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THE NATURE OF DARWIN'S SUPPORT FOR THE THEORY OF NATURAL SELECTION*

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When natural selection theory was presented, much active philosophical debate, in which Darwin himself participated, centered on its hypothetical nature, its explanatory power, and Darwin's methodology. Upon first examination, Darwin's support of his theory seems to consist of a set of claims pertaining to various aspects of explanatory success. I analyze the support of his method and theory given in the *Origin of Species* and private correspondence, and conclude that an interpretation focusing on the explanatory strengths of natural selection theory accurately reflects neither Darwin's own self-consciously held views, nor the nature of his support. Darwin's methodological and philosophical arguments were at once consistently empiricist and more sophisticated than such interpretations credit to him.

1. Darwin's Views. William Whewell and Sir John F. W. Herschel, the most influential writers in philosophy of science in the mid-nineteenth century, both held Newtonian physics aloft as the model form for a scientific theory. In order to demonstrate Darwin's sophistication concerning contemporary philosophical and methodological issues, I shall quote him extensively, in this section, from his private correspondence.

One crucial aspect of the laws of motion insisted on by philosophers and scientists alike was that they could be directly tested or proved. Darwin was well aware of the example provided by Newtonian physics, and was equally well aware that the theory of natural selection could not be tested by direct inference from the evidence.

> When we descend to details, we can prove that no one species has changed [i.e. we cannot prove that a single species has changed]; nor can we prove that the supposed changes are beneficial, which is the groundwork of the theory. Nor can we explain why some species have changed and others have not (Darwin 1919, 2:210).

On another occasion, Darwin wrote of F. W. Hutton:

> He is one of the very few who see that the change of species cannot

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> be directly proved, and that the doctrine must sink or swim according as it groups and explains phenomena. It is really curious how few judge it in this way, which is clearly the right way (1919, 2:155).

Darwin explained his approach as follows:

> I have always looked at the doctrine of natural selection as an hypothesis, which if it explained several large classes of facts, would deserve to be ranked as a theory deserving acceptance (1903, 1:139–140).

It is clear from the following letters that Darwin believed his hypothesis to be analogous in this respect to the physical hypothesis concerning light, and accordingly thought that presenting indirect evidence for this theory, as a parallel form of support, should be acceptable scientific practice. He wrote to Asa Gray (1919, 2:80):

> Your distinction between an hypothesis and theory seems to me very ingenious; but I do not think it is ever followed. Every one now speaks of the undulatory *theory* of light; yet the ether is itself hypothetical, and the undulations are inferred only from explaining the phenomenon of light. . . . It seems to me that an hypothesis is *developed* into a theory solely by explaining an ample lot of facts.

Darwin made an explicit comparison in a letter to Henslow (1967, p. 204):

> In a letter to me, [Sedgewick] talks much about my departing from the spirit of inductive philosophy. I wish if you ever talk on [the] subject to him, you would ask him whether it was not allowable (and a great step) to invent the undulatory theory of light—i.e. hypothetical undulations, in a hypothetical substance, the ether. And if this be so, why I may not invent [the] hypothesis of natural selection (which from analogy of domestic productions, and from what we know of the struggle of existence and of the variability of organic beings, is in itself probable) and try whether this hypothesis of natural selection does not explain (as I think it does) a large number of facts in geographical distribution—geological succession—classification—morphology, embryology, etc.—I should really much like to know why such an hypothesis as the undulations of the ether may be invented, and why I may not invent . . . any hypothesis, such as natural selection . . .. I can perfectly understand Sedgewick or any one saying that natural selection does not explain large classes of facts; but that is very different from saying that I depart from right principles of scientific investigation.

Having defended natural selection as a legitimate scientific hypothesis, Darwin supported it with considerations that served either to connect empirical facts to the theory in various ways, or to show that the hypothesis would be useful to biological science in other respects.

Much of Darwin's support for his theory offered in the *Origin* and in correspondence with other scientists consists in linking the theory to empirical evidence in widely varying branches of science. Darwin presented his specific claims regarding his theory in a letter to the journal, *Athenaeum:*

> As far as I can judge, no theory so well explains or connects these several generalizations (more especially the formation of domestic races in comparison with natural species, the principle of classification, embryonic resemblance, etc.) as the theory . . . of natural selection. Nor has any other satisfactory explanation been ever offered of the almost perfect adaptation of all organic beings to each other, and to their physical conditions of life (1919, 2:207).

