

## 11 The Evolutionary Contingency Thesis

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### 1 Introduction

As Stephen Gould recently put it, evolution is like a videotape that, if replayed over and over, would have a different ending every time (Gould 1989, especially pp. 45–52, 277–291).<sup>1</sup> Last time it featured, among other things, duckbilled platypuses and human beings. And while we can be pretty sure that future replays will be every bit as humorous in their own special way, we cannot expect them to be quite as edifying. We are all, humans included, unlikely outcomes.

Gould contrasts such contingent “details” as ourselves with general “laws” that guide the course of evolution: “Invariant laws of nature . . . set the channels in which organic design must evolve.” But, Gould emphasizes, “the channels are so broad relative to the details that fascinate us!” (Gould 1989, p. 289). In other words, laws of nature only *loosely* constrain the outcomes of evolution.

In this paper, I will further elaborate Gould’s thesis and further defend it. My version of the thesis may appear at first to contradict Gould’s, especially inasmuch as he emphasizes contingent “details,” while I emphasize contingent *generalities*. Correspondingly, my version may appear stronger, though I believe he intends his to be every bit as strong.<sup>2</sup>

The thesis that I will defend, most briefly put, is this: all distinctively biological generalizations describe evolutionarily contingent states of nature—moreover, “highly” contingent states of nature in a sense that I will explain. This means that there are no laws of biology. For, whatever “laws” are, they are supposed to be more than just contingently true. To anticipate one obvious objection, I will also argue that there are no laws of evolution—the principles of evolutionary genetics are themselves evolutionarily contingent states of nature.

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What I call the “evolutionary contingency thesis” is interesting in its own right. But it is also bound up with and bears upon a number of other issues in philosophy of biology, over and above the existence of laws of biology. Here, I will discuss its bearing on the explanatory ideals of biology, especially the “theoretical pluralism” so characteristic of biology, and also its bearing on the nature of controversy in biology, specifically the “relative significance” controversies that are so prevalent in the life sciences.

### 2 The Evolutionary Contingency Thesis and Laws of Biology

The evolutionary contingency thesis, somewhat more elaborately stated, is as follows:

All generalizations about the living world:

- a) are just mathematical, physical, or chemical generalizations (or deductive consequences of mathematical, physical, or chemical generalizations plus initial conditions), or
- b) are distinctively biological, in which case they describe contingent outcomes of evolution.

The first part of this claim is meant to acknowledge that there are generalizations about the living world whose truth values are not a matter of evolutionary history. Evolution has not and will not result in any forms of life that are not subject to the laws of probability, or to Newton’s laws of motion. Nor will evolution result in any carbon based forms of life that are not subject to the principles of organic chemistry. But while these sorts of principles are true of the living world, we do not call them “biological” principles.<sup>3</sup>

The second part of the evolutionary contingency thesis requires a lot more explanation than the first part. To begin, what is meant by the claim that all distinctively biological generalizations describe *evolutionary outcomes*? (After I discuss the sense in which they describe “evolutionary outcomes,” I will then consider the sense in which they describe “contingent” evolutionary outcomes.)

By saying that biological generalizations describe evolutionary outcomes, I mean to refer to the *rule-making* capabilities of the agents of evolutionary change. All distinctively biological generalizations owe the extent of their generality to evolution by one or another, or some combination of, evolutionary agents, like directed and random mutation, hybridization, natural and sexual selection, random drift, etc. In this paper, I will focus on the rule-making (and later, rule-breaking) capabilities of evolution by random mutation and natural selection.

The rule-making capabilities of natural selection were of particular interest to the physicist-turned-biologist Max Delbrück, who characterized natural selection as “the overly faithful assistant of a credulous professor, the assistant being so anxious to

*There are laws, just not biological ones*

*Rule-making due to natural selection*

*Claim: there are no laws of biology*

please that he discards all those data which conflict with his master's theory" (Delbrück 1952, p. 12). In other words, generalizations emerge as certain traits are selected for, and as other traits—exceptions to the emerging rule—are selected against.

Consider for the purposes of illustration (and for fun) a very modest generalization from physical anthropology: "Humans are relatively hairless." That is, we have a lot less body hair than our closest ancestors. Why should this be the case? This turns out to be a highly contentious issue! But what is not disputed is that an evolutionary answer is called for. A number of different evolutionary accounts have been proposed, most of them based on natural selection.

For example, it has been argued that body hair was disadvantageous for early humans because hair harbors ticks, lice, and other insects that spread disease (Olson 1966). Others have argued that body hair was disadvantageous for early humans because of the warm climates in which they lived. That is, quadrupedal mammals need body hair in part to protect them from the sun's heat, but our early bipedal ancestors did not expose as much of their surface area to the sun; their body hair merely trapped heat (Wheeler 1985). Others argue that body hair was not so much disadvantageous as superfluous once humans evolved more effective means of dissipating heat, through the acquisition of many (2.5 million) sweat glands (Brace 1966; Campbell 1966). Darwin argued in *The Descent of Man* that the loss of body hair among humans was mainly due to sexual selection. In this respect, he urged, it is well to bear in mind the New Zealand proverb, "there is no woman for a hairy man" (and presumably vice-versa; Darwin 1871, vol. 2, p. 378).

On all these accounts, natural selection generates the relative hairlessness rule by eliminating its exceptions. But while "humans are relatively hairless" may be a slightly provocative principle, it is hardly fundamental, and so this is not a very telling case.

Consider another example, which also illustrates how *distinctively* biological generalizations describe evolutionary outcomes. This one has to do with the ubiquity of a particular metabolic pathway—the Krebs cycle—among aerobic organisms:

In aerobic organisms, carbohydrate metabolism proceeds via a series of chemical reactions, including the eight steps of the Krebs cycle.

This generalization might at first seem so broad as to be just a matter of chemistry. When reformulated or drawn so as to exclude reference to aerobic organisms, and to include not only the substrates of the reactions (e.g., citrate or citric acid), but also the enzyme catalysts involved (shown in parentheses), the required reaction temperatures, the resulting generalization is just a chemical generalization (see figure 11.1).

But the ubiquity of the eight reactions of the Krebs cycle among aerobic organisms is not simply a matter of chemistry. It depends on genetically based aspects of those organisms, like their ability to synthesize the enzymes that facilitate the various reactions of the cycle. Genetically based traits are subject to changes in frequency due to

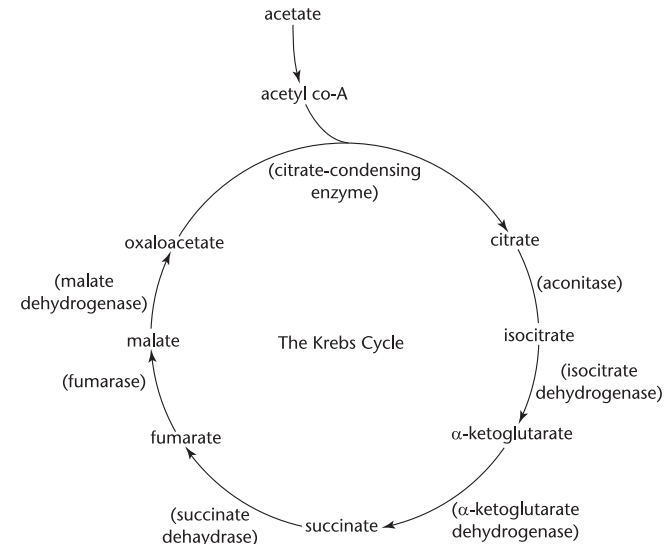


Figure 11.1

the various agents of evolutionary change, and so the prevalence of the Krebs cycle among aerobic organisms—and hence the truth of the generalization above—is a matter of evolutionary history. Having spent the early part of his career establishing the steps of the cycle, Hans Krebs spent the latter years of his life trying to give an account of its ubiquity in terms of evolution by natural selection (e.g., Krebs 1981; Baldwin and Krebs 1981). For instance, he argued that alternative ways of metabolizing acetic acid (the starting substrate of the cycle) are not as energy efficient.<sup>4</sup>

The case of the Krebs cycle is interesting not just because it is so fundamental, but also because, depending on how one generalizes about it, the resulting claim is either a chemical generalization whose truth value is not a matter of evolutionary history, or a distinctively biological generalization describing an evolutionary outcome.<sup>5</sup>

Consider one more example of the rule-making capabilities of evolution by natural selection. This example is intended to anticipate questions as to whether the generalizations of evolutionary biology themselves describe evolutionary outcomes. The example concerns Mendel's first "law" of inheritance, from which one of the central principles of evolutionary biology, the Hardy-Weinberg "law" is derived.

