

# Adaptation and Evolutionary Theory

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*There is virtually universal disagreement among students of evolution as to the meaning of adaptation.*

(Lewontin, 1957)

*Much of past and current disagreement on adaptation centers about the definition of the concept and its application to particular examples: these arguments would lessen greatly if precise definitions for adaptations were available.*

(Bock and von Wahlert, 1965)

*The development of a predictive theory [of evolution] depends on being able to specify when a population is in better or worse evolutionary state. For this purpose an objective definition of adaptedness is necessary.*

(Slobodkin, 1968)

The conception of adaptation was not introduced into biology in 1859. Rather what Darwin did was to offer a radically new type of explanation of adaptations and in so doing he altered the conception. As the above quotes indicate we have not in the last century sufficiently delimited this conception and it is important to do so.

In this paper we will analyse and, I hope, clarify one aspect of the conception of adaptation. One of the aims of this paper is a theoretically

adequate definition of relative adaptedness. As we will see such analysis cannot be divorced from an analysis of the structure of evolutionary theory. The other major aim of this paper is to expose this structure, to show how it differs from the standard philosophical models of scientific theories, and to defend this differentiating feature (and hence to show the inadequacy of certain views about the structure of scientific theories which purport to be complete).

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A note on defining is needed. Definitions are often thought to be of two kinds, descriptive and stipulative. (See, for example, Hempel (1966), chapter 7.) Descriptive definitions simply describe the meaning of terms already in use; stipulative definitions assign, by stipulation, special meaning to a term (either newly coined or previously existing). According to this view the project of defining a term is either purely descriptive or purely stipulative. This view is mistaken. The project at hand calls for neither pure linguistic analysis nor pure stipulation; it is much more complex. Briefly, we examine the conceptual network of evolutionary biology. We find that according to evolutionary theory there is a biological property, adaptedness, which some organisms have more of than others. Those having more of it, or those better adapted, tend to leave more offspring. And this is the mechanism of evolution. The project calls for conceptual analysis but such analysis is sterile unless it is coupled with an examination of the biological property which is the object of the conception. Any definition which fails to fit the conceptual network must be rejected, as must any which fails to apply to the property. The project calls for an element of stipulation but our stipulatory freedom is constrained both by theoretical and conceptual requirements and, one hopes, by the real world.

A note on the restricted scope of this paper is also needed. Biologists talk about the adaptedness of individual organisms and of populations. Selection occurs at the level of individuals and, presumably, at higher levels. That is, there is intrapopulational selection and interpopulational selection. It is vital that we keep these levels separate and that we see the relation between selection and adaptation.<sup>1</sup> Selection at the level of individual organisms has as its cause differences in individual adaptedness and its effect is adaptations for individual organisms. We will follow standard practice in calling selection at this level natural selection. Any benefit to the population from natural selection is purely fortuitous. One must distinguish between a group of adapted organisms and an adapted group of organisms. For instance, a herd of fleet gazelles is not necessarily a fleet herd of gazelles. Similarly group selection will have as its cause differences in group adaptedness and as its effect group adaptations. The theory of group selection is quite clear; its

occurrence in nature is controversial. One could speak of an abstract theory of evolution which covers natural selection, group selection and even the selection of tin cans in junk yards. But most of the interesting problems don't arise at this level of generality. In this paper we will be primarily concerned with natural selection, *i.e.* with intra-specific intraenvironmental selection. Thus we will be concerned with the adaptedness of individual organisms, not with the adaptedness of populations.

Let me illustrate the confusion that results from the failure to relate adaptedness to the proper level of selection. One of the more prominent definitions of relative adaptedness is due to Thoday.<sup>2</sup> Basically it says: *a* is better adapted than *b* if and only if *a* is more likely than *b* to have offspring surviving  $10^8$  (or some other large number) years from now. Either the long-range probability of offspring corresponds to the short-range probability of offspring or it does not. (Corresponds means: *a*'s long-range probability of offspring is greater than *b*'s long-range probability of offspring if and only if *a*'s short-range probability of offspring is greater than *b*'s short-range probability of offspring.) If it does correspond then we should stick to the more easily measurable short-range probability. If not, then since natural selection is not foresighted, *i.e.* it operates only on the differential adaptedness of present organisms to present environments, the long-range probability of offspring is irrelevant to natural selection.

Why has Thoday's definition been so favorably received? Because the long-range probability of descendants is important to selection at or above the species level. For instance, one plausible explanation of the predominance of sexual reproduction over asexual modes of reproduction is that the long-range chances of survival are greater for populations having sex (see Maynard Smith, 1975, pp. 185ff). But if one is interested in selection at the population level then the relevant notion of adaptedness would be that which applies to populations. Until recently even biologists have failed to distinguish intra- and inter-populational selection. Thoday's definition, not being selection relative, lends itself to this confusion. To keep matters as clear as possible we will only be concerned with natural selection and with that notion of adaptation which properly relates to it.

## 1. The Role of the Concept of Relative Adaptedness in Evolutionary Theory

The following three statements are crucial components of the Darwinian (or neo-Darwinian) theory of evolution:<sup>3</sup>

1. Variation: There is (significant) variation in morphological, physiological and behavioral traits among members of a species.
2. Heredity: Some traits are heritable so that individuals resemble their relations more than they resemble unrelated individuals and, in particular, offspring resemble their parents.
3. Differential Fitness: Different variants (or different types of organisms) leave different numbers of offspring in immediate or remote generations.

When the conditions described above are satisfied organic evolution occurs. A thorough examination into the history of our awareness of these conditions would be interesting and worthwhile but will not be attempted here (see Mayr, 1977). Suffice it to say that in Darwin's time each was a non-trivial statement. In what follows we will examine them predominantly from our own point of view.

Ignoring the parenthetical 'significant' (1) could not help but be true. The uniqueness of complex material systems is now taken for granted; and so we expect variation among individuals of a species. Their similarity needs explaining not their variation. (1) becomes less empty from our point of view when 'significant' is added. What sort of variation is significant? That which can lead to adaptive evolutionary changes. Though the world is such that individuals must be unique the recognition of this fact is of fairly recent origins and is necessary for an evolutionary world view.

Unlike (1), (2) is not at all trivial. There is no metaphysical necessity in offspring resembling their parents. (2) can now be derived from our modern theories of genetics; in Darwin's time it was an observation common to naturalists and animal breeders. Darwin's theories of heredity were notoriously muddled but fortunately a correct theory of genetics is not a prerequisite for a Darwinian theory of evolution (see Mayr, 1977, p. 325). What is important to note is that given

that there is variation, (1), and that some of the traits which vary are heritable, (2), it follows that the variation within a species tends to be preserved. (Of course this tendency can be counterbalanced by other factors.)

When (3) holds, when there are differences in reproductive rates, it follows from (1) and (2) that the variation status quo is disrupted, that is, that there are changes in the patterns of variation within the species. For our purposes we can count such changes as evolution. (For a fuller explication of the concept of evolution see Brandon, 1978.) Thus when (1)–(3) hold evolution occurs.