Darwin also supported his hypothesis of natural selection by appealing to its value to the science of biology as a whole through promotion of research:

> Whenever naturalists can look at species changing as certain, what a magnificent field will be open—on all the laws of variations, on the genealogy of all living beings, on their lines of migration, etc. (1919, 1:485).

At this point, it may seem quite plausible that Darwin is arguing for his theory chiefly on the basis that it provided the "best explanation" for the different phenomena from widely varying fields. Following a brief summary of the "inference to the best explanation" view of theory choice, I shall argue that such an interpretation of Darwin's theory support is inadequate and misrepresents Darwin's main concerns.

"Inference to the best explanation" has been claimed by Gilbert Harman to be the rule of rational inference basic to all non-deductive inferences (Harman 1965, p. 89). As a rule of inference governing theory choice, inference to the best explanation means that we should infer the hypothesis which explains a given set of evidence better than any competing hypothesis at hand. Harman's suggestions regarding the criteria used in determining *which* hypothesis is better include simplicity, plausibility, minimal *ad hoc-ness,* and ability to explain a larger quantity of evidence.

Paul Thagard has claimed that Darwin's support for his theory of natural selection is a clear-cut example of an argument to the best explanation; he claims that Darwin supported his theory chiefly on the basis that its explanations were consilient, simple, and analogical in nature, and thus fulfilled some of the prime criteria used in evaluating explanatory theories (Thagard 1978, p. 89). Thagard emphasizes that consilience, simplicity, and analogy (and explanation in general) are primarily concerned with the actual *use* of the theory within a specific social and historical context. Context-centered features of a theory should be seen in contrast to other features, such as its logical structure (logical relations inside the theory), or its semantic relations (the relations between the theory and the facts). I shall show that although Darwin did use arguments from consilience, simplicity, and analogy to support his theory, his main defense did *not* amount to claims concerning its explanatory power but rather to claims regarding its semantic properties. It should not, therefore, be considered a clear-cut case of an inference to the best explanation, nor be used as support for that view of theory choice.

2. Darwin's Support. Before proceeding to the actual discussion of Darwin's support for his theory, I would like to introduce an account of the structure of the theory which I will use throughout the rest of the paper. Morton Beckner has argued that natural selection theory is best understood as presenting a family of related models (1959, p. 160). A particular model used in an explanation is constructed by using principles of the theory in combination with certain assumed conditions; the outcome of the model is supposed to be consistent with observed empirical phenomena. A good example is the case of the emergence of two types of wolves, in which Darwin describes an imaginary situation wherein the outcome would be of a certain (testable) kind, given natural selection and granting certain conditions (1965, p. 90).

Particular models serve to show that the theory is compatible with observed phenomena, viz., empirical generalizations and particular facts of evolution, by providing a specific way in which the theory plus certain specific assumed conditions would produce a fit with the empirical results. This account of theory structure, called the "semantic" view, is a recently developed alternative to the so-called "received view" or covering law approach (see van Fraassen 1972, especially pp. 304–306; van Fraassen 1970, pp. 328–329; Beatty 1980, pp. 399–401, 419–420). Many interpretations of Darwin's support for his theory, including those by Ruse and Kitcher, are guided by the assumption that "good" or "scientific" theory structure must conform to the covering law view (Kitcher 1981, p. 509; Ruse 1979, pp. 109, 236, 270; see especially Ruse 1975a, pp. 221–224). It has been a special problem of the received view to search for empirical laws in theories under analysis; the semantic view circumvents this problem (see Beatty 1980). Throughout the rest of the discussion, I shall rely on a simplified semantic account of natural selection theory as a standard and unifying picture of the structure of the theory. Details concerning the use of natural selection theory in models will be discussed in section 2.4.

2.1. Consilience. Darwin, as quoted on p. 113, explicitly defended natural selection theory on the basis that "it explained several large classes of fact" (1903, 1:139). I would like first to consider the view that Darwin's claim to consilience is best interpreted as a claim regarding the theory's ability to produce explanations of a certain sort. Following a brief criticism of an explanation-based view of Darwin's claim, I shall suggest an alternative interpretation that grounds consilience instead in the semantic properties of the theory.