Mendel's first law concerns the way in which the genes of a sexual organism are partitioned ("segregate") among the gametes it produces. The law states that,

*Mendel's law*

*Evolution of hairlessness*

*Different ultimate causes proposed: diseases, heat, sexual selection*

*Carbohydrate metabolism*

*Its prevalence depends on evolutionary factors*

With respect to each pair of genes of a sexual organism, 50% of the organism's gametes will carry one representative of that pair, and 50% will carry the other representative of that pair.

*Its presumed  
ultimate causes*

Consider now that the process of gamete formation is itself a genetically based trait. There are genes that contribute to 50:50 segregation ratios, and genes that contribute to biased ratios (see, e.g., Sandler et al. 1968 and White 1973; see Magee 1987 for a review of the genetics of the process). Consider also that the degree of prevalence of any genetically based trait—50:50 segregation of genes included—is subject to agents of evolutionary change, like mutation and natural selection. The fact that Mendelian gamete production is so prevalent thus requires an evolutionary explanation—for example, some account of why 50:50 segregation ratios are adaptive. Indeed, this is currently a matter of considerable interest among evolutionary biologists (see the literature review by Bell 1982, pp. 438–442).

The fact that Mendel's law describes an evolutionary outcome is especially interesting because one of the central principles of evolutionary biology, the so-called Hardy–Weinberg “law” of gene frequency change, is a straightforward deductive consequence of Mendel's “law.” Hence, the Hardy–Weinberg “law” of evolution itself describes an evolutionary outcome (see also Beatty 1981; 1982; Rosenberg 1985, pp. 132–136). As population geneticist Marcy Uyenoyama has so plainly put it, “Just as the meiotic mechanism [of gamete formation] directs evolution through its effects on the pattern of inheritance, the process of genetic transmission itself evolves by natural selection” (Uyenoyama 1987, p. 21).<sup>6</sup>

*Rule-breaking  
capabilities  
described*

So much for the sense in which distinctively biological generalizations describe “evolutionary outcomes.” What does it mean to say that such generalizations describe evolutionarily *contingent* states of affairs? This has to do with the *rule-breaking* capabilities of the agents of evolutionary change: the agents of evolution not only make, but also break the rules that pertain to the living world. More formally, to say that biological generalizations are evolutionarily contingent is to say that they are not laws of nature—they do not express any *natural necessity*; they may be true, but nothing in nature necessitates their truth.<sup>7</sup>

*Laws and  
contingent  
generalisations  
contrasted*

Admittedly, as Bas van Fraassen complains, philosophers of science are better at illustrating this distinction than explaining it (van Fraassen 1989, pp. 1–129).<sup>8</sup> A common sort of illustration (van Fraassen's own, p. 27; see also Hempel 1966, pp. 54–58) contrasts the following two generalizations:

1. All solid spheres of enriched uranium ( $U_{235}$ ) have a diameter of less than one hundred meters.
2. All solid spheres of gold (Au) have a diameter of less than one hundred meters.

Suppose both claims are true. Still, there seems to be more to the former than the latter, by virtue of which we might accord the former but not the latter the status of law

(or perhaps in this case it would be better to suggest that the first generalization describes an “instance” of a more general law). The critical mass of uranium excludes the possibility of such a large sphere of the substance. But nothing that we know about gold excludes the possibility of such a large sphere of that material. Now if on these grounds we accord to the former claim but not to the latter the status of law (or “instance” of a law), then we acknowledge that there is more to being a law than just being true. That something more has to do with what nature necessitates or precludes.<sup>9</sup>

There are at least two senses in which nature *fails to necessitate* the truth of biological generalizations. These correspond to two senses of evolutionary “contingency,” one stronger than the other, although the weaker one is not absolutely weak. There are, in other words, at least two senses in which the agents of evolution can break rules as well as make them.

The weaker sense has to do with the fact that the conditions that lead to the evolutionary predominance of a particular trait within a particular group may change, so that the predominance of the trait declines. Somewhat more colloquially: what the agents of evolution render general, they may later render rare. Two sources of this kind of contingency are mutation, and natural selection in changing environments. Suppose that relative hairlessness owes its prevalence to the fact that it was favored under particular circumstances by natural selection—relative hairiness being selected against—selection acting, as Delbrück suggested, “like the overly faithful assistant” who “discards all those data which conflict with his master's theory.” Is there anything *naturally necessary* about the circumstances under which relative hairlessness was favored—something that could not change? Is the professor really so single minded? And are the loyalties of the professor's assistant really so unswerving?<sup>10</sup>

In the case of generalizations about the Krebs cycle, and also in the case of Mendel's “law” and the derivative Hardy–Weinberg “law,” we know that the assistant is *not* so loyal, or that the professor has not settled on one description of nature. There are so many exceptions. There are species of aerobic organisms that do not proceed through all the steps of the Krebs cycle, and that take different chemical routes from the same starting point to the same endpoint (e.g., organisms whose metabolism proceeds via the “glyoxylate shunt,” which bypasses the two steps of the Krebs cycle leading from isocitrate to succinate; Gottschalk 1986, pp. 120–121; Moat and Foster 1988, pp. 27, 30, 136–139; Brock et al. 1984, pp. 142–143). As biochemist P. D. J. Weitzman reasons, one should *expect* to find such variations since,

different organisms would be expected to make different demands on the several functions of the cycle and thus control the cycle in different ways in accordance with their individual metabolic “life-styles.” It seems reasonable to assume that the evolutionary paths to different organisms have been accomplished by the evolution of distinctive regulatory and other individual functional features in the CAC [the Krebs cycle] (Weitzman 1985, pp. 253–254).

*Biological  
contingency  
in the sense  
of  
changeability*

*Exceptions  
to biological  
laws*

And there are many pairs of genes, in many species, that do not segregate in a 50:50 fashion; in these cases there is instead a marked bias in the production of gametes containing one rather than the other representative of the pair (e.g., Crow 1979). As Graham Bell (1982, p. 439) recently acknowledged, many of his fellow evolutionary biologists who contemplate such issues actually find it easier to imagine circumstances in which unequal segregation of alleles among gametes would prevail than to imagine the circumstances which would favor evolution by natural selection of 50:50 segregation ratios à la Mendel.<sup>11</sup>

*Inapplicability contrasted with falsity* My line of reasoning up to this point—especially as it applies to Mendel’s “law”—has been criticized by Elliott Sober (1987; 1989) and Marc Ereshefsky (1991, 1992). Their objection is that the argument rests on a confusion between the *falsity* of a generalization, and its *inapplicability*. As they rightly point out, Mendel’s “law” can be recast in the conditional form, “if *A*, then *B*.” “*B*” is presumably 50:50 segregation of genes among gametes. “*A*” presumably describes some appropriately specified type of organism. This generalization would only be false if there were, in the past, present or future, organisms of type *A* that did not make gametes in the specified way. But just because some organisms do not make gametes in the specified way does not mean that the generalization is false, for those organisms may not be instances of *A*. The generalization is not falsified by these organisms, rather, the generalization does not apply to them. Of course, whether the generalization is false or just inapplicable depends on the formulation of *A*. The usual formulation of *A* has to do with being a sexual organism. If early sexual organisms did not all form gametes in the specified way, or if present sexual organisms do not all form gametes in this way, or if species of sexual organisms could evolve to the point where they do not all form gametes in this way, then Mendel’s “law” *as usually formulated* is either straightforwardly false, or describes a contingent outcome of evolution and hardly a law of nature, in which case Sober’s and Ereshefsky’s objection fails.

