrel population was due to the kind of random drift known as indiscriminate parent sampling. The action of wind conditions in Rosenberg's example is parent sampling, but it is *discriminate* parent sampling, because the long-necked giraffes were killed as a result of their long necks, not irrespective of their long necks. Discriminate parent sampling is generally considered to be natural selection; indiscriminate parent sampling is random drift.

However, indiscriminate parent sampling is only one kind of random drift. Beatty (1992) isolates three other kinds of random drift: indiscriminate gamete sampling, fluctuations in the rates of evolutionary processes (selection, migration and mutation), and the founder effect. Another kind of random drift has to do with the assortment of genes into gametes (Dodson and Dodson 1985). Brandon (1990) claims to have identified yet another kind of random drift. This leaves potentially at least six different kinds of random drift. The existence of these other kinds of random drift point to a further deficiency within Rosenberg's account, namely that he has failed to discuss and take into account the different kinds of random drift in his arguments.

For reasons of space, I will consider only gamete sampling and the founder effect. Gamete sampling takes place during the process whereby gametes are united to form zygotes. In any given population, the number of gametes (the "gene pool") is very large relative to the size of the population. On average, the genetic composition of the gene pool will be representative of the parents' generation. However, only a finite number of those gametes will become founders of the next generation; the number of zygotes is always finite. Thus the successful gametes (those that become zygotes) are a sampling of the total number of viable gametes in the gene pool. If each individual has an equal chance of contributing its successful gametes to the next generation, i.e., if the success of gametes is not based on any genetic differences between them, then there is indiscriminate gamete sampling. As a consequence, the successful gametes may form a non-representative sample of the gene pool (the gene frequencies among the former may differ from those among the latter). Indiscriminate gamete sampling, like indiscriminate parent sampling, is a form of random drift.

Mayr's founder effect focuses on the evolutionary effects of particularly unrepresentative samples. The founder effect occurs when a sub-population (the "founders") becomes isolated from the rest of a population and only a small fraction of the variation of the original population is represented amongst the founders. This isolation can occur passively, as when a river might split a population, or actively, by the migration of a group of individuals from the main population. Since the founders were not separated from the original population on the basis of their physical differences, we can say that they were sampled indiscriminately from that population. In this way, the founder effect can be considered to be a kind of random drift.

Indiscriminate parent sampling, indiscriminate gamete sampling, and the founder effect are all instances of random drift. Yet each is a distinct phenomenon. They are different from each other; furthermore, they are different from discriminate sampling, i.e., selection. Below, I will explore these differences, and show how they serve to argue against Rosenberg's claim that from an omniscient viewpoint the concept of random drift is unnecessary.

4. The Non-Eliminability of Random Drift. As we have seen, Rosenberg's account uses an impoverished notion of drift; it is limited to random drift as parent sampling only. Moreover, his conception is a disputable notion of drift, including cases more commonly classified as selection. Thus, in order to justify his claim for the eliminability of the conception of drift from an omniscient viewpoint, Rosenberg would have to show that clear-cut cases of random drift, of different kinds, are eliminable from an omniscient viewpoint. In this section I will argue that such a proof is not forthcoming—that random drift is not eliminable from evolutionary theory, even if one "knows all the facts." I offer three arguments in support of this position: 1) That biologists distinguish between different kinds of random drift suggests that random drift is not merely a cover for processes of which we are ignorant; 2) Instances of random drift cannot be spelled out in terms of selection; and 3) Random drift provides the means to explain non-adaptive change that cannot in principle be explained by natural selection, and is therefore necessary for any evolutionary theory, omniscient or otherwise. I will discuss each of these in turn.

4.1. The Importance of Different Kinds of Random Drift. I mentioned above that biologists differentiate between a number of different kinds of random drift. For example, Cain and Currey (1963, 2) emphasize the importance of distinguishing random fluctuations in selection, mutation, and migration (which Sewall Wright considered to be random drift) from parent and gamete sampling. They also agree with Dobzhansky's (1959) claim that parent and gamete sampling should be distinguished from the founder effect. So not only do biologists consider a number of different processes to be random drift, they think that it is important to retain the distinctions between them. Dobzhansky emphasizes that while the phenomena are "closely related" they are "different enough to make some distinction useful" (1959, 85). In other words, the different kinds of random drift account for different kinds of phenomena; furthermore, as Dobzhansky suggests, one kind may be more prevalent in one population, another kind more prevalent in another population.

