

10 Natural Selection as a Causal, Empirical, and Probabilistic Theory

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Darwin's conforming of his theory to the old vera causa ideal shows that the theory of natural selection is probabilistic not because it introduces a probabilistic law or principle, but because it invokes a probabilistic cause, natural selection, definable as nonfortuitous differential reproduction of hereditary variants.

Chance features twice in this causal process. The generation of hereditary variants may be a matter of chance; but their subsequent populational fate is not; for their physical property differences are sources of causal bias giving them different chances of survival and reproduction. This distinguishes selection from any process of drift through fortuitous differential reproduction in the accumulation of random or indiscriminate errors of sampling. To confirm the theory of natural selection empirically is to confirm that this probabilistic causal process exists, is competent, and has been responsible for evolution. Such hypotheses are both falsifiable and verifiable, in principle, if not in practice.

Natural selection has been accepted and developed by biologists with very diverse attitudes toward chance and chances. But the theory and its acceptance have always involved probabilistic causal judgments that cannot be reduced to correlational ones. So, the theory has contributed to a probabilistic shift within the development of causal science, not to any probabilistic rebellion in favour of science without causes.

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This chapter proposes a framework for integrating biologists' and philosophers' analyses of natural selection as a causal, probabilistic, and empirical theory of evolution. Throughout, the argument will be that the probabilistic character of the theory, whether in Darwin's day or ours, can only be properly understood when its distinctively causal and empirical character is kept in view.

Until fairly recently, perhaps only a decade and a half ago, philosophical commentary on natural selection rather rarely interested biologists, who were understandably impatient, for example, with endless variations on the old tautology complaint. Equally, biologists' disagreements over genetic drift, the classical and balance theories, group selection, and so on attracted little attention from philosophers.

I am much indebted here to discussions with John Beatty, David Hull, Larry Laudan, Rachel Laudan, Ernst Mayr, Bernard Norton, Michael Ruse, Sam Schweber, and John Turner. For the excellent interdisciplinary opportunities provided by two Bielefeld conferences, I am very grateful indeed. The present chapter incorporates material from an earlier piece, where some historical points were treated somewhat more fully: "Law, Cause, Chance, Adaptation and Species in Darwinian Theory in the 1830's, with a Postscript on the 1930's," in M. Heidelberger, L. Krüger, and R. Rheinwald, eds., *Probability since 1800. Interdisciplinary Studies of Scientific Development* (Bielefeld: Universität Bielefeld, 1983), pp. 287–330.

Happily, this phase is now past, as anyone will know who reads in such journals as *American Naturalist*, *Annual Review of Ecology and Systematics*, *Biology and Philosophy*, *Journal of Theoretical Biology*, *Paleobiology*, *Philosophy of Science*, *Studies in History and Philosophy of Science*, *Synthese*, and *Systematic Zoology*. For there one finds the technical resources provided by both biology and philosophy often combined and applied to problems of common concern to the two disciplines.¹

This chapter aims to contribute to this most welcome trend. But it does not set out to do so directly. Rather the hope is to clarify the probabilistic character of the theory of natural selection, as it concerns biologists and philosophers alike, by beginning from a point of departure that lies within the discipline of neither party.

This point of departure is an historical one, namely, Darwin's original understanding of the theory of natural selection as a causal, empirical, and so explanatory theory. There will be, however, no concern with history for its own sake, nor any attempt to settle current disputes by invoking venerable authority. Instead, it will be argued that Darwin's conception of the character of the theory is still appropriate today, because it conforms to what is common to the best explications of the theory given of late by biologists and philosophers. Accordingly, the proposal will be that those developments in this century—most notably in Mendelian population genetics and molecular biology—that have made the current versions of the theory no less causal, no less empirical, and no less probabilistic have also made Darwin's original conception of what kind of theory it is more, and not less, instructive.

Although this is a historical proposal, albeit an overtly normative one, it will not be defended by offering a narrative analysis of developments from Darwin to Dobzhansky and beyond. For it will be proposed that we can abstract and generalize, from the century and a quarter since 1859, and insist that answering certain enduring clusters of questions in certain ways has always been characteristic of any thoroughgoing commitment to natural selection as a theory of evolution.² The principal thesis will be, accordingly, a very simple, even simple-minded, one, namely, that in trying to understand the theory of natural selection, whether in the original Darwinian or in any subsequent neo-Darwinian context, it is always best to follow Darwin's own strategy and concentrate on distinguishing some four clusters of questions:

1. *The definition question*: What is natural selection? How is this process (or agency or force or whatever) to be defined?
2. *Existence, that is, occurrence and prevalence, questions*: Does it exist, is it going on anywhere? How widespread, how prevalent is it? Among what units and at what levels—organisms, colonies, species and so on—is it occurring?
3. *Competence, that is, consequence and adequacy questions*: What sorts, sizes, and speeds of change does it suffice presently to produce? What are its possible and actual consequences?
4. *Responsibility, that is, past achievement questions*: What has it done? For how much of past evolution has it been responsible? What is to be explained as resulting from it?

Obviously, such question clusters might be distinguished in other ways. But this way will serve our purpose here. For it will be argued throughout this chapter that any correct answers to the definition question will have as a corollary that all the other three clusters concern empirical questions, albeit very diverse questions, about probabilistic causal processes, questions that can be given answers that are testable in principle if not in practice.

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Before proceeding to argue for this thesis, however, mention should be made of three analytic resources that will be deployed in due course.

First, I have not assumed the privileged correctness of any particular account of testability, whether Carnapian, Popperian, Duhemian, or whatever. But I have assumed what I take to be accepted by most accounts of theory testing, namely, (a) the elementary logical point that “denying the consequent” is valid or deductively correct while “affirming the consequent” is not, so that a statement’s truth is not validly inferred from the truth of its consequences, while its falsity is validly inferred from their falsity; (b) the familiar epistemological point that theories can often only be made to have testable predictions as deductive consequences by conjoining them with additional auxiliary hypotheses, so that the elementary logical contrast does not in itself sanction any methodological imperative whereby predictive errors should always be instantly accepted as conclusively falsifying the theory rather than the auxiliaries; (c) the obvious methodological point that, in judging the respective merits of two or more theories confronted with some observational reports accepted as facts, we have to evaluate, among other things, the different sets of auxiliary hypotheses that need to be conjoined with those respective theories if they are to predict those facts.³

Second, I sometimes distinguish between something being true as a matter of definition or meaning and something being true as a matter of fact or experience. Now, thanks especially to the teachings of Quine (whose own position has shifted more than is usually appreciated), all such distinctions are often held to be difficult to defend.⁴ However, my uses of them do respect these difficulties. For it is not assumed here that something is definitionally rather than factually true independently of all contextual considerations; with changes in the theoretical context, especially, one might well want to revise earlier judgments as to what is best taken as definitional and what as factual. But that possibility only confirms that one can often clarify the assumptions constituting the theoretical framework current at any time by seeing how they make it reasonable to draw the line here rather than there. To drop all such distinctions would thus be to forgo needlessly a very useful source of light on those assumptions themselves.

Third, in conformity with Salmon’s developments of Reichenbach’s views, I take a causal process to be a physical process, one wherein energy is transformed and transmitted, and one whose later temporal stages can be altered by interfering with earlier stages.⁵ Thus, by contrast, an abstract, mathematical “process,” whereby

successive numerical values are "generated" by an algorithmic "operation," is not a causal process because not physical, while the successive positions of a shadow passing over the ground do not form a causal process because no alterations of later positions can be wrought by actions at earlier ones. Among the successive stages of a causal process there hold relations of causal relevance. And, in conformity with recent explications of what it is to be a causal factor, Giere's, for instance, I accept that relations of statistical relevance cannot in and of themselves constitute causal relevance.⁶ Accordingly, I assume that insofar as a demand for explanation is construed as a demand for an identification of what is causally relevant to what is being explained, then neither mere mathematical representations nor purely statistical description can by themselves meet this demand.

Finally, I should emphasize that I have not brought to this analysis of natural selection theory any one philosophical account of what a scientific theory is: the "received view," for instance, dominant in the heyday of logical empiricism, or its more recent rival, the "semantic view." Both of these have been shown to clarify some leading features of Darwin's own and later evolutionary theorizing.⁷ But no one such view is uniquely helpful in exhibiting the most instructive continuities in the roles of probabilistic notions in natural selection theory as those roles have developed over the last century and a quarter.

3

On going back now to our starting point in Darwin's work, it will be evident that for my purposes here it is not necessary to read into his writings any philosophical resources developed only in our own times. On the contrary, if our understanding of natural selection theory is eventually to benefit from those resources, we need to begin by taking Darwin on his own terms. We need an analysis of the problems he saw natural selection as solving, an analysis that brings out why he deliberately gave his argument for natural selection a very distinctive structure.

The structure is most easily discerned by comparing *On the Origin of Species* (1859) with its predecessors, the manuscript *Sketch* of 1842 and *Essay* of 1844. Then it is apparent that Darwin knowingly conformed his argument to the *vera causa* ideal for a scientific theory.⁸

The phrase *vera causa* meant not the true cause but a true cause, that is, a real cause, one known to exist, and not a purely hypothetical cause, merely conjectured to exist. So, the *vera causa* ideal, as Darwin sought to conform to it, required that any cause introduced in a scientific theory should be not merely adequate to produce the facts it is to explain on the supposition that it exists. For the existence of the cause is not to be accepted on the grounds of this adequacy. Its existence should be known from direct independent evidence, from observational acquaintance with its active presence in nature, and so from facts other than those it is to explain.

This *vera causa* ideal had been first given this formulation in the Scots moral and natural philosopher Thomas Reid's teachings on the import of Newton's first rule

of philosophizing, the one that specified that no causes are to be admitted except such as are both true and sufficient to explain the phenomena.⁹

Reid, going beyond Newton's own understanding of this principle, used his novel explication of it to argue for the conclusive epistemic superiority of the Newtonian gravitational force over the Cartesian ethereal vortices as explanatory of the planetary orbits. That force with its determinate law, unlike those vortices, was a well-evidenced cause for the orbits up there, because the orbits themselves were not the sole evidence for its existence. It was a real and true cause, not a hypothetical and conjectural one; for it was known to exist from our direct and familiar experience of swinging pendulums and falling stones down here on earth.

It was the teachings of Charles Lyell, in the three volumes (1830, 1832, and 1833) of his *Principles of Geology*, that mediated between this Reidian *vera causa* tradition, in the epistemology of physics, and Darwin's understanding of what evidential demands would have to be met in solving the problem of the origin of species.

All the causes of change on the earth's surface were presumed, in Lyell's system, to persist undiminished in intensity, and so in efficacy, into the present, the human period, and on into the future. Now, as at all times, habitable dry land is being destroyed by subsidence and erosion in some regions, while it is being produced by sediment consolidation, lava eruption, and elevatory earthquake action in others. Likewise, there is a continual, one-by-one extinction and creation of animal and plant species, a constant exchange of new species for old, adequate to bring about a succession of faunas and floras in the long run.¹⁰

Lyell's most explicit rationale for this presumption of the persistence of all such causes of change into the present and future was the ideal of explanation by *verae causae*, causes known to exist from direct observational evidence independent of the facts they are to be invoked to explain. Accordingly, his system was to exemplify, no less explicitly, an epistemological analogy. In geology, only causes active in the present, human period are accessible in principle, although often not in practice, to direct observation. So, in this science, the brief human present is to the far vaster prehuman past as the terrestrial is to the celestial in Newtonian physical astronomy.

We have here, then, in this *vera causa* ideal the source for Darwin's structuring his argumentation in the *Origin* as he did. For, to conform to this ideal, the argumentation on behalf of a causal theory had to make three distinct evidential cases: for the existence of the cause, for its adequacy for facts such as those to be explained by it, and, finally, for its responsibility for those facts. Thus the first two cases, in establishing that the cause exists and can produce effects of the appropriate sort and size, would constitute argumentation showing what the theory is, what cause it introduces, that it is a true theory, one of a true cause, and an adequate theory, one of a true cause capable of such effects, and so no mere conjectured hypothesis, while the third would constitute its verification, as the true theory for the particular facts it is to explain.

As anyone who has consulted the *Origin* will recall, the one long argument of that book does indeed make three distinguishable evidential cases for three theses about natural selection: first, that it is a really existing process, one presently at

work in nature; second, that, as it now exists, it is adequate for the adaptive formation of species and their adaptive diversification, in the very long run, into genera, families, and so on; third, that it has probably been the main agency in the production in the past of the species now extant and of those extinct ones commemorated in the rocks.

