Selection, Indeterminism, and Evolutionary Theory*

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I argue that results from foraging theory give us good reason to think some evolutionary phenomena are indeterministic and hence that evolutionary theory must be probabilistic. Foraging theory implies that random search is sometimes selectively advantageous, and experimental work suggests that it is employed by a variety of organisms. There are reasons to think such search will sometimes be genuinely indeterministic. If it is, then individual reproductive success will also be indeterministic, and so too will frequency change in populations of organisms employing such search.

1. Introduction. For some years now philosophers of biology have worried about whether or not evolution is an essentially indeterministic phenomenon. Most arguments for the indeterministic character of evolution have attempted to show that the statistical machinery employed by evolutionary theory is ineliminable, and so must be given a realistic interpretation; that is, these arguments aim to show that evolutionary theory is essentially probabilistic (Beatty 1984; Sober 1984). Responses have generally tried to undercut realist interpretations by showing that even if natural selection were thoroughly deterministic the statistical machinery of evolutionary theory would be useful, even essential, given our epistemic limitations (Horan 1994; Rosenberg 1988).

I think these discussions have by and large missed the strongest case for the claim that evolution is indeterministic. In this paper I develop that case and one of its implications for evolutionary theory. Some quasi-

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formal preliminaries are necessary. I take a phenomenon, e.g. the value \( v \) at time \( t \) of some variable \( V \) in some causally complete context \( C \), to be \textit{indeterministic} if in \( C \) contexts the frequency of \( v \) for \( V \) is strictly between 0 and 1; such indeterministic phenomena occur, if at all, as a matter of chance. It follows that if \( V \) depends causally on an indeterministic variable \( W \), then absent over-determination of one or another sort, \( V \) is also indeterministic and so also chancy. I take a theory to be \textit{probabilistic} if it is not deterministic in Montague's (1974) sense, and further describes some phenomenon in its domain as being indeterministic. Finally, I assume that the correct interpretation of quantum mechanics implies that some quantum phenomena are indeterministic.¹

Given these assumptions, the argument is this. Some animals exhibit random behavioral patterns. They do so because such patterns are selectively advantageous. There is good reason to think the behaviors conforming to such patterns are at least sometimes indeterministically generated. But the actual reproductive success of individual animals depends not on the pattern their behavior instantiates, but on the actual sequence of such behaviors. If such behavior is in fact indeterministically generated, then so too are the actual levels of reproductive success achieved by the animals. Hence, changes in the frequencies of types of these animals are indeterministic. A non-probabilistic theory cannot generate adequate explanations of indeterministic phenomena. Therefore, we have good reason to think evolutionary theory must be probabilistic.

In what follows I will flesh out the argument. I begin with a description of a particular kind of random behavioral pattern, random search, and briefly address the theoretical reasons for regarding such patterns as adaptive under various conditions. I then argue that there are good reasons to think that when random search is adaptive, actual search sequences will be generated by an indeterministic mechanism, and I describe one way in which indeterministic behavior generates indeterministic evolutionary phenomena. I finally turn to the implications of these results for evolutionary theory, addressing two objections recently raised by Graves, Horan and Rosenberg (1999), the first epistemic and the second methodological.

2. Random Behavioral Patterns: Random Search. Behavioral ecologists have described a number of different kinds of random behavioral patterns. Foraging theory provides a variety of examples. When forage is distributed homogeneously in an environment, the optimal strategy for finding