Distinguishing between the different kinds of random drift gives biologists the means to explain the differences between the evolutionary processes occurring in different populations.

For example, suppose there exists a population of snails, half of which are pink and half of which are yellow. Let us further assume that yellow snails are twice as fit as pink snails, due to their greater tolerance to heat from the sun. The snails are observed for a generation, and it is discovered that the proportion of yellow snails in the subsequent generation has changed from 1/2 to 2/5. In the absence of random drift we would expect that 2/3 of the snails would be yellow;[1] that only 2/5 of the snails would be yellow is an unlikely result of natural selection alone. A likely hypothesis is thus that random drift caused the change in gene frequencies. However, this in itself does not tell us very much; a deeper explanation would tell us *why* this change came about. For example, further analysis might determine that this particular summer has been very hot and dry, such that the corresponding decrease in the usual supply of shade-providing bushes causes snails of both colors to die in large numbers. Another possibility is that the original population has been split, leaving an unrepresentative sample. Either of these cases might produce the above result. However, in the first case, the change in gene frequencies would be due to indiscriminate parent sampling; in the second case, it would be due to the founder effect. Thus, distinguishing between the different kinds of random drift provides the tools to isolate and further specify the different kinds of processes which may be occurring in a population.

Yet the practice of distinguishing between different kinds of drift is puzzling on Rosenberg's account. According to Rosenberg, all drift explanations can, in principle, be put in terms of selection explanations; the problem is that non-omniscient biologists are unaware of the real selective events, and so must postulate random drift. Random drift on Rosenberg's account thus acts as a cover for our ignorance. However, biological practice belies this claim. Rather than being a cover for our ignorance, random drift is a general term for a number of distinct biological processes, such as indiscriminate parent and gamete sampling and the founder effect. In practice, it may be difficult to determine which process has predominated. But that is not to imply that such a task is impossible, nor does it imply that biologists cite random drift when they are unaware of the real evolutionary processes. On the contrary, biologists seek to determine which of the kinds of random drift has occurred in order to support and further expand upon their claims that random drift has been prevalent in a population. Since random drift is used to refer to a number of distinct biological processes, rather than being a cover for our ignorance, drift will not be eliminable from an omniscient account of the evolutionary process as Rosenberg claims. Even (or perhaps, especially) an omniscient being would need to take into account the different processes leading to evolutionary change which the term 'random drift' represents.

4.2. Random Drift Is Not Selection. Rosenberg's claim is that from the omniscient viewpoint, one could give an account of the evolutionary process that was so detailed in its enumeration of selective forces that one would have no need for the concept of drift. Rosenberg illustrates this claim through the use of the poacher scenario; he suggests that we who "know all the facts" would say that the changes in the giraffe population were due to selection, rather than random drift. Yet we saw that the poacher example was not a case of random drift, but of natural

[1]Expected frequency of yellow snails in the next generation = (frequency of yellow snails) (relative viability of yellow snails)/average fitness of snail population = $(.5)(1)/[(.5)(1)+(.5)(.5)]$

selection. If we examine a case of random drift, however, we will find that it cannot be replaced by an enumeration of selective processes.

Consider, for example, the process of indiscriminate gamete sampling. If all the viable gametes have an equal chance of success—if, in other words, they are equal in fitness—there may still be a change in gene frequencies. The frequencies of gametes may by chance fail to reflect the frequencies in the parent generation. This is random drift. However, without fitness differences, selection cannot occur; there is nothing upon which to select. It is therefore not possible to interpret indiscriminate gamete sampling in terms of selection. Indiscriminate gamete sampling is a phenomenon in its own right, distinct from selection. It is not eliminable from evolutionary explanations because even if we were omniscient, we would still see it as random drift. Although I will not argue the point here, I maintain that the other kinds of random drift likewise cannot be accounted for in terms of selective processes. Thus the omniscient viewpoint needs the concept of random drift; it cannot be supplanted by natural selection.

4.3. The Indispensable Explanatory Role of Random Drift. As we have seen, natural selection and random drift are distinct processes. This implies that there are phenomena that random drift can explain, but natural selection cannot. In this section, I will show how such an explanation would proceed, and suggest that even an omniscient being would need the concept of random drift to provide such explanations.