*The objection fails, since Mendel’s law applies to all sexual organisms*

Sober’s and Ereshefsky’s criticism is well taken only in connection with nonstandard formulations of Mendel’s “law” (which they do not specify). But perhaps there are ways to modify the antecedent of the usual version so that it no longer just refers to sexual organisms, and so that it would be inapplicable rather than false in the past, present or future when 50:50 segregation of genes among gametes fails to obtain. It might then express a naturally necessary state of affairs. Perhaps all biological generalizations can be so formulated (or reformulated).

Of course, we have to be careful not to build into the antecedent *A* the conditions from which the conclusion *B* is logically and mathematically derivable. Laws of nature are supposed to be true as a matter of *empirical fact*, and not just as a matter of logic and mathematics.

Consider to this end a general strategy for rescuing the law-like status of biological generalizations, by qualifying them appropriately. Suppose we were to conditionalize

generalizations about the prevalence of a trait upon the presence of the circumstances in which the trait would be expected to be favored by natural selection. These sorts of generalizations would correspond to what Sober calls “source laws” of natural selection, in the sense that such generalizations specify the sources of the selection pressures for the traits in question (Sober 1984, pp. 50–51, 58–59).<sup>12</sup>

So Mendel’s “law” as usually formulated may not really be a law, but there may be a law to the effect that *under particular circumstances* sexual organisms will produce gametes in the way Mendel described, because under those circumstances sexual organisms that produced biased ratios of gametes will be selected against. (Similarly, the Hardy–Weinberg “law” could be reformulated so as to be conditional upon the occurrence of the same circumstances.) The new version of Mendel’s “law” (and the new Hardy–Weinberg “law”) will then be inapplicable, rather than false, when those circumstances do not obtain. To be sure, evolutionary biologists who work on the evolution of 50:50 segregation ratios have hypothesized circumstances that they think would favor that arrangement.<sup>13</sup>

The generalization about the ubiquity of the Krebs cycle already comes close to conditionalizing the prevalence of a trait upon the presence of the circumstances that favor the trait. By referring to aerobic organisms, the generalization at least implicitly refers to the oxygen environments in which the cycle plays its important respiratory role (in addition to its various biosynthetic roles), and in response to which important steps of the cycle evolved.<sup>14</sup>

In fact, there are in biology many such correlations of traits with the sorts of circumstances that favor their predominance. There is, for instance, the category of so called “ecological rules” like Bergmann’s and Allen’s rules. According to Bergmann’s rule, given a species of warm-blooded vertebrates, those races of the species that live in cooler climates tend to be larger than those races of the species living in warmer climates. According to Allen’s rule, given a species of warm-blooded vertebrates, those races of the species that live in cooler climates have shorter protruding body parts like bills, tails, and ears than those races of the species that live in warmer climates. One common understanding of the correlation between body size and cooler climate is that increased body size results (other things being equal) in decreased surface area, which slows heat dissipation, which becomes more and more advantageous as the climate becomes colder and colder. Basically, the same reasoning applies to Allen’s rule (Mayr 1963, pp. 320–324).

The problem with such rules is that they are so riddled with exceptions, and for interesting reasons that have to do with the second, stronger sense in which all distinctively biological generalizations describe “contingent” states of affairs.<sup>15</sup> That stronger sense, which I intended earlier when I suggested that biological generalizations are *highly* contingent, has to do with the fact that evolution can lead to different outcomes from the same starting point, even when the same selection pressures are operating.

*A qualified version of biological laws*

*But this version still allows exceptions*

*The second sense of contingency: due to random mutation and functional equivalence*

There are many sources of this second form of contingency. One is so-called “chance” or “random” mutation, meaning that the probability of occurrence of a mutation is in no way proportional to the advantage it confers. A second source is “functional equivalence,” meaning that there are very different ways of adapting to any one environment.

Darwin employed both sources of this stronger form of contingency in his account of *The Various Contrivances by which Orchids are Fertilized by Insects* (Darwin 1862, esp. pp. 282–293; see also Darwin 1872, vol. 1, pp. 241–244).<sup>16</sup> The different reproductive contraptions of orchids had evolved, Darwin believed, from a common form (the original orchid species), in response to a common problem (the need for cross fertilization), and at least originally under virtually the same circumstances (e.g., the same range of available insects). Sometimes this part of the flower had been modified to entice or trap insects, sometimes another part had been modified to do the job. Even when the same parts had been modified to do that job, they did it in very different ways. Among the various orchid species, presumably derived from one, Darwin thus conceived the evolution of reproductive mechanisms occurring over and over again with no generally determined outcome except cross-fertilization. And this was to be expected on the basis of chance variations and the possibility of functional equivalence. Selection acts on whatever opportunities present themselves, with never the same order of useful modifications arising, and with equally functional results.

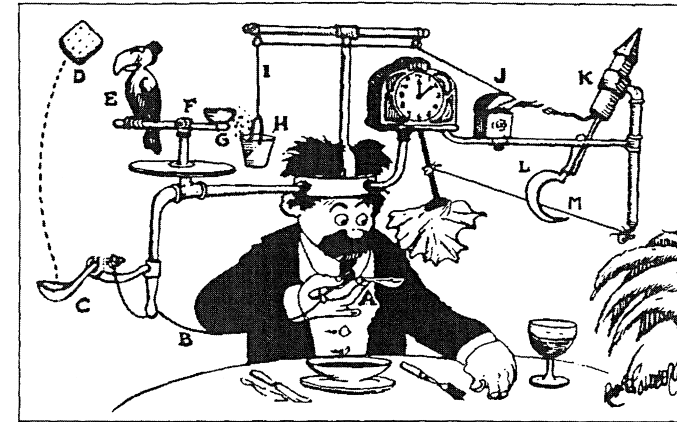
Somewhat more colloquially, natural selection is like a Rube Goldberg “tinkerer” (Jacob 1982, pp. 25–46; see also Grene 1988). Suppose that Mr. Goldberg were faced more than once with exactly the same problem (see figure 11.2). Who would ever expect him to solve it in the same way, even starting with the same materials?

The same line of reasoning can be used to throw doubt upon the status of any supposed source “law” of natural selection. Consider again Bergmann’s rule. Is decreased surface area the only way to limit heat dissipation? No. Heavier layers of fur or feathers will also do the job, as will behavioral innovations like burrowing. And it has long been argued that exceptions to Bergmann’s rule are best explained in these and still other ways. The exceptional groups evolved different, functionally equivalent solutions to the problem of heat dissipation (see, e.g., Mayr 1956; 1963, p. 321).

Similarly, supposing that we can agree on the circumstances that favored the evolution of 50:50 segregation ratios, can we rule out the possibility of a functionally equivalent solution? And once we agree on the circumstances that favored the evolution of the Krebs cycle, will we be able to rule out other, functionally equivalent solutions? These are the sorts of questions that we will have to answer in order to know whether we can formulate anything like biological laws via the source-law strategy.<sup>17</sup>

But those looking for biological laws are not going to give up so easily! Another strategy has been proposed for qualifying biological generalizations in order to render them laws. This strategy has recently been suggested by Ereshefsky (1991), and is currently

*A further  
comeback of the  
opponent: more  
conditionalisation*



...if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (Darwin 1862, pp. 383–284)

Figure 11.2

... if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for its present purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (Darwin 1862, pp. 383–384)  
© 1979 by Rube Goldberg (used with permission)

being developed in detail by Kenneth Waters (ms.), again with special reference to Mendel’s “law.”<sup>18</sup> Consider that 50:50 segregation of genes among gametes in sexual organisms might be guaranteed by the presence of the appropriate genes—the genes supposedly responsible for the Mendelian mechanism of gamete formation—together with the appropriate environments for the expression of those genes. A generalization correlating the presence of those genes (and the appropriate environments) with the presence of the Mendelian mechanism might really be a law. Similarly, we might formulate a law by conditionalizing the presence of the Krebs cycle on the presence of the appropriate genes (and environments). Note that such generalizations are claims about the expression of particular genes, and as such are very different from the standard generalizations about Mendelian inheritance and the Krebs cycle.



