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SELECTION, DRIFT, AND THE AIMS OF EVOLUTIONARY THEORY

1. INTRODUCTION

According to textbook presentations of evolutionary theory, evolutionary change is a result of the interaction of a number of biological processes that together shift a population away from Hardy-Weinberg equilibrium. Among the factors typically mentioned are genetic mutation, gene flow (emigration and immigration), nonrandom mating, selection, and drift ("chance").[1] By constructing equations which factor in specific values for each of these processes, evolutionary biologists try to explain why a population follows a particular evolutionary trajectory. Hence, much of evolutionary biology is concerned with the empirical determination of values for each process, and the ways in which the various processes can and do interact with one another to produce evolutionary change.

A common presupposition of this approach is that each of the evolutionary factors just identified represents a distinct biological process (or force), clearly delineated from the rest. For example, selection is understood as a quasi-deterministic sampling process operating on the basis of heritable variation in fitness among individuals at some level of the biological hierarchy. Drift, on the other hand, is understood as the consequence of random changes in gene frequencies, usually over several generations, due to "sampling error". As such it is an inherently stochastic process. "Selection" and "drift" are concepts designed to capture two distinct but interacting biological processes.

My aim in this paper is to critically examine this standard account, focussing on the processes of selection and drift. Are selection and drift really distinct processes in nature? What purpose(s) (if any)

P. Griffiths (ed.), Trees of Life, 133–161.

does the selection/drift distinction serve in evolutionary biology? My plan is to explore these questions by isolating the critical issues involved. My specific aim is to understand the precise relationship between selection and drift both in evolution and in evolutionary theory, in the hope that doing so will shed light on the nature of this theory, including its internal structure and how it relates to the living world it is designed to render comprehensible. I will argue that although selection and drift are not as distinct as a superficial reading of the textbook account would suggest, neither are they biologically identical. Rather, "selection" and "drift" are idealised concepts which represent endpoints on a continuum of biological sampling processes. Yet, despite the lack of any clear-cut distinction between selection and drift in nature, there is good reason to distinguish them in evolutionary theory because doing so serves certain explanatory and predictive purposes. I then draw some implications of this conclusion for understanding the nature and aims (and limitations) of contemporary evolutionary biology.[2]

2. THE CONVENTIONAL DISTINCTION

As John Beatty points out, both selection and drift can be understood as sampling processes.[3] Both processes involve the differential survival and/or reproduction of biological entities. What distinguishes these processes is whether the sampling process is "discriminating" or not. Sampling is "discriminating" when the survival and/or relative offspring contributions to the next generation are affected by physical differences among individuals. To take the classic example, consider light and dark moths living in a forest which, because of nearby industrial pollution, is becoming increasingly soot-covered. In the presence of avian predators which hunt by visual recognition of prey, the dark moths will have a survival advantage in this environment. The avian predators will "sample" the moth population, discriminating among moths on the basis of a physical difference between them. Over time, the proportions of dark to light moths will shift toward the dark morph. This is of course a classic example of natural selection producing evolutionary change.[4]

Sampling is "indiscriminate" when physical differences between individuals affect neither their own survival nor their relative offspring contributions to the next generation. Beatty gives the example of a forest fire which sweeps through an area killing some organisms and sparing others without regard to physical differences between them. He writes that, "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., colour) between the entities in question are irrelevant to whether or not they are sampled."[5] Repeated occurrence of such indiscriminate sampling in a finite population can result in the random drifting of properties (or gene frequencies) over several generations. Hence the name "random genetic drift".

The point of departure for my critical examination of the standard "textbook" account (as clarified by Beatty) is a modification of an example originally due to Michael Scriven but alluded to and elaborated on by many subsequent writers.[6] Suppose that two "identical" (i.e., monozygotic) twins are hiking along a mountain ridge when suddenly an electrical storm arises. ZAP! — One of the twins is struck dead by a bolt of lightning. The other twin, slightly singed, dazed but still alive, goes on to live a long and fruitful life, eventually fathering some dozen children, all of whom are equally prolific. What are we to say about this case? Is it an example of selection or of drift ("chance")? How can we decide which it is?

Most of the biologists I have posed this question to have concluded, after a moment's reflection, that it was a purely chance occurrence, and hence not selection.[7] This interpretation could be supported by the following considerations. There were, *ex hypothesi,* no genetic differences between the twins — they were genetically identical. Genetic identity does not guarantee phenotypic identity, of course, but we can assume for the sake of the example that neither twin has a developmentally or environmentally induced characteristic that would make it more or less vulnerable to a lightning strike. For example, neither twin was given pituitary growth hormone as a child, so that it grew twice as tall as its sibling, thus making it into a kind of natural lightning rod. In the absence of such phenotypic differences between the twins, the only recourse is to attribute the fateful occurrence to drift (chance).

My strategy in the next section will be, first, to defuse the most common argument that asserts that this cannot be a selection event by challenging the presupposition it rests upon, and then, second, to give a positive argument for the claim that the twin case is a selection event. This strategy will serve to bring to the surface the issues at stake in distinguishing selection and drift.[8] What is at stake here is not simply the best interpretation of a purely hypothetical abstract example. How one interprets the twin case bears on the validity of the selection/drift distinction in general. The case of the twins merely allows us to focus our attention on the relevant issues. Insights gained from this example can then be applied elsewhere in understanding evolutionary biology.

3. SELECTION OR DRIFT?

One might argue that the case of the travelling twins cannot be a selection event, by reasoning as follows. Both selection and drift are sampling processes. What differentiates these two processes is that the former discriminates on the basis of *fitness* differences among biological entities, whereas the latter does not. Selection is a form of discriminate sampling on the basis of fitness differences among biological entities, whereas drift is a form of indiscriminate sampling (i.e., not on the basis of fitness differences) among biological entities. So, according to Beatty[9], "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 differences between the organisms sampled." This argument rests on several important claims, all of which need to be critically examined, *viz.*: (1) fitness differences are essential for selection, (2) the twins do not differ in fitness, and (3) there are no physical differences characterizing the twins with respect to which the sampling could or did discriminate between them.