Let us again consider a case of indiscriminate gamete sampling. Suppose we have a small population of giraffes, 50% long-necked and 50% short-necked, and let us further suppose that length of neck confers no survival or reproductive advantage to the giraffes (perhaps there is an abundance of both tall and short trees for the giraffes to feed upon). Since it is a small population, the frequencies of the successful gametes (those that become zygotes) may not reflect the frequencies of the parent generation, since gametes are successful ("sampled") irrespective of their neck length potential. Thus the next generation of giraffes could, for example, consist of 40% short-necked and 60% long-necked giraffes. Now in the third generation, these frequencies may stay the same, or they may change in either direction. Moreover, it is possible that the proportion of long-necked giraffes to short-necked giraffes will increase in the third generation, and continue to increase over the course of subsequent generations, until the population consists entirely of long-necked giraffes. To a biologist observing the changes in gene frequency, the shift to a long-necked population would be puzzling if he or she only considered selection as a possible explanation, since there is no adaptive advantage conferred on the giraffes by virtue of having a longer neck. However, indiscriminate gamete sampling can provide an explanation for this nonadaptive change; nonadaptive change is a likely consequence of indiscriminate gamete sampling, especially in small populations where conspecifics have little selective advantage over one another.

This is just one example of how random drift can provide an explanation of a phenomenon, nonadaptive diversity, that selection cannot; explanations provided by other kinds of random drift or in different situations might proceed differently. (Note that I am not making an empirical claim about the prevalence of random drift or nonadaptive diversity; rather, my argument is an "in principle" one). Yet if random drift can explain what selection cannot, then our omniscient being will not be able to explain all instances of evolutionary change without the concept of random drift. In other words, the being's arsenal of explanatory tools would be incomplete. More specifically, the being will not be able to explain certain instances of nonadaptive change via natural selection. Thus the concept of drift is a necessary part of evolutionary theory, even from an omniscient viewpoint; it provides explanations where selection cannot.

In response to this argument, Rosenberg might argue that an omniscient being would know all the details of a gamete sampling event. Thus, even if the being could not explain a particular phenomenon in terms of selection, it could explain it by an elaboration of the processes which constitute the indiscriminate sampling event. This would suggest that random drift is eliminable from the omniscient viewpoint. Yet if random drift is eliminable in this sense, then so is natural selection. An omniscient being can just as easily discuss the processes which make up natural selection, through an elaboration of the fates of individual organisms. However, to do so would be to miss the population level explanations that the concepts of random drift and natural selection provide—and evolution concerns the fates of populations, not of individuals. More to the point, the option to eliminate selection from the omniscient account is not one that is open to Rosenberg, given the pivotal role that selection plays in his arguments for the instrumentalism of biology (1994, 15–16). Rather, he should acknowledge that random drift plays as essential a role in evolutionary theory as selection does.

5. Conclusion. Rosenberg offers us an intriguing and provocative account of evolutionary theory, one where the concept of random drift is necessary only because of our limited capacities as human beings. However, his arguments utilize an impoverished concept of random drift, one that is imprecise and not sufficiently elaborated. An examination of the different kinds of random drift shows that random drift is not eliminable from an omniscient perspective. Random drift is a term which covers a number of distinct biological processes, processes which biologists refer to in their explanations. Furthermore, random drift is a real phenomenon in its own right, distinct from natural selection; random drift cannot be replaced with an elaboration of selective processes. As a consequence, random drift can explain certain kinds of evolutionary change that selection cannot. Each of these considerations supports the claim that even an omniscient being would need the concept of random drift, as I have argued.

If random drift is an essential part of any theory of evolution, then some of Rosenberg's larger claims are cast into doubt. For one, in order for Rosenberg to support his claim that evolution is deterministic, he must demonstrate that random drift—in all its forms—is a deterministic process. Moreover, if random drift is a genuine process, and not merely a cover for our ignorance, it is a concept which reflects facts about the world; it is not about our limited capacities as human beings. If this is the case, then random drift cannot be used as evidence for the instrumentalism of biology. Evolutionary biology, at least in the limited cases that we have been discussing, is a realistic theory.

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