According to William Whewell, who coined the term, "consilience" can occur either when an hypothesis can explain at least two known classes of fact, or when it can predict or explain cases of a new and different kind from those cases considered in forming the hypothesis (Laudan 1971, p. 371; Butts 1977, p. 74). Note that these classes are not to be understood as arbitrary sets; evaluation of consilience presupposes a division of facts into natural classes. Whewell's notion has been adopted by Thagard, who claims that consilience can indicate *how much evidence* a theory explains (Thagard 1978, pp. 79–80). This notion can be used in a comparative way; for example, if Theory A explains three classes of facts, and Theory B explains four classes of facts, including the three classes explained by Theory A, then Theory B should be considered more consilient than Theory A. Since this definition is couched in terms of explanations, it seems that consilience is based upon the performance of the theory in explanation. Throughout this discussion, the term "explain" is used in a substantive sense, in which it is contrasted to mere description, prediction, fitting, or accounting for.

Consider, however, the specific support Darwin gave for his claim to consilience: despite his (quite ordinary) use of the word "explain", it does *not,* in fact, involve the level of complexity of an explanation-centered criterion. The use of the word "explain" is non-technical: it can be replaced by a more neutral term like "account for" without loss to the support given. He claimed that his theory explained "several large classes of fact" (see Darwin 1919, 2:13; 1903, 1:13); these explanations produced with natural selection theory were of a certain type and quality. Given that natural selection can be understood as presenting a family of related models, the form of an explanation using the theory must be a demonstration of how the observable phenomena in question *could* have happened, given moves authorized by the theory plus certain conditions. One evaluates a model by independently testing the assumed conditions and by comparing the outcome of the model with empirical observations, including observations not available at the time of model construction, if possible. In the case of natural selection theory, then, consilience of inductions would consist of the many models one has constructed, using the theory, which have been shown to be at least minimally empirically adequate. Thus, if consilience is defined strictly in terms of explanations, Darwin has not really defended his theory on the basis of consilience. If, on the other hand, consilience is seen as based on the relationship or fit between the theory and empirical data, we can make better sense of Darwin's actual defense, as follows. At the heart of Darwin's declarations of the importance of the consilient nature of natural selection theory was his conviction that the theory had proven capable of "saving" the phenomena. In other words, Darwin had shown himself, in the course of his researches, and using his strictest testing criteria, that the theory could be used to construct outlines of models which would give results that *conform to the empirical data*.

The semantic nature of the criterion of consilience is a problem for those who support inference to the best explanation as the rule for theory choice. Those who argue that many scientists have supported their theories on grounds of consilience are correct; the question is whether this support is based on the fact that their theory *explained* the most (in a substantive sense of "explain")—consilience seems to be an index of this sort—or whether consilience is seen instead as an index of the empirical adequacy of the theory, as argued in the preceding paragraphs. If the latter is the case, as I claim, then the inference being made and supported by consilience is *not* an inference to the best explanation, but rather an inference to the most empirically adequate theory.

The fact that Darwin supported his theory by claiming that it was consilient seems to indicate that he was concerned with the "explanatory power" or success of his theory. Since the notion of consilience is basically semantic, Darwin's defense can be more appropriately recognized as a set of claims about the fit of empirical data to various models constructed with the use of natural selection theory. The particular way in which Darwin tested his models, and thereby his theory, are the subject of section 2.4.

2.2. *Simplicity*. Simplicity, an important constraint on consilience, has been characterized as a function of the number and type of auxiliary hypotheses used in explanations provided by the theory under consideration (Thagard 1978, pp. 85–86). This apparently amounts to evaluation of the use of *ad hoc* hypotheses in explanation—an *ad hoc* hypothesis being one that is only good for explaining the phenomena which it was introduced to explain. I shall first reject the appropriateness of applying a criterion of simplicity of this sort to Darwin's argument. Then I shall discuss Darwin's claim that his theory was valuable because "so many phenomena can be thus grouped together and explained" (1903, 1:184), a claim that seems to involve *some* notion of simplicity.

Consider the nature of explanations from natural selection theory: they consist of models that include the basic theory plus certain empirical hypotheses. For example, an explanation of the present populations of mosquitoes in a certain area would include basic assumptions regarding the fitness of the present occupants' ancestors, in addition to details concerning the availability of food sources for the different species of mosquitoes present. An explanation which includes the additional hypothesis, "there have been no new species of food source plants introduced into the area during the last 200 years", could, when considering the question of the mosquitoes' present food source, make a *better* explanation, i.e. one more informative and more persuasive, than an explanation which omits this extra assumption. Thus, in natural selection, explanations are often *improved* by the addition of untested assumptions which were introduced only to explain the phenomenon in question. These empirical assumptions have a strong ring of *ad hoc-ness* until further research reveals more information about them. The initially plausible definition of simplicity based on the number of *ad hoc* hypotheses in the explanations seems therefore completely inappropriate to apply to natural selection theory.