Let us begin with the second claim. That there are no fitness differences in the twin case can be shown in two ways, providing the basis for two arguments that this was not an example of selection, but rather one of drift: (1) *Supervenience Argument:* Fitness is a *supervenient* property.[10] Hence, if the underlying properties of two biological entities are identical, they also have identical fitnesses. In the case of the twins, their underlying properties were identical. Hence they did not differ in fitness. Selection requires fitness differences. Hence it was *not* an example of selection. It was either selection or drift. Therefore, it was drift. (2) *Propensity Argument:* Fitness is a *propensity* (or disposition) to survive and produce viable offspring.[11] *Subargument #1:* Identity of underlying properties entails identical propensities. In the case of the twins, their underlying properties were identical. Hence, their propensities for survival and reproduction were identical. Hence, they did not differ in fitness. Selection requires fitness differences. Hence it was not an example of selection. Therefore, it was a case of drift. *Subargument #2:* Propensities are *ascribed* to entities in virtue of observed correlations between the possession of certain properties and certain effects (e.g., "fragility" and breaking easily when subjected to a sudden force). In the case of the twins there was no basis for ascribing different propensities for survival and/or reproduction to the twins because there were no properties of the twins that would allow us to determine *before the event* which one would be more likely to die from a lightning strike. One could argue that because the case of the twins is an utterly unique event, there is no basis for ascribing different propensities to them. Hence, there was no basis for ascribing fitness differences to them. Selection requires fitness differences. Hence it was not an example of selection. Therefore, it was a case of drift.

My response to these arguments has several parts. First, I agree that there are no fitness differences between the twins. Fitness is best construed as a supervenient propensity for survival and/or reproduction. The twins did not differ in fitness because there was no basis, before the lightning strike, for predicting their different fates in the context of an electrical storm.[12] Claim (2) above is correct.

My (first) disagreement concerns the claim that fitness differences are necessary for (and not just conducive to) selection events. I want to claim that contrary to many presentations of evolutionary theory, fitness differences are *not* necessary for selection (and hence cannot be used to distinguish selection and drift). My claim builds upon, and I think follows from, the very fact that fitness is a supervenient propensity for survival and/or reproduction.

As a *supervenient* property of an organism, fitness is grounded in an indefinite number of underlying properties that affect that organism's ability to survive and/or reproduce, properties such as disease resistance, visual acuity, protective colouration, fleetness, position in a dominance hierarchy, etc. In any given interaction with the environment, only a small subset of the properties determining an organism's fitness *actually* contribute to an organism's survival and/or reproduction. Most play no role whatsoever. When being pursued by a predator, an organism's coordination, reflexes, and speed become relevant factors, but the average litter size it is prone to produce may not. "Fitness" is a gauge of how biologically successful an organism is *likely* to be given its particular suite of characteristics and the environments it is likely to encounter. As such, it does not directly determine an organism's fate. What *directly* determines an organism's fate is the set of *actual* environmental challenges it encounters and its particular resources for dealing with these challenges.[13]

A consequence of the claim that fitness is a supervenient property of an organism is that organisms having identical fitnesses may nonetheless exhibit quite different underlying properties — differences which may determine differences in biological success. Fitness, as such, is not a property of an organism which directly interacts with the environment. As Sober (1984) has cogently argued, fitness is causally inert.[14] Yet selection is a causal process, one involving interaction between some aspect of an organism's phenotype and some "critical factor" in the environment.[15] It follows that selection can occur in the absence of fitness differences. Not only do fitness differences not guarantee selection, but fitness differences are not even necessary for selection.[16]

As a *propensity*, fitness describes an entity's typical behaviour when placed in specified circumstances. Propensities can be ascribed to entities in either (or both) of two ways. One can place a given entity in the desired circumstances a number of times, observing what effect this has, or one can note what properties an entity exemplifies, and observe how similar entities behave when placed in *similar* circumstances. The first method is more direct, but only works with entities which survive the treatment intact. The second method is more indirect, and only works when one can be sure that both the entities and circumstances considered *are* sufficiently similar to warrant an inference from one to the other. In either case, propensities are ascribed to entities in virtue of observed correlations between certain properties and specific effects.

A consequence of interpreting fitness as a propensity, and claiming that fitness differences are necessary for selection, is that no *unique* sampling event can be identified as a selection event. On this view, to identify a selection event requires identifying fitness and hence propensity differences. But propensities can only be ascribed in either of the two methods just outlined. In a unique sampling event, neither method is available. If the entities in question have never been placed in the specified circumstances before, and if the uniqueness of the situation precludes analogy with other "similar" cases, then there is no basis for ascribing differences in propensity, and hence in fitness, to the entities. But if selection requires fitness differences, then there are no unique selection events. On this view (which I think is mistaken), all selection phenomena are by definition repeatable. Singular selection events are a contradiction, and hence impossible.

Hidden in the propensity argument is the assumption that the correct description/interpretation of a sampling event is determined by locating the event in a larger pattern of "similar" events in which it is thought to be an instance. By definition, a selection event is part of a regular pattern, and one instance cannot constitute a pattern. Hence, a series of selection events is composed of individual events, no one of which is, taken individually, a selection event. It would commit us to saying that any given sampling event in nature cannot be, and hence cannot be identified as, a selection event *until* it can be seen in the context of many other "similar" sampling events.

If natural processes are to be understood as objectively real occurrences, and selection is a natural process, then selection events occur in nature quite independently of their description by biologists. Although their identification is made considerably *easier* when placed in the context of similar events of which they can be seen to be an instance, this does not entail that selection events do not occur *except* as parts of identifiable patterns. If a sampling event is unique in its characteristics, it may nonetheless be a selection event, despite the fact that it does not occur as part of an identifiable *pattern*, and hence does not occur because of an identifiable *propensity*, and hence does not occur because of identifiable fitness differences. Again, fitness differences are not necessary for selection events.

Finally, recall that there were three central claims in Beatty's argument that the twin case is an example of drift rather than selection, *viz.*, that: (1) fitness differences are essential for selection, (2) the twins do not differ in fitness, and (3) there are no physical differences characterizing the twins with respect to which the lightning could or did discriminate between them. I accepted the claim that the twins do not differ in fitness, but have been arguing that the claim that fitness differences are essential for selection is mistaken. I turn now to the third claim. Are there any physical differences characterizing the twins with respect to which the lightning could or did discriminate between them?

