Does Biology Have Laws? The Experimental Evidence

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In this paper I argue that we can best make sense of the practice of experimental evolutionary biology if we see it as investigating *contingent*, rather than lawlike, regularities. This understanding is contrasted with the experimental practice of certain areas of physics. However, this presents a problem for those who accept the Logical Positivist conception of law and its essential role in scientific explanation. I address this problem by arguing that the contingent regularities of evolutionary biology have a limited range of nomic necessity and a limited range of explanatory power even though they lack the unlimited projectibility that has been seen by some as a hallmark of scientific laws.

1. Introduction. Are there laws of biology? This is one of the oldest questions in the philosophy of biology (see, e.g., Hull 1974). In its first incarnations it was a way of getting at the question of whether or not biology, especially evolutionary biology, was a legitimate science. Nowadays I assume we all agree that evolutionary biology, laws or no laws, is a legitimate science. So the question takes on a different meaning for us; it now concerns the, perhaps special, character of evolutionary biology.

The title of this paper is intentionally ambiguous. One reading of it suggests putting the question of laws in biology to a direct experimental test. Although I do think that "big" questions such as this can be put to a sort of experimental test,[1] that is not what I am going to be doing in this paper. Rather I am going to argue that the character of experimental evolutionary biology can best be made sense of if we see much

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1. A sort of ensemble test like that described by Orzack and Sober 1994; see also Brandon and Rausher 1996. Brandon and Carson (1996) discuss an experimental test of determinism in biology.

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of it as being an exploration of *contingent* regularities. My aim is not to argue that biology is absolutely lawless, or to endorse a strong version of what John Beatty (1995) calls the *Evolutionary Contingency Thesis*. My thesis is weaker than that, I will argue that biologists are interested in contingent regularities, not for some purely sociological reason, but because of the nature of the evolutionary process. My argument will be that experimental evolutionary biology has the character it has because evolution produces contingent regularities. This thesis is compatible with there being some laws of biology, but incompatible with a view that sees the primary aim of biology as the search for fundamental laws.

2. Laws Of Nature. The basic conception of laws of nature coming out of the Logical Positivist, or Logical Empiricist, movement is that laws are universal generalizations that are true not in virtue of pure logic or mathematics (are not analytic), but rather are true in virtue of the way the world is (are synthetic). But not just any synthetically true generalization will count as a law. The positivists and their successors have all agreed that there is a crucial distinction between generalizations that are accidentally or contingently true and those that have something more to them, something we might call natural or nomic necessity (as opposed to logical or mathematical necessity). A standard example is the contrast between: (a) All spheres of pure gold are less than one kilometer in diameter; and (b) All spheres of enriched uranium are less than one kilometer in diameter. (a) is probably true, but its falsity would in no way violate the laws of physics. (b) on the other hand must be true if the basic laws of atomic physics are true. So (b) but not (a) is a law of nature. The mark of natural necessity is the ability to support the relevant counterfactuals. If we were to gather together enough gold to produce a sphere one kilometer in diameter we could. On the other hand if we were to gather together that much enriched uranium we would be in big trouble.

Laws also, according to the Logical Positivists, function in scientific explanation and prediction. To explain some phenomenon one subsumes it under the relevant law or set of laws. For instance, we explain some particular atomic fission explosion by showing that the relevant initial conditions (the structure of the bomb that brings together a critical mass of U_{235}) and the relevant laws necessitate the event to be explained. (Scientific prediction was supposed to work in essentially the same way, but for our purposes we will focus on explanation.)

To summarize what has been said thus far: Laws are true non-analytic universal statements that (1) have a sort of natural or nomic necessity, which is marked by their ability to support counterfactuals;

and (2) function essentially in scientific explanation. (1) and (2) are usually thought to be two sides of the same coin since laws have explanatory power because of their natural necessity. To explain an event is to show why it had to happen (see, e.g., Hempel 1965). This legacy from the Logical Empiricist movement is present is virtually all contemporary discussions of laws. Rarely noted, however, is a third feature of laws that at least some Empiricists thought absolutely crucial.