¹. The assumption is substantive. As far as I know, it is an open question whether or not anything is essentially indeterministic at the quantum level, and the assumption that at least some things are indeterministic is not idle in the arguments that follow.
forage is sometimes best described as a random walk, and such search strategies have been observed in fallow deer (Focardi, Marcellini and Montanaro 1996). When forage is non-homogeneously distributed, there are contexts in which the optimal search strategy for discovering prey within a patch is a biased random walk (Bovet and Benhamou 1991; Li, Roitberg and Mackauer 1992; Marschall, Chesson and Stein 1989). In some contexts, the optimal rule for determining patch residence time is indeterministic (Oaten 1977; Nishimura 1999). An initial result of fairly simple models of optimal foraging is the zero-one rule: given a range of kinds of prey items, optimal foragers either always attack items of a given kind, or never do. But as it turns out, that rule is systematically violated by actual organisms: real critters commonly exhibit partial preferences (see e.g. Werner and Hall 1974; Davies 1977; Lea 1979), these preferences are sometimes best modeled as probabilistic dispositions (McNamara and Houston 1987), and sometimes they are adaptive (Sirot and Krivan 1997). Random patterns of non-foraging behavior have also been observed. One sort of escape behavior involves taking an erratic and unpredictable path away from the location of an attacking predator (Driver and Humphries 1988), and has been observed in moths (Roeder 1962) and sticklebacks (Rodewald and Foster 1998). Here I focus on random search within a patch, though I think the argument could be developed with any of the above behaviors.

Those foragers typically occupying environments with non-homogeneous distributions of energy resources commonly exhibit two distinct sorts of searching behavior. A forager (typically but not always a predator) begins searching for patches of prey, i.e. local areas of the environment where prey items are more densely distributed than in the environment as a whole. Searches of this sort are commonly characterized by a relatively high velocity and low rate of turning. Patches are typically identified by the discovery of a prey item, though sometimes by responding to different environmental or physiological cues correlated with the presence of prey. For example, some parasitoid wasps apparently respond to the presence of honeydew, while adult ladybirds apparently respond to increases in gut content rather than directly to the detection of a prey item (Kareiva and Odell 1987). Once a patch has been identified, a quite different kind of search pattern is employed. This so called area intensive or area restricted searching is characterized by a much slower rate of speed, and a much higher rate of turning.

Area restricted searching is a common feature of the biological world. It has been documented in beetles (Carter and Dixon 1982), flies (Chandler 1969), parasitoid wasps (Li, Roitberg and Mackauer 1992), lacewings (Bond 1980), predatory mammals including badgers (Mellgren and Roper 1986) and moles (Fielden, Perrin and Hickman 1990), birds, including
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I will here describe just one case of area intensive search, that of Green Lacewing (*Chrysopa carnea*) larvae as described by Bond (1980). Lacewing larvae feed on aphids. When an aphid is discovered, the larva eats it, and then begins a period of area intensive search. Intensive search is characterized by a slowing of velocity, an increase in the rate of turning, and an increase in the width of the search path as compared with 'extensive' search. Velocity and turning rates depend both on the internal state of the larva and on the fact of prey capture. Bond found that 'extensive' velocities were on average \(0.562\) cm/s when larvae had been starved for 2 hours, and \(0.731\) cm/s when larvae had been starved for 8 hours. During intensive search, following the discovery of an aphid, mean velocities were \(0.354\) cm/s and \(0.282\) cm/s respectively for the two treatments. In extensive search the mean rate of turning measured in degrees per centimeter, called *meander*, was \(65.7\) °/cm for larvae starved for 2 hours, and \(42.8\) °/cm for larvae starved for 8 hours, while for intensive search the two groups were respectively characterized by means of \(155.4\) °/cm and \(224.7\) °/cm. Bond records typical extensive and intensive search paths, one each of which are reproduced below.

Different kinds of area restricted search patterns are possible. One such kind is called *random search*. It is so called because the paths and pattern of paths characteristic of organisms employing random search can be described as a first order correlated random walk. This sense of 'random' is important, and we shall return to it, but there is another, equally important, sense in which search patterns of this kind are sometimes random. Random search in this sense is best understood in contrast to its opposite, systematic search.

Figure 1. Intensive search trace from a lacewing larva. The distance between vertical bars represents \(2.5\) cm, dots represent \(1.5\) second intervals, and the second bar marks the end of intensive search. Modified from Bond (1980), Figure 2, page 13.
One option for a forager in an identified patch is to search the patch systematically, that is, to search in such a way that each part of the patch is not equally likely to be searched in a given interval of time. Two different kinds of search strategies will give rise to systematic search. First, search paths are sometimes spatially oriented. For example, ladybird larva search plants beginning with the leaves at the top of the plant, and then work down the plant, only occasionally returning to investigate the top leaves (see Hoffman 1990). Differently, if predators can sense clumps of prey within a patch at some distance, say by sight or smell, then their search paths will be systematic in the relevant sense, because they will be more likely to search areas of the patch containing prey items than those areas not containing prey items.