Actually, David Hull once suggested that the best candidates for biological laws were precisely such generalizations about gene expression: as he schematized such laws, “Any organism with the genetic makeup  $G$  in any environment ranging from  $E_1$  to  $E_n$  undergoing biochemical reactions  $R_1$  through  $R_n$  will come to have phenotypic characters  $C_1, C_2, \dots, C_n$ ” (Hull 1974, p. 80).

For Waters, this gene-expression strategy is an instance of a more general strategy for locating laws within biology. This involves distinguishing between two different kinds of generalizations in biology: 1) evolutionarily contingent “trends,” about the *distributions* of biological entities or properties (e.g., the distribution of 50:50 segregation among sexual organisms), and 2) non-evolutionarily contingent “laws,” about the *dispositions* of biological entities (e.g., genes) to behave in particular ways (e.g., to result in particular phenotypes). The general strategy, then, is to seek generalizations of type 2, of which generalizations about gene expression are an instance. Waters focuses on gene expression examples.

I do not dispute the possibility of formulating laws by the gene-expression strategy, although that will be very difficult. I do question the possibility of formulating *distinctively biological* laws in this way. Consider first the difficulties. Not surprisingly, generalizations correlating genotypes and phenotypes *may* describe evolutionarily contingent outcomes. That is because, first of all, genes interact in the production of phenotypes; one and the same gene may have very different effects depending on what other genes it occurs in combination with. And second, evolutionary changes with respect to those “other” genes may affect the phenotypic expression of the gene or genes in question. For instance, many evolutionary biologists entertain the idea that the extent of a beneficial gene’s dominance—the degree of phenotypic expression of that gene when it occurs in a single dose—evolves over time as natural selection favors the accumulation of other genes that enhance the expression of the gene in question (see e.g., Futuyma 1979, 374–376).

The problem of formulating any particular *law* of gene expression is therefore the problem of stating it in such a way that it would not be rendered false by further evolutionary change with respect to interacting genes. And that requires that we state a sufficiently inclusive set of genetic and environmental conditions. An appropriately conditionalized law of gene expression might then be rendered inapplicable by evolution—the conditions of the law no longer being met—but it might not be rendered false by evolutionary change.

What would such a law look like? It seems that one would be in a better and better position to know whether the set of conditions was sufficiently inclusive the more and more one knew about the chemical pathways leading from the sequence of nucleotide bases that make up the genes in question, to a physical-chemical specification of the phenotype in question. I suspect this is why Hull included the biochemical reactions linking genes to phenotypes in his schema of a law of gene expression.

Suppose that complete chemical pathways from genotypes to phenotypes could be formulated; and suppose that generalizations about these were indeed laws; still, I see no reason to regard them as *distinctively biological* laws. That is, I see no compelling reason to regard a description of a chain of chemical reactions—no matter that the reactants and products include DNA, RNA, and lots of enzymes—as “biological” generalizations. So to summarize this part of the discussion, the closer one’s generalizations about gene expression come to describing sequences of chemical reactions, the more certain one can be that they are laws, because one can be more certain that no evolutionary outcomes can contradict them. But at the same time, the generalizations will become less and less *distinctively biological*.<sup>19</sup>

There are two other issues concerning the meaning and justification of the evolutionary contingency thesis that I would like to address at least briefly. First, by focusing on the contingency of *distinctively biological* generalizations, I do not mean to suggest that the situation is entirely different in physics and chemistry; in particular I do not mean to suggest that there are generalizations in physics and chemistry that are not contingent. I really do not know. Perhaps all true generalizations in physics and chemistry will also prove to be “evolutionarily” contingent, at least in the sense of “cosmologically” contingent. It is worth noting, however, that some physicists, like the particle physicist and cosmologist Steven Weinberg (1992), do indeed have faith that there will be discovered “a final theory,” a most fundamental theory that explains everything else, all of cosmology included. Weinberg traces this ideal to Isaac Newton. I will have more to say shortly about this Newtonian ideal.

Second, by emphasizing *whether or not* biological generalizations are contingent, I do not mean to dismiss the possibility of different *degrees* of contingency manifested by different biological generalizations. The idea of degrees of contingency figures more prominently in the work of others. For example, Kenneth Schaffner recommends distinguishing between two degrees of contingency in biology: “essential” and “historical” accidents. “Historical accidentality,” he explains, is not so very accidental:

though initiating from a chance event [like random mutation, it] is augmented by additional nomic circumstances, such as strong natural selection. . . . Historical accidentality thus represents accidentality “frozen into” nomic universality. (Schaffner 1980, p. 90; 1993, p. 121.)

Schaffner follows Francis Crick (1968) in referring to the near (!) universality of the genetic code as a “frozen accident.” Crick argued that once the code was established in a particular lineage, any change in the code would have had enormous, cascading effects, resulting in changes in the amino acid sequences of many, many previously adaptive proteins. Such a change could not conceivably be beneficial overall. Thus, as Schaffner explains, “though the origin of specific coding relations may have (likely) been due to a chance mutation . . . , at present the code is sufficiently entrenched by natural selection that it is only historically accidental (Schaffner 1980, p. 90; 1993, p. 121).<sup>20</sup>

Stuart Kauffman (1993) further multiplies the degrees of contingency by stressing the *extent* of evolutionary contingency throughout the biological world. For instance, he is concerned to determine 1) the *extent* to which generalizable features of biological systems are due to self-organizing properties of their constituent parts, 2) the *extent* to which selection may displace biological systems from the states they would occupy on the basis of the self-organizing properties of their parts alone, and 3) the *extent* to which the self-organizing properties of biological systems not only constrain evolution by natural selection but also in certain respects enable evolution by natural selection to take place.<sup>21</sup>

Schaffner and Kauffman and others are surely right to stress that there are *more or less* contingent generalities in biology. The present formulation of the evolutionary contingency thesis may be misleadingly simplistic in this regard.

### 3 Theoretical Pluralism and Relative Significance Controversies

I want to switch now from articulating the evolutionary contingency thesis, to applying it. In particular I want to consider its bearing on the explanatory ideals of biology, especially on the “theoretical pluralism” so characteristic of biology, and also on the nature of controversy in biology, specifically the “relative significance” controversies that are so prevalent in the life sciences.

“Theoretical pluralism” has to do with the number of theories or mechanisms that are believed to be required to account for a domain of phenomena (see also Beatty 1994). A proponent of theoretical pluralism with respect to a particular domain believes that the domain is essentially heterogeneous, in the sense that a plurality of theories or mechanisms is required to account for it, *different items in the domain requiring explanations in terms of different theories or mechanisms*. There is no single theory or mechanism—not even a single synthetic, multi-causal theory or mechanism—that will account for every item of the domain. This is not merely a matter of insufficient evidence for a single theory; rather, it is a matter of the evidence indicating that multiple accounts are required.<sup>22</sup>

Theoretical pluralism contributes to, and is reflected by, a certain kind of controversy—the so-called “relative significance” dispute. What is at issue in a relative significance dispute is the *extent of applicability* of a theory or mechanism within a domain—roughly, the proportion of items of the domain governed by the theory or mechanism—not whether the theory or mechanism in question is *the correct* account of the domain.

Examples of theoretical pluralism and relative significance controversies occur at every level of investigation in biology. As we have already discussed, biochemists raise questions about the extent of applicability of the Krebs cycle among aerobic organisms, suggesting that alternatives to the Krebs cycle are more prevalent than commonly

acknowledged (Weitzman 1985, pp. 253–254). Geneticists raise questions about the ubiquity of the Mendelian mechanism of inheritance, arguing that non-Mendelian mechanisms are possibly very common (e.g., Crow 1979). Molecular geneticists wonder and argue about the extent of applicability of the lac operon (negative induction) model of gene regulation, as opposed to alternative negative repression, positive induction and repression, attenuation, etc. models (e.g., Lewin 1990, pp. 240–299; Yanofsky 1981, 1988). Immunologists and geneticists argue about the extent of applicability of alternative accounts of the generation of antibody diversity: e.g., germ-line vs. somatic cell theories (e.g., Kindt and Capra 1984). Physiologists, biophysicists, geneticists and evolutionary biologists working in the area of gerontology argue about the relative applicability of different mechanisms of aging: e.g., somatic mutations in dividing cells vs. “wear and tear” of post-mitotic cells (e.g., Comfort 1979; Maynard Smith 1966; Rose 1985; Finch 1990).