There is, however, a certain simplicity to natural selection theory to which Darwin appeals explicitly. I would like to suggest an alternate formulation of the notion of simplicity, intended to capture the characteristic by which Darwin actually supported his theory.

The set of related models which comprise natural selection theory could more accurately be called a group of model types. Van Fraassen has defined "model type" as the description of a structure in which certain parameters are left unspecified; "model" refers only to specific structures "in which all relevant parameters have specific values" (and van Fraassen has suggested that in its typical use by scientists, "model" has the sense of "model type") (van Fraassen 1980, p. 44). When natural selection theory is said to present a set of related models, it is meant that there are certain model types which are given in the theory to account for observed phenomena; the variables of these model types are specified and instantiated through hypothesis and testing in a recursive manner. For example, a model type used to explain the presence of certain instincts would contain variables corresponding to the possible range or variation of the instinct, its profitability in different sets of circumstances, and the economies of related behaviors, in addition to standard natural selection assumptions concerning the existence of fine gradations of instinct and change in instinct.

A slightly different model type might be used to explain the predominance of one species over related species. Such a model type would include variables representing each species' method of obtaining food, changes in the food supply, flexibility with regard to food supply, and climatic changes, in addition to basic natural selection assumptions regarding the effects of competition and the existence of natural variation. These model types serve as formats for explanations; the particular terms or factors in a model type vary in each application, depending on the outcome of the model and various assumed conditions.

One way to evaluate simplicity of a theory that consists of a set of models is to see how many separate models and terms are necessary to account for the phenomena; roughly, a simpler theory has fewer model types. If a theory is both *simple* in the manner defined above, i.e. consists of only a few basic model types, and is *consilient* as well, then it can be considered to *unify* the phenomena. Kitcher has recently given a similar interpretation which, except for its syntactic presentation, presents a similar view of the nature of the unification involved in Darwin's theory: "a theory unifies our beliefs when it provides one (or more generally, a few) pattern(s) of argument which can be used in the derivation of a large number of sentences which we accept" (1981, p. 514). Darwin often supported his theory on the basis of its unifying nature (cf. quote p. 113). This virtue is not one of consilience alone; it also involves the fact that the basic plans for explaining so many classes of phenomena are included in a relatively straightforward and small set of model types.

In other words, the manner in which natural selection theory is simple is that it consists of only a *few* interrelated model types, yet these model types can be filled in with contingent facts and assumptions for *any* specific phenomenon in the extremely large range of phenomena the theory claims to account for. This ability of outlines of evolutionary explanations to be instantiated with different details is also emphasized by Kitcher as a vital aspect of the success of the theory: "[an] eventual unification would consist in derivations of descriptions of these phenomena which would instantiate a common pattern" (1981, pp. 514–515). Thus, simplicity is a relation between the theory, the empirical data, and the explanations constructed from the theory; it cannot, therefore, be considered a relation concerned exclusively with explanation.

2.3. Analogy. As a form of theory support, analogies are generally supposed to improve the explanations provided by the theory. Such support seems to be heuristic support: take the case in which an analogy between phenomena improves the explanations because the first explanation provides a model for the second; the nature of this improvement is an improvement in understanding. Analogy is then playing a heuristic or psychological, rather than confirmatory, role in the justification of the theory.

Darwin's use of artificial selection in support of natural selection is usually brought forth as an example of analogical support; the "familiarity" of artificial selection is supposed to increase the explanatory value of natural selection theory (Thagard 1978, p. 91). Darwin did claim that "the belief in Natural Selection must at present be grounded entirely on general considerations including the analogy of change under domestication by man's selection" (1919, 2:210).

The stragety of Darwin's presentation, wherein the first two chapters of the *Origin* concern artificial selection and abundance of variation in wild organisms respectively, suggests that he was aware of an heuristic use of the analogy. The situation becomes less clear-cut, however, when we consider that contemporary popular and scientific opinion held that results from domestic variation and artificial selection were strong evidence *against* the transmutation of species (Ruse 1979, pp. 177, 203).