Random search may then also be understood as non-systematic search. So understood random search is to be distinguished from systematic
search in the following ways. Typically, if search is systematic, then the
time required to catch a particular prey item will be correlated with the
number of prey in the patch, or prey density in the patch (sometimes called
*patch quality* or *value*), and the time until the next prey item is encountered
will be correlated with the amount of time already spent in the patch
searching for prey (called *residence time*). Roughly, the longer the resi-
dence time, the smaller the volume in the patch that remains uninvesti-
gated and hence the more likely the predator is to encounter an as yet
undiscovered prey item in the next interval of time. Further, because pred-
ators commonly leave a patch when the time since the last capture becomes
sufficiently large (greater than the so called *giving-up time*), in systematic
search the number of captures in a patch and sometimes the path taken
through the patch will typically depend on the distribution of prey within
the patch. Finally, by definition, in systematic search, the probability that
a given area or volume of the patch is searched by a forager is not inde-
pendent of the search history: the probability of a new search of the area
is smaller if it has already been searched than if it has not.

None of these is true of random search. By definition, search is random
only if there is no correlation between the time to encounter with a par-
ticular prey item and the number of prey items in the patch, and similarly,
no correlation between the time to next encounter and residence time.
Success in a patch using random search depends on prey density, but not
on prey distribution, and the path taken through the patch will not depend
on prey distribution in the patch. Finally, in random search each area of
the patch is equally likely to be searched during a given interval, so the
search is random only if the probability of searching a given area or vol-
ume of the patch is independent of whether or not it has already been
searched.

Each of these differences has implications that can be used to test for
random search. One test is this. Define \( n \) as the number of prey items in
the patch at a given time, and \( T_n \) as the time until the capture of the next
prey item, and let \( t \) vary over temporal intervals. Then in random search
\( \Pr(T_n > t) = e^{-\alpha nt} \), where \( \alpha \) is some constant. This implies that the vari-
able \( g = nT_n \) should be exponentially distributed. So a standard way to
test for random search is to test for exponential distributions of \( g \) (for
discussion see Marschall, Chesson and Stein 1989).

Interestingly, random search so understood need not imply random
search in the first, more intuitive sense of random walk. Indeed, random
search in the second sense can be characteristic of sit and wait predators
who do not travel through their environment, provided that prey densities
in the immediate area of the predator evolve in the right way over time.
We, however, are interested in organisms that engage in search that is
random in both senses. Such search has been observed in at least two
different groups, bluegill sunfish (see Marschall, Chesson and Stein 1989, DeVries, Stein and Chesson 1989) and the parasitoid wasp *Aphelinus asychis* (see Li, Roitberg and Mackauer 1992). These organisms take paths through an identified patch that can be described as first order correlated random walks, and which are random in the sense of being non-systematic (e.g., \( g \) is distributed exponentially).

Search that is random in both of the above senses is predicted to be adaptive in various environments, as for example when prey move between patches, and under some conditions when prey move within a patch. If, for example, predators cannot detect prey at any distance and prey move within a patch, random search makes intuitive sense. In these conditions a search that is systematic with respect to prey distribution in a patch is impossible, since prey items cannot be detected at any distance, while a spatially systematic search will allow prey items to move from areas yet to be searched into areas that have already been searched, and so to go undiscovered. The intuitive idea has been formalized and tested in simulation trials. Li, Roitberg and Mackauer (1992), for example, model the random search of *Aphelinus asychis*. They show that when prey are non-homogeneously distributed in patches, but are at low densities even in patches, and move randomly within patches, random search produces greater numbers of prey encounters and also a higher efficiency, measured in prey captured per energy spent searching, and so this strategy has a higher fitness. Random search still does better than systematic search even when prey are at high densities within a patch, but the fitness differences are not as great.