We have seen that (1) is in a sense trivial and requires no explanation. We have also seen that (2) is non-trivial and is to be explained by modern theories of genetics, but that this explanation is not essential to Darwinian theory. In contrast, the distinguishing feature of a Darwinian theory of evolution is its explanation of (3).<sup>4</sup> The focus of this paper is the conception used for such explanations.

The distinguishing feature of a Darwinian theory of evolution is explaining evolutionary change by a theory of natural selection. Of course, that is not the only possible sort of explanation of evolution. In his own time Darwin convinced the majority of the scientific community that evolution has and does occur but hardly anyone bought his natural-selection-explanation of it. (For an excellent source book on the reception of Darwin's theory see Hull, 1973.) The alternatives of Darwin's day, *e.g.* divine intervention and the unfolding of some predetermined plan, are no longer scientifically acceptable. But there is one present day alternative we should consider.

It is not surprising that in finite populations of unique individuals some variants leave more offspring than others. We would expect such differences in reproductive success simply from chance. And if there are chance differences in reproductive success between two types of organisms (or similarity classes of organisms) we expect one type ultimately to predominate by what statisticians call random walk. If we can explain (3) and so the occurrence of evolution in terms of chance is the hypothesis of natural selection necessary?

It is becoming the received view in the philosophy of science that hypotheses are not evaluated in isolation but rather in comparison with rival

hypotheses. This view is, I think, for the most part correct but not entirely; some hypotheses we reject as unacceptable without comparison with specific alternatives. Unacceptable hypotheses are those that violate deeper-seated beliefs, theories or metaphysics. Similarly some forms of explanation are unacceptable in that no investigation into the particular phenomenon is required to reject them. We reject them without considering any particular alternative explanation simply because we believe there must be a better alternative. For example, accepting Darwinian theory we reject the explanation that bees make honey in order to provide food for bears without examining bees, bears or honey. (An acceptable form of explanation is not one which is necessarily correct or even accepted; it simply is one which is not unacceptable.)

The theory of evolution by chance or by random walk has been developed in recent years and is often called the theory of non-Darwinian evolution, or better, the neutrality theory of evolution (see King and Jukes, 1969). We cannot give it the discussion it deserves but it is worth pointing out that explanation in terms of chance is an acceptable form of explaining short term evolutionary change but not of any interesting sort of long term evolutionary change. (The truth of this hinges on what counts as interesting. I will not try to delimit interesting long term evolutionary change; suffice it to say that any seemingly directed change is interesting.)

The neutrality theory supposes that certain alternative alleles (and so certain protein molecules coded by them) are functionally equivalent, *i.e.* are selectively *neutral*. Given this supposition the neutrality theory predicts (and so is able to explain) the sorts of changes in frequencies of these alleles expected by a process of random sampling in different situations. As Ayala (1974) points out these predictions differ both qualitatively and quantitatively from those given by the selectionist theory. (Ayala presents data on different species of *Drosophila* which tend to corroborate the natural selectionist hypothesis and refute the neutrality hypothesis.) Whether evolution by random walk is a common or rare phenomenon we cannot reject *a priori* a chance-explanation of short term evolutionary change.

The situation is different for interesting long term evolutionary phenomena. Of course we

do not directly observe long term evolutionary change. What we observe and try to explain are the products of such change. Presumably any complex feature of an organism is the product of long term evolutionary change. On the one hand some complex features of organisms, such as the eye of a human, are so obviously useful to their possessor that we cannot believe that this usefulness plays no part in explaining their existence. That is, given Darwinian theory and the obvious usefulness of sight we have a better alternative to the chance-explanation. On the other hand there are features whose usefulness is unclear for which we still reject chance-explanations because of their high degree of complexity and constancy. Complexity and constancy are not made likely on the hypothesis of evolution by random sampling. A good example is lateral lines in fish. This organ is structurally complex and shows a structural constancy within taxa, yet until recently it was not known how the lateral line was useful to its possessor. In this case the rejection of a chance-explanation was good policy; studies eventually showed that the lateral line is a sense organ of audition. (This example is taken from G. C. Williams, 1966, pp. 10-11.)

One can contrast the lateral line in fish with the tailless condition of Manx cats. This feature is not even constant within the species and a non-existent tail is hardly complex. (Actually what is relevant concerning complexity is that the historical process leading from tailed to tailless is most probably not complex.) Furthermore legend has it that Manx cats originated on the Isle of Man in what would be a small isolated population; thus increasing the probable role of chance. The tailless condition of Manx cats may have evolved by natural selection but for all we know the best explanation of it is the explanation in terms of chance.

It is important to keep in mind the possibility of evolution by random walk for it is important that Darwinian explanations be testably different (at least in principle) from chance-explanations. What is the Darwinian explanation of (3)? The conventional wisdom is that Darwin explained (3) by his postulate of the 'struggle for existence' (or in Spencer's words, which Darwin later used, 'the survival of the fittest') and that this explanation, or this discovery of the mechanism of evolution, was Darwin's greatest contribution.

How does 'the struggle for existence' or 'the survival of the fittest' explain (3)? Following current practice let us define the *reproductive success* or the *Darwinian fitness* of an organism in terms of its actual genetic contribution to the next generation. I will not try to make this definition precise and complete. The genetic contribution to the next generation can usefully be identified with the number of sufficiently similar offspring when 'sufficiently similar' is sufficiently explicated. This would disallow, for example, sterile offspring from counting towards Darwinian fitness. There are two options: either let the Darwinian fitness of an individual equal its actual number of sufficiently similar offspring or let the Darwinian fitness of an individual equal the mean number of sufficiently similar offspring of members of the similarity class to which it belongs. In either case Darwinian fitness is defined in terms of numbers of *actual* offspring. I should point out that most biologists use the words 'fitness' and 'adaptedness' interchangeably. In this paper 'fitness' will only be used to refer to Darwinian fitness. Adaptedness, as we will see, cannot be identified with Darwinian fitness. (3) says that Darwinian fitness is correlated with certain morphological, physiological or behavioral traits. Why is there this correlation? Why is there differential fitness? Darwin's answer, which he arrived at after reading Malthus' *Essay on Population*,<sup>5</sup> was that since in each generation more individuals are produced than can survive to reproduce there is a struggle for existence. In this 'struggle' (which in its broadest sense is a struggle of the organism with its environment not just with other individuals, see Darwin, 1859, p. 62) certain traits will render an organism *better adapted* to its environment than conspecifics with certain other traits. The better adapted individuals will tend to be fitter (*i.e.* produce more offspring) than the less well adapted. Why are those who happen to be the fittest in fact the fittest? The Darwinian answer is: They are (for the most part) better adapted to their environment.

What does this explanation presuppose? It seems to presuppose the following as a law of nature:

- (D) If *a* is better adapted than *b* in environment *E* then (probably) *a* will have more (sufficiently similar) offspring than *b* in *E*.