Michael Ruse has argued, in the context of a discussion on the hypothetico-deductive nature of Darwin's theory, that "Darwin's discussions of artificial selection and of variation do have a justificatory role in his thought" (Ruse 1975a, p. 226). Ruse argues as follows: in the course of arguing for natural selection theory, Darwin claims that there *do* exist favorable and injurious variations, upon which populational and environmental demands can then exert differential pressure. What evidence does Darwin give for this assumption, crucial to natural selection theory? He argues from artificial selection: since variations that are useful to people have occurred in domestic animals, it should not be "thought improbable" that variations that are useful to the organism itself in "the battle of life" should occur spontaneously in wild organisms (Darwin 1964, pp. 80, 467).

The assumption that there are heritable variations useful to the (owner) organism should not be confused with the class of individual empirical assumptions that appear in particular applications of natural selection theory. The analogical argument serves as *supporting evidence* for the basic construction of the model types; after this assumption has been made, it becomes possible to assume the existence of *some* heritable favorable variation. The task is then to determine its nature through functional analysis or other research methods. The use of the analogy from artificial selection as supporting evidence for an assumption common to all natural selection model types clearly outstrips a merely heuristic application. Darwin does not use analogy just to improve the explanations by improving understanding (a use which has a basically psychological appeal), nor does the explanation in artificial selection simply serve as a model for explanation in natural selection; rather, analogy seems to be used by

Darwin chiefly as the strongest type of evidence by which he could support a certain assumption of his theory (see Ruse 1975a, p. 235; Ruse 1979, pp. 177–178, 203–205).

One last point: it could possibly be misleading to accept Darwin's own interpretation that the supporting role of artificial selection in natural selection theory is analogical. Van Fraassen has suggested that the case of artificial selection might have been serving as a specific, narrow case of a certain process; this process was then generalized from a limited, artificial environment to the natural environment (personal communication).

2.4. Independent Testing of Model Assumptions. The preceding sections contained several references to the fact that Darwin was concerned with testing his theory and its adequacy to empirical facts. I have found that Darwin's concern for consilience was based on his conviction that his models satisfy at least minimal conditions of empirical adequacy, and that theory support criteria which focus on characteristics of explanations *neglect* the type of argument, significant in terms of both volume and detail, which relates the theory to empirical data and observations.

Once a model is constructed which accommodates the phenomenon to be explained, we can test the theory only by eliminating the various assumptions of the model, that is, by *independently testing* its assumptions. A great deal of the first half of the *Origin* is devoted to providing empirical evidence for the fundamental assumptions implicit in the model types used in natural selection explanations. For instance, Darwin needed some evidence for his assumption that wild organisms spontaneously developed heritable variations that would be advantageous to their survival and reproductive vigor. Darwin needed to be able to take the existence of useful variations for granted; such a general assumption was necessary to create a variable in the model type which would then be instantiated in the construction of specific models.

The second half of the *Origin* can be understood as a collection of specific models constructed using the model types provided in the first half of the book, in combination with various specific assumptions. Darwin presents these models as explanations for phenomena already publicly known; the support for his theory consists of offering empirical confirmation for all of the special and specific assumptions which are needed, in combination with natural selection, to explain the phenomena. I shall present two cases in which Darwin offers empirical evidence for an empirical assumption of a model constructed with the use of selection theory.

Darwin argues in the *Origin* that one can explain the facts of the geographical distribution of organisms by using natural selection theory. In his famous set of examples involving the Galapagos Archipelago, Darwin hypothesizes that the fact that species inhabiting the islands resemble South American fauna and flora very closely, but are not identical to them, is a result of the migration of ancient South American forms to the islands and their subsequent transmutation through natural selection. In this explanation, the migration of all of the ancestral forms onto the islands is not *directly* testable. It should be proven, however, that such a migration would have been *possible* in order for the model to serve as indirect support for natural selection theory. Accordingly, Darwin discusses "means of dispersal" at length, defending his assumptions regarding migration with a multitude of various observations and experiments (1964, pp. 346–410).

On another occasion, Darwin described in a letter how he created an explanation and then tested an assumption of his model:

> There is a very curious point in the astounding proportion of Coleoptera that are apterous [wingless]; and I think I have guessed the reason, viz., that powers of flight would be injurious to insects inhabiting a confined locality, and expose them to be blown to the sea: to test this, I find that the insects inhabiting the Dezerte Grande, a quite small islet, would be still more exposed to this danger, and here the proportion of apterous insects is even considerably greater than on Madeira proper (1919, 1:404–405).

The apterous insect instance exemplifies a certain technique for independently testing assumptions: the assumption being considered must be isolated from the other assumptions in the model; this is done by comparing two or more models which have the assumption under question in common; through comparing these models with yet other models, the new assumption can be isolated as the *only* unestablished assumption in the models. This technique (theoretically) makes possible rigorous, though indirect, testing of each assumption in any natural selection model.