Bluegill (Marschall, Chesson and Stein 1989; DeVries, Stein and Chesson 1989) and some parasitoid wasps (Li, Roitberg and Mackauer 1992) both appear to face environmental conditions of these sorts. The behavior of the wasp *Aphelinus asychis* has been especially well described (see Gerling, Roitberg and Mackauer 1990, Boyle and Barrows 1978). Female wasps search for their aphid hosts by walking over the surface of leaves. They can detect aphids at ranges just less than 2 mm. Once detected, a wasp ‘antennates’ the aphid, positions herself in front of or behind the aphid, but facing away from it, and attempts to stab the aphid with her ovipositor. Aphids that detect wasps, either before or after being stabbed with the ovipositor, exhibit a variety of escape behaviors. Such behavior exhibited by one aphid may induce similar behavior by other aphids in the area. Finally, aphids can and do move within a patch, here a leaf.

So there are cases in which random search has been observed. These are also cases in which random search is, on the available evidence, adaptive. That search is random, however, does not entail that it is generated by indeterministic mechanisms. That inference requires a bit more work.
3. Random Search Strategies. Random search comes in different kinds, and the kinds are not selectively equal. It is easy to see why this is so. If on average the search paths taken by a predator maximize the proportion of the patch searched while minimizing the length of the path, the predator will maximize the number of prey encountered while minimizing the energy expended. Very roughly, then, a predator wants to generate random search paths that on average optimize what we might vaguely call the curvature of the path. Too little 'curvature', and not enough area is covered. Too much, and the predator spends too much energy for the return in prey caught. So some search patterns, those with more paths at optimal or near optimal 'curvature', are better strategies than others.

To account for patterns of motion, ecologists have developed various notions of kinesis and taxis. Roughly, taxis involves movement oriented with respect to an environmental gradient, while kinesis involves unoriented movement. We are here interested in models of kinesis. There are any number of concepts of kinesis. This is because there are any number of variables an animal might directly control or respond to when generating a path, and any number of subsets of these variables are sufficient to describe both the paths organisms take, and the patterns of such paths. I will here describe only one concept of kinesis meant to measure 'curvature', namely sinuosity. Measures of 'turning rate', or angular velocity, are more common in the literature, but sinuosity has various theoretical advantages and is here more directly relevant.

Suppose a predator generates a search path by taking a sequence of steps of constant length P, in between which steps it changes direction. Let R be a measure of direction change in radians, and suppose R is distributed normally with mean 0 and standard deviation σ, so that the actual path is represented as a first order correlated random walk. Bovet and Benhamou (1991) define the sinuosity S of the path as $S = \sigma / \sqrt{P}$, and estimate optimal sinuosity for a central place forager in a patchy environment. They find that optimal sinuosity is given by $S^\ast = (1.2 - 0.11 \ln(A/W^2))/\sqrt{W}$, where W is the width of the path searched, i.e. the distance on either side of the predator at which it can detect prey, and $A = i/d$ where i is the number of prey items the forager collects before leaving the patch and d is the prey density in the patch. At optimal sinuosity, R will have the standard deviation $\sigma^\ast = 1.2 - 0.11 \ln(A/W^2)$. While the optimal sinuosity may change with different predation strategies, phenotypes and environments, presumably for each such triple there will be some optimal sinuosity.

Nothing at issue here hinges on whether sinuosity or R are directly

2. See Fraenkel and Gunn (1961) for the classical discussion, and Benhamou and Bovet (1989) for a critical review.
regulated or their distributions are instead an artifact of the regulation of other variables. What does matter is that however search generating mechanisms work, such mechanisms will be adaptive only if they generate searches with optimal sinuosity. Optimal sinuosity requires that the pattern of search paths generated by the mechanism be characterized by a random variable, $R$. That provides good reason to think that the mechanisms generating random search paths are themselves random in the relevant sense, i.e. essentially indeterministic. Since $R$ is random, either it depends indeterministically on other variables, in which case $R$ is essentially indeterministic, or it depends deterministically on other variables, in which case at least one of those variables must itself be random, which randomness can again be accounted for only in the above ways.