Certainly if (D) is a true law then the Darwinian explanation is acceptable. Darwin seems to presuppose (D) but it is not to be found stated explicitly in the *Origin*. Nor is it to be found in modern evolutionary works. But if one examines work in modern evolutionary biology – the theorizing done, the inferences made, the explanations offered – one finds that (D) or something like (D) is required as the foundation of evolutionary theory. I take it that this conclusion will be so uncontroversial that it need not be further supported by examining examples of evolutionary reasoning. But later in this paper we will give some examples to show how (D) is to be employed.

Philosophers of science talk about laws more often than they display actual examples of them. In particular many people have discussed whether or not 'the survival of the fittest' is a tautology without displaying something other than that phrase which might be a tautology. (As for example J. J. C. Smart, 1963, p. 59.) The phrase itself, not being a declarative sentence, could not be a tautology. An exception is Mary Williams.<sup>6</sup> She has attempted to give a 'precise, concise and testable' version of that phrase, and so has attempted to give a precise, concise and testable version of the fundamental law of evolutionary theory.

William defines the clan of a set  $\beta$  as the members of  $\beta$  plus all their descendants. On a phylogenetic tree the clan of  $\beta$  would be those nodes which are in  $\beta$  plus all nodes after them which are on a branch which passes through one of the original nodes. A subclan is either a whole clan or a clan with one or more branches removed. A Darwinian subclan is a subclan which is held together by cohesive forces so that it acts as a unit with respect to selection (this crucial concept is not defined by Williams; she takes it as primitive). Informally Williams' version of the fundamental law of evolutionary theory states that for any subclan  $D_1$  of any Darwinian subclan  $D$ ,

If  $D_1$  is superior in fitness to the rest of  $D$  for sufficiently many generations... then the proportion of  $D_1$  in  $D$  will increase during these generations. (1970, p. 362)

(D) is a 'law'<sup>7</sup> about properties of individual organisms; Williams' version is a law about properties of sets of organisms. Which is fundamental? Some properties of sets (notable

exceptions being set-theoretic properties such as cardinality) are a function of the properties of the sets' members. In particular, as Williams herself points out (1973, p. 528), the fitness of a clan is to be identified with the average fitness of the members of the clan. Thus the property of individuals (or more precisely the property of individuals in some environment) – what we will call adaptedness, what Williams calls fitness – is fundamental. Likewise (D) is fundamental in that Williams' law can be derived from it and the laws of population genetics but not *vice versa*. Perhaps the only way of testing (D) is to apply it to fairly large populations and so to test something like Williams' law, but this does not change our conclusion. (D) is required as the foundation of evolutionary theory.

## 2. Four Desiderata of Definitions of Relative Adaptedness

We have seen the role the relational concept of adaptedness is to play in a Darwinian theory of evolution: It is the explanatory concept in what I have called the fundamental law of evolutionary theory. Philosophers have not been able to come up with a set of necessary and jointly sufficient conditions for scientific lawhood, but there is wide agreement on some necessary conditions. In particular laws of the empirical sciences are to be empirically testable universal statements. It is also highly desirable, whether or not definitionally necessary, that laws be empirically correct or at least nearly true. One cannot just look at the surface logic of a statement in order to determine whether or not it is a scientific law (as done in Ruse, 1975). To determine whether (D) is a scientific law we will have to look deeply into the conception of adaptation. My strategy is to try to construct a definition of relative adaptedness that makes (D) a respectable scientific law. In this section I will argue that from any definition (construction, explication) of this concept we would want the following: (a) independence from actual reproductive values; (b) generality; (c) epistemological applicability; and (d) empirical correctness. After arguing for the above desiderata I will show how current definitions fail to satisfy all four and then I will produce a general argument showing that no explication

of the concept will satisfy all four desiderata. In the final section I will attempt to draw the ramifications of this result.

### (a) Independence

The relational concept of adaptation is to explain differential fitness. To do so (D) must not be a tautology. Clearly if (D) is to be a scientific law rather than a tautology the relational concept of adaptation cannot be defined in terms of actual reproductive values. That is, we cannot define it as follows:

*a* is better adapted than *b* in *E* iff *a* has more offspring than *b* in *E*

('iff' is shorthand for 'if and only if'.) Most biologists treat 'fitness' and 'adaptedness' as synonymous and many define relational fitness in just this way. (See Stern, 1970, p. 47 where he quotes Simpson, Waddington, Lerner and Mayr<sup>8</sup> to this effect. Stern approves of this definition.) They thus deprive evolutionary theory of its explanatory power.

To avoid turning (D) into a tautology it seems we must also avoid defining relative adaptedness in terms of probable reproductive values. That is, the following definition also seems to render (D) a tautology:

*a* is better adapted than *b* in *E* iff *a* will probably have more offspring than *b* in *E*

(See Munson, 1971, p. 211 for a definition of this form; but he substitutes survival for reproductive values.) Actually things are not as simple as they seem to be. Whether or not the above definition makes (D) tautologous depends on the interpretation of probability being used. More will be said about this, but for the moment we may conclude the obvious: If the relational concept of adaptation is to play its explanatory role in evolutionary theory it must be defined so that (D) does not become a tautology. We will call this requirement the condition of independence from actual reproductive values.

### (b) Generality

As stated earlier we are primarily interested in intraspecific selection and so for the set of ordered triple  $\langle x, y, z \rangle$  which satisfy 'x is better adapted

than  $y$  in  $z'$  the first two members of those triples will be members of the same species. In other, less formal, words we are interested in what it is for one alligator to be better adapted than another alligator to their particular environment but not in what it is for one elephant to be better adapted than one swallow to their environment (since they are not in direct reproductive competition with each other, see Ghiselin, 1974). But we do expect one and the same explanation or definition of relative adaptedness to apply to ants, birds and elephants. That is, we want (D) to be a general law that applies to the whole biosphere.

Suppose for some precursors of modern giraffes it was true that one was better adapted than another to their environment if and only if it was taller than the other. (Suppose this only for the sake of this discussion. Even within a given species it is doubtful that any single-dimensional analysis of adaptedness will be adequate.) It won't do to define relative adaptedness in terms of relative height because even though such a definition may truly apply to some giraffe precursors it will not apply to most other plants and animals. Such a definition would make (D) a true law of giraffe precursors but make it false or inapplicable to other plants and animals. If (D) is to be a general law our definition of relative adaptedness must meet what we will call the condition of generality; that is, it must apply to all plants and animals.

(c) *Epistemological applicability*

One way of stating this requirement is to say that our definition of relative adaptedness must render (D) testable. However, I prefer to stress another side of what is perhaps the same coin and say that our definition of relative adaptedness should tell us something about how (D) is to be applied to particular cases. I choose this stress because I think testing (D) is a pipe dream, whereas applying it to explain certain phenomena should not be. (Such thoughts are in consonance with Scriven, 1959, and Mayr, 1961.)

One sometimes hears talk of adaptedness as a 'close correlation with the environment'. We could define relative adaptedness as follows:

$a$  is better adapted than  $b$  in  $E$  iff  $a$  is more closely correlated than  $b$  to  $E$

This is a good example of a definition which fails epistemological applicability. Without further information we have no idea how it applies to particular organisms, simply because we have no idea what it means. Consider the following:

$a$  is better adapted than  $b$  in  $E$  iff God prefers  $a$  to  $b$  in  $E$

At least for those theistically inclined there is no problem of meaning here. But this definition is clearly useless since we have no way of knowing which organisms God favors.