The two examples presented above are typical of the empirical support which Darwin cites as indirect evidence for natural selection theory. This evidence serves to confirm the individual assumptions that are necessary to the various specific models constructed when one uses natural selection theory.

2.5. Stimulation of Research. Concern with confirmation of empirical assumptions of the theory is outside the realm of explanation-centered theory evaluation schemes such as inference to the best explanation. Darwin himself emphasized the utility of natural selection theory in areas having little to do with the theory's performance in explanations; furthermore, he saw its success in research-related areas as support for some sort of acceptance of the theory. Darwin supported his theory numerous times, both in private correspondence and in the conclusion of the *Origin,* on the basis of its usefulness in scientific research (1903, 1:104; 1919, 1:485). He argued that "When we regard every production of nature as one which has had a history", a vast field of inquiry would be opened up, involving the causes and laws of variation, the affects of physical conditions, the means of migration, taxonomy based on rudimentary organs and embryology, and more (1964, pp. 485–489). Darwin believed that natural selection theory would be adopted because young scientists would find "that they can group facts and search out new lines of investigation better on the notion of descent, than on that of creation" (1919, 2:147).

Although this makes it sound as if success in serving as a foundation of a research program involves only the relation of the theory to its users, I shall argue briefly that this success is based for a large part upon the structural attributes of the theory.

There are four different ways in which natural selection theory can stimulate research. First, the types of explanations generated by the theory serve especially well as outlines for specific research programs. That is, any account of the action of natural selection allows for the possibility of many specific influences, e.g. predation, disease, food shortage, severe climate, etc. An explanation or model of a particular phenomenon must take into account the varying effects of the numerous possible causes of selection pressure. Because of the nature of an explanation using natural selection—i.e., that the phenomenon at hand is the *result* of certain assumed conditions plus natural selection—research is always necessary to fill in explicitly specified details during the construction of the model.

Second, natural selection theory provides a strategic plan and order for carrying out different types of research. This research might consist in eliminating alternatives, for example, leading to an hypothesis that selection pressures would most likely be in a particular direction. Once a particular model has been constructed, further research is necessary to confirm or disconfirm the assumptions or hypotheses. Many of these hypotheses, in modern terminology, are basically functional descriptions and analyses.

Third, the technique of isolating and testing the various assumptions of a given model stimulates the acquisition of new empirical information. The ideal situation for a model is when all of the details and assumptions have been rigorously tested independently and confirmed. This can be done by using the isolating technique described in the previous section and exemplified in Darwin's apterous insect example. Use of this technique itself actually stimulates research, since, if an assumption is found to be disconfirmed, a new model must be constructed on the basis of different assumptions. One result of this type of research is clearly the acquisition of a great deal of empirical data stemming from the necessity of confirming each assumption.

Finally, natural selection theory stimulates research by allowing the formulation of weak predictions. Researchers can construct a natural selection model based on (mostly) confirmed biological hypotheses, in which the outcome or *result* of the model has *not* been observed or empirically confirmed. In this case, the task of scientific researchers consists in directed searching for an entity or situation which is within the range of properties predicted, using natural selection theory (see the electric fish example, below).

Research promoted by natural selection theory can thus take various forms. If the explanations using natural selection are in the form of models that exhibit results compatible with available empirical data, the research program would consist in *constructing* specific models for specific phenomena, independently *testing* the assumptions in each model, and then *comparing* different models. Researchers can also generate models which *predict* the existence, and sometimes general form, of a certain entity or relation; the research suggestions resulting from this type of model would be directions for a real search.

I have outlined several of the ways in which the theory of natural selection is especially well equipped to promote and support a scientific research program. Success of this sort certainly depends upon the relation between the users and the theory; but this relation is not the source of its success and acceptance. Rather, the structural characteristics of the theory, e.g. its formulation in model types, are a primary source of its success in research.

2.5.1 Examples of Research Guided by Darwin's Theory. Darwin himself made use of natural selection theory as a guide for research in his taxonomic work on barnacles. He discovered that, in a certain species of barnacle, there were both male animals and hermaphroditic ones, the hermaphrodites having two tiny "supplemental males" attached on the outside. Darwin comments, "I should never have made this out, had not my species theory convinced me, that an hermaphrodite species must pass into a bisexual species by insensibly small changes; and here we have it . . ." (1903, 1:65).