4. Internal Sources of Indeterminism. On the available evidence, then, there are in some organisms mechanisms that produce behavior best explained as random. Genuine random search is, ceteris paribus, demonstrably optimal under some conditions, and there are actual biological populations which apparently exhibit random search under just those conditions. One way to insure that this search behavior is in fact random is to generate search paths indeterministically, e.g. to make $R$ indeterministic, or to make it depend directly or indirectly on one or more variables that are indeterministic. Nonetheless, deterministic algorithms can approximate random variables, so it is at least possible that the search paths these organisms take are really determined by some set of hidden variables, so that the distribution over $R$ which characterizes the pattern of their search paths, while not really random, is approximately so.

We would have reason to take this possibility seriously, that is, to doubt that random search behavior is genuinely random, if it were simply impossible for organisms to exploit indeterministic features of their own physiology or environment in generating search behavior. For even if indeterministic mechanisms are selectively advantageous in some circumstances, they will not be present if they are for some reason physiologically impossible.

Is there reason to think that indeterministic behavioral mechanisms are possible? I know of no explicit argument to the contrary, but one might wonder whether perhaps there simply is no sufficiently high-level physiological variable whose behavior is stochastic. Though I can cite no explicit cases, I think something like this presumption is common in both philosophy of science and certain brands of philosophy of mind. While initially plausible, if only because our own behaviors so rarely appear to be random, the worry flies in the face of much current evidence.

Whatever procedure is used to generate random behavioral patterns, and random searches in particular, at some level this procedure must com-
monly involve the operation of structures of cells. But there is reason to think such structures and their components behave indeterministically. Ion channels apparently behave stochastically (Merlushkin and Hawkes 1997), as do synapses (Faber et al. 1992), and in the former case this stochasticity appears to account for variations in cellular behavior. Indeed, there is evidence for stochastic behavior in both neurons (White et al. 1998; Wilders and Jongsma 1993) and in non-neural cells (Nemoto et al. 1995). In one of the former cases (White et al. 1998), there is evidence that this stochastic behavior has some effect on learning behavior.

On the current evidence, then, if indeterministic search mechanisms have not evolved, that is not because it is impossible for quantum indeterminacy to percolate to the level of macro-physiology or organismal behavior: there is reason to believe that it is not only possible for mechanisms to translate quantum indeterminacy into stochastic behavior at macro levels, but also that such mechanisms exist. Further, there are good reasons to think that if such mechanisms have occurred in the right contexts, they will have been preserved by natural selection. It is of course possible that mechanisms permitting the upwards percolation of quantum indeterminism have in virtue of exactly this indeterminism some as yet unknown but nonetheless significant selective disadvantage. But no such disadvantage has ever to my knowledge been proposed, and there is no evidence of which I am aware suggesting any such cost to indeterministic mechanisms per se. So while it might turn out that, as a matter of fact, there are no random behavioral patterns with underlying indeterministic physiological mechanisms, there is neither empirical nor conceptual reason, at this point, in favor of that conclusion. Moreover, were it a fact that no such behavioral patterns exist, it would be, as far as we can now say, simply an accidental fact: the generalization is backed by no conceptual reason, nor by any putative laws of nature, but rather depends for its truth on a happy sequence of evolutionary changes in which on every occasion where an indeterministic mechanism is possible and would be advantageous, no such mechanism ever arises.

So there are good reasons to think that in some cases the actual paths taken by foragers are random in the fullest sense: even given full information about the organism’s current state and the state of the environment, it is a matter of chance what path the forager actually takes through a given patch on a given occasion. And this implies that evolutionary change is indeterministic.

5. Indeterministic Search and Evolutionary Change. The implications of indeterministic search for evolutionary phenomena may be developed either by treating such mechanisms as playing a role in one or more selection
processes, or as constituting a source of drift. Here I will consider only the case for selection.