Thus the first case evidences both a tendency in wild species, as in domesticated ones, to vary heritably in changed conditions, and a struggle for life wherein variant individuals are surviving and so reproducing differentially, as when domesticated species are bred selectively by man. The second argues for the ability of this natural selective breeding—so much more sensitive and sustained, precise, and prolonged than man's as it is—to produce and diversify species in eons of time and changing conditions. Finally, the third adduces many facts of various kinds—geological, embryological, and so on—about extant and extinct species; and it is argued that these facts can best be explained—most intelligibly connected by referring them to unifying laws, that is—on the supposition that this cause was mainly responsible for producing and diversifying those species in irregularly ramified lines of descent diverging adaptively from more or less remote common ancestral stocks.

4

We have, then, to acknowledge that Darwin, in the *Origin*, was bringing to a problem in biology evidential and explanatory ideals first explicated, principally if not solely, in legitimating Newtonian celestial mechanics. But to acknowledge this is to raise at once an issue of immediate bearing on our efforts to understand the probabilistic character of Darwinian theory. How could Darwin have thought that such an ideal, originally legitimating the subsumption of the solar system under the laws of a deterministic classical mechanics, was at all appropriate to his arguments on behalf of a probabilistic causal process, natural selection as a cause for the adaptive formation and diversification of species? And, more generally, even if Darwin saw no inconsistency here, has it not turned out that Darwinian theory has developed since so as to make quite inappropriate his notion of the evidential and explanatory challenges raised by any commitment to natural selection as a theory of evolution?

These are questions that could be resolved by constructing and contrasting caricatures of "Laplacian" and "Darwinian" science, so as to secure a quick verdict, namely, that in its concern with what is "historical," "unique," "statistical," and so on, Darwinian science is utterly unlike any Laplacean program and must, therefore, have arisen in a repudiation of everything we associate with the French mathematician and physicist.

Nor surprisingly, to anyone who has studied how Darwin came to natural selection, while he was filling his *Notebooks* B–E and M–N in the years from July 1837 to July 1839, two decades before publishing the theory, this response is much too quick.¹¹ These decisive sources reveal a far more complicated history than this response can allow. Moreover, to see why these sources should do so, is to be in a

better position to decide how far such a response can be vindicated by what has happened to natural selection theory since Darwin.

In understanding how Darwin's notebook theorizing is related to the Laplacean heritage, or indeed to any prior precedents, it is indispensable to recognize that although Darwin had broken fundamentally with his mentor Lyell over the organic world, before *Notebook B* was opened in July 1837, he had not departed, nor would he ever, from Lyell's main teachings on the physical world of land, sea, and climate change.

On the physical side, then, Darwin remains in conformity with the Laplacean heritage. Lyell himself had revised but not repudiated the Huttonian theory of the earth, as it was upheld by John Playfair. A principal interpreter of Laplacean science to the British, Playfair, in his *Illustrations of the Huttonian Theory of the Earth* (1802), drew explicit analogies between Laplace's and Lagrange's conclusion as to stability in the solar system and the leading Huttonian thesis of a permanent stable balance in the actions of the igneous and aqueous agencies modifying the earth's surface.¹² John Herschel supported Lyell's neo-Huttonian position, in his *Preliminary Discourse in the Study of Natural Philosophy* (1830), and Darwin allied himself with Herschel in the late 1830s in efforts to construct a theory of crustal elevation and subsidence on the assumption that for the whole earth the forces arising from subterranean heating and cooling were balanced, and so subject only to reversible local fluctuations in the long run of the geological past, back at least to the time when the oldest known fossiliferous rocks were laid down.

Such commitments to stability and reversibility in the system of physical causation at work on the earth's surface were upheld in the face of explicit dissent from those, notably Sedgwick and Whewell, who thought these analogies between celestial mechanics and geology profoundly erroneous. As Lyell saw it, however, to give up this stability and reversibility was to forgo the possibility of meeting the *vera causa* ideal in geology. If it is to be possible to have direct evidence of the real existence of a cause deployed in explaining some past effects recorded in the rocks, then it must be at work still today. And if its adequacy for such past effects is to be properly evidenced, then we should be able to presume that it could, indeed must eventually, reproduce effects of that character and magnitude in the indefinitely long run of the future. So, this reproductive adequacy requirement presupposed limited variability in the conditions of working of these persistent causes. For, a terrestrial world without that limitation would not be one where the same causes continued to produce similar effects because working in similar conditions. Lyell held, therefore, that such a terrestrial world would not be one safe for analogical inferences from the short human period to the vast, past, prehuman periods, the inferences that allowed one to bring those periods within a science of geology conforming to the *vera causa* ideal essential to all inductive science.

For the inorganic world of land, sea, and climate changes, Darwin was always to uphold this teaching as he found it proposed by Lyell and seconded by Herschel. So we have to ask how far, in developing his own quite novel account of the organic world to complement this Lyellian one for the inorganic world, he was in intent and in effect departing from the presuppositions made by such presumptions of stability and reversibility.

5

Here, we need to consider Darwin's theorizing over the year and a half before he arrived at the theory of natural selection late in 1838. For, when he eventually constructed this theory, he drew on views about chance and chances and about *verae causae* that he had already been working with explicitly.

From summer 1837 on, his theorizing was dominated by two theses: first, that all structural change, and so all adaptive change, is ultimately due to the effects of changing conditions on the impressionable immature organization possessed by the offspring of sexual as distinct from asexual generation; second, that the outcome, in the long run, of the changes wrought by changing conditions is an irregularly branched tree of life, wherein species are multiplied when lines split without ending and become extinct when they end before splitting. So, sex is the immediate means and the tree of life is the eventual result of adaptation to an earth's surface everywhere changing à la Lyell.¹³

Direct experience indicates, according to Darwin, that sexual generation leads to adaptive heritable variation in altered conditions; it may then be a *vera causa* for unlimited adaptive diversification with unlimited time and changing circumstances. Equally, common ancestry is a known cause for similarities among relatives, especially similarities not creditable to common adaptations to common ends. So, in the tree of life, the resemblances among the species of some supraspecific group, a genus, family, or class, may be explained as due to a common inheritance from common ancestors, while their differences will be largely due to adaptive divergences.

Darwin was led to reflect on chance and chances in the propagation of the tree of life by the very considerations that led him to prefer branching descent over special, independent creations of species.¹⁴

Lyell had had each species created independently of any other. The character of a new species was not determined by the structure and instincts of any older species already in the area. Rather, its character and so its supraspecific type are entirely determined by the conditions where it is being created together with those conditions it is destined to meet subsequently on later spreading into other areas. Here, then, conditions determine character not only through present needs but also prospectively, in that the species, thanks to divine prevision, is provided in advance for future contingencies.

It was from this view that Darwin dissented directly. A new species, he argued, has the characters distinctive of its genus thanks to heredity, to inheritance from older congeneric species already present. And it owes the structures and instincts distinguishing it from its congeners not to any provisional adaptation to conditions not yet encountered, but to those conditions encountered during and so determining its divergence from those ancestral stocks.

To see how this alternative to provisional character determination by conditions led Darwin to reflect on chance and chances, consider how he used his new tree of life to reinterpret and extend various demographic analogies expounded by Lyell. For Lyell had developed an analogy between the births and deaths of human

individuals and the coming and going of species as quasi individuals. The intermittent recording in any region of species births, lives, and deaths, by the fossilization process, was thus compared with the periodic visits of census commissioners to one place in the nation.¹⁵

Darwin continued such demographic analogies in his *Notebook B*, in elaborating his branching tree representation of species multiplications and extinctions. He dwelt, especially, on the quantitative implications of high average degrees of relatedness, many species, that is, descending from a few ancestral species, "father" species in his phrasing. With high degrees of relatedness and a constant total species population, the chances are small of any individual species having living descendant species a long time from now; and the causes determining which ones will succeed in doing so may be impossible to analyze, just as with two flourishing human families, today, where many causes, such as hereditary disease and dislike of marriage, may eventually determine that one family rather than another has living successors.

These same genealogical, demographic analogies are elaborated further in considering the wanderings and colonizations whereby species settle in fresh sites, such as new land emerging from the ocean. Here Darwin again opposes prevision and provision; for he argues that, in any generic or familial group, those species that colonize some area do so because they happen to be fitted for it by structures and habits already acquired in adapting to conditions previously encountered. One would expect, then, Darwin reflects, that by the law of chances, larger groups of species would supply more successful colonists than others.

It is likewise with the structural diversifications whereby an ancestral stock may have one or more aberrant species among its descendants, a ground-dwelling species, say, arising in a group, such as the woodpeckers, that was originally and is still predominantly arboreal. Here, too, Darwin opposes providential plans in favor of adaptive opportunities and successes that accord with circumstantial contingencies and so numerical chances; such an aberrant species has been formed when some one species among an ancestral group has succeeded in adapting to the aberrant way of life, successful aberrances happening, therefore, more often in larger than smaller groups of species.

Pursuing these quasi-demographic and quasi-genealogical concerns, Darwin considers two ways whereby the adaptation in a father species may be related to the adaptations in descendants. It could be, he reflects, that in adapting to its own circumstances the father species ensures the adaptation of the offspring species to its circumstances. Or, over the long run, it could be that a father species is adaptively influenced by a succession of changing circumstances and produces numerous varieties, among which the best adapted alone are preserved and diverge to become species.

So far, then, in his *Notebook B*, Darwin is considering adaptive variety and species formation, and supraspecific group proliferation, without relating these changes to the individual maturations that are distinctive of sexual reproduction, and that ultimately make adaptive variation possible. In *Notebook C* he does take up this challenge, and he starts with two possibilities.

On the first possibility, adaptive species formation would trace to the production of "chance offspring" characterized by some slight peculiarity and by exceptional vigor, so that, among the males, they would be eventually more successful than others in winning mates in competitive combat and in passing on their peculiarity. By contrast, on the second possibility, the first step is not a chance prenatal innovation in an offspring, but a postnatal change in habits in some parents—as when some jaguars are tempted to swim after fish prey, on their region turning swampy, the changes in structure thereby acquired then being transmitted to their offspring.¹⁶

Now, it is this second possibility that Darwin develops most fully in the next six months, from spring to autumn 1838.¹⁷ And in developing it, he continues his opposition to prevision and provision in adaptive species formation. For, although the structural variations acquired in habit changes are not chance variations or chance productions, they are initiated by chance encounters with new conditions, and not in planned anticipations of changed circumstances.

Darwin makes these corollaries of his habit theorizing most explicit in his *Notebook M*, begun in July 1838, where he reflects on the human will and its apparent freedom.¹⁸ For in higher animals, new habits may arise from willed responses to whatever conditions or circumstances are being encountered. So, if willings are uncaused and unlawful, then structural changes tracing to habit changes may be too. To avoid this conclusion, Darwin takes a resolutely deterministic line. Free will is to mind, he says, as chance is to matter; that is, in both there is a misleading appearance, but only an appearance, of a lack of lawfully determining causation. Accordingly, Darwin insists that all responses to whatever is encountered are determined by existing hereditary organization and prior education and so on.

This determinism is complemented by a no less explicit materialism whereby everything mental arises from determinate material causation. In particular, any mental traits can be transmitted without conscious awareness in the material organization passing from one generation to another. By being subsumed within the corporeal, mental changes, such as instinct changes, are brought within the general account given for all adaptive change.

Darwin's reluctance, at this time, to credit adaptive change to chance variation is not then due to any misgivings about chance productions in general and as such. For his determinism makes chance variations the products of lawful, albeit hidden, causation. And here he was in conformity with the customary view that chance congenital variants, polydactylous offspring, for example, were not uncaused but, in accord with the commonplace ignorance interpretation of chance, caused by unseen prenatal conditions. For Darwin at this time, the most evident drawback to chance variations as a contribution to adaptive species formation in the wild was their rarity. Breeders, he emphasized, could deliberately pair rare, chance, congenital variants together and so make and perpetuate a race distinguished by that peculiarity. But, in the wild, free crossing ensured that such rare, chance congenital variation is counteracted. This contrast between species, as formed adaptively in the wild, and the products of the selective breeder's art was, for

Darwin, reinforced by the reflection that the artificial, selected varieties were monstrous, not adaptive, being fitted not to natural ends or conditions but human purposes.