Discussing the twin example, Mills and Beatty (1979) write that, "Surely in this case there is no difference between the two organisms which accounts for their difference in reproductive success."[17] Hence they conclude that this was not a selection event. I want to claim that, on the contrary, there *is* a physical difference between the twins that accounts for their differential biological success. Contrary to initial appearances, there is *one* respect in which the twins differ from one another — location on the mountain. It was the fact that they occupied different spatial coordinates when the lightning struck that was the crucial factor that resulted in their differential survival. The twins differed in *locational properties*, resulting in differential survival, and hence in selection.

It might be objected that being at a particular place at a particular time is not a property of an organism. Surely "locational properties" are pure fiction. But consider that location, like size, is a *spatial* property of an entity. Size is a function of volume and configuration, while location is a function of relationships to other entities in some coordinate system. Spatial properties such as size are recognised as important factors in evolution.[18] Likewise, biological success is *almost* always a function of where an individual is relative to other entities in its environment. Where an organism finds itself can be decisive for its moment to moment prospects for survival. To take but one example, a common explanation for schooling in fish is that predators generally take a disproportionate number of individuals from the periphery of the school. This results in a selective pressure to move toward the interior of the group, hence the tightness of the group and apparently coordinated group maneuvers. Such examples are not unusual. In an otherwise genetically and phenotypically homogeneous population, locational properties can be the decisive factor determining an individual's survival. Selection can operate on locational properties as easily as on any other kind.

It might be objected that locational properties, as I have described them, cannot play the role that I assign to them in selection events, because they do not constitute an *unchanging* part of an organism's phenotype. That is, one might argue that to ground a selection event, the properties in question must be stable, standing properties of an organism which persist from one environment to another. So, in the example of the travelling twins, had it been the case that one of the twins (the one that got zapped) had a stable *disposition* to walk along a more exposed (and hence more vulnerable) path during the electrical storm, then we could ascribe the differential survival to selection. In the example as described, however, there is no such disposition. That one twin got zapped while the other escaped unharmed seems more a matter of luck or coincidence than of selection. Hence it is not a case of selection.

To see what is mistaken in this argument, consider the following hypothetical experimental set-up. Imagine an artificial selection regime consisting of two containers of insects and a disk which spins freely. I put the containers on opposite sides of the disk which is then spun around. I stop the disk, remove the container from the left hand side, and kill all of its inhabitants. I then breed the insects in the remaining jar, form a new group that is then placed in the empty jar, spin the disk again, and again kill all the insects who end up in the left hand container. This procedure is repeated fifty times. Question: Is this selection? On what grounds could it be denied that it is?

In the artificial "selection" experiment above, organisms (or groups) were indeed selected on the basis of a locational property —

being on my left. The fact that a member of *Homo sapiens* was the selective agent is irrelevant to the analysis of the process. Those insects just happened to find themselves in an unusual environment. Plants on the edge of a volcano, or fruit flies in a geneticist's lab, also find themselves in unusual environments. It is true that in the case described one would not be able to *predict*, in advance, which organisms would survive and which would not. But this has more to do with our ability to look ahead than it does with the nature of biological events. One might argue that the property of being on my left is not a real property, because it is constantly subject to changing environmental factors. Besides begging the question, this objection overlooks the fact that any property, including all dispositional/intrinsic properties, can only be such in relation to environmental/external conditions. Being light-coloured is impossible without the presence of light.

I conclude that the organisms on the rotating disk do differ with respect to a property (the property of being on my left at time *t*), but they do not differ with respect to any "inhering property," such as colour, weight, visual acuity, etc. They don't differ with regard to *fitness*. What follows from this observation is simply that prediction is much more difficult in such cases, not that selection does not occur. Returning now to our hypothetical twins, we can say that they differed in what proved to be a very important property — location on the mountain. Because of this property difference, one was killed and the other survived. The fact that the property in question is not an enduring, stable characteristic of the organism is quite true but irrelevant. Hence this is, contrary to the common view, a selection event.[19]

Even if it is granted that locational properties are real and possibly important in some contexts, one could still argue that neither the case of the twins nor that of the insects on the rotating disk were examples of selection, because in neither case were the locational properties in question *heritable*. The surviving twin will not pass on to his offspring the property of being at location *x* on the mountain, nor the even more useful property of being in a safe location during an electrical storm. Likewise, the insects ending up in the right-hand container do not pass on to their offspring the property of ending up in the right-hand container — after all, *some* of the offspring of the "lucky" insects will, because of the experimental set-up, be placed in a container that ends up on the left-hand side during their "turn at the wheel"! Evolution by natural selection requires that the properties being selected be heritable. Hence neither the twin case nor that of the insects on the rotating disk is a selection event.

This argument rests on the mistaken assumption that selection only operates on heritable properties. It fails because it confuses the requirements for *evolution* with those for *selection*. Whereas evolution by natural selection does require heritable characteristics, selection (more precisely, phenotypic selection) does not. The issue of heritability is irrelevant to identifying a sampling event as a case of selection.[20]

Shifting attention from the nature of the properties that are operative in selection to the nature of selection itself, one could argue that the twin example is not a case of selection, as follows. Selection is an interaction between the properties of biological entities and the environment. To say that *location* is a property of an organism is to erase the organism-environment distinction, because it makes the environment *part* of the organism. But if there is no organism-environment distinction, then there is no room left for *interaction* between the biological entities and the environment. At most one could have interaction between some properties of an entity and some *other* properties of that entity. Hence, so long as selection is understood as an organism-environment interaction, the twin case is not an example of a selection event.[21]

This argument misunderstands the claim that location is a biologically significant property of an organism. Being at location *x* at time *t* is a property of an organism. Because of this property an organism may be affected by some factor in its environment — e.g., a predator or other natural agent. But to say that location is a biologically significant property of an organism is not to claim that *all* aspects of an organism's environment are part of its phenotype, nor that every environmentally-based property of an organism is biologically or selectively significant. The lightning which interacted with the phenotypes of the twins was a part of the twins' environment, not a part of their phenotypes. It was in virtue of this separateness that an interaction between it and the twins' phenotypes was possible. Some environmentally determined properties of the twins with respect to which they differed (e.g., in the shade or in the light, facing northeast or southwest, etc.) were not, in this case at least, biologically (i.e., selectively) significant. Just as components of fitness must be distinguished in order to understand why a particular selection event occurred, so too must *components* of an organism's phenotype (e.g., its location) and its environment (e.g., a lightning bolt) be distinguished. Hence the interaction objection fails.