I take selection processes to be those causal processes that account for differences in the relative rate of reproductive success among some set of kinds of organisms in a population. In the normal case, the differences in relative rates of reproductive success depend mathematically on the individual relative rates of success for each kind, and on nothing else. These in turn are artifacts of the absolute mean rate of success for each of the kinds. Each such absolute mean rate is a mathematical consequence of the actual reproductive success of each individual of the kind. The actual success of many such individuals depends causally, in part, on the foraging efficiency of the individual. This in turn depends on the number of prey items it captures and on the energy it spends searching for these prey items. Both of these variables depend causally on the search paths the individual actually takes through particular patches. For organisms employing indeterministic mechanisms for generating search paths, these mechanisms are a cause of the number of captures it makes and the energy it expends to make them. Hence, the mechanisms are involved in a causal process that accounts, in part, for differences in reproductive success, should any occur. Consequently the mechanisms are involved in a causal process that accounts for changes in type frequencies, and, equally important, for the rates of such changes. But if such mechanisms are causes of success, and so of evolution, they are indeterministic causes of that success. So selection, evolution and the rate of evolution are, sometimes, indeterministic.

So there seems good reason to think that evolutionary phenomena are at least sometimes indeterministic, i.e. occur only as a matter of chance. It is worth noting that this sort of argument is not uniquely afforded by foraging theory. The argumentative structure depends only on finding some random behavioral pattern where 1) the underlying mechanism is plausibly thought to be indeterministic and 2) the mechanism generates behavior that causes success. Several alternative phenomena immediately suggest themselves. It might be that at some loci DNA sequences more likely to mutate in one direction than in the reverse are selectively advantageous. Similarly, the mechanisms by which genotypes produce phenotypes are, at least in some cases, indeterministic (see McAdams and Arkin 1997, and references therein). To the extent that selection occurs at the phenotypic level, then, evolutionary changes will be indeterministic. Patterns of dispersion from natal territories are clearly under selection, and might well be produced by indeterministic mechanisms. Sensory mecha-

3. Note that this case does not depend on there being selection for an indeterministic behavioral mechanism M, though of course if M is adaptive it will presumably have evolved, and selection for M will be indeterministic.
nisms, especially those responding to electro-magnetic radiation, must certainly operate indeterministically at sufficiently precise levels of description. Doubtless there are other domains of evolutionary phenomena where the same kind of causal structure obtains and in which there is at least some modicum of evidence that the relevant mechanisms are essentially indeterministic.

6. Evolution and Its Theory. Recall that a theory is probabilistic if it is not deterministic in Montague's (1974) sense, and further describes some phenomenon in its domain as being indeterministic. It might seem obvious that if some evolutionary phenomena are indeterministic then any good evolutionary theory must be probabilistic, but it has not proved so. Notwithstanding apparent indeterminism in the phenomena, some have suggested that there are good reasons for attempting to find a deterministic theory of the phenomena, or at least for regarding the probabilism of any stochastic evolutionary theory as an expression of ignorance rather than a claim about how the world is. In a recent paper, Graves, Horan and Rosenberg (1999) advance a pair of arguments for this view. The first argument aims to show that even indeterministic evolutionary phenomena are reliably predictable by a deterministic evolutionary theory, on the grounds that evolutionary phenomena are 'asymptotically deterministic'.

Their argument is not entirely clear, but as I read them (1999, 143–146), this is what is going on. Deterministic theories of indeterministic phenomena face two sorts of error. There is error about what happens in a large set of trials with relatively frequent occurrences of each outcome in some space of outcomes, where the relative frequency of each outcome is to be predicted. A deterministic theory will presumably predict the expected frequencies with certainty, and so runs some risk of error. And there is error about what happens in a small set of trials where the frequency of one overwhelmingly common outcome is to be predicted. When the number of trials is small relative to the probability of the unlikely outcome, the deterministic theory will predict with certainty that the likely outcome has frequency 1. As I read Graves, Horan and Rosenberg, they claim that neither sort of error should worry us, because first, errors of either sort are very unlikely, and second, such errors as do occur give us no reason to reject the deterministic theory.