Nor did Darwin's thinking about chance variation in relation to species formation change on his assimilation of Malthus late in September 1838. For Darwin's immediate response was to see Malthusian superfecundity as complementing crossing in contributing to the adaptiveness of structural change in the wild. Crossing ensured that structure changes were adapted to the slow, permanent changes affecting a whole country in the long run of physical change studied by geologists. For, with crossing, any adaptive variation elicited by local fluctuating changes in conditions is eliminated through the blending in offspring of parental characteristics. Complementing this means of retention and elimination, the Malthusian crush of population ensures, further, that only variations that were adaptive for the whole life of the individual, from conception to adulthood, would be retained and so, in the course of many generations, embedded permanently in the hereditary constitution as structure is adapted to permanent long-run changes in conditions.

Such, then, was the drift of Darwin's thinking about chance and chances, in relation to sexual generation and the tree of life, before he came, most likely in late November 1838, to his positive analogy between artificial and natural selection as both means of adaptation, and so before he came to that deployment of probabilistic notions that is so characteristic of the theory of natural selection as known in the *Origin*.

Plainly, before the selection analogy was arrived at and before it transformed his thinking in decisive ways, he had already the conceptions of chance and chances that he would integrate in that analogy. Those conceptions had always been such as to rest on two assumptions for which there were ample precedents: first, that, in an individual, the future consequences of its properties may be determined by conditions that can arise independently of the conditions that produced those properties in it earlier in its life; second, that, in a population, physical property differences may be causally adequate to move outcomes away from what frequency differences, rarity and commonness, alone would determine.

To confirm that these assumptions were, in themselves, not innovative, consider how Darwin's conceptions of chance and chances relate to the old distinctions of chance, necessity, and design.

In accord with the ignorance interpretation of chance, Darwin is not ultimately working with a trichotomy of chance, necessity, and design, only a dichotomy between design and the rest. For, while he will judge a chance production unplanned, unintended, or undesigned, he will not call it uncaused. Although not known to be necessitated by discernible causal antecedents, it is presumed to be so, no less than is one of known necessitation.

As with chance, so with chances: only ignorance requires us to distinguish them from causes. Chances are what are determined by numbers, by quantitative differences, when as far as we know all else is qualitatively, physically, causally equal. When all we know of two families is that one is larger than the other, then we give it the better chance of having descendants centuries hence. As soon as we learn

that it is less healthy, that bet is off, for we now know a cause sufficient to shift the chances away from where they would be were the numerical difference all that nature was working with in determining what future will be produced from the present.

A distinction between accidental and necessary adaptations can then be upheld, by Darwin, as a distinction among productions that are, as all productions are, causally necessitated. For in an accidental adaptation, its productive causes are independent of its adaptive consequences, in that the conditions producing it are not those causing it to have consequences such as to make it count as adaptive. The fetal conditions producing extra length in some puppy's legs may be arising independently of the presence of the hares that make such legs post-natally advantageous. By contrast, a variant is a necessary adaptation if it is produced by the very conditions that make it advantageous, as in the thicker fur grown by puppies moved to a cold climate or the webbed feet developed by the swimming jaguars. Unlike necessary adaptations, then, accidental adaptations are chance productions, because they are produced by hidden causes acting early enough in life to be independent of the conditions encountered later, the conditions determining their advantageous consequences for survival chances.

In his conceptions of chance and chances, Darwin was not innovative; his leading distinctions relate in traditional ways to venerable contrasts between the accidental, the necessary, and the designed. We need next to see how, nevertheless, natural selection made a novel deployment of these conceptions.

6

As it emerged in late 1838 and early 1839, in *Notebook E*, Darwin's theory of natural selection made a dual deployment of chance and chances. Heritable variants sometimes arise "by chance," and among them will be some that have a "better chance" than the normal individuals of surviving to reproduce. It is thus a matter of chance as to what variations are arising in the conditions the species is now living in, but it is not a matter of chance as to which are most successful in surviving to reproduce.

Darwin did not have this dual deployment of chance and chances until he was explicitly drawing analogies between the selective breeding practiced by man and that going on in nature. To appreciate his own understanding of the place of these probabilistic notions in his new theory, it is necessary to consider his original rationale for developing these analogies as he did.

He seems to have come to these analogies, late in November 1838, in reflecting on sporting dog varieties, such as greyhounds; in these cases, man had not only made and maintained varieties adapted to his own purposes but also, in doing so, had given them structures and instincts that would be adaptive in the wild, in preying on hares, for example.¹⁹ Accordingly, Darwin was soon reflecting that the outward structural form distinctive of greyhounds could be produced by selective breeding away from all hunting and hares. So, he reasoned, the superior adaptive

power of the selective breeding going on naturally in the wild was not due to variation arising there differently from the case of domestication; rather, this superiority was due to the greater persistence and precision of the selection that would arise in a species making its living in the wild by hunting. So, those conditions of life would not be necessary for the elicitation of the requisite variation, but they would be determining the selective retention of it required for such an adaptation to be produced.

Going further, Darwin soon concluded that the conditions a structure was adaptive for would sometimes not be sufficient. To take an example he would elaborate later, he could not see how in an area the presence of woolly animals would affect the growth of plant seeds so that they became hooked and fitted for attaching themselves to the animals.

What Darwin's new theory did, therefore, was not to make changes in conditions less determining of adaptive change, but to make them less directly so. He was content to drop the thesis that conditions always had the power to determine adaptive change directly by working heritable effects upon growth and maturation, because the analogy with the breeder's art convinced him that adequate determination would come from the way different conditions determined chances of survival and reproduction among chance variants.

Darwin was used to considering the conjunctive chances of two rare chance variants coming together to breed and so to perpetuate their peculiarity.²⁰ He had emphasized that, in nature, their rarity made the chances very slight, there being no inherent tendency of like variants to pair together.²¹ So, on going over to selective breeding of chance variants in nature, Darwin was from the first concerned with the consequences of their rarity. He had long argued that, with the reproductive isolation of a few individuals, following migration to an island, say, the conservative effect of crossing could be circumvented as it was in the breeder's assortative matings. Selective breeding in nature was, then, for Darwin a cause that worked slowly because of the initial rarity of chance variants, and was effective despite the counteractive effect arising from the crossing of these new variants with commoner older ones.

In his new appeal to chance variation, Darwin was thus concerned not only with the lack of direct adaptive determination by conditions of variant growth in individuals but also with the determination, by frequency alone, of the populational fate of such variants, as long as no causal interactions were biasing their chances of survival and reproduction. So, natural selection was, from its very inception, a theory as to when and why frequency alone was not solely determining, because causes for bias in those chances were present.

As an agency working causally to bias population outcomes away from where frequencies alone would otherwise have them, nature as a selective breeder, in Darwin, may remind us of the demon in Maxwell.²² However, the resemblance must not be allowed to mislead us as to the contrasting rationales motivating the two theorists' essentially different proposals. Maxwell was concerned to dramatize how utterly improbable in nature is anything like the outcome secured by the

demon; for under all natural conditions there will be no such quasi-purposive interference as the demon exerts. By contrast, Darwin was out to establish that a quasi-designing form of selective breeding is an inevitable consequence of the struggle for existence and superfecundity, tendencies so ubiquitous and reliable as not to be construed as interferences at all.

These distinctive features of the theory were manifested vividly in Darwin's own earliest metaphors: of thousands of trials, that is, individual variations and struggles for survival over many generations, and of a grain in the balance, that is, of a consistent slight causal bias effective in a very long run in conformity with the law of large numbers.²³ Darwin did not need to have been a youthful aficionado of the gaming table, and of chemical paraphernalia, to find in loaded dice and tipped scales illustrations of the probabilistic causation constituting the process of change through the natural means of selection.

Darwin took the reiterated process of chance variants tried in the wild for adaptation, and so for causal bias in their chances of survival and reproduction, to be a quasi-designing process. At this time, he held ontogeny to recapitulate phylogeny; so he was also prepared to say that a growing mollusk was able to make a hinge for itself because it has in its heredity the innate, unconscious equivalent of a human craftsman's skill in making hinges, the skill gained by a long sequence of conscious trials, rejections of failure, and retention of successes.²⁴

One can say, then, that Darwin gave up having variation arise as "necessary" adaptations, as necessary effects of conditions, in favor of having it arise "accidentally" or "by chance," when and only when he came to see that its fate was under the quasi-designing control of a natural selection analogous to the skilled practice of the breeder's quasi-designing art.

Darwin's insistence on the analogy, ever thereafter, was no accident of expository tactics, but an essential component in the original construction of the theory. What he did give up later, before the *Origin* (1859), was his early thesis that the maturation distinctive of the products of sexual generation was what made possible all hereditary adaptive variation. He went over to the view that the production of the male and female elements, ovules and pollen in plants, eggs and sperm in animals, was a disruptible budding process that could provide chance variation with which natural selection could work perfectly well. So, instead of the variation that made adaptation possible arising in a proper, distinctive, functioning of sexual reproduction, it now arose in disruptions of the replicative function common to all generation, sexual or asexual.

There was thus no inconsistency between Darwin's commitment to the old ideal of known causes and his acceptance of the venerable ignorance interpretation of chance. It was only in the interpretation of the production of chance variation that Darwin invoked this ignorance; and in doing so he did not preclude arguing that the process of selection of that variation counted as a *vera causa*, a cause known—from the struggle for life—to be existent in nature, and known—from the breeders' results—to be efficacious in producing permanent adaptive change in structures and instincts.

7

We are now in a position to see more clearly how Darwin's theorizing, with its twofold invocation of chance and chances, stands in relation to the legacy of the physical sciences as found in Laplacean exemplars.

For a start, we can see the disadvantages in one tempting historiographic view of the probabilistic elements in Darwin's theorizing: the view that insofar as Darwin retained deterministic, nomological commitments to reversible, stable causation, he was still in the thrall of those Laplacean physics precedents, while, by contrast, insofar as he took seriously chance occurrences, accidental changes, statistical trends, circumstantial contingencies, and the like, he was being liberated from this thrall by those influences on him that came from the sciences of man and society, from Fergusonian conjectural history, Hartleyan associationist psychology, Queteletian societal arithmetic, Malthusian demographic theodicy, and the like.

This view is attractive because social theory obviously reflects social practice, so these influences could provide the mediation whereby Darwin's science was conditioned by his society, in accord with presumptions long made by many sociologies of knowledge.

The trouble with this view is that it tends to reduce all the diverse biological concepts of the early nineteenth century to so many echoes, emulations, borrowings, projections, extrapolations, analogies, and metaphors from physics, on the one hand, and social science on the other. And such reductions are very difficult indeed to square with all the traces we have of Darwin's deep indebtedness to rich traditions in physiology and natural history concerning vital forces, generation, geography, and so on. Moreover, it is surely arbitrary, as well as half-hearted, for a sociology of knowledge to presuppose that scientific theories are conditioned by their social context principally insofar as they are indebted to overtly social theories. More consistent and confident presuppositions for a whole-hearted sociological historiography would not require reading biological concepts and contexts out of the intellectual narrative, but would take them, and the physical science sources, too, as all suitable subjects for social conditioning, social construction, or social relations analyses.

To see one way whereby biological considerations led Darwin's theorizing away from the precedents set by the physics of the day, we may consider how heredity, for Darwin, could ensure long-run irreversibility. In Lyell, species losses, extinctions, are not reversible, in that no individual species returns once extinct; but any supraspecific group losses are reversible, for such a group may come to be represented again on the earth after a period when it has been temporarily missing. For that group, a genus or family or whatever, will reappear when conditions have changed, so as to be once more fitting for the creation of species with the structure and instincts characteristic of that group.

Darwin added heredity in explaining the spatial and temporal representation of supraspecific groups on the constantly changing Lyellian earth's surface. In doing so, he gave a genealogical interpretation of classificatory groups that denied the possibility of any reversibility such as Lyell upheld. For Darwin,

each supraspecific group has a single father, a monophyletic ancestry; and the assumption that a particular species never returns is extended to wider and wider groups, through the assumption that no group could ever arise again from a different future father species. This contingent impossibility was, for Darwin, confirmed by considering the cumulative changes in the lines leading from the simplest, remotest ancestral animals to the highest: birds and mammals. Here, he argued that heredity worked so that the oldest characters were most deeply embedded in the constitution, and so least susceptible to loss or alteration later. New characters would thus be added to these older ones and not substituted for them. The irreversibility of splitting and branching divergences likewise depends, for Darwin, on this same power of hereditary constitutional embedding, for inability or disinclination to interbreed depended on the accumulation and embedding of constitutional changes in two races descending from a common stock.