A related objection would argue that it is true that there must be *some* difference between the twins that accounts for their differential survival, but hold that it is not a difference in their *properties*. The twins do not differ in so-called "locational properties," or in any other properties for that matter. Rather, their differential survival is to be explained by recognizing that they simply occupy different *environments*. Twin *A*'s properties in environment *X* resulted in his survival, whereas twin *B*'s (identical) properties in environment *Y* resulted in his demise. This is no different from saying that a fast gazelle in one environment (say one lacking cheetahs) survives even though an equally fast gazelle in another environment (one populated by cheetahs) is predated. After all, it is obvious that whether or not a property of a biological entity makes any selective difference depends on the environment in which it occurs. In the case of the twins, they simply inhabit different environments, and properties that were an asset in one environment were a liability in another. In general, for two biological entities to participate in the same selection process they must be subject to a common environment. If it is claimed that the twins have different "locational properties," then this should be reinterpreted to mean that they occupy different environments. But if so, then they cannot be participants in the same selection process. Hence the case of the twins is not an example of selection.

There are two responses to this argument. First, to say that the twins differ in locational properties does not entail that they occupy different environments. If the relevant environment is (arbitrarily) *defined* as the mountain upon which they are hiking, then they occupy the same environment, and the difference in their fates must be explained on some other basis, e.g., on the basis of property differences between them.[22] Secondly, this objection, if correct, would prove too much. No two organisms inhabit identical (micro-) environments. Any two organisms will inhabit environments in which many, but not all, parameters are for all practical purposes the same. If it is argued that for selection to occur organisms must inhabit the identical environment, then selection never occurs. This objection either demonstrates too little or proves too much. Either way, it fails to establish its claim that the twin case is not an example of selection.

Finally, one could object that if the twin case is really an example of selection and not drift, then evolutionary theory falls prey to the charge of "panselectionism". If the twin case is really an example of selection, then it looks like all differential survival and/or reproduction are cases of selection. We can know, *a priori*, that a case of differential survival and/or reproduction is a case of selection without even examining the details. The result is that evolutionary theory is emptied of all of its empirical content. It becomes a trivial game of words, a pseudo-science on a par with astrology, palmistry, and alchemy.

I hope that is it obvious how silly this objection is. Nowhere am I claiming (or even presupposing) that (i) selection is all there is to evolutionary theory, nor (ii) that all evolutionary change is due to selection, nor (iii) that selection is even the most important factor in evolution. First, as stated at the outset of this paper, evolutionary theory attempts to factor together a number of distinct biological processes to account for evolutionary change. Among these factors are genetic mutation, gene flow, nonrandom mating, selection, and drift. My concern here is with selection and drift. I have said nothing about the distinctness, identity, or importance of the other factors.

Secondly, what I *am* claiming is that selection and drift, while conventionally distinguished as two distinct but interacting evolutionary processes, cannot in fact be distinguished so cleanly. Nowhere in this claim is it presupposed that selection is the only or even the most important evolutionary process, much less that selection is all there is to evolutionary theory. Clearly it is not.

Beatty is right to distinguish selection from drift by saying the former is discriminate sampling whereas the latter is indiscriminate sampling. But what is being sampled are *properties*. A sampling process may be undiscriminating with regard to some properties, but discriminating with regard to others. In the case of the twins, there is selection with regard to a spatial property with respect to which they differ (location relative to the lightning bolt), but not with regard to many others with regard to which they also differ (location with regard to Greenland, Margaret Thatcher, and the Hollywood Bowl). My claim is that in any case of differential survival and/or reproduction, there will be some property difference with respect to which selection is operative. Thus all supposed cases of drift can be reinterpreted as cases of selection. But it does not follow from this that we can know ahead of time which property was operative in any given sampling event. There is still plenty of room on the view advanced here for the empirical investigation of selection events to determine (i) *which* properties were actually operative, (ii) *how* they contributed to differential biological success, and (iii) what *effect* this event might have on questions of interest to evolutionary biologists. Knowing that all sampling events are selection events, far from putting evolutionary biologists out of work, instead makes it clear how much work there is still to do in explaining biological phenomena.

4. IMPLICATIONS

It is time now to summarise the argument thus far, and to indicate some of its implications. Conventional textbook presentations of evolutionary theory represent selection and drift as two distinct but interacting evolutionary forces (or processes). They are to be distinguished in terms of whether or not the sampling is caused by fitness differences. I argued that this method cannot be used to distinguish selection and drift, because *neither* process is caused by fitness differences. The twin case was introduced as a paradigmatic example of drift. Although commonly interpreted as a purely "chance" event, I argued that it is better interpreted as a case of selection. But if so, then the selection/drift distinction is called into question. Perhaps selection and drift are not biologically distinct processes.[23] Perhaps they are just two different descriptions for the *same* process. Just as "Morning Star" and "Evening Star" *appear* to describe two different entities, but are in fact identical (both are Venus), so too with selection and drift. If the case of the twins (which appears to be an example of drift if anything is) is in reality an example of selection, then it seems that the selection/drift distinction that underlies most textbook presentations of evolutionary theory does not capture a real distinction in nature.[24] The question is, are selection and drift merely identical processes with different names?