This is the rough outline of a prediction using natural selection theory. Darwin expected there to exist organisms of a certain approximate description because of certain assumptions in his theory. Although, in this case, he did not actually search for them, he seems to have "kept an eye out" for entities of the appropriate type (within bounds of the prediction). Notice also that Darwin makes the further claim that the phenomenon would not have been identifiable or explainable *unless* he had used a model type of his theory.

Another interesting incident resulted from Darwin's comment in the *Origin* that the electrical organs of fish provided a particularly difficult case for natural selection theory to explain (1964, p. 192). Darwin points out that "if the electric organs had been inherited from one ancient progenitor thus provided, we might have expected that all electric fishes would have been specially related to each other" (1964, pp. 192–193). But electric organs appear in only a few fishes, which are *not* closely related to each other. Thus, natural selection theory seems to suggest a general model which is disconfirmed empirically.

In 1860, a researcher in Dublin, R. McDonnell, wrote to Darwin that the difficulties were even worse; the electric organs were near the head in some fish, near the tail in others, and were supplied by completely different sets of nerves. McDonnell reported (to Darwin) that he realized "that if Darwin is right, there must be homologous organs both near the head and tail in other non-electric fish" (Darwin 1919, 2:145). McDonnell's subsequent search for these organs was successful, and he published his findings.

There are two ways to interpret this incident; one emphasizes model construction, while the other highlights its predictive aspect. When Darwin considered the problem, he seems to have constructed a model something like this: there was an electric fish which was the common ancestor of all the present-day electric fish (assumption); by inheritance and speciation, we would expect the existence of several species of electric fish with close affinities (outcome of the model type). As Darwin pointed out, under existing evidence, the initial assumption was disconfirmed empirically. McDonnell's approach was to turn Darwin's model around: there is a common ancestor of all electric fish (assumption); by inheritance and speciation, it produced the several species of electric fish (assumption); there *must be* some minimal morphological resemblance among all descendents of the ancestor fish; in particular, the electric organs must have homologues in the non-electric fish which are closely related to the electric ones (*prediction*). Note that the type of predictions that natural selection theory can produce are comparatively weak; in any predictive case, only a range of characteristics or possibilities can be specified—precise predictions involving *which* element in this range will be present are not supportable. That McDonnell's general empirical prediction was vindicated appeared to Darwin as strong support for this theory (1919, 2:145).

I take my final examples from the field of palaeontology. Darwin's theory exerted enormous influence on palaeontological research, some of which led to spectacular empirical discoveries, especially in the United

States (Pfeifer 1972). I can merely hint at the importance of these discoveries and their use as evidence for natural selection theory. Two related assumptions seem to serve as the basis for the most dramatic and well-known discoveries made with the use of natural selection theory: (1) given any two species, there existed some common ancestor at some point in the history of the world (1919, 2:121); and (2) given two species that occurred in different epochs but are related on the generic or familial level, it can be assumed that any species intermediate *between* the two species would also occur at a *time* intermediate between the two species (Darwin 1964, p. 462). These assumptions are confirmable through palaeontological evidence.

Albert Gaudry, a French palaeontologist, constructed tree diagrams presenting his evidence for the evolution of various mammalian families, and by doing so, established that new discoveries tended to *fill in* the gaps between previously known species and genera (Rudwick 1976, p. 240). Gaudry also showed that the forms discovered which were intermediate *anatomically* between the horse genus (*equus*) and other odd-toed ungulates were also intermediate in the geological time scale, thus supporting the second assumption. Confirming evidence of the first assumption mentioned above was provided by the discovery in 1861 in Bavaria of *Archaeopteryx,* a fossil bird with unmistakable reptilian traits. From the same location, *Compsognathus* was discovered, a reptile with bird-like anatomical features. Both of these fossils were argued by Thomas Huxley to provide "missing links" through showing that distinct classes of animals have had common ancestors (Rudwick 1975, pp. 250–251).

Subsequent palaeontological research continued to serve evolutionary theory in two ways. If one assumes that natural selection theory is a good theory, then there is a certain result which must not be disconfirmed, i.e. that lineages revealed by fossil remains conform to the expected temporal and anatomical succession. That palaeontological discoveries consistently produced this result served as strong confirmation of a fundamental assumption of all natural selection model types. The above examples demonstrate several related results from research promoted by natural selection theory. The testing of assumptions in various specific models led to new empirical findings in various fields, including classification, comparative anatomy, and palaeontology. Furthermore, by assuming specific assumptions while constructing models, researchers were able to predict the existence and general features of previously undiscovered entities or relations. The testing of assumptions and predictions served to focus and guide research efficiently into specific programs.