Heredity, although a principle of conservation, for Darwin, is therefore not at all closely analogous to the nearest equivalent principle in Newtonian physics: inertial mass. Nor, then, is the adaptive transformation and multiplication of species closely analogous to the outcome of successive actions of impressed forces on a body of constant mass. Selection, working with and complementing the powers of heredity, as Darwin judged it to do, was a force or cause with no close precedent in the exact sciences of the day.

However, in breaking with those precedents Darwin did not need, in his theory of natural selection, any new conceptions of chance and chances. As his heredity, adaptation, and selection theorizing developed, his twofold deployment of chance and chances could be made without breaking with available conceptions of these two.

Darwin could see natural selection as a *vera causa* because of his understanding of the relations between the short run and the long, especially as those relations were illumined by the analogy between artificial and natural selection. In the short run, in the hands of expert human practitioners, selective breeding was a causal, quasi-designing process with an approximately predictable outcome, in any instance, given a prior knowledge of the materials and the objectives. Superfecundity and the susceptibility of heredity to disruption in altered conditions entailed that an analogous process existed in nature, while comparison of that natural analogue with the achievement of the breeders indicated that, if they could produce marked racial differentiation in the short run, nature could produce distinct and diversely adapted species in her longer run.

There was the implication that the changes wrought by any selective breeding of hereditary variants would become less and less predictable, as one moved away from the shortest of artificial runs to the longest natural ones, but that loss of predictability was entirely tolerable, because Darwin was not seeking a theory as to why organisms of one particular group would tend to have descendants of another particular group: why fishes tend to have mammal descendants, or mastodons elephant descendants. There was for him no tendency in such descents, as so described. They had only happened once and were not expected to be repeated.

The ramifying, diversifying, complexifying tendencies for which Darwin sought

adequate causation were general and so could be introduced with referential anonymity. His tree diagram, in the *Origin*, is labeled abstractly with letters and numbers, not proper names, so that it can represent generalizations about types of trends. To fail to appreciate the implications of this generality and abstraction is to misunderstand the entire Darwinian enterprise in the *Origin* and ever since. For their most general explanatory purposes, the generalizations Darwin and his latter-day successors have needed to establish have had to indicate, for example, when adaptive divergence rather than convergence was more, rather than less, likely to occur, or when extinctions rather than species splittings are to be expected.²⁵ And, in this generality and abstractness of its predictive and explanatory functions, Darwin's natural selection was in conformity with such exemplary *verae causae* as the gravitational force.

There was a break with the gravitational theory precedent, however, in that there was no law that was to natural selection as the inverse square law with proportionality to mass products was to that force. For gravitation, this law enabled the exact consequences of that force to be deduced for certain simple, suitably specified cases of one mass in motion around another in an otherwise empty universe. Natural selection has no equivalent law because its very existence requires, causally, processes of reproduction, heredity, and variation; and while these processes may be and were presumed to be conforming to laws of their own, they cannot exist and conform to those laws in an empty universe void of complex interactions between what is changed and the conditions determining how it is changed.

These sources for the lack of any equivalent for the gravitational law do not entail that selective breeding is on all occasions as likely to produce one outcome as another. Indeed, Darwin does not have to deny that, if on some occasion exactly the same heredity and variation were to be subject to exactly the same selection as on some earlier occasion, then the outcome would exactly resemble the earlier outcome. However, it is not a possibility that will ever be approximately instantiated. What Darwin needs, for his explanatory purposes, is the presumption that the departures from the impossible sequence specified by that assumption are not capricious, but are occurring because of causation similar in kind, although different in degree, from those producing the controllable, approximately predictable results of the animal and plant breeders.

That the existence of natural selection requires the causal processes of heredity and variation shows that there is no Anselmian demonstration possible for its existence from its essence, no demonstration in the style of Anselm's ontological proof for God's existence, which argued that His essence, as completely perfect, must necessarily include the perfection of actually existing. In the *Origin*, Darwin introduced the term natural selection, definitionally, after he had argued for the existence of the process in nature. And so he proposed natural selection as an appropriate name because the process was analogous to artificial selection. But this analogical definitional procedure presupposed no Anselmian aim of making selection exist in nature by virtue of its very essence as stated in its definition. On the contrary, Darwin argued for the appropriateness of the name because of the character of the process—arising from heredity, variation, and the struggle for

existence—as already shown to exist in nature. He did not argue for its existence on the ground that its definition was such as to make that name appropriate.

We have seen how Darwin deployed traditional conceptions of chance and chances in a *vera causa* solution for his often unprecedented problem situation. And in doing so we are brought to see that it was intrinsic to his whole enterprise that he take up in certain distinctive ways various clusters of questions about the definition, the existence, the competence, and the responsibility of natural selection as a cause of evolution. We do well to work with such question clusters even after leaving Darwin behind.

8

On considering the first of these four clusters of questions, it will be evident that there are many ways to construe the definitional task it sets us. But that is only to be expected. Biologists call natural selection various things: an agency, a process, a factor, a cause, a force, and so on. Philosophers, meanwhile, always insist that definitions themselves come in several genres, although they rarely agree on what those genres are. The possible permutations are, therefore, plentiful for anyone proffering a definition of natural selection.

For our purposes here, however, one construal of this definitional task makes the best point of departure, for it introduces us directly to the issues of chance and causality raised by Darwin's and later versions of natural selection as a theory of evolution. On this construal, we confine ourselves, for a start, to intrapopulational selection of heritable traits distinguishing individual organisms. We take this selection to be a process, and we do what is always instructive for any process, namely, define it by stating the conditions necessary and sufficient for the process to occur. Such a definition allows us to integrate current textbook expository practices with longstanding themes about fundamental principles.²⁶

In textbook presentations of definitions for natural selection, it is instructive that everything goes along standard lines only up to a certain stage, and then different authors tend to go in one of two directions. Thus, as to necessary conditions, there is agreement that these include variation, heritability of variation, and differential reproduction of heritable variation. So we quickly reach differential reproduction of hereditary variants as indispensable to the definition, because necessary for the process. Moreover, there is almost always explicit recognition that some further condition is necessary, so that once this is given there will be a set of necessary conditions that are jointly sufficient. The need for the further condition is apparent, because in a finite population of hereditary variants, even without selection, there will be differential reproduction in genetic drift, that is, in the accumulation of any successive indiscriminate or random sampling errors in the same direction. And such drift must not be allowed to count as natural selection.

However, in proposing a further condition to distinguish selection from drift, some framers of definitions lay down that the differential reproduction in selection be "consistent" or "systematic" or "nonrandom," all terms with no peculiarly biological content and drawn often from the terminology of statistics, while other

authors insist that the differential reproduction must be due to differences in “fitness” or “adaptation,” terms characteristic of the biologists’, even formerly indeed the theologians’, lexicon, terms with an apparent teleological import.

Any diversity of definitional proposals reminds us that it is rarely easy to decide on what grounds one should be preferred over another. At a minimum, however, we have surely to take two sorts of considerations into account. First, there are judgments already being made, independently of particular definitional analyses, as to which real or imaginary processes count or would count as cases of natural selection. So, we need a definition that respects these judgments without merely reflecting them uncritically. Second, we should be guided by what has motivated the development of the theory of natural selection, and by what has influenced the way this concept is related to others, just as, to take another example, with the concept of mass in physics. For, with mass, awareness of the different presuppositions about space, time, motion, matter, and force, in Cartesian, Newtonian, and Einsteinian physics, has motivated decisions as to how to define mass itself and associated concepts such as weight, length, and so on.

Bringing these considerations to bear on natural selection, we are led, I shall argue, to one preferred resolution of the disagreements over what is needed, in defining selection, beyond differential reproduction of heritable variants. For we have to avoid two errors. On the one hand, we may be tempted to have a purely formal or mathematical restriction on differential reproduction in selection as distinct from drift: choosing a term such as “nonrandom” and then seeking for that term a purely formal or mathematical explication. On the other hand, we may be tempted to be finalistically biological rather than formalistically mathematical, and to require that the differential reproduction be due to differences in fitness or adaptation, with these terms explicated by reference to standards of design.

These two moves are errors, I submit, because their formalistic and finalistic quests lead us away from what is manifestly desirable: an explicit definitional insistence on causation itself, on, that is, its physical ingredients rather than on mathematical representations or teleological interpretations of its inputs and outputs. For, obviously enough, differential reproduction in selection is distinguished from any in drift by its causation; by contrast with drift, it is occurring because the physical property differences constituting the hereditary variation that is being differentially reproduced are not merely correlated with differences in reproduction—they are causally relevant to them.

When such causal relevance is present, we may call the differential reproduction nonfortuitous, a term better suited to biologists’ conceptions than nonrandom precisely on account of its connotation of causation rather than mere correlation. So, intrapopulational selection may be defined as what is occurring when and only when there is the nonfortuitous differential reproduction of hereditary variants.

9

To bring out the advantages in such a physicalist, causalist explication of the concept of natural selection, we may start with those corollaries of it that can be

clarified through elementary imaginary exemplars; then we can proceed to the issues raised by more complicated cases of intrapopulational selection, and by the extension of the explication to other levels, such as the interspecific. Elementary, imaginary scenarios are not to be dismissed as conceptually uninformative merely because they are unrealistic. The interactions that make up any process that counts as a cyclone are bafflingly complex, obviously; but to acknowledge this is quite consistent with holding that the concept of a cyclone is such as to be usefully explicated through its illustrative exemplification in elementary, imaginary scenarios.

Consider two small populations of butterflies. In both, the only variation is in color: half are red, half are green, and this difference is inherited. Both populations are living and breeding in green environments and only die from predation by birds. However, one population is preyed on by birds that are color-blind, the other by birds that are color-sighted. Now consider four particular runs of breeding and predation over several generations of the butterflies. In each population, it is found that there is one run in which the proportion of red butterflies goes down from a half to about a quarter, and one run where it rises to about three-quarters.

Presumptively, only one of these four runs involves selection rather than drift, because only in one population is the heritable color difference causally relevant to survival and so to differences in reproduction. Where the predators are color-blind, increases in red or in green are equally to be expected. In the other population the increase in red is presumably an unusual outcome, as the increase in green is not. However, even in this population, we have to admit the possibility that in a particular run the red butterflies may sometimes have been picked off at a higher rate by the color-sighted birds through the bad luck of landing up near the birds, perhaps at night, rather than as a result of being spotted on account of their color.

So, to presume that the differential reproduction in such a cause is nonfortuitous, rather than fortuitous, is to presume that in this environment this physical property difference is causally relevant to reproductive success.

In making this contrast between selection and drift, we maintain an obvious analogy with paradigm cases of discriminate versus indiscriminate samplings, when those samplings are considered as physical, causal processes. If a person, without looking, is picking balls out of a bag, some of them red, some white, and differing in no other property, there is indiscriminate sampling with respect to color differences, whereas if he is looking, and going for red ones deliberately, the sampling is discriminate. Even with indiscriminate sampling no ball jumps spontaneously out of the bag into the sampler's hand, out of the population and into the sample. So, likewise with the birds and the butterflies: no spontaneous uncaused deaths are occurring whether predatory sampling is indiscriminate or otherwise. What the balls, picked by the indiscriminate sampler from the bag, have in common is that they were in the right place at the right time to come to hand. And likewise, in indiscriminate predatory sampling, a disproportionate number of red or green butterflies may happen to be in the right place at the right time—or wrong place from the prey's viewpoint.

All these samplings, indiscriminate or otherwise, are physical, causal processes

with energy transformed and transmitted. So, it would be fallacious to think that because drift is a corollary of a mathematical property of the population, its finite size, while selection is a consequence of physical property differences among the individuals, it follows that drift is somehow a mathematical rather than a physical process. For selection in a finite population is sampling error, too, a discriminate sampling error. So, here, drift and selection are not to be contrasted as sampling with and without error, but as causally discriminate rather than causally indiscriminate erroneous sampling. An explanation that invokes drift invokes causation no less than a selection explanation does, but it invokes indiscriminate causation and so no causes of discrimination.

To explicate selection by contrast with drift allows for the indispensable distinction between selection for a property or trait and selection of a property or trait.²⁷ A property that is selected for is one that is itself causally relevant to its own differential reproduction. However, there will be selection of any properties that are correlated with one that is causally relevant, even though they are themselves not relevant causally. Thus if size differences are correlated with color differences and there is selection for color differences, then there will be selection of size differences, even if these size differences are not themselves of causal relevance, being only statistically relevant to this differential reproduction thanks to their correlation with those for which there is causal discrimination and so selection.