I think that an unqualified affirmative answer to this question would be near to the truth, but misleading. It may be true that selection events and drift events are indistinguishable when viewed as isolated, individual events, but it may also be true that they can be distinguished with the benefit of hindsight. We are often interested in the evolution of *adaptations*. Certain kinds of natural events lead to adaptations, whereas others do not. For the evolution of adaptations, repeated sampling is necessary *in the same direction*. That is, there has to be a consistent correlation between possessing certain properties and survival/reproduction. The property in question also has to be heritable. A property which sometimes aids survival and sometimes not, or is not heritable, will not evolve into an adaptation.[25] We call those events which do lead to adaptations "selection" events, and those which do not we ascribe to "chance" or "drift". (This is even true in Sewall Wright's shifting balance theory, for which drift without selection does not produce adaptations.) To be more precise, selection events are those sampling events that are judged to have a fairly high potential for producing adaptations, whereas drift events are those sampling events that are judged to have a fairly low potential for producing adaptations. The difference is one not of kind, but of *degree*. Every kind of sampling event is "unique" the first time it occurs. But if repeated for a sufficient number of times over enough generations, it *becomes* an example of selection which may result in the evolution of adaptations, or, alternatively, it leads nowhere, adaptively speaking, and hence is described as drift.[26]

This approach suggests an alternative to the two theses considered so far. According to what we can call (for lack of a better label) the *Distinctness Thesis*, selection and drift (along with assortative mating, mutation, and gene flow) are biologically distinct processes. Any given biological sampling event is either selection or drift, but not both. Selection and drift are distinguished in terms of whether sampling involves differences in fitness among the biological entities being sampled:

[Drift] <————interaction————> [Selection]
(No Fitness Differences) (Fitness Differences)

This thesis was criticised via the twin example. Selection and drift are not entirely distinct, at least when viewed as individual events. Neither process requires fitness differences. The distinctness thesis is too simple.

At the other extreme is what we could call the *Identity Thesis*. On this view, selection and drift are biologically identical. All biological sampling is selection:

[Drift = Selection]
(Both are sampling on the basis of property differences.)

This thesis was defended above, but then qualified. All sampling events, including those described as drift, can be interpreted as selection events when looked at in some detail. However, some sampling events tend toward adaptive traits (selection events), while others (drift events) do not. But if so, then there is a sense in which the processes are distinct, at least with the benefit of hindsight. The Identity Thesis is also too simple.

In contrast with the two theses just rejected which treat selection and drift as either entirely distinct or entirely identical, I want to propose one which attempts to tread a middle ground. According to what I will call the *Continuum Thesis*, selection and drift are biologically identical at the level of individual (isolated) events (the point of the twin example), but distinguishable at the level of series of such events (the relevance of adaptedness), and (in their pure forms) lie on the ends of a continuum of sampling processes having different selection coefficients:

[Drift .... Selection]
(Low Selection Coefficient) (High Selection Coefficient)
(Random *re:* adaptedness) (Tending toward adaptedness)

On this view, selection and drift are distinguished only with hindsight, in terms of the kinds of effects produced. The selection/drift distinction is ultimately a *pragmatic* one, based upon what we find interesting and important and worth accounting for (i.e., adaptedness). Were visiting extraterrestrial biologists to survey the same natural events, but be profoundly uninterested in adaptiveness, they would be disinclined to distinguish selection and drift. That selection and drift *are* thought worth distinguishing by biologists suggests implications for understanding the aims of evolutionary theory.

If, as I am suggesting, selection and drift are not clearly distinguishable in nature, why then are they treated as distinct processes (or forces) in evolutionary theory? What is gained by affirming in theory what is nonexistent in nature? The answer has to do with the very nature of the scientific enterprise. Scientists, as a rule, are interested in general truths about nature (e.g., natural laws), rather than in the explanation of particular, often unrepeatable, events. The distinction between explaining the general and explaining the particular is often the basis for distinguishing science from history, and biology from natural history. It is also the basis for distinguishing selection and drift in evolutionary theory.

Notice how selection and drift are usually distinguished — on the basis of whether the sampling is caused by fitness differences (selection) or not (drift). Recall that fitness interpreted as a propensity describes the characteristic behaviour of an entity or of the properties it exemplifies. "Selection" is a term used to describe sampling processes on the basis of properties which are exemplified in a number of different biological entities, which ground processes exhibiting a repeatable pattern, the causes of which are deemed worth investigating. "Drift" (or chance) is a term used to describe sampling processes on the basis of properties that are not widely exemplified, which ground unique events, the particular causes of which are at present unknown, and are deemed too particularistic (i.e., apparently lacking in general significance) to merit serious scientific investigation.[27]

"Drift" ("chance") in evolutionary biology is a term which expresses our inability to encompass in theory the complexity of causal interactions that occur in nature. When certain properties had by a number of biological entities seem to be consistently connected with differential biological success, we say that there is selection for such properties. When there is differential biological success among biological entities which is not obviously connected with certain common properties, then we ascribe this phenomenon to "drift" ("chance"). This is especially true when dealing with small numbers of biological entities, in which case there is less room for generalizing about the causal importance of common properties (because there are less entities which instantiate such properties).

The limit is reached when there are just two biological entities. Hence the difficulty of the twin case. Here, there are no general trends discernible that would allow us to easily identify selectively relevant properties and forces. This accounts for the tendency to identify this as a drift event. But strictly speaking all selection events are similarly individualistic in nature. The results of such individual selection events are "summed up" to give us a theoretically useful (i.e., explanatory, predictive) account of the kinds of forces at work in a population. "Selection" events are just sampling events grounded in commonly exemplified properties. "Drift" events are just sampling events grounded in properties lacking generally significant evolutionary effects. Selection and drift are two different descriptions for property discriminating sampling processes. In evolutionary theory, "selection" (like "fitness") is a term used to capture generalities, to isolate the features different sampling processes have in common — thereby providing the foundation for explaining general phenomena.