In 1843 John Stuart Mill wrote:

> Again, there are cases in which we reckon with the most unfailing confidence upon uniformity, and other cases in which we do not count upon it at all. In some we feel complete assurance that the future will resemble the past, the unknown be precisely similar to the known. In others, however invariable may be the result obtained from the instances which have been observed, we draw from them no more that a very feeble presumption that the like result will hold in all other cases. . . . When a chemist announces the existence and properties of a newly discovered substance, if we confide in his accuracy, we feel assured that the conclusions he has arrived at will hold universally, though the induction be founded but on a single instance. . . . Now mark another case, and contrast it with this. Not all the instances which have been observed since the beginning of the world in support of the general proposition that all crows are black would be deemed a sufficient presumption of the truth of the proposition, to outweigh the testimony of one unexceptionable witness who should affirm that in some region of the earth not fully explored he had caught and examined a crow, and had found it to be grey. Why is a single instance, in some cases, sufficient for a complete induction, while in others myriads of concurring instances, without a single exception known or presumed, go such a very little way towards establishing an universal proposition. (Mill [1843], 1887, Book III, 228, quoted in Scheffler 1963, 295–296)

About a hundred years later, Nelson Goodman makes the same point, and gives a diagnosis for the difference:

> That a given piece of copper conducts electricity increases the credibility of statements asserting that other pieces of copper conduct electricity, and thus confirms the hypothesis that all copper conducts electricity. But the fact that a given man now in this room is a third son does not increase the credibility of statements asserting that other men now in this room are third sons, and so does not confirm the hypothesis that all men now in the room are third sons.

> Yet in both cases our hypothesis is a generalization of the evidence statement. The difference is that in the former case the hypothesis is a *lawlike* statement; while in the latter case, the hypothesis is a merely contingent or accidental generality. Only a statement that is *lawlike*—regardless of its truth or falsity or its scientific importance—is capable of receiving confirmation from an instance of it; accidental statements are not. (Goodman 1965, 73, emphasis in original)

(It is interesting to note that in both quotes the lawlike generalizations are from physics or chemistry while the accidental generalizations concern matters biological.) Goodman developed his elaborate and controversial theory of projectibility to explicate the difference between lawlike and accidental generalizations. We will not go into that here. But it is important to note that for Goodman, as well as for Mill, we can learn to separate the lawlike from the accidental, the projectible from the non-projectible, only from experience.[2] Nothing about the formal (syntactic) or purely semantical features of a generalization can tell us whether it is projectible or not.

If we take Goodman (and Mill) seriously we will have to add to our characterization of laws. Laws are true universal generalizations that:

(1) have nomic or natural necessity (and so support counterfactuals);
(2) are used essentially in scientific explanation; and
(3) receive confirmation from (a small number of) their positive instances.

In the final section of this paper I will argue that this is not the best conception of laws for biology. It is too restrictive. It does not allow for statistical laws, although it could be easily amended to do so. The more fundamental problems with this conception have to do with the fact that (1), (2) and (3) do not go together as a neat unit. But before we get into that, we need to examine the experimental practice of biology.

3. Experimental Practice in Biology. Elsewhere (Brandon 1994) I have argued that to understand just what an experiment is, it is necessary to see what it is not. Two contrasts are helpful here. The first is between experiments and observations. The second is between experimental work and descriptive work. The key to the first distinction is the manipulation of nature. In experiments we actively manipulate nature to produce certain conditions. In contrast, observations are passive in the

2. See Mill 1887, Book III, 232; Goodman 1965, Ch. IV; and Scheffler 1963, 295–314.

sense that they utilize conditions already in nature. This idea is perhaps best put in functional terms. If we think of the phenomena to be observed as a variable dependent on certain other independent variables, then the deliberate change and/or control of some or all of these independent variables is what I mean by manipulation.

The key to the second contrast—that between experimental and descriptive—is less obvious, but I think it corresponds to the difference between testing hypotheses and measuring values of parameters. This distinction is orthogonal to the first: a measurement of a parameter value—say, the strength of natural selection in some particular population in some particular selective environment—may require considerable manipulation. For instance, if the question is whether a particular herbivore is a selective factor for a particular population of plants, one could introduce the herbivore in an experimental plot and measure its effects on the survival and reproduction of various genotypes of the plant. Here, one is manipulating an independent variable, presence or absence of the herbivore, to measure the selective response of the differing genotypes of the plants. One can do this, and often biologists do things like this, without any specific hypothesis in mind.