Defining selection as nonfortuitous differential reproduction is consistent with accepting that the instantiation of fortuitousness is description relative, so that, in our drift scenario, the deaths of the red butterflies were not fortuitous events *qua* deaths of butterflies, but were *qua* deaths of red butterflies in a population also including green ones preyed on by color-blind predators in green surroundings. For, even with such description relativity, it is still an empirical, causal matter whether a particular process of differential reproduction instantiates some description under which the process is not^{*}fortuitous.

Again, explicating selection by contrast with drift allows for—indeed encourages—the admission that in real life the ecology and genetics of butterflies and their predators may include some changes that are equally plausibly categorized as selection or drift.²⁸ Once one considers such familiar complications as linked genes, correlated responses to selection, patchy environments, frequency dependent effects, habitat preferences, and so on, it is possible to think of scenarios for which it is impossible to draw a sharp line between fortuitous and nonfortuitous differential reproduction. But, here, as always, it is to be emphasized that such impossibilities do not nullify the rationales for making the conceptual distinction.

To see why the distinction is indispensable, consider what sorts of causal theories of evolution are left once we have set aside orthogenetic and saltationist views that deny gradual change under the control of environmental conditions. To be schematic, we could draw up four options: two selectionist positions and two neutralist positions, where neutralism is the view that ascribes evolution to the populational fixation by drift of mutations that are adaptively neutral. For there would be Lamarckian selectionism and Weismannian selectionism, and likewise two versions of neutralism. Thus, in Lamarckian selectionism neither individual

generation of hereditary variation nor its populational fate would be a matter of chance in relation to conditions. By contrast, in Lamarckian neutralism the generation but not the fate of the variants would be a matter of chance.

Now, in the last half-century, Lamarckian views have declined greatly, the relation between phenotype and genotype implied by the molecular biology of protein synthesis making them very implausible in most eyes. So, to seek to define selection in contrast to drift, as one of two options to go with Weismannist presuppositions about hereditary variation, is now the more appropriate.

10

Such a definition is implicit in Wright's familiar classification of factors of evolution. He starts from the point that in any selection, by contrast with drift, the direction and amount of the gene frequency change increment may be determinate in principle; and he concludes that selection is a "wastebasket category" including all causes of directed change in gene frequency not involving mutation or introduction of hereditary material from outside. Biologically speaking, he stresses, it will include factors as diverse as differential viability, dispersal beyond the breeding range, fertility differences, and so on.²⁹

One advantage of this classificatory characterization of all selection is that we can circumvent the difficulties inherent in drawing lines between natural versus artificial selection or between natural versus sexual selection. This is an advantage, because insofar as all selection is nonfortuitous, drawing such lines is not desirable definitionally.

Another line, drawn within the category of selection, is inappropriate if our definitional proposal is acceptable; and that is Lewontin's suggested contrast between "tautological selection" and "functional selection."³⁰ In cases of the first, he says, we do not know why some genotype difference is subject to selection, but we think that it is and hence have to presume, tautologically as it were, that there must be some cause for its being so, while in the second the selection is arising from the known relation of a trait, such as color, to a known function, such as concealment from predation. Now, the very use of the unfortunate term tautological here may carry an unwelcome suggestion, albeit presumably unintended by Lewontin, namely, that if the causal workings constituting some selection are not manifest, then we are somehow reduced to asserting even the existence of this selection, Anselm style, for reasons to do with the way selection as such is defined. But by any reasonable definition this will not be so. For a process to be nonfortuitous rather than fortuitous, in the requisite sense, is for it to be so quite independently of how far we have succeeded in observing the causal bases for the causal relevance. There have been many cases—some chromosomal polymorphisms in *Drosophila* being once a famous one—where it was accepted that some genotypic differences are causally relevant to survival and reproduction differences, and so subject to selection rather than merely to drift; and yet it remained unknown as to how and why these genotypic differences are making for this reproductive success difference.

To conclude that there is causal relevance does not require knowing, much less observing, how it works. Many experimental routines with caged populations of *Drosophila* establish that, under some range of conditions, one genotype or karyotype will improve its frequency far too consistently for drift to be a credible explanation; and yet the causal basis for this consistent superiority in reproductive performance is undisclosed.

Consider next how this definitional explication of selection can be extended to levels other than the intraspecific. Here, one needs to keep constantly in mind the conditions that must be met if the different contrasts of Lamarckian versus Weismannian and selectionist versus neutralist are to work. Failure to keep them in mind has led to confusions. Thus, for instance, it is sometimes suggested that evolution in some prebiotic molecular systems is somehow Lamarckian. But in the absence of any distinction between analogues of germ plasma and somatic tissue, or phenotype and genotype, the contrast between Lamarckian and Weismannian modes of change loses all force. Again, we have been offered various games as models for selectional processes whereby life might originate. But on inspection, it often turns out that the games are equally good models for neutralist drift scenarios, in that there is differential reproduction but it is left open as to whether it is fortuitous or not.³¹

Going the other way, to higher levels of organization than the species, there are proposals current as to "species selection." The proposals appear to presuppose a quasi-Weismannist rather than quasi-Lamarckian view of the relation between changes in conditions and the generation of interspecific differences; and the term "species selection" indicates an implicit contrast with a species level analogue of drift. But the proposals would often be clearer than they are if the quasi-Lamarckian and quasi-neutralist analogues had been argued against more explicitly.³²

Hull has suggested that any selectionist proposal for any level can be clarified by insisting that it distinguish between replicators and interactors, examples of these being, respectively, genes and organisms at the familiar level of intraspecific selection. He emphasizes, what is more, that causal interactions, as a basis for consistent differential reproduction, are required, definitionally, if the process is to be properly called selectional. However, even Hull does not always sustain successfully the contrast between all selectional processes and any drift processes. Thus he defines a replicator as "an entity that passes on its structure directly in replication" and an interactor as "an entity that directly interacts as a cohesive whole with its environment in such a way that replication is differential." And he defines the selection process as one "in which the differential extinction and proliferation of interactors cause the differential perpetuation of the replicators that produced them."³³ Hull makes it clear, then, that he is as resolved as anyone to distinguish, causally, selectional from drift processes. However, the definition may not do this as it stands. After all, in our color-blind predation scenario there was differential extinction and proliferation of interactors (organisms) causing differential perpetuation of the replicators (genes) that produced them. So, once again, we need to insist that the differential perpetuation be caused nonfortuitously, that is, as a

result of the causal relevance for reproductive success differences of those particular physical property differences.

For, consider how a difference can fail to be causally relevant, how it may be causally neutral. A genotype difference may make no phenotypic difference, or it may make a phenotypic difference that the environment cannot detect and causally discriminate. By contrast, then, we should count as selection any differential reproduction of any genotypic variation that is occurring because of the causal effects of that genotypic variation. This will include, therefore, Lewontin's "tautological selection." All that some gene may do for its possessors is to enhance their enzymatic heat stability, and it may do this independently of any particular environmental conditions; but if its doing that makes a difference causally to reproductive survival, then its frequency must be credited to selection, not drift.

It will now be evident why the mathematics associated with the theory of natural selection may mislead us as to how to demarcate selection definitionally from drift. When the so-called coefficient of selection is introduced in textbooks, it is introduced merely as a coefficient of differential reproduction. So the manner of its introduction makes it equally applicable to differential reproduction in drift, provided that the drift has already occurred. Indeed, we can imagine a teacher of theoretical population genetics setting an instructive exam question. Here the student is told how some consistent differential reproduction in each generation has happened by luck, by drift, in some small population, and he or she is asked to use the mathematics introduced for selection to work out the resultant change in genotype frequencies. In an infinite population, granted, there is no random sampling error, and so any differential reproduction is selective, not drifting; and if the coefficients of selection are constant and all other sources of uncertainties are suppressed *ex hypothesi*, then the selection equations can be deterministic, not stochastic. It is only under such conditions that the so-called selection coefficient is appropriately termed; otherwise, it can mislead us in our efforts to understand selection as nonfortuitous by contrast with drift. It is on grounds of metaphysical presuppositions and empirical findings about causation, not for purely mathematical reasons alone, that we accept that deterministic equations become better representations of selective differential reproductions as population size gets larger.

Just as the implications of the mathematics of selection must be supplemented with physicalist and causalist notions as to their applicability, if they are not to mislead us in explicating the concept of selection, so with considerations of adaptation and fitness; these too will mislead us unless supplemented similarly.

11

There is no canonical explication of adaptation as it is understood in evolutionary biology. But there seems widespread agreement that adaptation is relative, in that an organism or an organ is not judged to be adapted unqualifiedly, but to be adapted or to be an adaptation, for example, to low rainfall or a herbivorous diet or for heat regulation or defense. Moreover, it seems accepted that such judgments

often presuppose decisions as to how to distinguish one feature from another in the organism, and also decisions about the problems, resources, and constraints involved in its way of life. Here, the application of what have been called engineering criteria of structural and functional efficiency are often thought to have heuristic value.

On all such proposals for the explication of adaptation, we would have two ways of relating adaptation to selection. We might define adaptation narrowly enough so that some variation not counting as adaptive could nevertheless be subject to selection. Thus we might decide that a heritable prolongation of the period of fertility is not an adaptive difference even though it has selectional consequences. On the other hand, we might make having selectional consequences definitionally part of what is meant by adaptation. Either way, however, what is indispensable to the concept of selection remains the same to this extent: whether some adaptive differences are judged to be selectional differences as a matter of fact or whether all are to be so as a matter of definition, a selectional difference may still be, by definition, only one that is causally relevant to reproductive success. Putting the point another way: we should define selection by contrast with fortuitous differential reproduction. And if we do that, we may—although I see no strong reason to do so—define adaptation in terms of selection so defined. And even if we did this, selectional explanations would not lose their force when given for structures judged to be adaptations. It would be an empirical question whether a particular structure was produced by selection or not. And that question could not be justifiably settled merely by declaring in advance of inquiry into its history that it is adaptive; because for that judgment to be justified one would have had to make that inquiry. So, whatever empirical or definitional relations we decide do hold between adaptation and selection, the appropriateness of a physicalist, causalist explication of selection is not compromised.³⁴

Turning now to fitness, we should note that many authors use this term more or less synonymously with adaptedness. But the concept of fitness that is of concern here is the one standard in population genetics, where the fitness of a genotype is defined in terms of the expected contribution of offspring made to the next generation by individuals of that genotype.

That fitness so defined is an expected quantity makes it appropriate to see it as a reproductive expectancy analogous to a life expectancy. Now, expectancies are in themselves not causal and so without explanatory content. If Jones has outlived Smith we cannot explain this difference by establishing that he earlier had the higher life expectancy and arguing that this duly caused him to live longer. It is physical differences that can make a causal difference and provide explanations; perhaps Smith smoked while Jones jogged. But expectancies estimated from physical differences can neither constitute causes nor provide explanations. For these reasons, it is misleading to conceive of fitness differences as causally mediating between the causes of a difference in reproductive performance and the difference in performance itself. We should not suppose that physical property differences somehow make organisms differ in fitness and that those fitness differences then somehow make them reproduce differentially. The contrasts between an expectancy and a

performance or outcome must never be overlooked. According to the reference class to which an individual is assigned, he may have a high life expectancy or a low one. A smoking jogger has one qua smoker, another qua jogger, and a third—not algorithmically computable from the other two—qua smoking jogger. Likewise, then, for the genotype of an individual organism when referred to its various allelic classes, it has many reproductive expectancies. But the organism eventually makes only one reproductive contribution performance, and that is free of all reference class relativity.³⁵

Because the relationship between fitness differences and reproductive performance differences is not causal and explanatory, we do not need one common but mistaken strategem in defending natural selection against the tautology charge. It is often thought that a successful defense depends on showing that fitness differences are contingently and fallibly rather than definitionally and infallibly related to performance differences. And it is often thought that to show this requires establishing criteria of fitness independent of reproductive success.³⁶ But this whole line of defense is mistaken because no such defense is appropriate. All that is needed if selection is to be saved from charges of tautology is that it be an empirical question as to whether any differential reproductive performance be nonfortuitously or fortuitously caused. Suppose in some case that the expectancy judgments are turning out false. As the tautology objector insists, they can always be revised retrospectively so as to be made true retroactively. But where the tautology objector and his opponent are both mistaken is in thinking that this point about fitnesses is decisive for the empirical rather than tautologous status of selection theory. What fitness estimates are being made ahead of time, and what revisions of them are made later, does not determine whether the physical differences the estimates are based on are or are not causally relevant to the reproductive performance differences. We now know that smoking is causally relevant to lung cancer, and to know this is to know that it is so whatever odds the life insurance companies are offering the tobacco companies' best customers.

