Section I

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Adaptation and evolutionary theory*

> There is virtually universal disagreement among students of evolution as to the meaning of adaptation. (Lewontin, 1957).
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> 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).
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> 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 analyze 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).

A note on defining is needed. Definitions are often thought to be of two kinds, descriptive and stipulative. (See, for example, Hempel (1966), Chap. 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.[1] Selection at the level of individual organisms has as its cause differences in individual adaptedness and its effect is adaptions 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 junkyards. 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 intraspecific 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.[2] 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 interpopulational 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:[3]

(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.

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(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 explain-
ing 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 notorious-
ly 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, 1978a.) 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).[4] 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 occurred 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 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 members 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 corre- lated 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*,[5] was that since in each generation more individuals are produced than can survive to repro- duce 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 evolutionaty 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 Smart, 1963, p. 59.) The phrase itself, not being a declarative sentence, could not be a tautology. An exception is Mary Williams.[6] 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 β as the members of β plus all their descendants. On a phylogenetic tree the clan of β would be those nodes which are in β 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'[7] 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[8] to this effect. Stern approves of this definition.) They thus deprive evolutionary theory of its explanatory power.