Evolutionary biology, ecology, biogeography, and systematics are rife with relative significance controversies. For instance, evolutionary biologists argue about whether selectionist theories have greater applicability to microevolutionary changes than neutralist theories (e.g., Lewontin 1974; Kimura 1983; Endler 1986; Gillespie 1991). They argue about whether gradualist, adaptationist theories of macroevolution have greater applicability than the punctuated equilibrium theory (e.g., Gould 1980; Lande 1980). They argue about the extent of applicability of the various mechanisms of the evolution of sex, from the “red-queen” hypothesis to the “tangled-bank” hypothesis to the “genetic-load” model to the “DNA-repair” model (e.g., Michod and Levin 1988; Kondrashov 1988). Evolutionary biologists and systematists argue about the extent of applicability of each of the multitude of theories of speciation, from each of the various forms of sympatric speciation, to parapatric speciation, to each of the various forms of allopatric speciation (e.g., Bush 1975; White 1978; Otte and Endler 1989). They also argue about the relative significance of different accounts of the relationship between ontogeny and phylogeny (e.g., the relative applicability of “von Baer’s law”; see, e.g., Gould 1977). They argue about whether vicariance accounts of biogeographic patterns have greater applicability than dispersalist/center-of-origin accounts (e.g., Nelson and Platnick 1981a; 1981b).

Ecologists debate the extent of applicability of alternative theories of community structure, from competition theory, to predation and abiotic factor theories, to random colonization models (e.g., Schoener 1982; 1983; Connell 1983; Sih et al. 1989). Again, these are all disputes about the *extent* of applicability of alternative theories or mechanisms within a particular domain, not whether this or that account is *the* universally true one within that range.

I believe there are reasons to be a theoretical pluralist with respect to *every* domain of distinctively biological phenomena, and reasons to anticipate relative significance controversies within every domain. The main reason is that the contingencies of evolu-

Pluralism of  
different  
mechanisms

Plurality of  
biological  
explanations

tionary history preclude the existence of laws of biology. It is not surprising that a biologist should be more interested in the *extent of applicability* of a theory within its intended domain than in its possible *universality* within that domain. Not expecting universal generalizations to hold within a domain, biologists expect instead to have recourse to a plurality of theories to cover it.<sup>23</sup>

#### Newton's ideals

The theoretical pluralism so prevalent in biology contrasts strikingly, I believe, with a traditional ideal, namely, to explain a domain of phenomena in terms of as few as possible different mechanisms, and best of all one single mechanism. This ideal was expressed particularly well by Newton, and so I will call it the Newtonian tradition. Newton elaborated it most succinctly in the first two of his three “rules of reasoning in philosophy” (Newton [1686] 1934, p. 398). According to the first rule, “We are to admit no more causes of natural things than such as are both true and sufficient to explain their appearances.” As Newton clarified the rule, “To this purpose the philosophers say that Nature does nothing in vain, and more is in vain when less will serve; for Nature is pleased with simplicity and affects not the pomp of superfluous causes.” Newton’s second rule states my point more clearly: “Therefore [i.e., it follows from the first rule that] to the same natural effects we must, as far as possible, assign the same causes.” As he proceeds to illustrate the rule: “As to respiration in a man and in a beast, the descent of stones in Europe and America, the light of our culinary fire and of the sun, the reflection of light in the earth and in the planets.”

Judging by their acceptance of theoretical pluralism, and by their waging of relative significance disputes, many biologists seem not overly impressed by this rule of reasoning. Indeed, by their *promotion* of theoretical pluralism they seem to *repudiate* the Newtonian ideal.

For example, in their reviews of the modes of speciation, Bush (1975) and White (1978) staunchly defend a pluralistic approach against assumptions or attempts to show that there is a single correct account of the domain. As White insists,

however much evolutionists of the future may synthesize in the field of speciation, we can be confident that the diversity of living organisms is such that their evolutionary mechanisms cannot be forced into the straightjacket of any narrow, universal dogma. (White 1978, p. 349)

This pluralism is also characteristic of the recent anthology and state-of-the-art summary, *Speciation and its Consequences*, edited by Otte and Endler (1989).

McIntosh (1987) recently summarized the trend toward theoretical pluralism in ecology, away from the ideals of the sixties and early seventies when ecologists like Robert MacArthur envisioned that all of ecology would ultimately be “embodied in a small number of simple laws.” Recent anthologies, for example the anthology on community ecology edited by Diamond and Case (1986), proclaim pluralism in the preface and throughout. The editors explicitly distance themselves from the ideals of Newtonian mechanics:

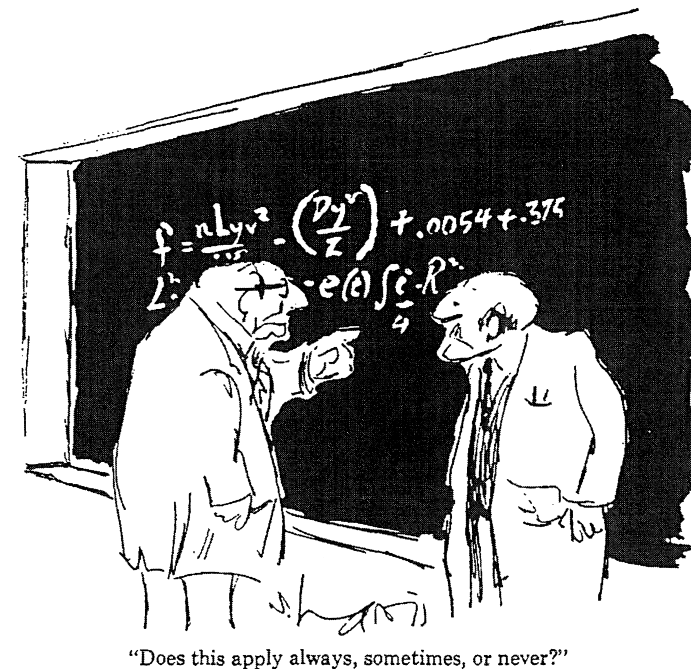


Figure 11.3

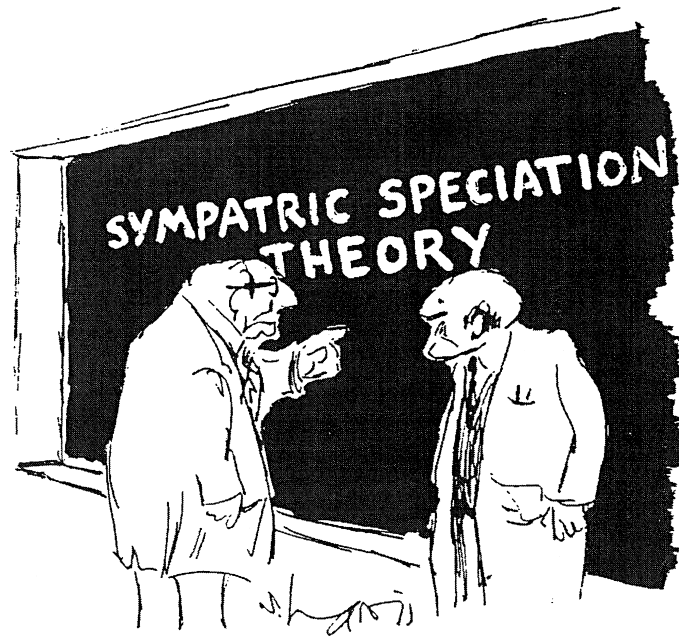
© 1977 by Sidney Harris (used with permission)

Until recently, philosophy of science focused on relatively homogeneous fields such as classical mechanics. As a result, many scientists have been trained to regard pluralistic approaches as soft, unrigorous, unscientific, and indicative of a retarded field. Even scientists who work in pluralistic fields tend to view how science “should” be pursued in ways that are mismatched to their field’s special needs. (Diamond and Case 1986, p. x)

The Newtonian tradition may prevail more in the physical sciences (at least in the non-historical—e.g., non-geological, non-cosmological—physical sciences). The difference between that tradition, and the tradition of relative significance controversies that prevails in biology, is well illustrated by the following Sidney Harris cartoon (see figure 11.3) of two physicists (they’re not mathematicians—mathematicians don’t wear white coats).

