POPPER'S SHIFTING APPRAISAL OF EVOLUTIONARY THEORY

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Karl Popper argued in 1974 that evolutionary theory contains no testable laws and is therefore a metaphysical research program. Four years later, he said that he had changed his mind. Here we seek to understand Popper's initial position and his subsequent retraction. We argue, contrary to Popper's own assessment, that he did not change his mind at all about the substance of his original claim. We also explore how Popper's views have ramifications for contemporary discussion of the nature of laws and the structure of evolutionary theory.

1. Popper's Evolving Interest in Evolution

Although our main focus is on Popper's 1974 and 1978 papers, his interest in evolutionary theory (ET) started considerably earlier, and a review of this history will be useful in locating Popper's two papers within his larger intellectual trajectory. Popper's book *The Poverty of Historicism* was published in 1957, but much of it (including the material on evolution) was given as lectures in the 1930s, and the book was first published in three parts in *Economica*, in 1944–45. Although Popper does not assert in *The Poverty of Historicism* that ET contains no empirical laws, and this is the central issue in his 1974 and 1978 papers, he advances philosophical theses about ET in that earlier book that helped shape his subsequent thought. In fact, he there defends what seems like a logically stronger thesis—that there are no laws of evolution, period.

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In section 27 of *The Poverty of Historicism* (called "Is There a Law of Evolution? Laws and Trends"), Popper argues that there are no general laws governing the evolution of societies, the evolution of organisms, or the evolution of the whole universe. He claims this despite granting that many laws are used in explaining the phenomena discussed in the social sciences, in evolutionary biology, and in cosmology:

> The crucial point is this: although we may assume that any actual succession of phenomena proceeds according to the laws of nature, it is important to realize that practically *no sequence of, say, three or more causally connected concrete events proceeds according to any single law of nature*. If the wind shakes a tree and Newton's apple falls to the ground, nobody will deny that these events can be described in terms of causal laws. But there is no single law, such as that of gravity, nor even a single definite set of laws, to describe the actual or concrete succession of causally connected events. . . . The idea that any concrete sequence or succession of events (apart from such examples as the movement of a pendulum or a solar system) can be described or explained by any one law, or by any one definite set of laws, is simply mistaken. There are neither laws of succession nor laws of evolution. (Popper 1957, 117)

In the same section of the book, Popper faults Comte and Mill for thinking that there are laws of succession, each of which describes the sequence of states through which a system of given type must move. Popper admits that there are historical trends, but he says that trends cannot be characterized by universal generalizations and so are not laws.

We have a few criticisms of these claims from *The Poverty of Historicism*. Popper shifts between saying that there is no "single" law of evolution and saying that there is no "one set of definite laws." The first of these requires a principle for individuating laws. If L_1, L_2, . . . , L_n are each laws, why is their conjunction not a single law? And conversely, a sentence that seems to express a single law can easily be rewritten as a conjunction, each conjunct of which expresses a law. For this reason, Popper's point is better put by using the second formulation that "there is no one set of definite laws." In any event, we do not think that Popper gives a good reason for accepting this thesis. He grants that there are laws of change for pendulums and solar systems but never makes it clear why there are not laws of evolution for other objects. We also see a problem in Popper's expressing his thesis that there are no laws of evolution by assuming that laws must be deterministic. Why can a law not be probabilistic? Popper is right to separate laws from mere trends. However, even if statements

like "events of type T_1 are often followed by events of type T_2" are not law-like, this leaves it open that probability statements sometimes are. After all, there are objective interpretations of probability statements that do not equate probabilities with actual frequencies. This is a point that Popper later took to heart when he proposed a propensity interpretation of probability (Popper 1959b). Quantum theory does more than describe de facto trends. Trends depend on initial conditions, as Popper says, but this does not rule out the possibility that there are probabilistic laws that are independent of initial conditions.

Popper's interest in ET broadened in the 1960s (Simkin 1993; Watkins 1995; Munz 2006). There were three reasons why. Popper came to believe that there is a close relationship between his method of trial-and-error elimination in science and the process of natural selection (Ruse 1977; Nanay 2011). He also saw new ways in which ET is relevant to his views on historicism. And finally, he became convinced that ET is the only significant scientific theory that bears on the mind-body problem and on the problem of freedom in a physical universe.[1]

As Popper delved deeper into ET, he came to believe that the principle of natural selection (NS) is a priori. This was a conclusion that puzzled him. On the one hand, he maintained that scientific theories are empirical, not a priori, but on the other hand, he was convinced that ET is the most successful theory in its domain and has no serious competitors. Popper (1974, 1978) attempted to reconcile these ideas, although he reached different conclusions in the two papers. His solution in the 1974 paper was to suggest that ET is not a theory of forces like Newtonian theory but rather involves what he calls "situational logic." This formed part of his thesis that ET provides in-principle explanations without supplying actual explanations of particular phenomena, since actual explanations of a given event must cite empirical laws. In the 1978 paper, Popper additionally suggested that there is an alternative formulation of the principle of NS that is not a priori. The 1974 a priori principle and the 1978 empirical reformulation are these:

> (PNS) If traits T_1 and T_2 are found in a population, T_1 is fitter than T_2, the two traits are heritable, and no other evolutionary causes impinge on the population, then T_1 will increase in frequency.[2]

1. Clear statements of his interest in ET regarding the relationship between ET and his evolutionary epistemology can be found in Popper (1957, 133; 1959a, 91; 1972, 261; 1974, 133; 1994a, 12). For Popper's view about how ET bears on the mind-body problem and on freedom in a physical universe, see Popper (1972, 1978, 1994a).

2. Popper (1974) does not explicitly indicate which statement about NS he thinks is a priori, but he does say that given the statistical definition of fitness, the principle he has in mind is a priori. This is our justification for saying that Popper thinks that PNS is a priori.

(PNSR) All traits in all organisms evolved because of natural selection.[3]

Popper (1978) says that the distinguished evolutionary biologists C. H. Waddington, G. G. Simpson, J. B. S. Haldane, and R. A. Fisher all attribute great explanatory power to PNS. Popper replies to this pantheon by pointing out that PNS is a tautology and that the explanatory power of a tautology is zero. PNS's tautological status stems from the fact an organism's fitness is defined as its degree of actual reproductive success. By proposing the PNSR reformulation, Popper hoped to increase the empirical content of ET by turning its main principle into an empirically testable statement. As we explain in what follows, Popper (1978) thought that PNSR is false. Given this, it is questionable how much ET is improved by replacing the trivial claim PNS with the false claim PNSR.