If one thinks of these two independent distinctions as dichotomies, Figure 1 suggests itself. Each of the four boxes of Figure 1 represents something realized in the practice of science, and certainly in the practice of evolutionary biology. The lower right box represents nonmanipulative descriptive studies, e.g., a cataloguing of the flora of western North Carolina. The human genome project falls here as well. The lower left box represents manipulative descriptive work. Here one manipulates some one or more independent variables and measures the response variable, but without a specific hypothesis in mind to test, as in the example of the last paragraph. Nonmanipulative tests of hypotheses fall into the upper right box. This box is heavily populated, most work using the comparative method fits here, as do so-called "natural experiments" (Diamond 1986). Finally, the upper left box corresponds to manipulative hypothesis testing. Much work in that part of evolutionary biology that is oriented towards elucidating the mechanisms of evolution fits here. For instance, to test the hypothesis that sexual reproduction is advantageous in heterogeneous environments, one could take some organisms capable of both sexual and asexual reproduction, manipulate them to produce offspring of both types, and then put those offspring into a heterogeneous environment to compare their fitnesses (see, e.g., Antonovics et al. 1988). Work in this box most clearly fits our ideas about what constitutes an experiment.

Do we then categorize only the upper left box as experimental? Do we, in a more inclusive spirit, count all but the lower right box as

EXPERIMENT / OBSERVATION

DESCRIPTIVE / EXPERIMENTAL		Manipulate	Not Manipulate
	Test hypothesis	Manipulative hypothesis test	Non-manipulative hypothesis test
	Measure parmeter	Manipulative description or measure	Non-manipulative description or measure

Figure 1. The two-by-two table formed by two separate distinctions relevant to the question of what is an experiment. Each of the four cells represents a type of investigation important in evolutionary biology.

experimental? But before worrying too much over these questions, let me suggest that both of the dichotomies used to set up our table are not really dichotomies but rather are better thought of a continua.

Clearly manipulation admits of degrees. We can change and/or control one or many independent variables, and our control can be more or less precise. Thus the first distinction—that between experiment and observation which we explicated in terms of manipulation vs. non-manipulation—forms a continuum rather than a rigid dichotomy.

At first glance our second distinction—that between procedures that test hypotheses and those that measure parameter values—seems more dichotomous than continuous. It might seem that an investigation either tests a hypothesis or it does not. But things are not this simple. Take, for example, a paradigm case of parameter measurement in evolutionary biology, a study measuring the strength of natural selection in some natural population (for citations of many such studies, see Endler 1986). Such a study would consist of the identification of various types (phenotypes or genotypes) in the population and the measurement of some component(s) of fitness of those types. But the very same data could be used to test hypotheses. We could use them to test the hypothesis that Type 1 is selectively favored over Type 2 in the population, or we could use them to test the blander hypothesis that natural selection is occurring in the population.

So, is such a study a test of a hypothesis or is it merely the measurement of a parameter value? This is a complicated issue, but I have argued elsewhere (Brandon 1994) that we decide such questions using criteria that are more continuous than dichotomous. Basically, the relevant scientific community decides how to describe such a study on the basis of two things: how important is the hypothesis to be tested, and how important is the test of that hypothesis. This idea explains why such a study conducted in 1996 would most likely be considered a measurement of a parameter, whereas conducted in the 1950s it would have been considered more of a hypothesis test. Nowadays we have plenty of demonstrations of the existence of natural selection in natural populations, but it was not that long ago that such was not the case. The importance of the hypothesis that natural selection occurs has not decreased in evolutionary biology. It is the basis for the application of the theory of natural selection to populations. But the importance of testing it has certainly declined with each new demonstration of natural selection. On the other hand, some "hypotheses" are not important enough to be so called. One very general class of such "hypotheses" are those that can always be formed after the fact of any sort of parameter measurement. After the fact, one can always recast a parameter measurement as a test of the hypothesis that the parameter takes the value that we have just observed.

Much more could and should be said about the notion of importance at work here. For instance, importance presumably varies with the generality of the hypothesis and its interconnectedness with other theoretical hypotheses. I simply want to point out that importance, as we have been discussing it, is a matter of degree and so our second distinction is best thought of as continuous.

Thus Figure 1 should be rejected in favor of Figure 2 which represents a field of experimentality where we do not have a rigid experimental/nonexperimental distinction but rather a field in which studies can be located and described as more or less experimental. The closer a study is to the upper left corner, the more experimental it is.