The thesis I am defending — that selection and drift are not entirely distinct in *nature*, yet are clearly distinguished in evolutionary *theory* — has implications for understanding the methods and aims of evolutionary biology, and its relationship to the nature it seeks to comprehend. Evolutionary theory, like all scientific theories, faces a dilemma of competing values. Scientific theories are judged (among other things) on the basis of theoretical generality and empirical specificity. Both are required of any scientific theory, but both are not attainable to the highest degree. To generalise is to look for recognizable patterns in the often chaotic flux of phenomena. To do so requires abstracting from the particulars of specific cases. Empirical specificity, on the other hand, is concerned with the precision of fit of theory to actual, highly specific, situations. The most empirically accurate theory would be one which simply describes, in infinite detail, each event occurring in its intended domain. But to do so would hardly resemble science as we know it at all. Between the competing values of generality and specificity, the former usually takes priority. But the latter value can be just as important, depending on the purposes at hand.[28] Here, as elsewhere, values determine practice.[29]

5. CONCLUDING REMARKS

Evolutionary theory succeeds in explaining biological phenomena of general interest (adaptedness, diversity, etc.) because it utilises "aggregative" terms like "fitness," "selection," and "drift". Individual biological phenomena are explained in terms of such general concepts, or are left unexplained until they are seen to be an instance of a more general phenomenon. As Sober points out, "In a sense, individual organisms are not really what the theory [of evolution] is *about*." [30] It is about populations. "The point is not to isolate the unique constellation of factors that most precisely circumscribes the fate of a single organism. Rather, the idea is to bring out patterns that apply both within and among populations."[31] Yet nature consists of both general trends *and* such individuals. Evolutionary theory (at present) deals only with the former. Hence, there are phenomena which escape the net cast by the theory.[32] Whether such phenomena are considered important depends of course on the reference frame one selects for assigning measures of importance.

To illustrate this last point, consider two cases which seem to lie at opposite ends of the spectrum of evolutionary importance. Each case can be seen as a variation of the twin case discussed in some detail above. Consider first the commonplace observation of the mangled body of some small animal in the middle of or alongside a rural thoroughfare. Where I grew up — Upstate New York — it was common to see the remains of a opossum that was obviously hit by an automobile as it tried to make its way across the road. ("Playing dead" before the threat of a Buick is a highly mal-adaptive behaviour.) Suppose two opossums are crossing the road. One is hit by an automobile and is killed, while the other, having started the trek across the road a moment later, makes it to the other side unscathed. What are we to say about this case: Is it a case of selection or of drift (chance)? I can imagine the response that it really does not matter what we call it, because it is such an isolated, insignificant event. But viewed from another perspective, it is neither isolated nor necessarily insignificant. If I added up all the dead opossums I've seen along roadways, the total number would be impressive. How can one be sure that there is no significant selection going on here? In addition, one of the beauties of evolutionary theory is that it offers a comprehensive framework for understanding the often chaotic events in the living world. In principle, *every* event involving living beings, and especially those involving differential survival, should be describable within a broadly evolutionary framework. Viewed from this perspective, to ask whether the road-kill one is now contemplating is a case of selection is simply to apply the evolutionary perspective in a comprehensive manner. Evolutionary theory *should* have something to say about it.

Finally, consider a more "serious" example. In a recent book, Stephen Jay Gould discusses the ancient decimations evident in the Burgess Shale of British Columbia.[33] Analysis of the data suggests that certain body-plans were eliminated from the history of life, not because of any evident structural inferiority, but simply by being at the wrong place at the wrong time, i.e., by chance. A scientific explanation for the present distribution of organismic body plans will be concerned with functional morphology, laws of physiology, and general evolutionary principles. But an equally important part of the explanation will be concerned with particular episodes in the history of life which decisively eliminated certain body plans from the competition, making radiation from the others possible. Start the tape of life over again, Gould suggests, and we could easily be spectators to a totally different history of life on earth. Or, rather, we would not be spectators, because the body plan that led to chordates (and hence to us) might well have been one of the unlucky victims of blind fate. Or was it selection? When the isolated, unique event in question is something as momentous for the history of life as the decimations Gould describes, the question of whether it was due to selection or to drift, and of the relationship between them, displays its true significance.

NOTES

Acknowledgements: I would like to express my sincere gratitude to Elliott Sober, Paul Griffiths, Susan Oyama, John Endler, Linda Zagzebski, and an anonymous referee for helpful suggestions on an earlier draft of this paper.

[1] See, for example, D. Futuyma (1986), *Evolutionary Biology*, 2nd ed. (Sunderland, MA: Sinauer), pp. 85-87.

[2] As John Endler has pointed out to me, most biologists do not think of selection and drift as distinct processes, but rather as ends of a continuum. This can be expressed quantitatively by noting that selection may take on any value from zero to a large value. "We speak of selection and drift as ends of a continuum, to focus our attention on the mechanisms and to show that they operate" (Endler, personal communication). Part of my aim in this paper is to present novel reasons in support of this view, and to draw out its implications for understanding evolutionary theory.

[3] J. Beatty (1984), 'Chance and Natural Selection', *Philosophy of Science* **51**:183-211.

[4] H. Kettlewell (1973), *The Evolution of Melanism* (Oxford: Oxford University Press).

[5] Beatty (1984) [note 3], p. 189.

[6] M. Scriven (1959), 'Explanation and Prediction in Evolutionary Theory', *Science* **130**:477-482; R. Brandon (1978), 'Adaptation and Evolutionary Theory,' *Studies in History and Philosophy of Science* **9**:181-206; S. Mills and J. Beatty (1979), 'The Propensity Interpretation of Fitness', *Philosophy of Science* **46**:263-286; J. Beatty (1984) [note 3]; E. Sober (1984), *The Nature of Selection* (Cambridge, MA: MIT/Bradford Press).

[7] In this paper, I am treating drift as the "chance" factor in evolutionary theory. This is in keeping with most formal and informal presentations of the theory. The concept of "chance" has had and continues to have other meanings in evolutionary biology, such as coincidence, ignorance of causes and as "accident". I have explored these different notions elsewhere; space prohibits me from doing so here.

[8] The *class of* issues at stake in considering the selection/drift distinction all concern cases in which factors other than selection coefficients (assignments of fitness values) affect the fates of organisms, populations, and species. According to Mayr's "founder principle," for example, a new species may originate from the genetic divergence of a peripheral isolate of a population. Which individuals form the isolate, and which survive the initial displacement, may have very little to do with their selection coefficients, but may have very great evolutionary consequences in the long run.