2. Difficulties concerning A Priori Formulations of ET

In his 1961 Herbert Spencer Lecture (which appeared in print as Popper [1972]), Popper says that it is a mistake to compare ET to Newtonian physics: "Darwin's discovery of the theory of natural selection has often been compared to Newton's discovery of the theory of gravitation. This is a mistake. Newton formulated a set of universal laws intended to describe the interaction, and consequent behavior, of the physical universe. Darwin's theory of evolution proposed no such universal laws" (267). Popper claims that Darwinism's success resides in its providing in-principle explanations: "Nevertheless, Darwin's revolutionary influence upon our picture of the world around us was at least as great, though not as deep, as Newton's. For Darwin's theory of natural selection showed that it is *in principle possible to reduce teleology to causation by explaining, in purely physical terms, the existence of design and purpose in the world*" (267).[4] Two paragraphs later, Popper says: "Although this was a great achievement, we have to add that the phrase *in principle* is a very important restriction. Neither Darwin nor any Darwinian has so far given an actual causal explanation of the adaptive evolution of any single organism or any single organ. All that has been shown . . . is that such explanations might exist (that is to say, they are not logically impossible)." Thus, the reason Popper thinks it is a mistake to liken ET to Newtonian theory is that ET does not postulate empirical laws; it offers a

3. This is how we interpret Popper's (1978, 345) claim that "all organisms and especially all those highly complex organs whose existence might be interpreted as evidence of design and, in addition, all forms of animal behavior have evolved as the result of natural selection."

4. In this quotation, the use of italics is Popper's. The same holds for italics in subsequent quotations, unless otherwise noted.

priori mathematical models, which at best can show how it is possible in principle to explain adaptations in causal terms.

How, according to Popper, did evolutionary biology lapse into tautology? In his 1961 Herbert Spencer Lecture, he alludes to the source of this problem: "What I regard as Darwin's central idea—his attempt to explain genetic changes which led to *better adaptation in the sense of better chances for the individual animal or plant to survive*—has recently suffered an eclipse. This is due very largely to the fashionable pursuit of mathematical exactness, and to the attempt to define survival value statistically, in terms of actual survival (of a gene, or some other genetic unit, in a population)" (Popper 1972, 271). In the next two paragraphs, Popper argues that such mathematically exact theories cannot explain complex adaptations. Popper addresses this topic in his "Science: Problems, Aims, Responsibilities," initially presented at the Plenary Session of the 47th Annual Meeting of the Federation of American Societies for Experimental Biology and published in the Federation Proceedings in 1963 but subsequently republished as chapter 4 of his *The Myth of the Framework*: "There is a difficulty with Darwinism. While Lamarckism appears to be not only refutable but actually refuted (because the kind of acquired adaptations which Lamarck envisaged do not appear to be hereditary), it is far from clear what we should consider a possible refutation of the theory of natural selection. If, more especially, we accept the statistical definition of fitness which defines fitness by actual survival, then the theory of the survival of the fittest becomes tautological, and irrefutable" (1994b, 94).

Although Popper talks about the difficulty of formulating empirical laws about NS that use a statistical definition of fitness in his 1961 Herbert Spencer Lecture, it is only in his 1963 talk that he claims that this way of describing NS is tautological. However, Popper does not give a full treatment of the issue in that talk. He just adds to the above quoted remarks that we should avoid the mistake of thinking that NS is the only mechanism that can lead to apparently goal-directed adaptations. The way forward, he suggests, is to conceptualize alternative mechanisms and then design crucial experiments to decide between them and NS. We note that this is and has been common practice in evolutionary biology, where drift is often taken to be an important competitor to NS.

The issue of tautology reappears in Popper's 1965 Arthur Compton Memorial Lecture: "Quite apart from evolutionary *philosophies*, the trouble about evolutionary theory is its tautological, or almost tautological character: the difficulty is that Darwinism and natural selection, though extremely important, explain evolution by 'the survival of the fittest' (a term due to Herbert Spencer). Yet there does not seem to be much difference, if any, between the asser-

tion 'those that survive are the fittest' and the tautology 'those that survive are those that survive' " (Popper 1972, 241–42). Popper raises the same issue in his 1969 Emory University Lectures:

> Biologists (especially Fisher) felt compelled to *define* as "more fit" those which more often survive. Thus, what once looked like a promising explanatory theory becomes quite empty. The statement "Evolution tends to produce higher forms because only the fittest survive" may sound like an explanation. But if we substitute here for "the fittest" its defining phrase, we get: "Evolution tends to produce higher forms because those forms which more often survive more often survive." So our "because" phrase has degenerated into a tautology. But tautology cannot explain anything. *All tautologies are equivalent to "All tables are tables" or "Those who live long are those who live long*." (Popper 1994a, 54, emphasis added)[5]

The tautology issue comes up again in chapter 2 of Popper's *Objective Knowledge*, but this time he goes a little further in his treatment of the subject: "A central problem of evolutionary theory is the following: according to this theory, animals which are not well adapted to their changing environment perish; consequently those which survive (up to a certain moment) must be well adapted. This formula is little short of tautological, because 'for the moment well adapted' means much the same as 'has those qualities which made it survive so far.' In other words, a considerable part of Darwinism is not of the nature of an empirical theory, but it is a logical truism" (Popper 1972, 69).