The distinctions that form Figure 2 help us address the question of why we use experimentation as a scientific method. We divide that question into two. First, why manipulate? The answer to that is, I think, fairly straightforward. We manipulate because nature does not

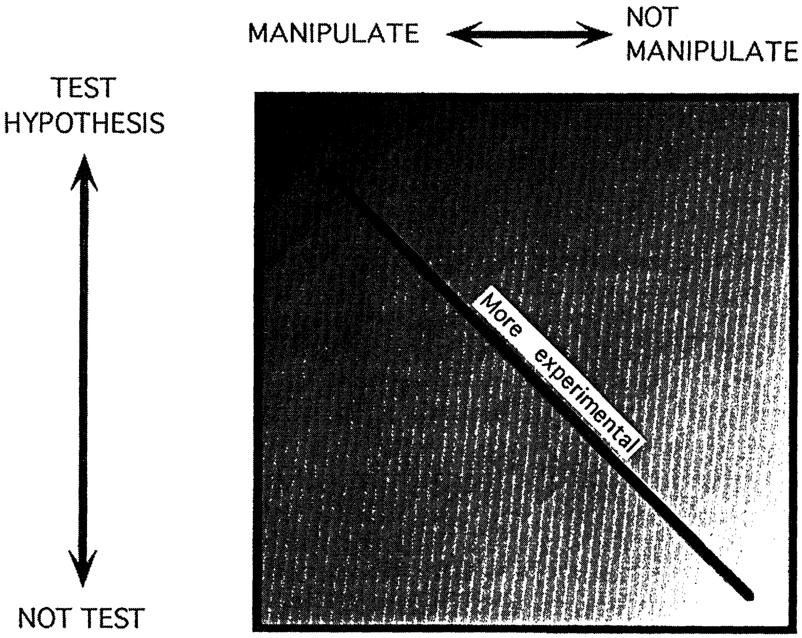

Figure 2. The representation of the space of experimentality formed by two continua relevant to the question of what is an experiment. Investigations located more toward the upper left corner are more experimental.

reliably and repeatably produce the conditions we need to observe in order to answer the empirical questions we pose. Second, why do we test hypotheses rather than sticking to descriptive studies that measure certain aspects of nature? The answer to this is less straightforward and touches on some of the central questions of the philosophy of science. Basically, we test hypotheses because we want to build theories that systematize our knowledge of the empirical world and testing hypotheses is the most powerful way to advance this theoretical knowledge.

These answers are by no means complete, but they do give us a better appreciation of why experimentation is a good thing in science. But, I now want to argue that in evolutionary biology, more experimental is not always better than less. This will give us insight into the distinctive character of evolutionary biology.

Consider the manipulation continuum. In some areas of evolutionary biology, such as paleontology and much of systematics, the manipulations we might like to make are practically impossible. This situation is by no means unique to evolutionary biology; it is the same in much of geology and astrophysics. Where manipulation is not possible, it is not done. More interesting is the situation in that part of evolutionary biology that studies the mechanisms of evolutionary change. These processes are in operation all around us and are manipulable. But the best work in evolutionary population biology does not hug the left side of Figure 2. Rather, I will argue, it clusters in the middle of the upper region. Why is this?

The most manipulative population biology studies are those that most tightly control the relevant independent variables. Typically this is only possible in laboratory studies. But it is all too easy to create in a laboratory setting conditions that are nowhere found in nature and that have only dubious relevance to what is going on in nature. For instance, a laboratory study that creates what has been shown theoretically to be the most favorable conditions for group selection, and then records a group selection effect, will not go very far in convincing group selection skeptics of the importance of group selection in nature, if those skeptics think those conditions are unrealistic. Similarly, a study that throws together two geographically and phylogenetically unrelated organisms and records a competitive interaction between them says little or nothing about the distribution and abundance of those species in nature.

The contrast with contemporary high energy physics is striking. The argument physicists made, unsuccessfully as it turns out, for the Superconducting Super Collider was that it was needed to test the most fundamental theories in physics. The phenomena it would have created would have been highly artificial, they would have existed either rarely or nowhere else in the universe. But physics, at least certain areas of it like high energy physics, is a science driven by the search for fundamental laws. No phenomena are too "artificial" to be of relevance to it. Indeed, as Hacking (1983) argues persuasively, much of modern physics is driven by these laboratory-created phenomena. The phenomena of cannonballs and falling apples do not help these days in developing physical theory.