In mathematical deductions of the consequences of a fitness having a given value, understood as an expected value, no epistemic gap, so to speak, between expectation and outcome ever arises. But this does not mean that the presence of such an epistemic gap is all that distinguishes real selection processes in nature from mathematical representations of them on paper. When we ask what it is that allows us to put some empirical content with the otherwise empty formalisms of the mathematics of selection theory, the answer should not refer to the riskiness as predictions of prospective estimates of fitness differences, but to the empirical status of our conclusions about causally relevant physical property differences.

Such an emphasis on these property differences can accommodate frequency dependent effects, as when a color variant in a prey population is at an advantage in survival and reproduction only as long as it is rare. In specifying the environmental conditions wherein a physical property difference has causal relevance to survival and reproduction, we may have to specify what the populational proportions of the variants are. But to do this is not to substitute mathematical for physical factors, for the frequency differences only make a causal difference because they

have different physical consequences for such processes as predator discrimination learning.³⁷

Considerations of fitness, then, its probabilistic and frequency dependent aspects included, bring us back to causation rather than away from it in any explication of what selection is, in the sense of how it is to be definitionally demarcated.

These considerations also confirm that it is fundamentally mistaken to answer the question as to what selection is by proposing that it is a law of nature, like a gas law, or, alternatively, that it is a framework principle, perhaps like the principle of the uniformity of nature.³⁸ In answering the question as to what natural selection is, we need only to insist that there is the term "natural selection," that the term's meaning can be given in a definition, that a concept is thereby explicated, and that when that is done natural selection is, definitionally, a kind of causal process, and so neither a law nor a principle. It is these reasons for this conclusion, as much as the conclusion itself, that are useful when we turn to those further question clusters concerning the existence and the competence and responsibility of natural selection for evolution.

12

The existence, competence, and responsibility questions are not independent of one another in every way. If selection does not really exist, it cannot be competent, nor therefore responsible for evolution. Again, if selection is judged to exist and to be competent for the job and is also thought to be the only conceivable cause competent, then it must be thought responsible. Thus Dawkins has argued along these lines for this last conclusion. His argument is not Anselmian, that is, solely from the essence of a cause, as expressed in a definition, to its existence; rather, as he acknowledges, it is in the Paleyan manner of the old arguments from and to design. For he argues that selection must have been responsible for evolution because no other cause could have done it. And his reasoning explicitly depends not only on premises concerning what selection is, definitionally, deemed to be, but also on premises concerning what anything adapted and complex enough to count as organisms will be like, whether here on earth or anywhere else where they have been produced.³⁹

What I ask to be conceded is thus merely that some answers to these questions leave the answers to the others open. If selection is judged to exist but not to be competent, then that rules out responsibility; but if it is judged to exist, that leaves competence as an open question, and if it is judged competent, that leaves responsibility open. For, by competence is meant competence for the sorts and sizes of change that the whole past course of evolution includes; and by responsibility is meant responsibility for these past changes. Obviously, if any selection exists in nature, it is having some consequences and so is competent and responsible for those consequences, but this does not imply competence and responsibility for evolution in the senses needed here.

It should be stressed that in this century, as in the last, the disagreements have

often been over matters of more or less rather than all or none. Neutralists, today, agree with their selectionist opponents that selection exists; but they think that there is less of it. They agree that it can produce and has produced some major changes. They agree with selectionists that manifestly adaptive structures such as vertebrate limbs should be credited to evolution by selection. They doubt, however, that selection can bring about changes as quickly as drift sometimes can; they also think drift responsible for much past evolution of molecular structures. Equally, for their part, selectionists admit some drift as existing and even as competent and responsible for some evolutionary changes.⁴⁰

The controversies between selectionists and neutralists have thrown into a clear light the relations among various answers to existence, competence, and responsibility questions. The controversies themselves, and the acceptance on both sides that empirical findings bear decisively if not conclusively on their resolution, undermine entirely any notion that natural selection as a theory of evolution is somehow forced on us a priori because it is merely tautological in the truth-functional sense of a logic text. If any such version of the tautological view were correct, selectionists and neutralists should have sought a verdict on their dispute using only a lexicon of definitions and a table of truth functions. As has rightly been observed, if selectionism is tautologous, then neutralism is contradictory.⁴¹ Any historical and philosophical analysis of natural selection as a theory of evolution must make plain why these recent controversies have not been about whether to prefer a tautology over a contradiction.

We may start by considering the existential issue. Here we should distinguish modest claims from sweeping ones, specific claims from general ones, and claims for one level from those for others. Thus someone might hold not merely that there is some selection going on, but that for most heritable traits there exist organism-environment interactions making those traits causally relevant to reproductive success. And such a general claim for intrapopulational selection might be matched by equivalent ones for interspecific selection, for example.

The generality of such a claim allows for it to be supported empirically in many ways. One might point to particular instances where selectional causation is established, and then argue that these instances are typical.⁴² Or, more in the manner of Darwin, one might argue that, from what is known generally concerning hereditary variation and concerning life, breeding, and death in natural conditions, it is probable that there is plenty of selection going on. And both lines have been taken, as can be seen from any recent survey of selectionist work.

The quantificational form of any claim may have implications for its testability: its verifiability or its falsifiability. And two points, familiar especially from Popper's teachings, should be introduced here.

The first, an uncontroversial corollary of what entailment includes, is a quite general one about falsification and verification. It is that one can falsify any statement deductively by falsifying what it entails, that is, by falsifying what can be deduced from it, but not verify it deductively by verifying what it entails, while, conversely, one can verify a statement deductively by verifying what entails it, but not falsify it by falsifying what entails it.

The second point, far from uncontroversial in its entirety, comes when Popper applies this first one to law statements. Law statements, he holds, have unrestricted universal form; the law that all metals expand when heated is universal and unrestricted in that it is about all metals and about them wherever and whenever they are, here today or on Mars a million years hence. Now, Popper insists that we cannot learn the truth of such a law statement through deductively valid inferences from any statements that we can verify. For we can verify only statements about the existence of finite numbers of instances of such a law, as we only have experiential access to these instances. However, we may have experiential access to a counterinstance, and so can learn the falsity of the law through a valid deductive inference from a statement of the existence of a counterinstance.⁴³

For law statements there is thus, Popper insists, an asymmetry; they are deductively falsifiable but not deductively verifiable. Moreover, for unrestricted existentially qualified statements the reverse holds. The unrestricted statement that there exist centaurs, somewhere at some time, is deductively verifiable by finding some centaurs at a particular time and place, but not falsified by not finding some at any particular time and place. And human experience is always limited, Popper holds, to finite findings at particular times and places.

For our purposes what is decisive, as Popper himself emphasizes, is that for statements that are not unrestricted these asymmetries do not hold. A restricted statement of universal form may be both falsifiable and verifiable, as the statement is that all the finite number of snails in my finite garden during this finite summer day are hermaphrodite. This can be falsified or verified by checking its finite instances. Equally, the statement that there exist now some fish in some particular pond is an existentially qualified statement that, thanks to its restrictedness, is both falsifiable and verifiable through finite observational findings.

We see, then, that if universal or existential statements are restricted in these ways, how easily falsifiable or verifiable they are depends on their content, it being much easier to verify or falsify a claim that there is an elephant in the room now than a claim that there is a gravity wave in the room now, or the claim that there was an elephant in Scotland in Roman times.

Now, as Popper seems to appreciate, testing natural selection as a theory of evolution involves testing claims that are restricted.⁴⁴ Consider even the very general selectionist claim that for most heritable traits there exist some organism-environment interactions making them causally relevant to reproductive success. This claim is of mixed quantificational form; the logic of *most* (very different from that of *all*, obviously) and of *exists* are both in play. But also we have to appreciate that there are several restrictions implicit in the content of the claim. Organisms cannot interact now with past or future environments, only with present ones; they cannot interact instantaneously with distant present ones. That the interactions are causal means that they are subject to restrictions that hold for all causation; further, as organism-environment interactions they are implicitly restricted even more.

Nothing I have said suggests that testing existence claims on behalf of natural selection is possible in practice, much less easy. The selectionist-neutralist controversy has highlighted the difficulties. But testability in principle cannot be denied.

13

There are many diverse issues involved in the competence question cluster. We have to distinguish between real competence, that is, the abilities of natural selection as it is found to exist in nature, and the hypothetical competence of selection as specified in abstract idealized models or imaginary scenarios. There is the obvious distinction between the short-run abilities of selection as experimentally accessible to us and its long-run powers. Again, very diverse questions can be asked about the ability of selection to cause equilibrium states or to cause change, to produce a particular sort of structure, such as the python's jaw, or to produce very general trends in adaptive diversification.

What is most instructive about the answering of all such questions is that nothing is thought to be true of all the workings of natural selection—except the definitional truth that they all include the conditions necessary and sufficient for selection to occur. In that sense there is no law of natural selection, no law of action for this cause.

One should not be surprised by this lack of law. For we would not expect all the cases of causal bias in the differential reproduction of hereditary variants to have anything in common that could be summarized in a statement of law, any more than we would expect all the cases of causal bias in any other sort of process to do so. A famous attempt to legislate for natural selection, Fisher's so-called fundamental theorem, only confirms this point. The proportionality it asserts between genetic variance in fitness and rate of increase in fitness only holds under some conditions, and so is not equivalent to the proportionalities asserted for gravitational attraction by Newton. As for the comparison Fisher made between his theorem and the second law of thermodynamics, this comparison is weakened on the same account. The reasons for his theorem not holding when it does not are not matched by any equivalent limitation on the applicability of the second law of thermodynamics.⁴⁵

It is tempting to say that there is no nondefinitional general statement of law to be made about all the workings of natural selection, because what its consequences are depends on what materials it is working with and what conditions it is working in. But this would be misleading in that it would suggest that natural selection is somehow an agency distinguishable from the hereditary materials and their interaction with their environmental conditions. And, of course, that is just what natural selection consists of—the processes of interaction—and that is why there can be no such general statement of law.

This lack of law does not make it impossible in principle to have well-confirmed generalizations about the workings of selection in specified ranges of conditions and with genetic systems of specified properties. And the contribution here of mathematical theory and experimental inquiry seems to be much as it is in most physical sciences.

Mathematics can provide the means for consequence extractions. And in this role it leaves open the status of the premises, assumptions, or axioms whose consequences it extracts. These premises can be completely conjectural or they can

be statements of more or less well-confirmed generalizations about what is found in nature. In either case, the issue of responsibility for past evolution may be left untouched. Fisher knowingly invoked all the phrases associated with the old *vera causa* ideal when he explained, in the preface to his *Genetical Theory of Natural Selection*, what his book was intended to do. For it was to develop, mathematically, the generally theory of natural selection without reference to the responsibility issue. Indeed, he emphasized in correspondence that most of his book would stand if the world turned out to be created a few thousand years ago as in the Bible account.⁴⁶

Many writers have dwelt on the deductive structures that can be given to the theory of natural selection. But what is meant and not meant by this has to be kept in mind. One may deduce a consistent differential reproduction in a postulated system of suitably variable, reproductive entities. In that sense a formal modeling of natural selection can be exhibited as a theorem derivable from an appropriate set of axioms.⁴⁷ Again, one can postulate that the conditions of Hardy-Weinberg equilibrium are satisfied by some Mendelian system, and one can then add supplementary specifications as to a coefficient of consistent differential reproduction, and so, much as in classical rational mechanics, deduce the equations for the resultant change.⁴⁸

The fact that deductive techniques of consequence derivation have such application to formal representations of selective processes does not mean that in the defining of natural selection, and in the asking and answering of existence, competence, and responsibility questions about it, biologists are matching closely what is done by physicists working with a theory, such as Newtonian gravitation theory, that has a force law intrinsic to its very formulation. However, framing and testing generalizations about the competence of natural selection is not made impossible by the lack of such a force law analogue. A causal process can have testable causal consequences, and the theory of such a process can have derivable logical consequences, notwithstanding that lack. *

Most natural selection theorists have, of course, wanted to go beyond questions about consequences, causal or logical, to the responsibility issue. They have sought to establish whether or not natural selection really did it, or at least most of it.