[9] Beatty (1984) [note 3], p. 192. A sampling event may be "indiscriminate" with regard to some properties, but not with regard to certain others. Balls drawn out of an urn by a blindfolded man have been sampled indiscriminately with regard to *colour*. But perhaps not with regard to location (top or bottom of urn). In the example, the twins were sampled indiscriminately with regard to presence of an X chromosome (they both possessed at least one), but perhaps not with regard to location (higher or lower on the ridge). One might contend that if there has been sampling at all, then there *must* be some properties in virtue of which some were taken out, and others left in. The questions then concern (a) the nature of such properties, and (b) the role they play in (i) evolution and (ii) evolutionary theory.

[10] A. Rosenberg, A. (1978), 'The Supervenience of Biological Concepts', *Philosophy of Science* 45:368-386.

[11] Mills and Beatty (1979) [note 6].

[12] I am here assuming that the/an *epistemic* interpretation of probability is correct, that is, that probability claims are judgments as to the likelihood of a given event in light of evidence we have of past events of this sort. Probability claims, on this view, are always relevant to a body of evidence known by one or more inquirers. On a *propensity* interpretation of probability, according to which certain events have a probability of occurring quite independently of any evidence had by any inquirers, it could be assumed that the two twins had different probabilities of being struck my lightning before the momentous train of events that transpired that day on the mountain began. We could then say that the twins differed in their (objective) propensities for being struck by lightning, and hence differed in fitness with regard to lightning strikes. The twin that survived had a greater fitness than the one that died, and hence this was a selection event. This way of looking at the twin case would allow one to preserve the link between fitness differences and selection. Note, however, that it would result in the same judgment of the twin case: on either interpretation of probability, this case turns out to be an example of selection.

[13] Fitness is a theoretical concept which has its use in evolutionary theory — to capture generalizations — but is not part of the causal explanation of a particular selection event. It is not the case that *A* outsurvived *B* because *A* had greater fitness. If *A* outsurvived *B*, it was because *A* possessed some set of properties, *P*, that *B* lacked. One can say that *A* outsurvived *B* because of *A's* superior fitness, but this is just a shorthand technique which leaves entirely open precisely *why A* fared better than *B*. For this one needs to identify relevant property differences. To see how selection can discriminate between organisms which have identical fitnesses, consider the following example. Organisms *A* and *B* have the characteristics listed below (numbers represent arbitrary values of components of fitness — i.e., specific prop-

erties — which together determine overall fitness):

	Organism A	Organism B
Disease Resistance	8	2
Visual Acuity	6	4
Protective Colouration	5	5
Fleetness	4	6
Social Status	2	8
Total Fitness:	25	25

In this case, both organisms have identical fitness. But suppose that a disease epidemic breaks out, killing Organism *B* (with low resistance) but sparing Organism *A* (with high resistance). I would argue that this is an example of selection, despite the lack of overall fitness differences between the two organisms. Fitness is a useful *predictive* tool, but is not a causal factor in selection events.

[14] Sober (1984) [note 6], pp. 88-96.

[15] L. Darden and J. Cain (1989), 'Selection Type Theories', *Philosophy of Science* **56**:106-129.

[16] This is not to deny that fitness differences may be *conducive* to (or correlated with) selection events. The greater the fitness differences among organisms, the greater the chance that they differ significantly in underlying properties. The greater the difference in underlying properties, the greater the potential for selection. The important point to note here is that it is underlying property differences, not fitness differences, that are causally significant with respect to selection.

[17] Mills and Beatty (1979) [note 6], p. 268.

[18] Some recent studies on body size as an ecological and evolutionary factor include: R.H. Peters (1983), *The Ecological Implications of Body Size* (Cambridge: Cambridge University Press); W.A. Calder III (1984), *Size, Function, and Life History* (Cambridge, Mass.: Harvard University Press);

K. Schmidt-Neilsen (1984), *Scaling: Why is Animal Size So Important?* (Cambridge: Cambridge University Press); M. LaBarbera (1989), 'Analyzing Body Size as a Factor in Ecology and Evolution', *Annual Review of Ecology and Systematics* **20**:97-117.

[19] Elsewhere [T. Shanahan (1990a), 'Evolution, Phenotypic Selection, and the Units of Selection', *Philosophy of Science* **57**:210-225] I have argued at length that selection can operate on properties that may be quite temporary in their duration. Position in a dominance hierarchy, holding of a territory, and possession of mates are all highly significant factors determining reproductive success. Yet each of these can change in value many times during the life of an individual. Such characteristics may not reflect any underlying disposition for dominance, resource holding power, or sexual charisma, but rather may simply be a function of *history*: Whoever stakes out a territory (or builds a harem) first may enjoy a competitive advantage simply in virtue of being *first*. Displacement from the position of advantage and later reintroduction often results in a disfavored position. The point is that characteristics need not be stable properties of an individual to be highly significant for selection.

[20] A beautiful example of nonheritable phenotypic differences that have great selective significance: Sterility or fertility in Hymenoptera is determined by environmental conditions during growth (e.g., kind of food given), and is mediated physiologically by hormonal titers. See C.D. Michener (1974), *The Social Behavior of the Bees* (Cambridge: Harvard University Press). As Wcislo (1989, p. 157) points out, "The feedback relationships between behavior and demographic factors, and social organization and life-history traits, imply that social structure determines which reproductive opportunities will be available to individuals" (W.T. Wcislo [1989], 'Behavioral Environments and Evolutionary Change', *Annual Review of Ecology and Systematics* **20**:137-169). For more on this point, see S.A. Altmann and J. Altmann (1979), 'Demographic Constraints on Behavior and Social Organization', in I.S. Bernstein and E.D. Smith (eds.), *Primate Ecology and Human Origins* (New York: Garland), pp. 47-63, and T. Shanahan (1990b), 'Group Selection and the Evolution of Myxomatosis', *Evolutionary Theory* **9**:239-254.

[21] According to Sober, "The sort of environment an organism inhabits is part of its phenotype" (Sober 1984 [note 6], p. 119). But if so, then how can an organism interact with its environment? At most an organism can interact with part of its own phenotype! If the environment is a part of the phenotype, then selection is impossible, since selection is an interaction between phenotypic properties and critical factors in the environment.