Evolution, on the other hand, continually creates new and unique phenomena. It results in branching phylogenies. Each monophyletic group, each branch of the tree of life is unique. Furthermore, these unique groups live in, and construct, unique selective environments (see Brandon and Antonovics 1996). All this forces evolutionary biologists to have a keen interest in the actual, that is, to be concerned with the realism of their experimental conditions. This realism can be assured in properly designed and executed field experiments, but the costs are high. Field experiments tend to be labor intensive, they are often conducted under difficult conditions, their results are less certain due to less control of known or unknown independent variables (Diamond 1986). And finally, and for us this is the most important point, the generality of results of field experiments can only be established by further field experiments. The results of field experiments are like Mill's black crows or Goodman's third sons. They are not automatically projectible. Why, given these costs, do evolutionary population biologists do field experiments? Because it is simply too easy to create phenomena in the laboratory that have no relevance to what is going on in nature.

Consider now the hypothesis test/parameter measurement continuum. Again there is a striking contrast with fundamental physics. In physics there are thought to be only a few fundamental constants, e.g., Planck's constant (Weinberg 1992). These parameter values are called constants because they are supposed to hold everywhere and everywhen. When measured accurately once, they need not be measured again. In evolutionary biology, on the other hand, there are no fundamental constants. The most important parameter values in evolution, things like the strength of selection, mutation rate, migration rate, are not at all constant. Even when measured accurately at one place and time, they must be constantly remeasured for different populations in different environments. Thus it makes sense that much more time and energy is spent measuring parameters in evolutionary biology than in contemporary physics. Again this is because biological parameters seem to lack the projectibility, or the lawlikeness, of the fundamental constants of physics.

To briefly summarize this section, I have argued that there are two dimensions of experimentation, and that along both of them evolutionary biology is less experimental than is physics. I explained this in terms of the phenomena of biology being less projectible or less lawful than those of physics. Put another way, experimental evolutionary biology takes on the character it has due to the fact that it is largely investigating contingent regularities.

4. Bringing Philosophy of Science and the Phenomena of Biology Together. The previous two sections of this paper create a tension between philosophy of science and evolutionary biology. In particular, if the characterization of laws given in §2 is correct and §3 is correct in its characterization of the phenomena investigated in evolutionary biology, then the generalities discovered in evolutionary biology are not lawlike, and so evolutionary theory is not explanatory (given that laws are essential components of scientific explanations). If you think, as I do, that evolutionary theory is not just explanatory, but has perhaps the greatest explanatory power of any theory in the history of science, then there is tension. Of course, we could revise this view and hang on to the philosophy of science developed in §2. I think the great success of evolutionary theory argues against that tack, so I will pursue the opposite one—revising the philosophy of science.

Recall that laws are supposed to be generalizations that:

(1) have nomic or natural necessity;
(2) are used essentially in scientific explanation; and
(3) receive confirmation from (a small number of) their positive instances.

It is easy to see why it might be thought that (1), (2) and (3) all go together to describe some unitary concept of law. (1) and (2) go together in that explaining a phenomenon is showing why it had to happen, which is to show that it follows from some generalization(s) that is (are) nomically necessary. (1) and (3) are the same in that (3) distinguishes nomically necessary generalizations from accidental or contingent ones. Thus (1), (2) and (3) all describe the same thing.

I think there is a fallacy in the above argument, a fallacy that involves an equivocation concerning the scope of relevant generalizations. I will explain this shortly, but first let me just state my positions with respect to evolutionary biology. It is that there is a gulf between (1) and (2) on the one hand and (3) on the other. That is, in biology some generalizations used in explanation do not receive the sort of confirmation from their positive instances that Mill and Goodman envisioned for laws.

There are two different classes of such generalizations. First, in biology there seem to be a number of nonempirical, i.e., analytic, generalizations that are genuinely explanatory. We will explore such cases briefly, but they are not directly relevant to the main thesis of this paper. Directly relevant are members of the second class—generalizations that are empirical, but are only contingently true. They are explanatory and have a limited sort of nomic necessity; or so I will argue.

Foremost among the generalizations fitting in the first class is the Principle of Natural Selection. As I have argued extensively elsewhere (Brandon 1978, 1981, 1990), this is the central organizing principle of the theory of evolution by natural selection. It plays an essential role in all explanations of evolution by natural selection. And finally, it, as a general schematic law, is without empirical content. It is simply an instance of a law of probability theory (the principle of direct inference). Other examples are easy to find. For example, the Hardy-Weinberg Law is, as anyone who has derived it knows, just a bit of fairly simple mathematics. Still it seems to play an explanatory role in population genetics. Galton's explanation of regression to the mean is another example. Thus one might want to extend the status of law to such explanatory analytic generalizations (as Elliott Sober argues in this issue). We will return to this suggestion presently.