The definition discussed above in terms of relative height is a good example of a definition which meets the requirement of epistemological applicability. We know what it is for one organism to be taller than another. Unfortunately this definition lacks generality (or if general then it is empirically incorrect).

To say a definition is epistemologically applicable does not imply that there is an easy mechanical test for its application. Perhaps a paradigm for an epistemologically applicable definition of relative adaptedness is the definition in terms of actual reproductive values (which explains its popularity). But if we try to apply it to two female Pacific salmon in the sea we are faced with real difficulties. We would have to try to follow them up river to their spawning ground. And if we managed to do that and if they both managed to make it we would be faced with the task of counting numerous eggs dispersed in the water. And then we would have to follow each egg's progress to sexual maturity or to death.

But these practical difficulties need not matter. What matters is that theoretically we know what it is for  $a$  to be better adapted than  $b$  in  $E$  and that for at least some cases we can apply it and so test (D) and in those cases where we cannot test (D) we have a good explanation of why we cannot. Thus by requiring epistemological applicability I do not mean to require an operational definition, theoretical applicability is enough.

(d) *Empirical correctness*

I hardly need to argue that we want our definition of relative adaptedness to be empirically correct but I do need to say something about what it is for our definition to be empirically correct and how we go about determining its correctness.

There may be many features of organisms, such as strength, beauty or even longevity, which we will be disappointed to find out are not invariably selected. In fact quite often there is no selection for higher fecundity.<sup>9</sup> The best adapted may not always be the strongest or the most beautiful or even the most prolific. But natural selection, rather than personal or collective taste, must be the ultimate criterion against which we test our explication of adaptedness.<sup>10</sup> If we define natural selection in terms of relative adaptedness (as we will, see below p. 111) then those selected will by definition be the better adapted. Yet it does not follow that those organisms with higher reproductive values will by definition be better adapted. (If it did then (D) would be tautologous.) We must allow that some instances of differential reproduction are not instances of natural selection.

If natural selection is to be defined in terms of relative adaptedness how can we use it to test the empirical correctness of our definition of relative adaptedness? Suppose for a certain species of organisms we pick out 2 similarity classes of members of this species, A and B. (For our purposes these classes should be formed on the basis of the functional or epigenetical similarity of the genotypes of the members, see Brandon, 1978.) Suppose further that by our definition of relative adaptedness all members of A are better adapted than any member of B to their mutual environment. Our theory of natural selection, of which (D) is a major component, tells us that in statistically large populations (where chance differences in fitness are cancelled out) A's will have a higher average reproductive rate than B's. If repeated observations (either in the lab or in the field) show that A's do in fact outreproduce B's then our definition of relative adaptedness fits these facts of natural selection and so is corroborated; if not then it is on its way to being falsified (of course no one observation would falsify it).

It should be clear that any definition that fails to satisfy the condition of independence from actual reproductive values will fail to be testable in the way described above. Yet it is important to note that once we accept some theory of adaptedness, that is, some theory of what it is for an organism to be adapted to its environment, we can criticize a definition failing (a) as empirically incorrect. In fact, as we will see, on any decent theory of adaptedness any definition failing (a)

will also fail (d).<sup>11</sup> We want our definition of relative adaptedness to fit the facts of natural selection. We cannot accept a definition which renders (D) false.

To summarize, our strategy is to construct a definition of relative adaptedness that makes (D) a respectable scientific law (from the received point of view of philosophy of science). Requirement (a) is that (D) cannot be a tautology. Requirement (b) is that (D) must be general, *i.e.* universally applicable throughout the biosphere. Requirement (c) is that (D) not be so vague or so obscure that we have no idea how to apply it to particular cases (or that (D) be testable). And requirement (d) is that (D) must not be false (or more precisely, that (D) must be nontautologically true).

### 3. Current Definitions and the Possibility of Satisfying the Four Desiderata

Let us now examine current approaches to the problem of defining relative adaptedness in the light of the four desiderata discussed above. As I said earlier the simplest approach is perhaps the most popular: *a* is better adapted than *b* in *E* iff *a* has more offspring than *b* in *E*. Besides making (D) a tautology and so stripping the concept of its explanatory power this approach totally ignores the fact that natural selection is a statistical phenomenon. Differential fitness may be correlated with certain differences in traits but the correlation is not expected to be perfect. For example, in a certain population of moths darker winged individuals may on average produce more offspring than lighter winged individuals but this certainly does not imply that for every pair of moths the darker winged one will have a greater number of offspring than the lighter winged one. Appreciating that natural selection is a statistical rather than a deterministic process has led some theorists to suggest a more sophisticated approach to our problem (see Mayr, 1963, pp. 182–184).

This more sophisticated approach would define relative adaptedness in terms of the statistical probability of reproductive success. How is this probability to be determined? Suppose we separate the members of a population (of moths,



for example) into similarity classes formed on the basis of the functional or epigenetical similarity of their genotypes. To fix ideas let us say that we form two such classes and that the members of one are all darker winged than any of the members of the other (this difference being the result of genetic differences between members of the two classes). Further suppose that these classes are epistemically homogeneous with respect to reproduction; *i.e.* no other division of this class of moths that we can make (based on our knowledge) will be statistically more relevant to reproduction, except divisions based tautologously on actual reproduction. We can now determine the probability of reproductive success of any individual as a simple function of the average reproductive success of the members of the similarity class to which it belongs. And so the reproductive success of the individual is statistically determined by the functional properties of its genotype.

This approach, which we will call the statistical approach, fits some existing paradigms of statistical explanation (see Salmon, 1970), but, as I will show, it fails not only desideratum (a) but also (d). The statistical approach is most closely related to the frequentist interpretation of probability which identifies the probability of an event with its relative frequency 'in the long run'. The leading proponents of this interpretation have been Richard von Mises and Hans Reichenbach. In what follows I am only criticizing the application of this interpretation of probability to defining relative adaptedness. This, of course, does not constitute a general criticism of that interpretation. In the next section I will suggest a definition using a rival conception of probability.

Since the statistical approach uses actual reproductive values its empirical correctness cannot be tested by prediction and observation. It can only be tested against certain general theoretical principles. Consider the following case. Four dogs are on an island; two German shepherds one of each sex and two basset hounds one of each sex. Both bitches go into heat, basset mounts basset and German shepherd mounts German shepherd. While copulating the shepherds are fatally struck by lightning. The bassets, on the other hand, raise a nice family. Are the bassets therefore better adapted to the island environment

than the shepherds? To put the question another way, do we count this differential reproduction as natural selection?

Biologists usually define natural selection simply as differential reproduction (of genes, genotypes or phenotypes). But this is due to carelessness not lack of understanding. Most biologists would agree that the above case is not an instance of natural selection but rather a case of chance differences in fitness. (Not that it could not be natural selection, but nothing in the story indicates that it is. We can elaborate the story in ways that make it clear that it is not a case of natural selection. For instance, the only food source for dogs on our island might be animals whose size and ferocity would make it relatively easier for the larger shepherds to eat than the bassets. Furthermore lightning might be a rare phenomenon and indifferent between bassets and shepherds.) How then shall we characterize natural selection? The concept must be defined in terms of the as yet undefined notion of adaptedness. Natural selection is not just differential reproduction but rather is differential reproduction which is due to the adaptive superiority of those who leave more offspring.