The assumption behind the cartoon—what makes it funny—is that physicists are not supposed to argue about such matters. But what makes us think these are physi-





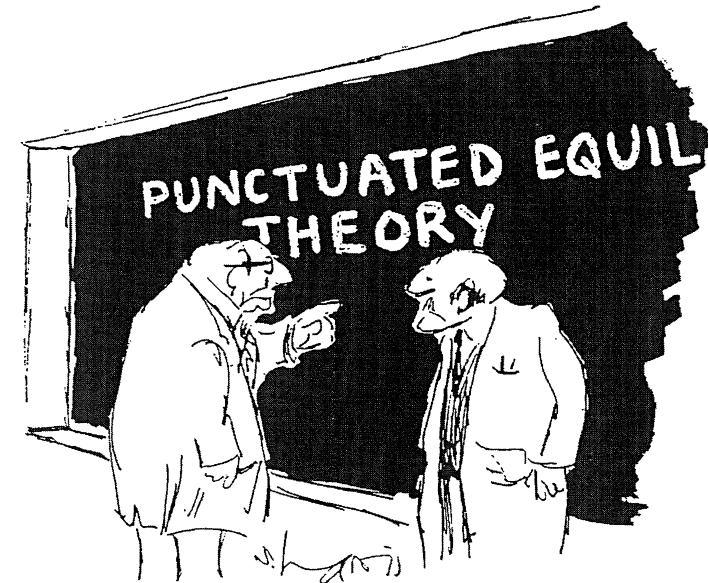
"Does this apply always, sometimes, or never?"

Figure 11.4

cists? Well, if they were not, it would not be funny. Imagine that they are evolutionary biologists arguing about theories of speciation, or theories of the rate of evolutionary change (figures 11.4 and 11.5). Now this is not a joke. It is rather the fact of the matter. To some it is the sad fact of the matter. Which leads me to temper my remarks about theoretical pluralism in biology.

It is important not to exaggerate the differences between the biological and physical sciences. The Newtonian tradition has considerable appeal in biology as well, and not only in the more ahistorical branches of biology, like molecular biology. One also finds it in the more historical areas like systematics, ecology and evolutionary biology. For example, Carson chides his pluralistic peers in the area of speciation for giving up too easily in this regard:

Despite much modern work in plant and animal population biology, there has been a regrettable lack of unification of theory relating to the modes or processes involved in the origin of new species. I find two reasons for this. First, there is a tendency not to be reductionistic, that is, to accept



"Does this apply always, sometimes, or never?"

Figure 11.5

many disparate theoretical notions about the way in which species may arise (e.g., White 1978). In the face of this, long and complex classifications of various conceivable modes of speciation (e.g., allopatric, sympatric, parapatric, stasipatric, etc.) have been constructed, discouraging those who seek unifying principles. (Carson 1985, p. 380)

Numerous other biologists are pluralists, but only reluctantly, as if pluralism falls short of the Newtonian ideal. For example, Ghiselin concludes a review of mechanisms of the evolution of sex by admitting that, "Perhaps we shall *have* to accept a pluralistic assemblage of explanations." And again, "From the point of view of having an adequate explanation for all the data, we may *have* to accept more than one hypothesis" (Ghiselin 1988, p. 23, my emphases). And as James and Carol Gould admit, "We have, it seems, an embarrassment of plausible hypotheses to account for the evolution and maintenance of [sex]" (Gould and Gould 1989, p. 65, my emphasis).

Many natural historians reveal the limits of their tolerance for theoretical pluralism by conducting their relative significance arguments in the manner described by Gould and Lewontin:

In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but circumscribe its domain of action so narrowly that it cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an ecumenical chap. (Gould and Lewontin 1978, p. 585)

To a certain extent, as Gould and Lewontin suggest, systematists, ecologists and evolutionary biologists often acknowledge the need for theoretical pluralism, but try to keep it under control by minimizing the significance of all but a couple, or even one, possible account of a domain of phenomena. For example, James and Carol Gould predict with regard to theories of the evolution of sex that one account will turn out to be “*the major factor*,” although “there may well be *special cases* in which the [ecological] pressures posited by other models will be critical” (Gould and Gould 1989, p. 65; my emphases).

There are other means by which biologists try to eliminate or contain theoretical pluralism. One important means is by splitting a heterogeneous domain, governed by multiple theories, into two or more homogeneous sub-domains, each governed by only a couple of theories or perhaps even a single theory. For example, the evolution of sex can be partitioned into two sub-domains, the *origin* of sex and the *maintenance* of sex. Some biologists believe that the DNA-repair hypothesis will be *the* account of the origin of sex, while multiple theories may be needed to explain the maintenance of sex. Similarly, attempts are often made to distinguish the domain of microevolutionary changes within which selectionist theories are most significant, from the domain in which neutralist theories are most important (e.g., Endler 1986, Chap. 8; Gillespie 1991, pp. 289–290). Interestingly, while Diamond and Case (quoted above) promote theoretical pluralism in community ecology, they nonetheless seriously entertain the possibility that “one can at least partition communities among a modest number of types and devise a model for each type” (Diamond and Case 1986, p. xi). Douglas Allchin (1991) devotes considerable attention to the strategy of domain partitioning.

But the fact that tactics like these are employed to contain theoretical pluralism indicates that theoretical pluralism is indeed widespread, however much some biologists with Newtonian inclinations may regret it. As Michael Gilpin acknowledges in objecting to a fellow ecologist’s pluralistic approach:

I must confess that I am saddened by [his book’s] honest realism, its unabashed pluralism. Something of a romantic, I long for the heady days of an earlier decade when the [alternatives considered by him] vied one against the other to be the organizing principles of our science. (Gilpin 1986, pp. 200–201)

I can imagine an argument for adhering to the Newtonian ideal, independently of its romantic qualities. That is, one might suggest that theoretical pluralism reflects more about the state of our ignorance than about the state of nature: there may actually

be laws of biology, and a unitary or unifying theory for each domain of biological phenomena, but we have yet to discover these important generalizations. Whether theoretical pluralism reflects the nature of the biological world, or the state of our ignorance, we cannot at present know. Nonetheless, we should aim for unitary or unifying theories. Then, if the biological world is really so contingent, and each domain inescapably heterogeneous, we will ultimately be forced to deal with theoretical pluralism. But if we begin by advocating theoretical pluralism, then we may never find the unitary or unifying theories that might actually be true. We might rest happy with multiple accounts when a unitary account is possible and could be discovered with just a little more effort. I am not just imagining this argument, it is a lot like David Hull’s argument in favor of a single species concept. According to Hull, defenders of a unitary vs. a pluralistic species concept,

are carrying on in the best scientific tradition of opting for one perspective and pushing it for all its worth. Perhaps species as genealogical [individuals]...may prove ultimately inadequate. Science does march on. If so, then this monism will have proved to have been only temporary, but the only way to find out how adequate a particular conception happens to be is to give it a run for its money. Remaining content with a variety of slightly or radically different species concepts might be admirably open-minded and liberal, but it would be destructive of science ... (Hull 1987, p. 178)

This is a difficult argument to counter.<sup>24</sup> The best I can do is to offer an alternative argument (or rather, sketch of an argument), which rests on the following premise: scientific methodology, including injunctions to seek unified accounts of each and every domain, should be scientifically (in this case evolutionarily) informed. This is, for example, the assumption that structures Elliott Sober’s analysis of the evolutionary grounds underlying the parsimony criterion in phylogenetic systematics. As Sober puts it,

The idea of a presuppositionless “scientific method” implies that methodology is static and insensitive to what we learn about the world. But with theory and method linked by a subtle nexus of interdependence, progress on theories can be expected to improve our methods of inquiry (Sober 1988, p. 239).

Similarly, why should we adhere to a methodology that dictates the search for unitary accounts of each domain of biological phenomena—e.g., a unitary account of inheritance, or a unitary account of carbohydrate metabolism, or a unitary account of gene regulation, or a unitary account of speciation—unless we have reason to believe that the outcomes of evolution are *highly* constrained?