After this paragraph, Popper attempts to separate, to our knowledge for the first time, the empirical and the a priori parts of the theory. He says that the empirical claims are these: the environmental conditions in which organisms live change slowly, organisms are sensitive to such changes, the only way organisms can survive such changes is by producing mutations some of which respond to these changes, and useful mutations sometimes occur. Popper then describes what he thinks the a priori part of this theory is: "If the process of adjustment has gone on long enough, then the speed, finesse, and complexity of the adjustment may strike us as miraculous. And yet, the method of trial and of the elimination of errors, which leads to all this, can be said not to be an empirical method but to belong to the *logic of the situation*. This, I think, explains (perhaps a little too briefly) the logical or *a priori* components in Darwinism" (1972, 70). Popper is here constructing a conditional statement whose

5. We see things differently; although all mathematical truths are mathematically equivalent, some help explain empirical phenomena while others do not (Sober 1984, 2011a).

antecedent describes properties of organisms and environment and whose consequent is about the emergence of novel adaptations. The conditional, he says, is a priori, although the antecedent and the consequent are both empirical. Logically speaking, Popper's conditional resembles "if someone is a bachelor, then he is unmarried." Popper does not take the discussion any further in this work.

Popper's first thorough treatment of the tautology issue and ET was in section 37 of his 1974 autobiography (entitled "Darwinism as a Metaphysical Research Program"), which appeared in the Schilpp volume on Popper. Here Popper announces that ET "is not a testable scientific theory, but a metaphysical research program—a possible framework for testable scientific theories." He clarifies what he means by a metaphysical research program in footnote 242: "The term 'metaphysical research programme' was in my lectures from about 1949 on, if not earlier; but it did not get into print until 1958, though clearly in evidence in the last chapter of the *Postscript* (in galley proofs since 1957). I made the *Postscript* available to my colleagues, and Professor Lakatos acknowledges that what he calls 'scientific research programmes' are in the tradition of what I described as 'metaphysical research programmes' ('metaphysical' because nonfalsifiable)" (Popper 1974, 175).

This remark requires clarification. Although Popper thought that ET is a "metaphysical research program," he did not think that Newton's theory or Einstein's theory falls in this category. Lakatos, in contrast, held that all three are "scientific research programs" because all three contain hard-core assumptions that are unfalsifiable because of the Duhem-Quine problem. For this reason, Lakatos proposed that such programs should be evaluated by their overall ability to solve theoretical and empirical problems. The latter part of what Lakatos says in fact coincides with what Popper says about metaphysical research programs. Popper decides whether a theory is metaphysical on the basis of whether its purported laws are empirical (Stamos 2007); he does not deny that genuine physical theories may also deploy metaphysical assumptions. It is in this connection that Popper sees a difference between ET on the one hand and Newton's and Einstein's theories on the other.

It is important to recognize that just because Popper labeled ET as metaphysical, we should not jump to the conclusion that he took ET to be a pseudoscience (Hull 1999). For Popper (1978, 344), "the doctrine of natural selection is a most successful metaphysical research programme." Psychoanalysis and astrology are not in that league; Popper thinks they are pseudosciences. Popper then explains Darwinism's success as a metaphysical research program in terms of "situational logic": "I think that there is more to say for Darwinism than that it is just one metaphysical research programme among others. In-

deed, its close resemblance to situational logic may account for its great success, in spite of the almost tautological character inherent in the Darwinian formulation of it, and for the fact that so far no serious competitor has come forward" (1974, 135). The a priori character of ET's main principle does not lead Popper to dismiss the theory; rather, he tries to provide a philosophical explanation of how ET could be scientifically successful.

Popper then clearly states that by Darwinian theory or Darwinism he is referring to the modern synthesis theory of evolution. He says that this theory involves two main theses:

> (1) The great variety of the forms of life on earth originate from very few forms, perhaps even from a single organism: there is an evolutionary tree, an evolutionary history.
> (2) There is an evolutionary theory which explains this. It consists in the main of the following hypotheses. (Popper 1974, 135)

Popper then lists four hypotheses that flesh out this second component. The first says that heredity is faithful. The second says that small variations arise in populations caused by accidental mutations. The third says that NS is a mechanism that eliminates unfit variants. The fourth says that the variability (what Popper calls the 'scope of variation') found in a population is subject to NS. This last hypothesis basically says that the hereditary mechanisms that give rise both to mutations and to mostly faithful reproduction are themselves the products of NS. It is in this sense that NS is said to determine the scope of variation.

It should be clear that the two main theses of ET are not tautologies, and neither are the first, second, and fourth hypotheses that Popper mentions. Popper thought that unrestricted existential claims are not falsifiable and therefore not empirically testable; however, he also thought that existential statements are falsifiable if they are restricted to specific space-time regions (Popper 1963, 195–96).[6] This is how common ancestry and the three hypotheses should be understood—they each pertain to life on planet Earth.[7] It follows that there are important parts of ET that are empirically testable. The only element that is a candidate for being a tautology is the third hypothesis. If this analysis of what Popper says is correct, then the only reason Popper has for thinking that ET is not a testable scientific theory is that the third hypothesis is a tautology.

6. Others do not require much in the way of background theories; "there are five apples in the basket now" can be refuted just by counting them apples.

7. The idea that common ancestry is a historical hypothesis, not a general law, is already in *The Poverty of Historicism*; see Popper (1957, 106–7).

The problem, he thinks, is engendered by the definition of fitness that biologists use: "Adaptation or fitness is defined by modern evolutionists as survival value, and can be measured by actual success in survival: there is hardly any possibility of testing a theory as feeble as this" (Popper 1974, 137).

Although Popper speaks of the "synthetic theory of evolution," he evidently is not thinking of all the propositions in that "theory" when he says that the theory is feeble or tautologous. We suggest that when he here considers what "evolutionary theory" is, he is looking for laws, so all the singular empirical statements in the "theory" are set to one side. What remains, he says, is a lonely tautology. We emphasize that the fact that PNS is a tautology does not show that there are no laws in ET. Otherwise, Newton's theory would fall by the wayside if "$F = ma$" turned out to be a definition of force. Popper thinks that PNS is the main principle of ET and the only candidate law that ET offers. For Popper, PNS is the common thread of ET that connects all the other evolutionary claims he lists; if it fails to be empirical, what we are left with is a bunch of unconnected claims.