[22] The determination of the relevant environment for a given selection event is conceptually as well as empirically problematic. Environments cannot be distinguished along sharp boundaries. In any case, there is (as yet) no completely non-arbitrary way to individuate environments, so claims that the organisms occupy the same or different environments must necessarily be inconclusive. Fortunately, selection does not require a common environment. What is required for selection is rather common "critical factors" in the environment, i.e., a common selective *agent* (Darden and Cain, 1989 [note 15]). Selection is not an interaction between an organism's fitness and its environment. Just as not all components of an organism's fitness are relevant to a selection event, so too not all components of an organism's environment are relevant. The "environment," like "fitness," is causally inert.

[23] A word of clarification: Strictly speaking, it is not that there is no biological distinction between selection and drift, because if one of these processes is more likely to lead to adaptations than the other, then there *is* a biological distinction. Rather, there is no *hard and fast* biological distinction: the two processes lie on a continuum. What differentiates selection and drift is not the nature of the events transpiring *per se*, but the kinds of *effects* or *results* one can expect from the process when different kinds of conditions obtain, e.g., whether selection takes place on widely exemplified properties, whether it is in a consistent direction, whether it results in adaptations, etc. In a previous discussion of selection and drift [T. Shanahan (1989), 'Beatty on Chance and Natural Selection', *Philosophy of Science* 56:484-489.] I argued that selection and drift are clearly distinct, and are distin-

guished on the basis of whether sampling is on the basis of fitness differences or not. I now think that this is mistaken, or at least too simple. Evolutionary theory distinguishes selection and drift in terms of whether or not fitness differences are thought to be causative in differential biological success. But strictly speaking fitness differences have no causative power, and thus this way of distinguishing selection and drift as distinct processes *in nature* fails.

[24] Sober (1984) [note 6, p. 115] argues that "Separating selection and drift yields concepts that are needed to mark important biological distinctions." As I understand his argument, two populations may be characterised by identical sets of selection coefficients. Yet, if they differ in size they may experience quite different evolutionary careers. (In a smaller group the chances of random fixation of genes is greater.) On this view, the concept of "drift" is a way of capturing the importance of population size for evolutionary change. I would interpret this claim as follows: "Drift" is a concept used to fill in the space left between the predictions of abstract theory and the facts of concrete biological reality. Selection coefficients are educated guesses about the likely effects of certain properties in specified environments. When factored into a population genetics equation which assumes infinite population size, a prediction can be made about the change in gene frequencies in a population. But as selection coefficients are at best guesses (based on past correlations between properties and effects), they can be off the mark in actual biological scenarios. Thus, the concept of "drift" is introduced to account for changes in populations that deviate from those expected on the basis of selection coefficients. My claim is that the events described as "drift" are not different in kind from events described as "selection," but differ only in that drift events are not predictable to the extent that selection events are. Drift events are, by definition, the residue left over when populational changes fail to accurately reflect selection coefficients. Selection and drift are distinguished in theory even though they are not entirely distinct in nature.

[25] Such properties will consequently not be of great interest to many evolutionary biologists. A distinction needs to be made between those entities which function is the process of selection, and those which

function in processes of adaptation. Those biological entities that are the objects of phenotypic selection are units of selection. The objects of natural selection (which requires heritability) are units of adaptation. Units of adaptation are always units of selection, but units of selection are not always units of adaptation (Shanahan 1990a [note 19]).

[26] Rosenberg (1988) suggests two alternative interpretations of drift: (1) Drift is a cover for unknown nonevolutionary (i.e., non-adaptational, non-selective) forces. (2) Drift is a cover for selective (i.e., adaptation-producing) forces of which we are ignorant. Rosenberg seems to prefer (1). My position is neither (1) nor (2), but a third (hybrid) position: Drift is a cover for selective forces of which we are ignorant [as in (2)], but it is also non-adaptational [as in (1)]. "Drift" is a term used to cover selective events which have a low probability of leading to adaptational change. "Drift" refers to non-adaptational selective events.

[27] According to Pierre Laplace, "We regard a thing as the effect of chance when it offers to our eyes nothing regular or indicative of design and when we are moreover ignorant of the causes which have produced it. Thus chance has no reality in itself; it is only a term fit to designate our ignorance concerning the manner in which the different parts of a phenomenon are arranged among themselves and in relation to the rest of Nature" (P.S. Laplace, 'Memoire sur la probabilite' des causes pour les evenements', *Oeuvres completes*, VIII, 27-65; quoted in K.M. Baker (1975), *Condorcet: From Natural Philosophy to Social Mathematics* (Chicago: University of Chicago Press).

[28] When one is considering something like the origin of *Homo sapiens,* which occurred only once in the universe, one needs both general principles *and* plenty of specific details pertaining to early proto-hominid environments, etc. In a case like this, one might well choose to know everything there is about the origin and evolution of this one species, rather than settle for general principles that apply to *Homo* and lots of other primate groups as well.

[29] And scientific values determine scientific practice. As Rosenberg (1988, p. 189) points out, "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" (p. 188). If it turns out that the phenomena are deterministic but that we frame our theory in statistical terms because doing so is pragmatically expedient, "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" A. Rosenberg, A. [1988], 'Is the Theory of Natural Selection a Statistical Theory ?' in M. Matthen and B. Linsky (eds.), *Philosophy and Biology* (Calgary: University of Calgary Press), pp. 187-207.

[30] Sober (1984) [note 6], p. 117.

[31] Sober (1984) [note 6], p. 134.

[32] According to the Hardy-Weinberg Equation, in an infinite population drift (sampling error) is ruled out. At the other extreme, in a "population" of two organisms, one might say that whatever happens to these is, according to the theory, a case of drift (sampling error). Predictive power of the theory is proportional to population size: The larger the population, the less potential for sampling error; the smaller the population, the greater the potential for sampling error. Explanatory accuracy is inversely proportional to population size: The smaller the population, the greater the potential for determining precisely why a given sampling event occurred. Predictive power and explanatory accuracy are inversely related in evolutionary biology. Rosenberg (1988) [note 29] makes a similar point, when he points out that usefulness and realism are inversely related.

[33] S.J. Gould, S.J. (1989), Wonderful Life: The Burgess Shale and the Nature of History (New York: W.W. Norton).

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