Even without a definition of relative adaptedness we can be confident that cases like the basset-shepherd case are not instances of natural selection. Given that natural selection is a statistical phenomenon it should not be surprising that in small populations Darwinian fitness is not always correlated with adaptedness. Yet the statistical approach to defining relative adaptedness cannot recognize this. According to our story the basset-shepherd case is unique; no such population of dogs has ever been nor will ever be on this island nor on any sufficiently similar island. Thus our four dogs exhaust the data available for the statistical approach. So according to the statistical approach the bassets are better adapted to the island environment than the shepherds. Yet by ecological analysis, in which we determine what it takes for a dog to survive and reproduce on our island, we conclude that the shepherds are better adapted to the island than the bassets. This conflict raises questions concerning the empirical correctness of the statistical approach.

If the basset-shepherd case were just an *ad hoc* counter-example dreamed up to refute the

statistical approach then perhaps we should ignore it. But statistically small populations are not uncommon in nature and they are of considerable evolutionary significance (especially for speciation by what Mayr calls the *founder principle*, see Mettler and Gregg, 1969, pp. 130–135; and Mayr, 1963). When applied to small populations the statistical approach will quite predictably conflict with our best analyses of the organism-environment relation, and so we are led to conclude that this approach which renders (D) a tautology is also empirically incorrect. (It should be clear that defining the relative adaptedness of an individual in terms of *its* actual reproductive success is likewise empirically incorrect.)

Let me criticize the statistical approach in a slightly different way to show the connection between its empirical incorrectness and its explanatory failure. The role in evolutionary theory of the relational concept of adaptation is to explain differential fitness. The question is: Why are those features which happen to be highly correlated with reproductive success in fact highly correlated with reproductive success? The Darwinian answer is: Organisms having these features are (for the most part) better adapted to their environment than their conspecifics lacking them. This higher degree of adaptedness causes the fitter organisms to be fitter and is the explanation of their higher fitness. The idea behind the statistical approach to defining relative adaptedness is that high statistical correlations between certain features and Darwinian fitness will indeed be causal connections and so will explain differential fitness. Yet we have seen that there are conceptually clear-cut types of cases (involving small populations) where the high statistical correlation is not a causal connection (in any interesting sense) and so cannot be used to explain differential fitness. In our basset-shepherd case certain distinctively basset features (such as shortness and color of coat) are perfectly correlated with fitness. Yet our bassets are fitter than our shepherds not because they are shorter or are a certain color, but rather because the shepherds were in the wrong place at the wrong time. In our case it's not that shepherds are characteristically in the wrong place at the wrong time but just that they happened to be once. Due to small population size once is enough and so an essentially random process has radically altered our island

population of dogs. Here differential fitness is explained (some might worry over how this is an explanation – I can't concern myself with that here) in terms of a chance process and small population size. Thus if evolutionists are to explain what they want to explain, if they are to have the sort of explanatory theory they want, some other approach to the problem of adaptation is needed.

Early in this paper we were led to distinguish adaptedness from Darwinian fitness. As we have seen from the basset-shepherd example, in small populations the two do not always coincide. Are there other types of cases where the two do not coincide? I can think of only three candidates for such cases: cases of artificial selection, cases of domestication such as in modern man where selection seems to have been relaxed and cases of sexual selection. But none of these types of cases are ones where the correlation of fitness and adaptedness should not be expected and it is important to see why this is so. I will focus my attention on artificial selection; what is said about it can easily be applied to the other two types of cases by analogy.

Artificial selection quite often results in organisms which could not survive in their 'natural' habitat. Organisms which under 'natural' conditions would be the fittest are prevented from breeding while other organisms, less fit under 'natural' conditions, are allowed to breed. By such a process we end up with chickens without feathers, dogs so small they can fit in your hand and fruit flies with legs where they should have antennae. Such cases, it could be claimed, are clear cases where Darwinian fitness does not coincide with adaptedness. But how could one argue for this claim?

Suppose we are following the relative frequency of a segregating genetic entity, say a chromosome inversion in a population of fruit flies. We divide this population into two genetically identical subpopulations, leave one sub-population in its original habitat and move the other to some new and different habitat. After a few generations we observe that the frequency of this chromosome inversion has changed in the moved population (while remaining the same in the control population). Are we to conclude that this change in frequency is the result of some divergence between fitness and adaptedness, since some flies

which would have been less fit in the original environment have had a higher relative fitness in the new environment? Obviously not. Whatever adaptedness is it has something to do with the organism-environment relation. With a change in environment a change in relative adaptedness is not unexpected. Man is often thought of as the zenith of evolution yet he can hardly get by in his fishy ancestors' environment.

Artificial selection is just a human induced change in environment. I presume that it is true that a fly with leg-like antennae would not be as well adapted to his ancestral home as many of his more normal relatives. But is he not much better adapted than his normal relatives to the laboratory where the experimenter is selecting for an extra set of legs? In this environment he is much better able to survive and reproduce than his more normal colleagues. The flies are living and breeding in the laboratory; what would be their relative adaptedness in the wild is irrelevant to an assessment of their relative adaptedness in the lab.

To argue that in cases of artificial selection fitness and adaptedness do not coincide is clearly to ignore the environment in which the selection is taking place; in particular it is to ignore the experimenter's or breeder's part in this environment. But that is no more justified than ignoring the part of predators in the prey's environment and is a bit of anthropocentrism. To objective biologists experimenters and breeders are no different than those English birds who for hundreds of years have steadfastly selected against (*i.e.* eaten) moths not cryptically colored.

Thus artificial selection is just a type of natural selection. This point will have a crucial role to play in an argument later in this paper so I should make it clear that it is not a quibble over words. How would we reply to one who says that by 'natural selection' he means all cases of selection excluding those involving man? To this we should reply that the concept he has defined is not as useful for theoretical purposes as the more inclusive concept we have defined. He can try to use words however he wants, but he can't justify an anthropocentric point of view towards the concept of adaptedness.

We have seen that the simplest approach to defining relative adaptedness, which does so in terms of actual reproductive values, and the

more sophisticated statistical approach fail both desiderata (a) and (d). This failure, especially the failure to meet (a), is fairly apparent and is presumably due to the neglect of theorists to formulate desiderata concerning the concept of relative adaptation. However there is the novel approach by Walter Bock and Gerd von Wahlert (1965) which might be taken as an attempt to meet (a)-(d); at least it does not obviously fail them.