As already noted, Popper thinks that the way to understand how ET can be successful despite its lacking empirical laws is by understanding its deployment of situational logic. To get a grip on what Popper has in mind here, consider the following remark: "Models, as here understood, may be called '*theories*,' or be said to incorporate theories, since they are attempts to solve problems—problems of explanation. But the opposite is far from true. Not all theories are models. Models represent typical initial conditions rather than universal laws. And they therefore need to be supplemented by 'animating' universal laws of interaction—by theories which are not models in the sense here indicated" (Popper 1994b, 165).[8] Popper thinks that in the natural sciences there are two kinds of *explananda*—token events and types of events. Token events are explained or predicted by the conjunction of universal laws and initial conditions. However, types of events are explained by constructing models that "represent typical initial conditions," which are always idealizations (164). Popper's example of a token event is the occurrence of a particular lunar eclipse, and his example of a type of event is the periodic recurrence of lunar eclipses. The idea is that if you want to either explain or predict a single occurrence of a lunar eclipse, you just write down some laws and relevant initial conditions and then show that the event in question follows from them. However, in explaining why lunar eclipses have a periodic cycle, you need to build a model representing typical initial conditions and show that under these typical initial conditions lunar eclipses periodically recur. In the sec-

8. This quotation is from *The Myth of the Framework*. The chapter is based on a talk Popper gave in 1963.

ond case, laws enter into explanations only indirectly in the sense that the models are built or constructed in accordance with those laws.

Although Popper says in the passage previously quoted that a model-based explanation must always have universal laws in the background, he says a page later that model-based explanations can go forward in the social sciences even though they are not backed up by universal laws: "I wish to propose the thesis that what I have said about the significance of models in the natural sciences also holds for models in the social sciences. In fact, models are even more important here because the Newtonian method of explaining and predicting singular events by universal laws and initial conditions is hardly ever applicable in the theoretical social sciences. They operate almost always by the method of constructing *typical* situations or conditions—that is, by the method of constructing models" (1994b, 166). Constructing a model in the social sciences proceeds by describing a typical situation, the problem in that situation, the parts of the typical situation that are relevant to the problem at hand, and the aims of an agent. Popper thinks that these models do not require the specification of any psychological laws. All you need to assume, according to Popper, is a so-called rationality principle. This principle says that agents act in accordance with the requirements of the situation for achieving their aims.

Although Popper seems to think that the only candidate for a law in the social sciences that resembles Newtonian laws is the rationality principle, he says that this principle is not a law; he thinks it is almost empty. This is because he holds that the rationality principle is just an assumption about how a typical agent would behave in a given typical situation, and in this sense it does not necessitate an outcome in the way that Newton's laws together with initial conditions have entailments about Uranus's orbit.

Right after he asserts that there are no testable laws in ET, Popper (1974, 135) says that Darwinism is an application of situational logic. His point is this: First you describe a population of objects that is somewhat stable, but not exactly, and that contains small variations where some of those variations help their possessors to better cope with the conditions in which they find themselves. Then you "add to this the assumption of the existence of a special framework—a set of perhaps rare and highly individual conditions—in which there can be life, or more especially, self-reproducing but nevertheless variable bodies. Then a situation is given in which the idea of trial and error-elimination, or of Darwinism, becomes not merely applicable, but almost logically necessary" (134). Here again, Popper is formulating a conditional in which the assumptions of the model are the antecedent and statements about resulting adaptations are the consequent; the whole conditional is a priori. In accordance with this general framework, you can construct specific models for a specific situa-

tion; the specific case is an instance of a general type of event. The models, then, are testable but not the framework itself. All you can say about this framework is how often it is realized in nature.[9] In contrast, Newtonian theory as a whole is empirically testable and so are its applications in specific models.

For Popper, what holds things together in a model in the social sciences is the so-called rationality principle, while in ET what holds things together is PNS. However, in the case of the social sciences, the rationality principle is obviously false if you interpret it as an empirical claim; therefore, this principle is better interpreted as a regulative principle in the construction of models.[10] In the case of ET, the situation is different, in that the PNS "law" is true a priori. Even so, there is something that ET and the social sciences have in common; for Popper, the point of building models in both is not to test these general "laws" but to test singular models constructed in accordance with those "laws."

Popper's demand that a genuine scientific theory must include empirical laws shaped his view of what a scientific explanation is. For him, a causal explanation of a token event must cite at least one empirical law: "To give a causal explanation of an event means to deduce a statement which describes it, using as premises of the deduction one or more universal laws, together with certain singular statements, the initial conditions" (Popper 1959a, 38). Popper was therefore driven to conclude, not just that ET contains no empirical laws but that it cannot provide causal explanations of the adaptive features that organisms actually possess.

It is interesting that Popper thinks that a model-based explanation is about the "typical situations" that a kind of system occupies. Does this mean that the system usually obeys the model's postulates? If so, Popper's usage of "model" is at variance with what scientists and philosophers now often mean by that term. They have in mind the idea that models contain idealizations that render them false. Far being true of what a system is like in the kinds of situations it usually occupies, the model is true only in situations that the system never occupies.

3. A Change of Heart or the Old View in Disguise?

We now return to Popper's famous talk delivered in 1977 at Darwin College, Cambridge, which was published in *Dialectica* in 1978. Although Popper says

9. Brandon (1990) endorses this position.

10. Popper (1994b, 169) says that the rationality principle is a consequence of a methodological rule: "The adoption of the rationality principle can therefore be regarded as a by-product of a methodological postulate. It does not play the role of an empirical postulate." PNS in ET, however, cannot be interpreted as a methodological or regulative rule since it is an a priori truth. Yet, according to Popper, their functions in the construction of models are the same.

that he has changed his mind about the absence of testable laws in ET, we will argue that Popper in fact did not change his mind at all (see also Hull 1999, 485). He begins by describing an evolutionary claim that is empirical: "In its most daring and sweeping form, the theory of natural selection would assert that *all* organisms, and especially all those highly complex organs whose existence might be interpreted as evidence of design and, in addition, *all* forms of animal behaviour, have evolved as the result of natural selection. . . . If formulated in this sweeping way, the theory is not only refutable but actually refuted" (Popper 1978, 345). Popper mentions two reasons for thinking that this PNSR formulation is falsifiable—sexual selection and drift. To discuss sexual selection, Popper uses Darwin's example of the peacock's tail. Peacocks evolved gaudy tails because peahens preferred to mate with gaudy males. Popper sees this as a counterexample to PNSR because he accepts Darwin's assumption that sexual selection is not a species of NS. Many biologists would now disagree. They would say that when males evolve gaudy tails in response to the mating preferences of females, this is just like polar bears evolving thicker fur in response to the weather's getting colder. Sexual selection is a special kind of NS wherein the selective environment experienced by one sex is created by properties of the other. As for Popper's idea that drift is a counterexample to PNSR, he does not mention any actual examples of drift; rather, he notes that an organ may look adaptive and that this may lead us to mistakenly conclude that it was produced by NS. He says this can be a mistake because it is possible for an organ to be a product of drift and become adaptive only later. However, the mere possibility of this scenario is not enough to show that PNSR is false; one needs an actual case. Given the assumption that there are such cases, Popper can conclude that some organs and behaviors have evolved without NS's being the cause.