3. Evaluation of Support. Darwin thought that he had no direct evidence for natural selection equivalent to the supposedly direct evidence offered by Newtonians for the laws of motion, the paradigm of scientific theory at the time. He moved the fight into a more appropriate arena by drawing a parallel between the hypothesis of natural selection and the hypothetical wave theory of light. As a result, any demands for direct evidence for natural selection theory made by Darwin's contemporaries were countered by the claim that perfectly good and accepted scientific theories could be supported by indirect evidence and support of various kinds. Darwin accordingly provided a vast amount of indirect evidence in the form of support for the various assumptions necessary for model types and particular models constructed from natural selection theory. Considered in this context, Darwin's evidence cannot be considered inferior either by the standards of his contemporaries or by today's.

A major objection, raised against Darwin ever since 1860, is that natural selection theory does not make testable predictions. I have discussed several examples of predictions resulting from the application of natural selection theory to model construction. Mary Williams has recently argued that modern evolutionary theory yields testable predictions, supporting the status of natural selection theory, a subset of modern evolutionary biology, as a predictive theory (1982, p. 304). In addition, natural selection models constructed from confirmed assumptions led to specific successful research programs. The success of the research lay not just in the fact that new empirical information was acquired; the new facts also indirectly *confirmed* the models and the theory. In the case that the new facts were of the sort suggested by a model constructed using natural selection theory, the success of the research must therefore be closely related to the predictive success of the theory.

Darwin's specific support of his theory of natural selection consists of various sorts of arguments. Several of these, particularly his claims to consilience, simplicity, and analogy, seem, *prima facie,* to be aspects of the explanatory use of the theory. Upon closer examination, though, Darwin's claim that his theory was highly consilient actually amounts to the claim that the theory had exhibited empirical adequacy in a large variety of instances, according to all available data. The notion of consilience is therefore not primarily a characteristic of explanations; rather, it is a semantic relation, based on the relation between the theory and the empirical data.

In addition, a criterion of simplicity that focuses on the form or content of the explanation is not an element of Darwin's support for natural selection. The simplifying and unifying aspects of the theory to which Darwin *does* refer are not merely relations between the theory and users but involve essential relations of the theory to empirical facts. Considering the analogical inferences in Darwin's theory as merely heuristic devices does not accurately represent their role in Darwin's argument. The existence of heritable variations is an assumption basic to all model types representing natural selection, and this assumption is supported by analogical evidence, and possibly generalization from a limited to a total environment. Analogical evidence is a semantic issue, and does not directly concern various features of explanation, as assumed by proponents of an inference to the best explanation view of Darwin's defense.

Aside from the fact that explanation-centered criteria are inappropriate for characterizing the nature of the above aspects of Darwin's support for his theory, such criteria omit a crucial line of his defense: the role of the theory in stimulating scientific research. Thus, the structure of natural selection theory, regarded as presenting a set of related model types, makes it particularly suited to serve as a foundation for scientific research. Research generated by the theory, according to my simplified version, serves either to test assumptions of particular models or to search for or identify entities or relations which are predicted by speculative models.

I have summarized some instances of the vindication of predictions which were supplied by models using natural selection theory. Such successful research also contributes to the support of natural selection theory itself. I conclude that the support offered by Darwin and other nineteenth century researchers is *not* inherently weaker than, or of a kind inferior to, support offered for other scientific theories. Darwin supported the assumptions contained in the model types of natural selection by extensive empirical evidence. Under the covering law approach taken by Ruse, Kitcher, and others, interest is focused on Darwin's formulation of various "empirical laws" which can be fitted together into a partial axiomatization of the theory of natural selection (see especially Ruse 1975). In contrast, the conception of natural selection theory as presenting a family of related model types suggests an interpretation of Darwin's argument which emphasizes and clarifies the role of his empirical evidence.

Explanatory power either involves relations strictly between the user and the theory, or among the user, theory, and data; theory structure and empirical adequacy, on the other hand, are relations founded in the logical structure of the theory itself and the fit between empirical data and theory—relations that are much less context-oriented than those heavily involving users. Contrary to the claim that Darwin supported his theory chiefly on the basis of its explanatory power, I have argued that the structure of the theory and its relation to empirical evidence, as shown both in explanation and in research, served as Darwin's primary support for his theory.

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