Errors are thought to be very unlikely, I take it, for the following reasons. Indeterministic macroscopic behavior is 'asymptotically deterministic' when produced by many complex causal processes. That is, when population sizes are large, deterministic theories can predict the frequencies of these sorts of behaviors. Biological populations are large, and evolutionary theory need not predict the behavior of individuals, but only the frequency of types of behavior in the population. Moreover, the qualita-
tive predictions about which types in the population go to fixation or some
stable equilibrium requires only precise, not exact, predictions of behavior
frequencies. While some individual behavior may be indeterministic, the
probability distribution over alternative behaviors is such that each of
them is expected to occur regularly in any large population of trials. So
the law of large numbers can be usefully applied and consequently deter-
ministic theories can predict the frequencies of the relevant behaviors in a
population with great precision and high accuracy.

There remains of course the chance that an error of the second sort will
occur, i.e. there is a small chance that any given prediction about the
behavior of a population will be in error. But that chance is really vanish-
ingly small. Since the number of populations is relatively small, the relative
frequency of predictive errors made by a deterministic theory will be ex-
ceptionally small, perhaps even zero. And now comes the second part of
their response. Even if such an error should occur (i.e. the theory is, by
chance, falsified), that ought not bother us since such events will occur so
very, very rarely. One error in zillion ought not matter between a theory
and its friends, as it were (c.f. 1999, 145).

If I have got the argument right, then there are any number of diffi-
culties with it. Not all populations are large, and, depending on how one
partitions lineages into populations, there are very many populations. The
argument focuses on qualitative predictions about the outcome of evolu-
tionary processes, but ignores the much more sensitive predictions regard-
ing the rate of evolution. Moreover, there are contexts in which determin-
istic treatments of indeterministic evolutionary phenomena will lead to
systematically mistaken predictions (see Oaten 1977). Finally, for all that
the methodological recommendation will be endorsed by any number of
practicing biologists, it strikes me as quite desperately wrong.

These difficulties aside, I want to develop a different objection, to my
mind the most pressing. Suppose, for the sake of argument, that there is
reason for rejecting a theory as predictively inadequate only if the theory
generates predictions that are, in some relevant domain, systematically in
error, and suppose it is possible to produce a deterministic evolutionary
theory that is never systematically in error, even when the phenomena it
predicts are essentially indeterministic. I think one still ought reject the
theory, not because it is predictively inadequate, but because it will yield
mistaken explanations.

One is not in general concerned merely with prediction, and with respect
to evolutionary theory one is quite specifically, and quite deeply, con-
cerned with explanation. And here matters are very different indeed.
Whether or not the phenomena to be explained by a theory are asym-
totically deterministic is simply irrelevant to the adequacy of the ex-
planations generated by the theory if those explanations are causal. A non-
probabilistic theory can presumably generate only explanations that describe all the causes they do describe as being deterministic causes, and therein lies the difficulty.

If random search mechanisms exist and are adaptive, then presumably they evolved, if only in respect of changing distributions of $R$ in response to changing distributions of patch value over the history of the lineage. There ought therefore be an evolutionary explanation for the frequency of any such mechanism $M$. Any evolutionary explanation of the frequency of $M$ either will or will not describe $M$ as a cause of the success of its carriers.

Suppose the explanation does not describe $M$, but rather begins the causal description with an appeal to the distribution of search paths or net energy gain among organisms in the population. In this case the explanation is incomplete and so inadequate for certain legitimate explanatory requests. Hence evolutionary theory must be capable, at least in principle, of describing $M$'s role as a cause of search paths, and hence of net energy gain, on pain of being explanatorily incompetent for some of the phenomena in its domain.

But suppose that a deterministic theory does describe the role of $M$ as a cause of search behavior. Then it must mis-describe $M$ as a deterministic cause of such behavior, in which case some of the explanations afforded by the theory are false. Worse, one cannot systematically offer explanations that describe indeterministic causes as deterministic and at the same time limit the explanatory errors to just that mis-characterization of the relevant causes.