Bock and von Wahlert argue that a measure of adaptedness should be expressed in terms of energy requirements. First they point out that the energy available to an organism at any given time (from both internal and external sources) is limited and that there is interindividual variation in the amount of energy available to organisms (as well as intraindividual variation over the life-span of an individual). Next they point out that for an organism to maintain the proper relation to its environment (*i.e.* to stay alive) it must expend energy. The amount of energy expended will vary depending, for example, on whether the organism is resting or escaping predation. Since an organism must expend energy to live and reproduce and since its available energy is limited it is advantageous, they argue, for the organism to minimize the amount of energy required to maintain successfully its ecological niche (p. 287). Thus the following definition is suggested by their work:

*a* is better adapted than *b* in *E* iff *a* requires less energy to maintain successfully its niche in *E* than does *b*.

There are a number of problems with this definition. First we must ask whether it really meets requirement (a). Stern (1970, p. 48) suggests that it does not. He asks what it means to *successfully* maintain a niche. He quotes Bock and von Wahlert as follows: 'The relative factor of survival or the relative number of progeny left which is usual when comparing the adaptedness of individuals is accounted for by the relative nature of the term "successful"' (Bock and von Wahlert, p. 287). This, according to Stern, 'is tantamount to admitting that their criterion is really subservient to reproduction, and that success in adaptation is still to be measured by more conventional means. That a niche will be maintained more successfully if less energy is required is clearly only an unsupported conclusion, not a matter of

definition.' (Stern, p. 48). But here Stern misses the point. Bock and von Wahlert clearly assert that 'unsupported conclusion'. They say, "The less energy used, the more successfully . . . the niche will be maintained." (p. 287). If they are right then differences in fitness can and will be explained in terms of differences in energy requirements. It remains for us to ask whether they are right.

We may not be able to answer this question. Although their definition of relative adaptedness seems to be applicable (*i.e.* it seems to satisfy desideratum (c)) it may not be. We can turn to Bock and von Wahlert for suggestions on how their definition is to be applied to particular cases. Unfortunately they do not discuss intraspecific comparisons; but from their discussion of comparing the energy requirements of sparrows *vs* woodpeckers for clinging to vertical surfaces we can reconstruct how they would make such a comparison (see Bock and von Wahlert, pp. 287 ff.). They would determine the amount of energy expended in clinging to a vertical surface by measuring the amount of oxygen consumed. Thus for two woodpeckers they would determine which is better adapted to clinging to vertical surfaces by measuring their oxygen consumption while clinging to some surface. One would be better adapted than the other if it used less oxygen than the other. Recall that we want to explain differential reproductive success. One could test the hypothesis that if one woodpecker requires less energy to cling to a vertical surface than another then it (probably) will have more offspring than the other. But it is not likely to be true. Even for woodpeckers there is more to life than hanging on trees. What seems to be needed is a determination of all the activities necessary for survival and reproduction in a particular environment. We would then compare the relative adaptedness of two organisms by comparing their energy requirements for these activities. But would not these activities have to be weighted according to their importance? How would they be weighted? And isn't it possible, and even fairly frequent, that one organism can bypass some 'necessary activity' because of some difference from his conspecifics in morphology, physiology or behavior? These questions lead me to believe that the Bock and von Wahlert definition is in fact not epistemologically applicable (*i.e.* it fails (c)) but I will not pursue this further.

Rather let us grant for the sake of argument that it is applicable and ask whether or not it is empirically correct.

I have already outlined how to test the empirical correctness of a definition of relative adaptedness (see above, pp. 110–111). In brief, we take paradigmatic cases of natural selection and see if the definition fits the case. In the well known case of melanism in English moths we would check to see if darker winged moths required on average less energy than lighter winged moths. I have raised doubts whether the Bock and von Wahlert definition is so testable and since I can't overcome the problems raised for its testability I can't subject it to this case-study type of test. But if it is testable (or epistemologically applicable) it can, I will argue, be shown to be empirically incorrect.

Suppose we have in our laboratory a population of genetically diverse individuals whose diversity is phenotypically expressed in an easily recognizable manner. By Bock's and von Wahlert's definition some variants are better adapted than others. I, as a perverse Popperian, prevent the so-called 'better adapted' from breeding while allowing the so-called 'less well adapted' to breed. I do this in a large population over a number of generations. Since artificial selection is just a type of natural selection we have here a case of natural selection which does not fit Bock's and von Wahlert's definition. If more falsifying cases are wanted we can produce them. And so, it seems, if Bock's and von Wahlert's definition is epistemologically applicable it is not empirically correct. Clearly this argument applies not only to the Bock and von Wahlert definition but to all definitions which meet desiderata (a)–(c).

This argument is not conclusive. When we begin to select for the so-called 'less well adapted' we change the environment of the organisms. It is open for the theorist whose definition we are criticizing to claim that our change of environment has reversed his estimations of adaptedness, adaptedness being environment relative. This doesn't deter us; again we try to refute the implications of the definition. But what if our most perverse efforts fail to contradict the proposed definition? Here I think we must conclude that empirical correctness has been purchased at the price of epistemological applicability. (Consider

how one would try to defend the Bock and von Wahlert definition against such counterexamples.) That is, the definition has become so vague and malleable as to make (D) unfalsifiable. My claim is that for any proposed definition of relative adaptedness satisfying desiderata (a)–(c) I can produce cases showing that it fails (d) (*i.e.* is empirically incorrect) and that to resist falsification by artificial selection is to give up (c) (*i.e.* is to cease being epistemologically applicable or testable). To exhaustively prove this would be to take every possible definition of relative adaptedness and produce the relevant counterexamples. It is not surprising that I can't do this. But I do hope my argument is convincing.

I'm sure some will feel that this argument from artificial selection is a cheap victory. If we could find a definition of relative adaptedness that truly applied to all organisms in 'natural' environments wouldn't we be justified in ignoring counterexamples produced by artificial selection? That is a difficult theoretical question but we can say this: Such a definition would represent a tremendous advance in our knowledge of ecology and would be welcomed. But artificial selection is as much a natural phenomenon as predation, starvation, mate selection, *etc.* The argument from artificial selection should, if nothing else, decrease the plausibility of the possibility of such a definition. Naturalists are well aware that natural selection is an opportunistic process, often leading to evolutionary dead ends and extinction. Are not some 'natural' cases of selection just as bizarre as our concocted cases?

The point emphasized in the argument from artificial selection is this: The environments in which organisms find themselves competing are radically different from each other, and at least practically speaking there is no way to specify all possible environments. Thus there is conflict between desiderata (c) and (d). To make (D) testable is to expose (D) to falsification from some radically new ecological situation. And to protect (D) from such falsification is to make it so general that it ceases to be applicable. This point should be accepted even by those who fail to subsume artificial selection under natural selection. Having given good reasons to doubt that any definition of relative adaptedness will satisfy (a)–(d) the question should be: Is there any reason to suppose such a definition possible? I've found none.

#### 4. A Suggested Definition

The attempt has been to construct a definition of relative adaptedness that renders (D) an explanatory law. Accepting the received view of philosophy of science I pointed out that for (D) to be an explanatory law it must be nontautologous, general, testable and true. I argued that for (D) to be such the definition of relative adaptedness must satisfy desiderata (a)–(d). Finally I showed that no definition of relative adaptedness can satisfy (a)–(d). In the light of these conclusions I will now suggest what I take to be the best possible definition of relative adaptedness.