Popper's point about PNSR is fair enough; it is falsifiable. However, that does not show that PNS is empirical or that ET contains an empirical law. Popper has not changed his mind at all; he has merely changed the subject, from PNS to PNSR. This is also evident from another remark in the 1977 Darwin lecture: "The fact that the theory of natural selection is difficult to test has led some people, anti-Darwinists and even some great Darwinists, to claim that it is a tautology. . . . I mention this because I too belong among the culprits. . . . My solution was that the doctrine of natural selection is a most successful metaphysical research programme. . . . I still believe that natural selection works in this way as a research programme. Nevertheless I have changed my mind about the testability and the logical status of the theory of natural selection" (Popper 1978, 344–45). When Popper says that "the theory of natural selection" is testable, he presumably has PNSR in mind. He grants that this principle is not true. If laws must be true, then PNSR is not a law. But is it law-like? That

is, if it were true, would it be a law? Maybe not; perhaps PNSR resembles the claim that all cancers are caused by cigarette smoke. If this statement were true, would it be a law? We think not. It could be an accidental generalization. It violates no law of nature to suppose that some cancers have other causes. As noted, Popper thinks there actually are other causes of trait evolution apart from NS. But what is actual is also nomologically possible. This suggests that even if PNSR were true, it would not be a law.

Although Popper (1974) is grappling with a genuine philosophical puzzle concerning the conceptual structure of ET, Popper (1978) achieves something that is rather trivial; he simply constructs a statement about NS that is testable and (let us grant) false. Similar constructions can be carried out in phrenology and psychoanalysis, but Popper would never dream of viewing those constructions as vindicating those two pseudosciences. Popper steadfastly maintained that a scientific theory must contain one or more empirical laws; his picture of ET, both in 1974 and in 1978, is that the theory lacks this crucial element. The thought occurs to us that Popper may have seen that point quite clearly.

4. Evaluating Previous Interpretations of Popper's Views about Laws in ET

Hull (1999), citing Popper (1978), says that Popper was misled by Fisher, Haldane, Simpson, and other evolutionary biologists. Hull claims that the definition of fitness as actual survival is an idealization introduced to make the mathematics work well; for this reason, it should not be considered an essential part of ET. Hull further submits that biologists are aware that such idealizations are needed for the theory to be operationalized. We do not think that this reply to Popper is successful. For one thing, the mathematics of ET does not require that one equate an organism's fitness with its actual degree of reproductive success. This is something that the propensity interpretation of fitness (Brandon 1978; Mills and Beatty 1979) made clear. Second, "operationalizing" a theory that contains probabilistic parameters requires estimates of those parameters' values; it does not require that one define probability to mean actual frequency. And third, even if we reject the statistical definition of fitness, the question remains of what should replace it. Defenders of the propensity interpretation of fitness have suggested the following replacement:

> (PNSP) If traits T_1 and T_2 are found in a population, T_1 is fitter than T_2, the two traits are heritable, and no other evolutionary causes impinge on the population, then T_1 will probably increase in frequency.

PNSP is just like PNS, except that "probably" has been inserted. Popper's problem remains, since PNSP appears to be a priori, given the definition of fitness as a probabilistic propensity.[11]

Nanay (2011) claims that Popper changed his account of the scientific process of conjectures and refutations after the 1960s under the influence of Lakatos, Zahar, and Worrall and that he came to think that new scientific conjectures are not generated at random; rather, they are influenced by scientists' beliefs concerning which earlier conjectures have been refuted and which have been left standing. According to Nanay, since Popper thought that there was a strong analogy between ET and his theory of the growth of knowledge, applying his new views to ET led Popper to offer an alternative theory of evolution. Ruse (1977) also claims that Popper was misled by his attempt to understand ET from the perspective of his theory of the growth of knowledge, since there are important differences between the two. We claim that there is a deeper philosophical reason behind Popper's proposing an alternative theory of evolution: he believed that ET provides in-principle explanations for typical events but can never provide actual explanations for particular phenomena, and he thought this because he believed that the main principle of ET is a priori.

Stamos (1996) argues that it is a consequence of Popper's philosophy that ET is not a genuine empirical science. Central to Stamos's argument is the idea that Popper held that a genuine scientific theory must postulate universal laws and that they and only they are falsifiable and empirical in the strict sense; see also Stamos (2007). Starting with Popper's discussion of whether there are laws of evolution in *The Poverty of Historicism*, Stamos claims that it is a consequence of Popper's position that the hypothesis of common ancestry is not a genuinely scientific claim. However, as we explained in section 1, Popper does not make any claim about the scientific status of ET in *The Poverty of Historicism* (Ruse 1977; Hull 1999). Popper rightly denies that the Darwinian hypothesis of common ancestry is a law, since that hypothesis is about the living things on Earth; it is a singular statement about that token biota. Popper does not deny that such spatiotemporally restricted existence claims are falsifiable (Hull 1999).

In his later treatments of ET, Popper clearly states that there are testable empirical parts of ET. And even Popper (1959a) is clear that only whole theoretical systems are falsifiable, not the parts thereof.[12] Therefore, we object to

11. Given that Popper (1959b) proposed a propensity interpretation of probability, it is curious that he never saw that there could be a propensity interpretation of fitness.

12. This holistic stance on testability encounters the well-known "tacking problem." If U is untestable and T is testable, then U&T will often be testable.