If I have stressed the factors that broaden the range of evolutionary possibilities, that is not because I think they are intrinsically more interesting or important than the factors that limit the range. But unless we believe that the outcomes of evolution are always severely constrained, then perhaps we should be *on the lookout* for multiple

*Biological  
naturalism*

accounts of each domain. Only a naive Newtonian would rest satisfied with a unitary account, when, with a little more effort, a multiplicity of accounts might be found!

#### 4 Conclusion

I will summarize very briefly. Gould contrasts the “laws in the background” with the “contingent details” in the foreground of biology. What this means to me is that there *may* be genuine laws that are relevant to biology (e.g., laws of physics and chemistry), but those laws are not distinctively biological. What is distinctively biological are the contingent details, allowed but not necessitated by the presumed laws. The details can have most any degree of generality—and the degrees of generality of those details may change over time. And all the while evolution is making new rules and breaking old rules, the rules of evolution are themselves changing.

This evolutionary contingency thesis bears upon a number of other issues in philosophy of biology, including the explanatory ideals manifested in “theoretical pluralism,” and the nature of “relative significance” controversies. Just as a scientific hypothesis derives support from the phenomena it successfully explains, so, too, the evolutionary contingency thesis derives support from these other general features of biology that it makes sense of.

#### Notes

1. This essay is dedicated to Lorenz Krüger, who made me think hard about chance, and who made it fun.

I am very grateful for improvements that I owe to Peter Abrams, Douglas Allchin, Robert Brandon, Richard Burian, Joseph Cain, James Curtsinger, Daniel Dennett, Marc Ereshefsky, Ronald Giere, Stephen Gould, Ernst Mayr, Robert Richardson, Peter Sloep, Kelly Smith, Kenneth Waters, and also to audiences of philosophers and biologists at Duke, Johns Hopkins, Michigan, Tufts, and Virginia Polytechnic Institute. I am also appreciative of the very thoughtful suggestions made by my commentators, Martin Carrier and Kenneth Schaffner.

2. Richard Lewontin (1990) defends a similarly strong version in his review of Gould.

3. I should probably emphasize early on a point to which I will return later. That is, the evolutionary contingency thesis has nothing at all to say about whether there are laws of physics and chemistry. The physical and chemical generalizations that are true of the living and non-living worlds may also be contingent—presumably not evolutionarily contingent, but perhaps cosmologically contingent. I should probably also allude to one other point to which I will return later. That is, the evolutionary contingency thesis is compatible with there being *degrees* of evolutionary contingency. Distinctively biological generalizations may be *more or less* contingent.

4. Acetic acid can be oxidized and CO<sub>2</sub> produced by a simpler series of reactions, which does not involve attaching the acetyl unit to the oxaloacetate carrier. But this reaction does not lead to

the production of as many energy rich ATP molecules. The use of the oxaloacetate carrier—qua carrier—also makes sense of the cyclical nature of the Krebs reactions. In this way the carrier is regenerated, so that organisms do not have to ingest massive amounts of it in order to carry out acetic acid metabolism. See also Stryer (1988, pp. 392–393).

5. Of course, to say that a particular generalization about the Krebs cycle is not merely a chemical generalization, but also describes an evolutionary outcome, is not to say that the principles of chemistry are irrelevant for understanding it. It is just to say that evolutionary reasoning is also relevant. The evolutionary contingency thesis does not divide generalizations about the living world into those that can be explained entirely in terms of mathematics, physics and chemistry, and those that can be explained entirely in evolutionary terms without reference to principles of mathematics, physics and chemistry. The distinction is rather between those generalizations that can be explained entirely in terms of mathematics, physics and chemistry, and those that require an evolutionary perspective *in addition*.

6. Fisher’s “fundamental theorem of natural selection” also depends on Mendel’s first “law.” That is, it also fails in some cases of abnormal meiosis. Indeed, population geneticists often “prove” the fundamental theorem (or perhaps, given the notorious vagueness of the theorem, it is better to say that population geneticists “interpret” it) by deriving it from the Hardy–Weinberg “law” (e.g., Spiess 1977, pp. 402–436).

Shimony (1989) invokes a line of reasoning very much like the evolutionary contingency thesis to argue that there is no fundamental (independent of genetics) “principle” of evolution by natural selection.

7. My discussion of the existence of laws of biology owes much to the classic (but otherwise very different!) analyses by J. J. C. Smart (there are no laws of biology—1963, pp. 53–59), Michael Ruse (yes there are—1973, pp. 24–31), and David Hull (it is a very difficult issue!—1974, pp. 70–100).

My discussion also owes much to Ernst Mayr’s analysis of laws of biology. Mayr does not explicitly state the evolutionary contingency thesis, but I believe that it is central to his denial of the existence of laws of biology, and also central to his broad conception of the nature and identity of biology (Mayr 1982, pp. 32–76). However, it would take a separate paper to defend this point properly.

Philip Kitcher (1985) and John Dupré (1993) have also recently questioned the existence of laws of biology (see also note 23).

The most rigorous defense of laws of biology to date is by Kenneth Waters (ms.), which I discuss later in the text.

8. Van Fraassen actually argues that there are *no* unproblematic criteria for laws of nature; he proposes that we dispense with the category. His criticisms of the most commonly ventured criteria are indeed persuasive. Perhaps there are no laws in *any* science, at least no “laws” in any sense that we can successfully explicate. My concern here, however, is just to show that there are in any case no laws of *biology*.

9. Many philosophers of science argue that the ultimate criterion for determining whether a generalization is a law is its ability to support “counterfactual conditionals.” Thus the first claim

above is a law because we could infer on the basis of that generalization that if any object *X*—say a 100 meter sphere of some substance *besides* uranium—*were* (contrary to fact) a solid sphere of enriched uranium, *then* it would cease to exist. Whereas we would not infer on the basis of the second generalization that if any object *X*—say a 100 meter sphere of some substance *besides* gold—*were* gold then it would instantaneously shrink or cease to exist. But surely it is on the basis of what we believe is precluded or allowed by nature that we feel the first but not the second inference is justified. So the counterfactual conditional criterion is actually derivative upon the criterion of natural necessity.

10. Hull (1978, pp. 353–355) raises a similar objection to the lawlike status of many so-called “laws” of biology on behalf of his “taxa-as-individuals” thesis. That is, if taxa are spatiotemporally individuated lineages, then they are the sorts of entities that can evolve (the best argument for construing them as lineages!), in which case generalizations about taxa are only ever temporarily (in evolutionary time) true. However, my argument is broader than Hull’s, because it pertains not only to generalizations about particular taxa (e.g., humans), but also to generalizations *across taxa* (e.g., generalizations about sexual organisms). Ereshefsky’s most recent criticism of my position overlooks this point (Ereshefsky 1992, pp. 93–96).

11. There are many other sources of this weaker form of contingency, like random drift of gene frequencies in small populations and/or among selectively equivalent genotypes, which could also render temporary any genetically based generality. However, I prefer to emphasize the respects in which evolution *by natural selection* (vs. by mutation alone, or by random drift) can have contingent outcomes. This is because selection has traditionally been conceived and labeled as a “determinate” or “deterministic” agent of evolution (in contrast to mutation and drift—see, e.g., Wright 1949, p. 369; Sober 1984, p. 110). Thus, for instance, Richard Dawkins (1986, p. 41) exclaims, “Mutation is random; natural selection is the very opposite of random.” This might leave one with the unfortunate impression (not that any of the authors I just cited ever explicitly sanctioned this inference) that outcomes of evolution are contingent only to the extent that they are due to mutation alone or to random drift, and non-contingent to the extent that they are due to selection. The second sense of contingency to be discussed shortly makes clear why this would be an especially unfortunate conclusion to draw.

12. Sober does not actually invoke any particular criteria characteristic of laws of nature; while it is clear what he means by “*source law*,” it is not clear what he means by “*source law*.” He may not intend as strong a sense of “*law*” as is employed here.