Recall our desiderata. Apparently we will have to give up at least one of them. We should retain (a) and (d); tautologies and false statements explain little (one should note that giving up (a) would also entail giving up (d)). As we will see there is a trade-off between desiderata (b) and (c) and my suggested definition will, in a sense, preserve both.

First I will suggest a non-technical definition of relative adaptedness and then a more technical version. The non-technical version follows:

(RA) *a* is better adapted than *b* in *E* iff *a* is better able to survive and reproduce in *E* than is *b*.

This definition avoids tautology, that is, it is independent of actual reproductive values. (We can confidently assert that a particular Mercedes-Benz 450 SEL is *able* to do 150 mph while knowing that it never has and never will go that fast.) It is also a general definition and it is empirically correct (insofar as this makes sense, at least it is not empirically incorrect). But how are we to apply it to particular situations? I think it is clear that as it stands (RA) is not epistemologically applicable. So this suggested definition has the effect of preserving (a), (b) and (d) at the expense of (c), and given that we cannot have all four, (RA)'s obvious failure of (c) is a virtue. It is an unpretentious definition; it wears its epistemological inapplicability on its sleeve.

We can construct a more technical (and more pretentious) definition. Earlier I criticized what I called the statistical approach to defining relative adaptedness. This approach identified adaptedness with the statistical mean of observed reproductive rates. As pointed out then it is not too distorting to call the interpretation of probability used

in this approach the frequentist interpretation. There are other interpretations of probability. Some, for instance the logical and subjective interpretations (associated with Carnap and de Finetti respectively), are here irrelevant. But the approach, best expounded by Hacking (1965) (also see Popper, 1959), on which probabilities are deduced from theory rather than identified with observed frequencies is relevant.

In discussing the basset-shepherd case I said that observed reproductive rates can conflict with estimations of adaptedness based on ecological analysis. Suppose our ecological theories to be so well developed that for any given environment and organism we could deduce the distribution of probabilities of the number of offspring left by that organism (in the next generation). That is, from our theories we deduce for each organism  $O$  and environment  $E$  a range of possible numbers of sufficiently similar offspring,  $Q_1^{OE}, Q_2^{OE}, \dots, Q_n^{OE}$  and for each  $Q_i^{OE}$  our theory associates a number  $P(Q_i^{OE})$  which is the probability (or chance or propensity) of  $O$  leaving  $Q_i$  sufficiently similar offspring in  $E$ . Given all this we define the adaptedness  $O$  in  $E$  (symbolized as  $A(O, E)$ ) as follows:

$$A(O, E) = \sum P(Q_i^{OE})Q_i^{OE}$$

That is, the adaptedness of  $O$  in  $E$  equals the expected value of its genetic contribution to the next generation. (The units of value are arbitrary. All that matters here are the ordinal relations among the numbers associated with each pair  $\langle O, E \rangle$ . Outside of this context the numbers have no significance.) Our new more exacting definition of relative adaptedness,  $(RA')$ , is as follows:<sup>12</sup>

$$(RA') \quad a \text{ is better adapted than } b \text{ in } E \text{ iff} \\ A(a, E) > A(b, E).$$

Two things should be clear: First,  $(RA')$  only makes sense for intraspecific intra-environmental comparisons. Second,  $(RA')$  is a step in the right direction only on the proper interpretation of probability.

Before evaluating  $(RA')$  I should say something about its basic presupposition: *viz.* that from detailed ecological analysis we can give good estimates of the probabilities of reproductive

success of organisms in environments independent of observations of their actual reproductive success. For example, given the characteristics of a certain island environment and the particular characteristics of some basset hounds and German shepherds such theories should be able to predict the relative reproductive success of each even without any relevant statistics. Clearly such predictions are falsifiable (as falsifiable as any statistical hypothesis), but do we have any reason to expect them to be successful? There are few, if any, outstanding examples of such success in the corpus of biological science. On the other hand, there seems to be no theoretical obstacle to successful predictions of this sort.

The informal definition of relative adaptedness suggested above,  $(RA)$ , satisfied desiderata (a), (b), and (d) but not (c). How does  $(RA')$  fare on our desiderata? Given the proper interpretation of probability it satisfies (a). On this interpretation the probability of reproductive success (or expected genetic contribution to future generations) is some biological property of the organism and its environment (just as the probability of heads for a coin is a physical property of the coin and the tossing device). The organism in its environment has this property even if it is struck by lightning prior to leaving any offspring (just as the chance of heads may be  $1/2$  for a coin even if it is unique and is melted before it is ever tossed). Thus  $(RA')$  is independent of actual reproductive values. The occurrence of 'probably' in (D) may be confusing but  $(RA')$  does not turn (D) into a tautology.<sup>13</sup>  $(RA')$  clearly satisfies (b); that is, it is general. Like  $(RA)$ ,  $(RA')$  is not empirically incorrect and so we will say it satisfies (d), *i.e.* that it is empirically correct. Although  $(RA')$ 's failure to satisfy (c) may not be as apparent as  $(RA)$ 's it also fails to be epistemologically applicable. If there were a single all encompassing theory of adaptedness from which we could derive the adaptedness (as defined above) of any organism in any environment then  $(RA)$ 's would be epistemologically applicable. But, as I've argued, no such theory is possible. (I presented Bock and von Wahlert's theory as an attempt at such completeness.)

How is the suggested definition useful? It is useful as what we might call a schematic definition. It is neither applicable nor testable but particular instances of it are. What do I mean by an

instance of (RA')? Formally, in an instance of (RA') we fix the value of the environmental parameter '*E*' and limit the range of the individual variables '*a*' and '*b*' to a particular population of organisms living in *E*. Such an instantiation would represent a hypothesis concerning what it takes for certain types of organisms to survive and reproduce in a certain type of environment. Good hypotheses of this kind can only result from detailed ecological analysis. (Where 'ecological' is used in a broad, perhaps too broad, sense. I would include in such analysis the study of the sorts of genetic variation that occur and are likely to occur in the relevant organisms and the study of the phenotypic effects of this variation.)

For a simplified example suppose that the only variation in a certain population of moths is in wing color. These moths all rest on dark colored tree trunks during the day. Birds prey on the moths by sight in daytime. We analyse this simplified situation as follows: The darker the wing color the closer it is to the color of the tree trunks. Moths whose wings are colored most like the tree trunks are least likely to be eaten by birds. Moths less likely to be eaten are more likely to leave offspring. Thus we instantiate (RA') as follows:

Moth *a* is better adapted than *b* in (our specified) *E* iff *a*'s wings are darker colored than *b*'s (in *E*).

(I am here primarily interested in illustrating certain logical points, but I don't want to appear to take an overly naive and sanguine view towards the sort of ecological analysis necessary for complex organisms in complex environments.) Lewontin (1977) discusses some of the problems involved. Suffice it to say that although successful ecological analysis is difficult it does not seem to be impossible.

With a schematic definition of relative adaptedness (D) becomes a schematic law, and with an instantiation of (RA') we get an instantiation of (D). For our moths (D) says:

If *a* is darker winged than *b* (in *E*) then (probably) *a* will have more offspring than *b* (in *E*).