Stamos's (1996) claim that Popper thinks ET is not a genuine scientific theory because it contains untestable existential statements. Popper's problem with ET is that PNS is a priori. As Hull (1999) pointed out, this sort of misunderstanding of Popper's views stems from the false dichotomy in which the only alternatives for Popper are genuine science and pseudoscience. Popper thought that some theories in the social sciences and in psychology are pseudoscientific; however, he did not think that all sciences that fail to postulate universal laws of nature are thereby pseudoscientific.

In Popper's view, there are three categories into which you can place a theoretical system: sciences that generate empirical knowledge and understanding through the postulation of universal laws of nature, sciences that do not postulate such laws but nonetheless generate knowledge and understanding through the proposal of methodological rules and the construction of models, and pseudosciences that do not generate empirical knowledge and understanding at all. Popper is placing ET in the second category, not in the third. His position coincides with the positions taken by several other subsequent philosophers who claim that evolutionary biology or biology in general lacks universal empirical laws of nature in the strict sense; this position is defended in different ways by Smart (1963), Rosenberg (1994), and Beatty (1995).[13] For criticisms of Rosenberg's and Beatty's arguments, see Sober (1997).

With respect to the issue of tautology, Stamos cites Gould as an authority and claims that Popper failed to see that fitness does not need to be defined in terms of actual survival. Consequently, when Popper thought that NS is a tautology, he was being misled by biologists who failed to understand how fitness should be defined. Our reply, noted before, is that defining fitness as a probabilistic propensity gives rise to tautologies of its own. In addition, it is well understood today that Fisher's fundamental theorem of NS really is an a priori mathematical truth (Price 1972; Ewens 1989; Lessard 1997). Thus, Popper did not make a mistake in thinking that there is a tautology problem that needs to be addressed. His question was how a science like this can be valuable despite the fact that it does not postulate universal empirical laws. This in itself is an interesting philosophical problem regardless of the issue of what the best understanding of fitness is.

Ruse (1977) argues that what Popper said in *The Poverty of Historicism* agrees with the received view of evolution, rather than being a criticism of it. Ruse thinks that Popper's mistake lies elsewhere, especially in his *Intellectual Autobiography*, where Popper claims that Darwinism is not a testable scientific

13. Mitchell (1997, 2000) and Woodward (2000) argue that biology can do without strict universal laws. This, of course, involves no commitment as to whether there are such laws.

theory. After citing Popper's claim that Darwinism does not predict the variety of life forms, Ruse explains in detail under what sort of initial conditions ET would issue in this type of prediction. Ruse lists the following conditions: there is a mainland with large populations and there are isolated areas with varying conditions, populations vary genetically and phenotypically, and organisms in the mainland sometimes get to those isolated areas. Ruse then writes: "Had one reason to believe that life on the planet was fairly old (e.g., through the fossil record or general complexity of structure), yet were one to find that absolutely no speciation at all had occurred, then I suggest that, *contra* Popper, modern evolutionists would be worried. *Their theory, parts of it at least, would have been falsified.* The claims that they make about speciation would seem not to hold" (1977, 645, emphasis ours).

The first question to ask about Ruse's argument is whether "speciation has never occurred" is an observation. If it is not, the fact that it is incompatible with ET does not show that ET is falsifiable. But which part of ET conflicts with "speciation has never occurred"? It conflicts with the hypothesis of common ancestry, but that hypothesis is not law-like, as it describes the history of life on Earth. Popper grants that there are empirical elements in evolutionary biology. What he denies is that there are empirical laws. Similar comments apply to Hodge's (1987, 233) point that Popper grants that spatiotemporally restricted statements are both falsifiable and verifiable, and so are scientific. Hodge correctly notes that such statements are to be found in evolutionary biology. However, this point does not touch Popper's contention that ET lacks universal empirical laws.

Evolutionary biologist John Maynard Smith (1986, 5) says that "the theory of evolution is not falsifiable in the sense required by Popper." He says that the theory is a "logical deduction" and that Popper is demanding something more—that "a scientific theory must say something about the world, and not merely about logical necessity." Maynard Smith goes on to say that "Darwinism as a testable scientific theory can take various forms. I will give it first in the form in which Darwin himself proposed it, and then in a 'neo-Darwinist' form in which most biologists hold it today." Maynard Smith then says that the hypothesis of common ancestry is "clearly falsifiable . . . as a single fossil rabbit in Cambrian rocks would be sufficient." This is a double mistake. The discovery that Maynard Smith describes would require an important reworking of when various taxa first appeared and how different taxa are genealogically related, but neither of these changes shows that the hypothesis of common ancestry is false. And even if it did, that does nothing to establish that there are falsifiable universal laws of evolution. Maynard Smith next turns to what he regards as the second component of Darwinian theory, that NS was the major, but not the only, cause of evolution.

He says "it would be falsified if one could show that organisms lack one of the three necessary properties of multiplication, variation, and heredity." Here again, what is falsified is not a law. When Maynard Smith then turns to the modern theory of evolution (6–7), he notes three innovations, but says that they are "changes of emphasis rather than substance." He does not say whether the modern theory satisfies Popper's requirements.

More than a decade later, the biologist Ernst Mayr reacted to Popper in a lecture Mayr delivered in Stockholm when Mayr received the Crafoord Prize from the Royal Swedish Academy of Science: "Despite the initial resistance by physicists and philosophers, the role of contingency and chance in natural processes is now almost universally acknowledged. Many biologists and philosophers deny the existence of universal laws in biology and suggest that all regularities be stated in probabilistic terms, as nearly all so-called biological laws have exceptions. Philosopher of science Karl Popper's famous test of falsification therefore cannot be applied in these cases" (Mayr 2000, 82). It is ironic that Mayr saw physicists and philosophers as devotees of determinism. By 1999, quantum mechanics had been around for a long time. It is a probabilistic theory, and many physicists and philosophers regarded it as making a strong case for indeterminism. However, Mayr is right that probability claims are unfalsifiable under Popper's (1959a) strict definition of that concept; if a coin lands heads in each of a thousand tosses, this does not falsify the claim that the coin's probability of heads on each toss is 1/2. Even so, Popper (190–97) supplemented his strict definition of falsifiability with something more liberal. This relaxed definition of falsifiability says that the hypothesis that the coin is fair is refuted by the thousand heads, since the hypothesis says that that outcome is "sufficiently" improbable. It should be noted, however, that Popper thinks that it is a matter of convention how improbable an outcome needs to be if it is to "falsify" a hypothesis. In any event, the deeper question raised by Popper (1974, 1978) lies elsewhere. The question is not whether laws can be probabilistic but whether they must be empirical. Quantum theory is empirical, but PNSP is not.[14]