To establish this, more is required than merely making it plausible that selection could have caused evolution. Reconciling the supposition that it did with the fossil record or biogeographical data is not enough. Beyond that, from Darwin on, upholders of the theory have sought to show the explanatory superiority of that supposition over rival theories, in relation to such facts, and thereby to confirm that supposition itself. Insistence on some such link between explanation and confirmation has been a commonplace for centuries, and is not distinctive of biology, much less evolutionary biology. Nor is there a source of difficulty here that is sometimes thought to be peculiarly damaging to Darwinian explanations. For most structural or functional characters, it is easy to construct, imaginatively, some selectionist scenario for its production as an adaptation. Such scenarios have been deprecatingly dubbed "Just So" stories in recollection of Kipling's tale as to how, for instance, the leopard got his spots.⁴⁹ But, as the deprecators have appreciated, there is little that is surprising or distinctive about natural selection in the way it

lends itself to such exercises of imaginative ingenuity. To have any theory supply a reasonably confirmed rather than merely a conjectured explanation, it has to be supplemented with auxiliary assumptions, if only assumptions as to initial conditions, and these assumptions must themselves be independently confirmed from their own evidence.

In the standard cases, such as industrial melanism in moths or sickle cell anemia in man, the requisite auxiliary assumptions about the genetics of the variation and ecology of the interactions with the environment are evidentially pretty well secured. Securing such assumptions is never easy, and it is conspicuous that in very few cases indeed has this been done. There is a vast way to go if biologists are ever to have for the evolution of reptiles from their fish ancestors any selectionist explanation that is on a par, evidentially, with what they have for the melanism and anemia cases. But moving further toward such a goal is possible in principle, if often impossibly difficult in practice; and this shows that responsibility theses on behalf of natural selection are empirical theses, testable in principle.

14

In taking natural selection as a theory of evolution conforming to the old *vera causa* ideal, we are led, therefore, to appreciate the tremendous complexities inherent in any sophisticated articulation and thoroughgoing acceptance of the theory. Simple-minded though it may be, the approach suggested by that old *vera causa* ideal can show us clearly why such acceptance cannot be reduced to anything at all simple, such as "belief in natural selection or the survival of the fittest." The answers to the existential, competence, and responsibility questions involved in accepting the theory have always been highly complex answers, conceptually and evidentially, for reasons arising from the distinctive probabilistic, causal, and empirical character of the theory itself, as it has descended historically from Darwin's own exposition. Inevitably, many writers on the theory, even today, may think their analytical obligations to the theory can be largely met by formulating some single propositional expression of a "law" or "principle" of natural selection, exhibiting its "structure" and then arguing for its "status" as "falsifiable" or "nontautologous" or whatever. But such exercises cannot be counted as seriously engaging the theory as it has been developed, conceptually and evidentially, over the last century and a half. Equally, anyone working in some domain beyond evolutionary biology, whether linguistics, epistemology, or immunology, who wishes to represent his theorizing as Darwinian or selectionist, in some serious sense, should always be asking whether there are in his proposals any significant and not merely superficial analogues to the definitional, existential, competence, and responsibility issues that biologists have always had to face in making up their minds about natural selection.

This last declaration may seem to presume that there has always been a consensus among selectionists in biology over all fundamental matters. But, on the contrary, one virtue of approaching the theory from the old *vera causa* ideal is that we can see how the theory could be embraced and developed by people with strikingly contrasting metaphysical and ideological orientations.

Consider for a moment what diverse metaphysical and ideological attitudes toward chance itself are found within the Darwinian tradition. Darwin's own attitude was ultimately negative, in that he never saw the chanciness of chance variation as itself making a positive contribution to adaptation or progress. For him the decisive contrast was between the chanciness in the generation of chance variation and the determinacy in its populational fate insofar as that was directed by selection. Here, then, were echoes of all those schemes, such as Plato's in the *Timaeus*, with Manichaeian affinities. Variation, as chancy, is wild, chaos, error, so many failures of orderly replication, adding up to nothing when left to themselves, while selection is the cosmogonic, quasi-designing shaper of this otherwise helpless material.

Among dominant figures in our century, Fisher can be seen as largely perpetuating similar attitudes. Moved by Christian sympathies and thermodynamical preoccupations as well as eugenic zeal, he gave us a view of the living world as subject not only, as the inanimate world is, to the degenerative tendency entailed by the second law of thermodynamics but also to another, counterdegenerative agency, natural selection, so that this natural selection, although formally comparable, according to Fisher, with the second law, is, cosmologically, to be contrasted with it, as he emphasizes quite explicitly. Thus, for Fisher, gene mutations, as errors in gene replication, and drift, as erroneous genetic wanderings in populations, can never add up to anything by themselves except bigger errors and wider wanderings. So, on the variation side, where there rule such disordering tendencies as the living world shares with the inanimate world, small is beautiful; for small variations can be most precisely shaped by selection and made into what they cannot make themselves. To have small mutations in large populations is thus the optimal combination, for then drift is minimal and variation is plentiful, while even small selection pressures can control the outcome. Thus, too, was Fisher attracted to indeterminism, as required by free will and creativity in man. For, to exercise the possibility of free will and creativity is to master and direct, as natural selection does, what is, insofar as it is indeterminate, merely a material contribution to any adaptive progress, such as human eugenic advances.⁵⁰

By contrast, Wright, drawing on his Wundtian panpsychism and his shorthorn cattle breeding strategies, has seen chance processes as able, by virtue of their very chanciness, to contribute to the overcoming of the limitations arising from the determinacy of selection. For Wright, the stochastic exploration, by drift, of the field of variational possibilities can lead to a population moving to new adaptive peaks through selectional forces that would not otherwise have been brought into play.⁵¹ So, a population structure that entails such drift is in the long run more optimal than one that does not. One can even think of such a population structure as a quasi-designed error machine.

Likewise, sexual reproduction itself, when it includes meiosis, with its randomized combinatorial consequences, can be conceived of as a well-designed mechanism for making replicative mistakes at the individual level. So, from such reflections, a much more positive attitude toward chance can arise, one that allows for a teleology of chance. For, if the mechanisms, such as meiosis, that now supply

natural selection with its material, have themselves evolved by earlier selection, then the benefits of chanciness in variation, when changing through natural selection in an unpredictably changing world, are decisive for any understanding of how that evolution took place.⁵²

Finally, an approach to natural selection through the old *vera causa* ideal does not have to deny that the theory has often been championed and elaborated by people, such as Pearson, who have followed Comtean and other positivist precedents in repudiating the very notion that science can and should construct causal rather than correlational theories and laws. The contribution of Pearson and other biometrical correlationists included new quantitative analyses of variation and differential reproduction. However, such measurement and computation analyses could proceed purely correlationally, avoiding issues of causal discrimination and relevance, only as long as questions about adaptation and population size in nature were not confronted. For, when biologists of the Pearsonian persuasion, as Weldon was, sought to instantiate empirically their claim for the effectiveness of selection in changing structures gradually and adaptively, they appealed to the sensitivity and intricacy of organism-environment interactions, as providing adequate causes, and so explanations, for the preservation of particular structures in natural populations; and in making that appeal they never claimed to reduce all their causal judgments to correlational ones.⁵³ It should now be plain why such a reductive claim was not made. Statistics may be a science of probabilities and correlation may be a statistical measure; but it does not follow that natural selection insofar as it is probabilistic is correlational rather than causal. A historical view of the theory confirms what philosophical examinations and scientific expositions suggest; the theory arose as a probabilistic contribution to causal science, not as a rebellious rejection of causation in favor of science without causes.⁵⁴

A proper appreciation of Darwin's place in the probabilistic revolution can be enhanced, therefore, by recalling our own historical location. From Comte, in Darwin's day, to Hempel, in our own, empiricism in its more positivistic forms has construed the main questions about evidence and explanation in science as questions about universal statements of law rather than existential claims for causation. Darwin worked in an older, *vera causa*, tradition of empiricism than the Comtean one. We have had now two decades of philosophers priding themselves on seeing the limitations in any positivistic form of empiricism. So, perhaps, the present is an appropriate time to develop further the original interpretation of natural selection as a causal and empirical theory.

Notes

1. Two books by Michael Ruse introduce many of the issues and much of the literature: *Is Science Sexist? And Other Problems in the Biomedical Sciences* (Dordrecht and Boston: D. Reidel, 1981) and *Darwinism Defended. A Guide to the Evolution Controversies* (Reading, MA: Addison-Wesley, 1982). An invaluable collection of papers is now available: Elliott Sober, ed., *Conceptual Issues in Evolutionary Biology. An Anthology* (Cambridge, MA: The MIT Press, 1984). See also Sober's *The Nature of Selection* (Cambridge, MA: MIT Press, 1984), a masterly analysis of natural selection theory.

2. Peter Bowler brings out well the usefulness of analyzing enduring clusters of questions regarding evolution in his excellent study, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades around 1900* (Baltimore: Johns Hopkins University Press, 1983). In doing so he acknowledges direct debts to Stephen Gould.
3. For a lucid introduction, see R. Giere, *Understanding Scientific Reasoning* (New York: Holt, Rinehart and Winston, 1979).
4. S. Haack, *Philosophy of Logics* (Cambridge: Cambridge University Press, 1978), introduces the complexities in Quine's position.
5. See, especially, W. Salmon, "Causality: Production and Propagation," *PSA 1980: Proceedings of the Biennial Meetings of the Philosophy of Science Association* (Philosophy of Science Association: East Lansing, Michigan, 1981) vol. 2, pp. 49–69, and earlier papers cited there.
6. Giere, *Understanding Scientific Reasoning* and "Causal Systems and Statistical Hypotheses," in L. J. Cohen, ed., *Applications of Inductive Logic* (Oxford: Oxford University Press, 1980). Giere's views are discussed in relation to natural selection theory in an important trio of articles: E. Sober, "Frequency-Dependent Causation," *The Journal of Philosophy*, 79 (1982), 247–253; John Collier, "Frequency-Dependent Causation: A defense of Giere," *Philosophy of Science*, 50 (1983), 618–625; and R. Giere, "Causal Models with Frequency Dependence," *The Journal of Philosophy*, 81 (1984), 384–391. The contrast between mathematical and causal considerations is insisted on in E. Sober and R. Lewontin, "Artifact, Cause, and Genic Selection," *Philosophy of Science*, 49 (1982), 147–176, an article reprinted in Sober, ed., *Conceptual Issues in Evolutionary Biology* (note 1).
7. Ruse prefers the received view, for example, in the essay "The Structure of Evolutionary Theory" in his collection *Is Science Sexist?* (note 1). J. Beatty argues for the semantic view in "What's Wrong with the Received View of Evolutionary Theory?" *PSA 1980: Proceedings of the Biennial Meetings of the Philosophy of Science Association* (Philosophy of Science Association: East Lansing, Michigan, 1981) vol. 2, pp. 397–426.
8. M. J. S. Hodge, "The Structure and Strategy of Darwin's 'Long Argument,'" *The British Journal for the History of Science*, 10 (1977), 237–246.
9. L. Laudan, "Thomas Reid and the Newtonian Turn of British Methodological Thought," in his *Science and Hypothesis: Historical Essays on Methodology* (Dordrecht and Boston: D. Reidel, 1981), pp. 86–110.
10. R. Laudan, "The Role of Methodology in Lyell's Science," *Studies in History and Philosophy of Science*, 13 (1982), 215–249; M. J. S. Hodge, "Darwin and the Laws of the Animate Part of the Terrestrial System (1835–1837): On the Lyellian Origins of His Zoological Explanatory Program," *Studies in History of Biology*, 6 (1982), 1–106.
11. *Notebooks B–E* were published in G. De Beer, M. J. Rowlands, and B. M. Skramovsky, "Darwin's Notebooks on the Transmutation of Species," *Bulletin of the British Museum (Natural History). Historical Series*, 2 (1960), 27–200, and 3 (1967), 129–176; and *Notebooks M–N* were published by Paul Barrett in H. E. Gruber, *Darwin on Man* (New York: E. P. Dutton, 1974).
12. On matters concerning reversibility in this period, see S. G. Brush, *The Kind of Motion We Call Heat: A History of the Kinetic Theory of Gases in the 19th Century* (New York: North-Holland, 1976) and "Irreversibility and Indeterminism: Fourier to Heisenberg," *The Journal of the History of Ideas*, 37 (1976), 603–630.
13. For a more detailed account of Darwin's pursuit of these theories, see M. J. S. Hodge and D. Kohn, "The Immediate Origins of Natural Selection," in D. Kohn, ed., *The Darwinian Heritage. A Centennial Retrospect* (Princeton: Princeton University Press, 1986).
14. Darwin's early thinking on chance and chances has been discussed in S. S. Schweber, "The Origin of the Origin revisited," *The Journal of the History of Biology*, 10 (1977), 229–316, and in E. Manier, *The Young Darwin and His Cultural Circle* (Dordrecht and Boston: D.