The second class contains the sort of contingent regularities evolution produces and evolutionary biology studies.[3] These range in generality from the near ubiquity of the genetic code for life on earth, to generalizations that may hold of only a particular population for only a few years. Start at the low level of generality. Suppose we investigate a particular population of plants in a field over a period of three years. Suppose further that we discover a pattern of spatial and temporal heterogeneity of their selective environment that would favor sexual over asexual reproduction. How do we generalize this finding? Recall that according to both Mill and Goodman the projectibility of a hypothesis is something that cannot be known a priori, but can only be discovered by empirical investigation. It is only through empirical investigations that we are confident in projecting from a single sample of a particular metal and finding that it conducts electricity to the generalization that all samples of that metal will similarly conduct electricity. It is only through empirical investigation that we have learned that the physical world has that sort of uniformity. Through empirical investigation we have learned, like it or not, that the biological world is not so uniform. That one population has exhibited a certain pattern of selective environmental heterogeneity over a few years gives us little reason to believe that all or even most have. Thus, at present, we simply do not know how far we can project the discovered regularity.

But suppose that we have good reasons to believe that the conditions we are currently observing in this population have held for a considerable time, say a hundred generations. And suppose these plants are capable of producing seeds both by sexual outcrossing and asexually, but that the majority of the seeds are sexual. It seems to me that our regularity is not then without explanatory power. We can invoke it to explain the prevalence and maintenance of sexual reproduction in this particular population. Furthermore, this observed regularity certainly supports a limited range of counterfactuals. For instance, it supports the counterfactual assertion that this particular plant would be selected against if it were, contrary to fact, to produce all its seeds asexually. But our regularity certainly does not support a broad range of similar counterfactuals applied to quite different organisms in quite different environments. So it has at least a limited (limited to this population over the relevant time period) range of nomic necessity. Thus (1) and (2) seem to be separated from (3).

3. That evolution produces contingent regularities is one of the central themes of Beatty 1995.

What has been said about our low-level generalization concerning patterns of selective environmental heterogeneity holds for the highest level contingent generalizations in biology, for instance that almost all life on Earth shares the same genetic code. That is very general because, presumably, it evolved early in the history of life and deviations from it now would be fairly costly. Thus it is a "frozen accident." The code is certainly explanatory (explaining, for instance, protein synthesis) and it has a moderately high level of nomic necessity to it. But if we were to discover life on Mars, or somewhere else in the universe, we would be foolhardy to project that it would share our genetic code (unless, of course, we thought it shared a common origin with life on Earth).

Thus my thesis is that the contingent regularities of biology have (a limited range of) nomic necessity and have (a limited range of) explanatory power, but lack the unlimited projectibility that Mill and Goodman saw as one of the hallmarks of scientific laws. Put this way, and I think this is the right way of putting it, it seems less clear that I have separated (3) from (1) and (2). That is, given exactly the same scope, (1), (2) and (3) do seem to hang together. They are separated when (1) and (2) are restricted in scope while (3) has the sort of unrestricted scope that Mill and Goodman clearly intended to characterize laws of nature.

Let me end this paper by considering how we, as scientists and philosophers of science, do use, and should use, the term 'law'. We as a community can decide to use it however we like. We can avoid the tension set up between §2 and 3 of this paper by a much more promiscuous use of the term. Let us call the low-level contingent regularities we use in low-level explanations 'laws'. Let us also label the logical and mathematical generalizations, such as the PNS and the H-W law, 'laws'. Then the tension disappears.

But promiscuity often has its costs and this case is no exception. If experimental physics differs from experimental biology in the ways I outlined in Section 3, and if that is best explained in terms of the former being a science devoted to searching for fundamental laws and the latter being a science largely devoted to investigating contingent regularities, then promiscuity robs us of that explanation. Furthermore it blurs the very important distinction between the logical/mathematical truths used so centrally in biology and the generalities whose truth depends on the contingent details of the evolution of life. Thus, although I do not want to argue too much over how we end up using the term 'law', my recommendation is one of linguistic conservatism. Let us keep the Empiricist characterization of law. But let us also recognize that things other than laws can have explanatory power. This includes both analytic statements (such as the PNS) and contingent regularities. The latter, we should also recognize, can have a limited range of nomic necessity. Thus my recommendations, although linguistically conservative, greatly expand the cluster of concepts that went into the traditional conception of law.

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