5. Popperian Themes in Current Philosophy of Biology

In this section, we relate Popper's views on whether ET contains empirical laws to some more recent literature. Popper claims that ET cannot be interpreted as

14. Although we have said something about the reception of Popper (1974, 1978) among philosophers and scientists, there is another story to be told concerning the papers' reception among creationists. For some discussion of this, see Numbers (2006).

a theory of forces, but we disagree. The different evolutionary causes that impinge on a population (e.g., selection, mutation, migration) are represented in the theory as vectors that combine to produce a resultant. Indeed, the Hardy-Weinberg law functions as a zero force law in population genetics, and, as such, it resembles the law of inertia in Newtonian physics. And PNS (or better, PNSP) functions like the law of gravitation in that it describes how a system will behave when a single force acts on it (Sober 1984).[15] Even if Popper had known about these analogies, we think he would have dismissed them on the grounds that these evolutionary principles are a priori statements rather than empirical laws. Our response (to be fleshed out more in what follows) is that laws need not be empirical. Matthen and Ariew (2002) agree with Popper that ET should not be interpreted as a theory of forces, although their reasons differ from Popper's.

As discussed earlier, Popper claims that ET can provide in-principle causal explanations but cannot provide actual causal explanations of single events. Although the distinction between how-possibly and how-actually explanations is now standard in philosophy of biology (Brandon 1990; Plutynski 2004, 2005; Lange and Rosenberg 2011),[16] it is a further step to claim that a priori models furnish only the former and that empirical laws are needed to furnish the latter. We think that a priori models can do both (Sober 2011a). We further suggest that a priori dynamical models deserve to be called laws, since they do the same explanatory and predictive work that empirical laws perform (Elgin 2003). And while empirical causal laws are hard to find in evolutionary biology, they obviously exist in physics. This marks an interesting difference between the two sciences.

The package of ideas just described has come in for criticism. Lange and Rosenberg (2011) criticize Sober (2011a) by arguing that explanations built by using a priori models of NS are not causal explanations. Our response is that Lange and Rosenberg's thesis about explanation is perfectly compatible with the claim that there are a priori causal models of NS, a claim that Lange and Rosenberg do not dispute. We also think that Lange and Rosenberg fail to provide a convincing criterion for when an explanation is causal (Elgin and Sober 2015). Díez and Lorenzano (2015) develop a different line of criticism; they do not contest the claim that there are a priori causal models in evolutionary biology but argue that the same is true in physics. Our reply is that Sober (2011a) already noted that a priori models can be constructed in any science that con-

15. See Hitchcock and Velasco (2014) for further discussion of whether the force idea applies to ET.

16. Ewens (2004) thinks that there is a difference between models in physics and models in evolutionary biology in that the former are more realistic and less idealized.

tains empirical laws. The fact remains that there are few if any empirical laws in evolutionary biology but that such laws obviously exist in physics.[17]

Popper's idea of situational logic resembles two ideas that continue to be well received in philosophy of science. The first is Giere's (1979, 1999) approach to the structure of scientific theories. According to Giere, a theory (regardless of whether it is physical or biological or social) can be divided into two components. First, there is an a priori definition of a kind of theoretical system; for example, Newton's three laws of motion plus his law of gravitation define what it means to be a Newtonian system. The second component is empirical. It involves the claim that this or that token physical system is a Newtonian system. Notice that neither of Giere's components is both general and empirical. Popper's analysis of ET as a situational logic is similar. For Popper, ET provides a collection of statements that define a certain kind of object; let's call it a Darwinian system. We then apply this definition to an actual case by saying that it is an instance of a Darwinian system. Although the definition of a Darwinian system is not empirically testable, specific instances of models constructed by using this definition are. When some of these specific instances are refuted, we learn something about the world—namely, that the assumptions that define a Darwinian system are not satisfied in those cases. However, this does not show that the definition of a Darwinian system is wrong. For Giere, this pattern applies both to physics and to biology, but for Popper there is an important difference because in physics at least sometimes the background laws of a theory can be empirically refuted. Popper can grant that Giere's formulation applies to both sciences and still maintain that there is an important philosophical difference between them.

The second point of contact between Popper's "situational logic" and more recent ideas in philosophy of science is the semantic view of theories. Beatty (1981), Thompson (1989), and Lloyd (1994) argue that ET should be interpreted by using this framework; Ereshefsky (1991) disagrees. These authors are responding to the same problem that exercised Popper; they all are trying to provide a philosophical explanation of ET's success despite the apparent fact that ET's only "law" is a priori. Popper was against "conventionalism" (his term for the view that so-called laws are mere definitions) in the context of physical theories, although he thought that conventionalism is a coherent and consistent philosophical view. His position on the social and biological sciences is close to the semantic view of theories, and he embraces conventionalism about the status of social and biological "laws."

17. We do not claim that there cannot be empirical laws in evolutionary biology; our thesis concerns the science as it now is constituted.

6. Are There Any Empirical Laws in ET?

Popper argues that PNS is a priori, but he claims something more; he additionally claims that there are no empirical laws at all in ET. What is his argument for this stronger thesis? The same question arises if you think that PNSP is a better rendering of the probabilistic concept of fitness. Popper is neglecting the possibility that ET contains both source laws and consequence laws (Sober 1984).[18] PNS and PNSP are consequence laws; they purport to describe the changes that will occur (deterministically, or with some degree of probability) if certain initial conditions obtain. It is a separate task to describe the circumstances that make one trait fitter than another. These sources of fitness difference can be found in the physical environment that a population inhabits, in the biotic environment outside of the population (e.g., the prey, predators, parasites, and diseases that the population has to deal with), and in the population itself (as described by theories of sexual selection and of sex ratio evolution). Source laws specify the synchronic supervenience bases for variation in fitness; they have the form

> If a population contains traits T_1 and T_2 at time *t*, and its environment has properties E, and the organisms in the population have other traits $O_1, O_2, \ldots, O_n$ with frequencies $p_1, p_2, \ldots, p_n$ at time *t*, then T_1 will be fitter than T_2 at time *t*.