Such an instantiation of (D) is clearly testable (in fact it has been tested, see Kettlewell, 1955 and 1956). Moreover it does what we want it to do, it explains differential reproduction and so

explains evolution by natural selection (as in this instance we explain the evolution of industrial melanism in certain species of English moths).

To summarise; I have suggested that we give up epistemological applicability and adopt a schematic definition of relative adaptedness, (RA'). This correlatively makes (D) schematic and so not testable. When we instantiate (RA') we give up generality for applicability. Likewise instances of (D) becomes testable and explanatory but not general.

## 5. The Structure of Evolutionary Theory

(D) is the fundamental law of evolutionary theory. What sort of foundation is (D) for a scientific theory? Critics have often maintained that evolutionary theory rests on a tautology. As I hope I have made clear, (D) is not a tautology. But I have shown that no definition of relative adaptedness can render (D) non-tautologous, general, testable and true. (D) as a schematic law is not testable, instantiations of (D) are not general. This may not be so bad. If disconfirming an instantiation of (D) disconfirms (D) then (D) may be a respectable law. But this relation between (D) and its instances does not hold. That is, no amount of falsification of instances of (D) even begins to falsify (or disconfirm) (D).

Consider the instantiation of (D) concerning moths. If through experiments and observations it proved to be false then our response would be and should be that we have incorrectly analysed the ecological situation. Perhaps the birds prey on these moths using heat-sensing devices, making color variation irrelevant (unless that variation is correlated with variation in heat irradiation). We reanalyse the situation and test our new hypothesis. If the falsification of one instance of (D) doesn't even begin to cast doubt on (D) will large numbers of falsifications change matters? If, as is the case, some instances of (D) have proved successful then even large numbers of falsifications of instances of (D) will not cast doubt on (D). If no instance of (D) ever succeeded then we would doubt the usefulness of (D) but even this would not lead us to say (D) is false. In our world (where some instances of (D) have successfully explained and predicted certain

phenomena) no set of test results could falsify (D). Thus (D) is unfalsifiable.

With this in mind and given that through informative instantiations of (RA') we get testable and explanatory instances of (D) one might question the status of the schematic (RA') and (D). Neither meets our philosophical expectations so why should they be granted any status in our expurgated science? To answer this question we must consider some of the aims of scientific inquiry and some of the criteria by which theories are judged. Perhaps the distinguishing feature between science and myth is that science, unlike myth, aims at testable explanations. So theories and laws are judged according to their (in-principle-) testability. Instantiations of (D) fare well on this criterion, (D) itself does not. But scientific inquiry also aims at the systematic unification of broad bodies of diverse phenomena. Without (D) there is no theory of evolution, there are only low level theories about the evolution of certain organisms in certain environments. (And at present there are very few of those.) With (D) Darwinian theory is possible.

I have not simply presented a case where philosophy of science is at variance with actual science. Rather I have presented a case where two philosophical principles conflict. There is, as I have shown, a trade-off between desiderata (b) and (c), and so a conflict between testability and systematic unification. I have suggested adopting (RA') and so treating (D) as a schematic law as the best possible solution to this dilemma.

## 6. Summary

The conception of adaptation has been one of the most troublesome and yet one of the most important concepts in the biological sciences. I hope that this paper has cleared up much of that trouble. We have constructed an adequate definition of relative adaptedness. Our analysis of the conception of relative adaptedness went hand in hand, as it had to, with an analysis of the structure of evolutionary theory. We found that Darwinian evolutionary theory has as its foundation what I called a schematic law; thus its structure does not fit any existing philosophical paradigms for scientific theories. Heretofore schematic definitions and schematic laws have not

been recognized or investigated by philosophers of science.

In constructing a definition of relative adaptedness we posited the biological property of adaptedness. In this paper I said much about what this property is and what it is not. But its particular ontological status has not been discussed and remains somewhat mysterious.

## Notes

- 1 'G. C. Williams (1966) does an excellent job of clarifying these matters. Also see Lewontin (1970).
- 2 Thoday (1953) and (1958). Actually he uses the word 'fitness' not 'adaptedness' but I think he is like most biologists in using the words interchangeably.
- 3 This characterization of evolutionary theory is adopted from Lewontin (1977). For less satisfactory versions see Lewontin (1968) and (1970). For a more historical and fuller sketch of the major components of the theory see Mayr (1977).
- 4 Perhaps one should not speak of *the* distinguishing feature of Darwinian theory. One should recognize that evolutionary theory is not a monolithic whole. For instance, theories of speciation are quite distinct from the part of Darwinian theory on which we are focusing; *viz.* the theory of evolution within a species by natural selection. *A propos* the history of the subject it is useful to distinguish four subtheories or four parts of Darwin's theory (pointed out to me by Ernst Mayr): (a) Evolution at all; (b) Gradual evolution; (c) Evolution by common descent; and (d) Evolution by natural selection. Nevertheless both from a historical and contemporary perspective the most salient feature of a Darwinian theory of evolution is its explanation of evolution by natural selection.
- 5 Malthus (1798). It seems that Malthus was more of a coagulant than a catalyst for Darwin's ideas on this matter. See Hull (1973), pp. 344, 345, and Mayr (1977).
- 6 Another exception is Michael Ruse (1971). He has attacked the problem from a historical perspective and has tried to show that what Darwin said on natural selection was not tautologous.
- 7 In speaking of (D) as a 'law' I could continue to put 'law' in scare-quotes in order not to prejudge its status, but I will not. We will, in due course carefully evaluate its status.
- 8 Mayr, it seems, was quoted out of context. See Mayr (1963), pp. 182-184.



- 9 As shown by Lack (1954). This must be quite surprising to those with only a superficial understanding of evolution. For example Popper (1972, p. 271) thinks it is 'one of the countless difficulties of Darwin's theory' that natural selection should do anything other than increase fecundity. The explanation is really quite simple: Increased fecundity often results in a decreased number of offspring surviving in the next generation. See Williams (1966, chp. 6) for discussion.
- 10 To some unfamiliar with the problem of adaptation this may not be obvious. Rather than reargue the generally accepted I refer the reader to Stern (1970) which is a good introduction into the relevant literature.
- 11 See below pp. 110–111. Of course one might wonder how a definition could fail both (a) and (d), or how a tautology could be empirically incorrect. It can be in just this sense: *given* an adequate theory of adaptedness we have a notion of adaptedness which differs from any notion failing (a) (*i.e.* any notion which identifies adaptedness with actual reproductive success). These two notions will not be extensionally equivalent. So, from the standpoint of our theory, the definition which fails (a) will also fail (d).
- 12 The move to this sort of definition was suggested to me by Hilary Putnam.
- 13 (D) becomes something like an instance of what Hacking calls the Law of Likelihood and is analogous to the following: If the chance of heads for coin *a* is  $\frac{1}{2}$  and the chance of heads for *b* is  $\frac{1}{4}$  then (probably) when both coins are tossed a small number of times *a* will land on heads more than *b* will.

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