- Reidel, 1978), pp. 117–122. For a comprehensive survey of notions of chance and chances in the biology of this period, see O. B. Sheynin, “On the History of the Statistical Method in Biology,” *Archive for the History of Exact Sciences*, 22 (1980), 323–371.
15. M. J. S. Rudwick, “Charles Lyell’s Dream of a Statistical Paleontology,” *Paleontology*, 21 (1978), 225–244, is an invaluable study.
 16. *Notebook C*, MS pp. 61–63 (note 11).
 17. See, further, Hodge and Kohn, “The Immediate Origins of Natural Selection” (note 13).
 18. See *Notebook M* in Gruber, *Darwin on Man* (note 11).
 19. For the details, again, see Hodge and Kohn, “The Immediate Origins of Natural Selection” (note 13).
 20. See his *Notebook D* (note 11).
 21. Compare, for example, the discussion of congenital variation in Darwin’s *Notebook C* (note 11), with the view of chance varieties in J. C. Prichard, *Researches into the Physical History of Mankind*, 2nd ed., 2 Vols. (London: T. Hughes, 1826), Vol. 2, p. 548. Whether Darwin had read Prichard by this time is not clear.
 22. S. S. Schweber, “Aspects of Probabilistic Thought in Great Britain: Darwin and Maxwell,” in Heidelberger, Krüger, and Rheinwald, eds., *Probability since 1800: Interdisciplinary Studies of Scientific Development* (Bielefeld: Universität Bielefeld, 1983), pp. 41–97.
 23. Hodge and Kohn, “The Immediate Origins of Natural Selection” (note 13), gives a fuller account of these metaphors and analogies.
 24. See, for example, Darwin’s notes on this, probably from March, 1839, published in Gruber, *Darwin on Man*, p. 420 (note 11).
 25. On the themes of this paragraph, see D. Hull, *Philosophy of Biological Science* (Englewood Cliffs, NJ: Prentice Hall, 1974). The view that evolutionary theory is not predictive is effectively countered in two articles by M. B. Williams: “Falsifiable Predictions of Evolutionary Theory,” *Philosophy of Science*, 40 (1974), 518–537, and “The Importance of Prediction Testing in Evolutionary Biology,” *Erkenntnis*, 17 (1982), 291–306.
 26. See, for example, F. J. Ayala and J. A. Kiger, *Modern Genetics* (Menlo Park, CA: Benjamin-Cummings, 1980), pp. 657–658, and D. J. Futuyma, *Evolutionary Biology* (Sunderland, MA: Sinauer, 1979), pp. 300–301, for careful attention to the definitional issue. For complementary emphasis on physical properties and property differences, see Sober and Lewontin, “Artifact, Cause, and Genic Selection” (note 6).
 27. On the importance of this distinction, see E. Sober, “Force and Disposition in Evolutionary Theory,” in C. Hookway, ed., *Minds, Machines and Evolution. Philosophical Studies* (Cambridge: Cambridge University Press, 1984), pp. 43–62.
 28. See the incisive analysis of discriminate and indiscriminate samplings in selection and drift in John Beatty, “Chance and Natural Selection,” *Philosophy of Science*, 51 (1984), 183–211.
 29. S. Wright, “Classification of the Factors of Evolution,” *Cold Spring Harbor Symposium on Quantitative Biology*, 20 (1955), 16–24.
 30. R. Lewontin, “Testing the Theory of Natural Selection,” *Nature*, 236 (1972), 181–182.
 31. See Beatty’s critique, in his “Chance and Natural Selection” (note 28), of a game proposed by Eigen and Winkler.
 32. J. Maynard Smith raises such questions about such proposals in “Current Controversies in Evolutionary Biology,” in M. Grene, ed., *Dimensions of Darwinism. Themes and Counter-Themes in Twentieth-Century Evolutionary Theory* (Cambridge: Cambridge University Press, 1983), pp. 273–286.
 33. D. Hull, “Individuality and Selection,” *Annual Review of Ecology and Systematics*, 11 (1980), 311–332—see, especially, pp. 317–318.

34. There is now a sizable literature devoted to adaptation. Two influential contributions by biologists are G. C. Williams, *Adaptation and Natural Selection. A Critique of Some Current Evolutionary Thought* (Princeton: Princeton University Press, 1966), and R. Lewontin, "Adaptation," *Scientific American*, 239 (1978), 212–230. See, further, R. N. Brandon, "Adaptation and Evolutionary Theory," *Studies in History and Philosophy of Science*, 9 (1978), 181–206. Brandon's article is in Sober, ed., *Conceptual Issues in Evolutionary Biology* (note 1), together with other related discussions of adaptation, including one by Lewontin. Many recent proposals are discussed in valuable analyses by R. Burian, "Adaptation," in M. Grene, ed., *Dimensions of Darwinism* (note 32), pp. 241–272, and by C. B. Krimbas, "On Adaptation, Neo-Darwinian Tautology and Population Fitness," *Evolutionary Biology*, 17 (1984), 1–57.
35. The literature on fitness also grows apace. In relating my suggestions to others, it would be best to start, perhaps, with R. Brandon and J. Beatty, "Discussion: The Propensity Interpretation of 'Fitness'—No Interpretation Is No Substitute," *Philosophy of Science*, 51 (1984), 342–357. There is much in the propensity interpretation, with its application of the propensity view of probability associated with Popper, that I can agree with; but a confusion surely remains precisely where we need to be unequivocal: are fitnesses as propensities causal and so explanatory or are they not? The difficulties inherent in population-genetic fitness definitions and measurements are discussed in R. Lewontin, *The Genetic Basis of Evolutionary Change* (New York: Columbia University Press, 1974); R. Dawkins gives an instructive attempt to relate population-geneticists' and ecologists' notions of fitness in his book *The Extended Phenotype* (San Francisco: Freeman, 1982), Chapter 10. For a fuller discussion of fitness and the reference class relativity of probabilities, see S. Mills and J. Beatty, "The Propensity Interpretation of Fitness," *Philosophy of Science*, 46 (1979), 263–286, reprinted in E. Sober, ed., *Conceptual Issues in Evolutionary Biology* (note 1). See also A. Rosenberg, "Fitness," *Journal of Philosophy*, 80 (1983), 457–473, and E. Sober, "Fact, Fiction and Fitness: A Reply to Rosenberg," *Journal of Philosophy*, 81 (1984), 372–383.
36. See, for example, S. J. Gould, *Ever Since Darwin* (Harmondsworth: Penguin Books, 1978), pp. 39–48, reprinted in E. Sober, ed., *Conceptual Issues in Evolutionary Biology* (note 1).
37. See Collier, "Frequency-Dependent Causation: A Defense of Giere" (note 5).
38. I can agree, then, with many points made by H. C. Byerly against E. S. Reed's proposal that natural selection is a law of nature; but I cannot accept his own suggestion that it is a framework principle: E. S. Reed, "The Lawfulness of Natural Selection," *The American Naturalist*, 118 (1981), 61–71; and H. C. Byerly, "Natural Selection as a Law: Principles and Processes," *The American Naturalist*, 120 (1983), 739–745. I am in full agreement with Beatty when he insists that there is no law or principle of natural selection. See his discussion in "What's Wrong with the Received View of Evolutionary Theory" (note 7); see also on this question, in the same book, R. N. Brandon, "A Structural Description of Evolutionary Theory."
39. R. Dawkins, "Universal Darwinism," in D. S. Bendall, ed., *Evolution from Molecules to Men* (Cambridge: Cambridge University Press, 1983), pp. 403–425.
40. Futuyma, *Evolutionary Biology* (note 26), provides a good introduction here. See, also, R. Lewontin, *The Genetic Basis of Evolutionary Change* (note 35).
41. M. Ruse, *Darwinism Defended*, pp. 140–141 (note 1).
42. R. Lewontin, "Testing the Theory of Natural Selection" (note 30).
43. For these themes in Popper, the best introductions are his own books, *The Logic of Scientific Discovery* (London: Hutchinson, 1959) and *Conjectures and Refutations* (New York: Harper and Row, 1968).
44. Popper's views on natural selection are discussed in Ruse, *Is Science Sexist?* (note 1).
45. Fisher's original account is in his *Genetical Theory of Natural Selection* (Oxford: Clarendon Press, 1930), a revised edition of which was published by Dover in 1958. On the conditions

for the theorem holding, see J. R. G. Turner, "Changes in Mean Fitness under Natural Selection," in K. Kojima, ed., *Mathematical Topics in Populations Genetics* (New York: Springer-Verlag, 1970), pp. 32–78; G. R. Price, "Fisher's 'Fundamental Theorem' Made Clear," *Annals of Human Genetics* (London), 36 (1972), 129–140; and R. C. Olby, "La Théorie Génétique de la Sélection Naturelle Vue par un Historien," *Revue de Synthèse: Actes du Colloque R. A. Fisher et L'Histoire de la Génétique des Populations*, 103–104 (1981), 251–289.

46. Thus Fisher to J. S. Huxley, 6 May 1930: "... if I had had so large an aim as to write an important book on Evolution, I should have had to attempt an account of very much work about which I am not really qualified to give a useful opinion. As it is there is surprisingly little in the whole book that would not stand if the world had been created in 4004 B.C., and my primary job is to try to give an account of what Natural Selection *must* be doing, even if it had never done anything of much account until now." J. H. Bennett, ed., *Natural Selection, Heredity, and Eugenics. Including Selected Correspondence of R. A. Fisher with Leonard Darwin and Others* (Oxford: Clarendon Press, 1983), p. 222.

47. M. B. Williams, "Deducing the Consequences of Evolution: A Mathematical Model," *The Journal of Theoretical Biology*, 29 (1970), 343–385, and "The Logical Status of the Theory of Natural Selection and other Evolutionary Controversies," in M. Bunge, ed., *The Methodological Unity of Science* (Dordrecht: D. Reidel, 1973), pp. 84–101. Hull, in his *Philosophy of Biological Science* (note 25), brings out the advantages and limitations of Williams's approach. See also Sober, "Fact, Fiction and Fitness" (note 35).

48. M. Ruse, "The Structure of Evolutionary Theory," in his *Is Science Sexist?* (note 1).

49. S. J. Gould and R. C. Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme," *Proceedings of the Royal Society of London, Series B*, 205 (1977), 581–598.

50. Fisher's views on drift and related issues are discussed authoritatively, in this volume, in J. R. G. Turner, "Random Genetic Drift, R. A. Fisher, and the Oxford School of Ecological Genetics." For Fisher on determinism, free will, and associated subjects, see the correspondence published in J. H. Bennett, *Natural Selection, Heredity, and Eugenics* (note 46), and two published papers: "Indeterminism and Natural Selection," *Philosophy of Science*, 1 (1934), 99–117; "The Renaissance of Darwinism," *The Listener*, 37 (1947), 1001. Both are in the *Collected papers of R. A. Fisher*, edited by J. H. Bennett (Adelaide: University of Adelaide, 1971–1974). See further J. R. G. Turner, "Fisher's Evolutionary Faith and the Challenge of Mimicry," *Oxford Surveys in Evolutionary Biology* 2 (1985): 159–196.

51. The classic sources are S. Wright, "Evolution in Mendelian Populations," *Genetics*, 16 (1931), 97–159, and "The Roles of Mutation, Inbreeding, Crossbreeding and Selection in Evolution," *Proceedings of the VIth Congress of Genetics*, 1 (1932), 356–366. Wright's metaphysical views are instructively related to his biology in his "Biology and the Philosophy of Science," *The Monist*, 48 (1964), 265–90. W. B. Provine has a biography of Wright in preparation.

52. Here, issues are relevant that go back to H. J. Muller and, beyond him, to Weismann, and are now pursued in, for example, J. Maynard Smith, *The Evolution of Sex* (Cambridge: Cambridge University Press, 1978), and G. C. Williams, *Sex and Evolution* (Princeton: Princeton University Press, 1975).

53. B. J. Norton, "The Biometric Defense of Darwinism," *Journal of the History of Biology*, 6 (1973), 283–316.

54. (Added in proof) On causation, probability, and explanation, see now W. C. Salmon, *Scientific Explanation and the Causal Structure of the World* (Princeton: Princeton University Press, 1984). For all of these topics the reader should now see Sober's *The Nature of Selection* (note 1).