Deterministic causes bear different explanatory relations to their effects than do indeterministic causes. Deterministic causes can over-determine an effect; probabilistic causes cannot. If there is a deterministic causal relation between two properties or event kinds, the presence of an instance of the effect may be deduced from the presence of an instance of the cause; not so if the connections are indeterministic. Deterministic causes can contrastively explain the occurrence of their effects; probabilistic causes cannot on standard accounts of such explanation. When more than one cause of an effect is present and causation is deterministic, we commonly use back-tracking considerations to determine which of several causes present actually operated to produce the effect; if such discriminations are possible when causation is indeterministic, that is not how they are to be made. Indeed, because indeterministic causes are commonly non-additive, in the indeterministic case the assumption that only one of the causes present contributed to the effect is frequently mistaken. If we mis-characterize the causes of an event as being deterministic when in fact they are not, we

invite, indeed imply, further errors about the causal origin of the event, some of which are of quite serious methodological import. If, for example, we assume there is no over-determination, then when we believe $A$ to be a deterministic cause of $E$ in circumstances $C$, there is no point in looking for some co-causal factor not incorporated in $C$. If $A$ is in fact indeterministic though we treat it as deterministic, we will frequently fail to discover a range of co-causes of $E$.

Hence, if there are cases of random search where the underlying physiological mechanism is indeterministic, no complete, non-probabilistic theory of evolution can be explanatorily competent for the full domain of relevant phenomena. So even if Graves, Horan and Rosenberg were right about the predictive adequacy of deterministic evolutionary theories and about the methodological principle required to defend such theories, I think we have good reasons to reject any such theory. We care about explanation, and getting the explanation of indeterministic phenomena right requires a probabilistic theory, in this case one that permits us to describe indeterministic causes as indeterministic.

7. Indeterminism and Scientific Method. So there seems to me ample ground on which to defend at least the tentative judgment that evolutionary phenomena are sometimes essentially indeterministic, and that consequently any complete and correct evolutionary theory must be probabilistic. Still, there remains a methodological challenge to this conclusion, which is the second of the objections advanced by Graves, Horan and Rosenberg (153–154). They argue that the assumption of indeterminism is a methodological disaster because it is only by assuming that evolutionary behavior is deterministic that we come to search for the causes of such behavior. Such search is the raison d'être of science, so to abdicate the assumption, and hence the search, is to give up on the scientific project.

The point is clearly a double edged sword: if some of the causes of evolutionary behavior are indeterministic, we shall never recognize that fact if we take it as a requirement of methodologically competent scientific investigation that such investigations should assume determinism. Moreover, the assumption of indeterminism, or even of probabilism about evolutionary theory, requires neither that the search for causes nor that the search for deterministic causes be abandoned. Reliable search procedures for non-deterministic causal systems depend on the satisfaction of one further assumption than do such procedures for deterministic and pseudo-indeterministic systems (the assumption can be proved to hold for deterministic systems under normal conditions), but are not for that reason either unreliable or non-scientific (see Spirtes, Glymour and Scheines 1993). In any case, the standard search procedures employed by biologists, procedures such as regression and analysis of variance which are of more
or less unknown reliability for either sort of system, are frequently used in contexts where no presumption at all is made about whether the causal processes affecting individual organisms are deterministic or indeterministic.

Hence, I suggest, the general injunction to assume determinism is without even a modicum of justification. It is simply not a methodological requirement of the search for causal structure, never mind a requirement of good science. It is also plainly at odds with current evidence and the implications of current theory. There may be particular phenomena, even particular evolutionary phenomena, where something already known about the phenomena or the mechanisms generating them strongly suggest the relevant mechanisms are deterministic. But if the penultimate result in section 4 is right, if it is that all behavioral mechanisms are deterministic, if they are, only by accident, then not only is there neither conceptual nor empirical support for the general injunction, there are good reasons for thinking that some relevant mechanisms are indeterministic. And if even one such mechanism really is indeterministic, then evolutionary theory, on pain of explanatory inadequacy, had better be probabilistic.

REFERENCES


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