Some propositions of this form, like the models of sex ratio evolution constructed by Carl Düsing, R. A. Fisher, and W. D. Hamilton, are mathematical truths (Sober 2011b), but are there any empirical laws that have this form?

There is another way to pursue the question of whether there are empirical laws of evolution while granting that PNS and PNSP are not examples. Instead of trying to determine whether there are empirical source laws, one might consider something like the converse of PNS and PNSP. PNS and PNSP are both "forward-directed" conditionals; they say (roughly) that if there is variation in fitness at a given time, then you should expect change in trait frequency sometime later. Campbell and Robert (2005) propose a "backward-directed" conditional that approximates the converse of PNS and PNSP, namely,

> (D*) For almost every pair of variant organisms *a* and *b* that occupy the same environment, if *a* is complex and is generally more reproductively successful than *b*, then there exist heritable traits of *a* and *b* which, in

18. Popper is not the only philosopher who ignores the possibility that the theory of NS contains source laws; Fodor and Piattelli-Palmarini (2010) make the same mistake.

> interaction with *a* and *b*'s environment, cause *a* to be more reproductively successful than *b*.

This is an English paraphrase of the D* statement that Campbell and Robert put in logical notation. The word "generally" in D* leads us to think that *a* and *b* are types of organisms, not tokens. The same word also indicates that D* is not about some brief period of time in which *a* happens to out-reproduce *b* but rather concerns a sufficiently long stretch of time. Campbell and Robert (2005, 673) say that they prefer to call D* a model rather than a law.[19]

The existential quantifier in D* is meant to mark the fact that the selection process that makes trait T_1 fitter than trait T_2 in environment E_1 need not be the same as the selection process that makes T_3 fitter than T_4 in environment E_2. Perhaps T_1 and T_2 are traits of a butterfly species and T_1 is fitter than T_2 because of predators, whereas T_3 and T_4 are traits of an elm species and T_3 is fitter than T_4 because of diseases. Here Campbell and Robert are taking on board the fact that the property of fitness is multiply realizable (Brandon 1978; Rosenberg 1978; Mills and Beatty 1979; Sober 1984); this has the consequence that the property a population has of undergoing a selection process is also multiply realizable. Campbell and Robert emphasize that their D* has the quantifier order "for each pair of traits, there exists a story about natural selection" not the quantifier order "there exists a single story about natural selection that applies to all traits." We hope that our English rendering of D* captures this point.

Richmond and Robert argue that D* is testable, and we agree. Our question is whether D* would be a law of nature if it were true. Richmond and Robert do not consider this question, but the question is worth asking in the context of the current article. What we said earlier about Popper's PNSR reformulation of PNS is relevant here. Popper said that PNSR is false because of sexual selection and drift. We likened PNSR to the claim that all cancers are caused by cigarette smoke. Our point was that PNSR is not law-like; even if it were true, it would not be a law. We suggest that the same point applies to D*. For D* to be a law, it must be nomologically impossible for there to be a process other than NS that could often bring it about that one trait generally is more reproductively successful than another. Here is a reason to doubt that this is so: for any finite temporal interval, if the two variants *a* and *b* are equally fit and thus

19. Campbell and Robert formulate their D* in reply to Brandon's (1978) contention that explanations of specific evolutionary outcomes that appeal to NS are empirical, but that a general "principle of natural selection" will be a tautology or will be so vague that it cannot be tested or will be empirically false.

evolve by the nonselective process of pure drift, there is a nonzero probability that *a* will generally out-reproduce *b* during that interval. This claim about a single pair of traits applies to *n* such pairs, for any finite *n*.[20] Even if D* is not an empirical law of nature, the question remains whether there are other backward-directed propositions about evolution that are.

7. Concluding Comments

We have argued that Popper's (1974) reason for holding that ET is not a testable scientific theory is that he thinks that ET lacks empirical laws. He thinks this even though he grants that there are testable statements in ET. As Stamos (2007) points out, postulating testable empirical laws is, for Popper, a necessary condition for a theory to be scientifically testable. This is why Popper concludes that ET is a metaphysical research program. Popper does not conclude that ET is a pseudoscience; instead, he unsuccessfully attempts to reformulate PNS and also tries to explain ET's success in terms of his idea of situational logic.

Those who agree with Popper that laws of nature must be empirical may want to resist Popper's conclusion by insisting that a theory can be testable without its containing testable laws. Indeed, this suggestion finds a happy home in Popper's own concept of falsifiability; if S is a falsifiable statement, and S and A are logically compatible, then S&A is falsifiable. The fact that S is not a law and A is a tautology does not change that fact. We suspect that Popper was misled by the examples he found in physics; Newton's theory, relativity theory, and quantum mechanics are testable theories, and the laws they propose are testable. As noted earlier, Popper does not hesitate to speak of evolutionary "theory," but he does demand that it conform to the pattern he found in physics. Finding that it does not, Popper concludes that ET is a "metaphysical research program," not a testable scientific theory. However, if testable theories need not contain testable laws, there is no need to draw Popper's conclusion.

This is a good reply to Popper, but we take issue with the assumption that laws of nature must be empirical. Modern evolutionary biology is replete with mathematical models that are mathematical truths. They describe the proba-

20. There is an additional point: even if D* is an empirical law, it does not do much to explain why one trait generally out-reproduces another. In this respect, D* resembles "adaptationism," at least on some interpretations of that *ism*. Both D* and adaptationism are generalizations that can be tested by case-by-case analyses of different traits in different populations, and if you believe these generalizations, they will play a heuristic role, guiding your search for specific explanations (Orzack and Sober 1994).

bilities that populations have of changing their trait frequencies, given the population's initial and boundary conditions. These dynamical models explain and predict in the same way that empirical laws do; this is why we want to drop the requirement that scientific laws must be empirical. We are not suggesting that "bachelors are unmarried" is a scientific law; to say that some laws are a priori is not to say that all a priori statements are laws. Popper was right that ET is different from theories in physics, but that does not mean that ET is untestable or that it is not a genuine scientific theory.

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