13. On one such scenario, equal segregation of genes among gametes is a good way to maintain, and hence take advantage of, widespread overdominance (a form of advantage of heterozygotes over homozygotes—see Liberman and Feldman 1980; see also the discussion by Bell 1982, p. 439). An appropriate conditional might therefore be, “whenever overdominance is widespread . . .”

14. Some researchers have proposed that biosynthetic fragments of the cycle were already present in very primitive anaerobic ancestors of aerobes, before oxygen was present in the atmosphere; the cycle was then completed during the evolution of early aerobes in an increasingly oxygen-rich atmosphere (e.g., Gest 1987; Weitzman 1985).

15. Ruse (1973, pp. 59–62) and Hull (1974, p. 79) long ago raised basically this same objection to the lawlike status of such ecological rules.

16. See Michael Ghiselin’s excellent discussion of Darwin on orchids (Ghiselin 1969, pp. 131–159; see also Gigerenzer et al. 1989, pp. 132–140).

17. There are still other sources of this stronger sense of “contingency,” that is, besides random mutation and natural selection leading to functional equivalence. For instance, random drift of gene frequencies in small populations can lead to different evolutionary outcomes from the same starting point, even under the same selection regimes, and even when there is no difference in the order and timing of the introduction of mutations into the process. For reasons discussed in note 11, though, I continue to emphasize the contingent aspects of evolution *by natural selection*.

18. I want to make it clear that I am referring and responding to a *draft* of an essay by Waters. I know I will have my hands full dealing with the completed version!

19. There is another strategy for formulating laws that should be mentioned. This “*ceteris paribus*” or “*disturbing condition*” strategy is much more general than the source-law and gene-expression strategies; indeed, the latter two strategies can be viewed as instances of the former.

It is sometimes suggested that generalizations like Mendel’s “*law*” can be saved from their exceptions, and rendered true laws, by conditionalizing them upon the occurrence of all the appropriate “*ceteris paribus*” conditions, and/or the *non* occurrence of all the relevant “*disturbing conditions*” (e.g., Ereshefsky 1991). Thus, appended to the end of every biological law would be one or both of the following two clauses: “except when any of the following *ceteris paribus* conditions fails to obtain [ceteris paribus conditions listed], and except when any of the following disturbing conditions occur [disturbing conditions listed].”

As Nancy Cartwright notes, we most often translate “*ceteris paribus*” as “other things being equal,” but what we really mean is “other things being just *right*” (Cartwright 1983, p. 45). But the conditions that are just right for the evolution of a biological generality are exceedingly difficult (impossible?) to enumerate for reasons that we have been discussing. Similarly, it would be exceedingly difficult to enumerate all the relevant disturbing conditions—all the evolutionary scenarios that would result in exceptions to—a previously evolved generality.

Instead of actually listing the *ceteris paribus* and disturbing conditions, we could just refer to those two general categories. For example, in the case of Mendel’s “*law*,” we might generalize, “among sexual organisms, there is 50:50 segregation, except when any of the appropriate *ceteris paribus* conditions fails to obtain, or when any of the relevant disturbing conditions occurs.”

But there is an often noted problem with this strategy of lawmaking. Namely, it seems to purchase the truth of the supposed “*law*” at the cost of its empirical status. Presumably, laws of *nature* are supposed to be true as a matter of *empirical fact*, and not simply logically true. But how are we to interpret “the appropriate *ceteris paribus* conditions” and “the relevant disturbing conditions” so as to make the Mendelian generalization empirically and not merely logically true? In other words, how do we avoid the interpretation, “among diploids, there is 50:50 segregation, except when there obtain conditions that lead to non-50:50 segregation?” The problem is not *ceteris paribus* and disturbing conditions per se, but rather our inability to enumerate them (see, e.g., Giere forthcoming).

20. I appreciate Schaffner's point about degrees of contingency, but his example is interestingly problematic. However well "entrenched by natural selection" the genetic code may be, it has well known exceptions. The code is not universal. There is considerable variation, and not simply as a result of recent mutations that have yet to be eliminated by natural selection. There are "predictable" differences (not just due to recent mutations) in codes between mitochondrial and non-mitochondrial nucleic acids, and also among non-mitochondrial nucleic acids of different taxa. There are even predictable, site-specific code differences in the mitochondrial nucleic acid of a single taxon, and also site-specific code differences in the non-mitochondrial nucleic acids of a single taxon (see the general review by Fox 1987). Given the possibility that these differences are due to evolution by natural selection (which is at present unknown), then in what sense could selection properly be said to have "frozen" the code into "nomic universality?" Schaffner is surely right that there are degrees of contingency in the biological, as in the physical world. But just as surely, the degrees are more continuous than he suggests. Moreover, between his "essentially" accidental and merely "historically" accidental generalizations fall most (all?) distinctively biological generalizations.

21. Kauffman's own position is that self-organizing properties of biological systems place considerable constraints upon the outcomes of evolution, so that there may be distinctively biological generalizations that are contingent, but they are not *highly* contingent. I am not proud to say this, but I admit that I cannot judge the merits of Kauffman's arguments regarding the degree of contingency that actually obtains. It seems to me possible that the greatest merit of his work lies in his *focus* on the extent to which the outcomes of evolution are constrained. As he persuasively argues, it has been the tradition to focus instead on the extent to which the outcomes of evolution are not constrained—e.g., the extent to which evolution by natural selection is a Rube Goldberg tinkerer. Unfortunately, that puts me in the old-fashioned camp. In which case, I can only hope that I have elaborated the old-fashioned position clearly!

22. "Theoretical pluralism" has multiple meanings in the literature. One that is quite defensible, but different from the sense that I will be discussing, has to do with the idea that there are multiple causes for any particular biological phenomenon. For example, 1) a particular phenotypic trait is the result of the interaction of genotype *and* phenotype, 2) the presence of a trait may be viewed from an "ultimate," evolutionary perspective, *and/or* a "proximate," developmental perspective, 3) no evolutionary change is the result of natural selection *alone*—in any finite population random drift plays *some* role, etc. See Mitchell (1992) for a careful discussion of pluralism in this sense. In contrast, by "theoretical pluralism" I mean to refer to the way in which biologists explain a *domain* of phenomena, rather than any *individual* phenomenon. Another form of pluralism, perhaps more closely related to theoretical pluralism, is the form explored in John Dupré's recent book, *The Disunity of Science* (1993). Dupré defends a brand of ontological pluralism based on the rejection of essentialism. Thus he argues that there are no natural kinds in any strong sense in biology. He articulates his anti-essentialist position in several different ways, one of which is related to the non-existence of biological laws. I will return to Dupré's notion of pluralism in note 23.

23. This seems to bear upon what Dupré means by pluralism. The sense of pluralism that he defends involves a denial of the existence of natural kinds, by which he means in part that there

are no true laws of nature (Dupré 1993, pp. 63, 65). One important difference between Dupré's treatment of pluralism and mine is that I offer a *causal explanation* of why pluralism prevails in biology—in terms of the evolutionary contingency thesis—whereas it seems to me that Dupré is most concerned to document or *establish* pluralism.

But Dupré might not agree with my explanation, because in a sense it gives evolutionary thinking a unifying role in biology, and Dupré is concerned to defend the *disunity* of biology. My approach does not unify biology in terms of any particular evolutionary generalization, because evolutionary generalizations are highly contingent just like other biological generalizations. Nevertheless, my approach does suggest a unifying role for evolutionary thinking more broadly speaking: we can make biological sense of pluralism by thinking evolutionarily.

24. My position is similar to but also different from Dupré's (1993, pp. 52–53). Dupré argues that Hull begs the question—that Hull's viewpoint "is plausible only if one is already committed to the view that science requires, in the end, a unified biology with a wholly univocal concept of the species" (p. 53). I think Hull's argument is more sophisticated. To elaborate once more on the argument as it applies to theoretical pluralism, *if* nature is inescapably heterogeneous, the Newtonian would not forever overlook that fact, but would be faced with nature's heterogeneity over and over again. The Newtonian would ultimately be forced to acknowledge theoretical pluralism in that case. According to this argument, theoretical pluralism is possibly misleading, whereas the Newtonian tradition is, at worst, inefficient.

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