

“Adaptation”¹

In this chapter, I examine three concepts of adaptedness and adaptation found in Darwin and two additional concepts of “Darwinian fitness” employed in current population biology and evolutionary theory. The examination reveals a number of conceptual confusions within evolutionary biology and shows that much of the philosophical literature about evolutionary theory has been concerned with vulgarizations of that theory. A number of recent controversies in evolutionary theory, all of which focus on the degree of control that natural selection exercises over traits of organisms, are mentioned in passing. These controversies have been plagued by confusions regarding what it is for a trait to be an adaptation, the kinds of evidence required to support such a claim, and the units of analysis appropriate to applications of the concept of (an) adaptation. Removal of these confusions may contribute to the attempt to resolve the underlying biological disagreements about the relative importance of various units of selection, the existence of neutral mutations, and “selfish” DNA, etc.; but it will not be sufficient, by itself, to resolve those disagreements. Removal of these confusions will also serve as an important step toward a deeper and more fruitful understanding of the structure and content of evolutionary theory.

Adaptation and Adaptedness

In a recent book on *The Development of Darwin’s Theory* of evolution by natural selection (Ospovat 1981), the late Dov Ospovat argues, in effect, that a major key to understanding Darwin and his theory is provided by grasping the changes in Darwin’s concepts of “adaptation” and “adaptedness” and the subsequent changes that Darwin’s work helped to bring about in the use of cognate concepts by biologists. Although I am not entirely persuaded by all the details of Ospovat’s account of Darwin’s concepts of adaptation,² I shall employ some of his views, uncritically, as a starting point. The issues about the content and character of the concept of adaptation that I shall be exploring will not be greatly altered (though they may be clarified) by further historical scholarship regarding the path that Darwin followed.

Before proceeding, I must address one terminological point. As will become apparent in course of this chapter, the use of such terms as “fit,” “adapted,” “fitness,” and “adaptation” in the biological and philosophical literatures has been confused and

¹ This is the submission version of Chap. 4 of my *The Epistemology of Development, Evolution, and Genetics*, originally published in Marjorie Grene, ed., *Dimensions of Darwinism* (New York and Cambridge: Cambridge University Press, 1983), pp. 287-314. Reprinted with kind permission of Cambridge University Press. This chapter has benefited from criticisms by F. Ayala, C. Bajema, R. Brandon, L. Darden, S. Gould, M. Grene, K. Guyot, Ph. Kitcher, E. Mayr, R. Richardson, P. Richerson, A. Rosenberg, G. Simmons, and many others, including discussants at the Reimers Stiftung, Bad Homburg, the Committee on History and Philosophy of Science of the University of Maryland, and the seminar on History and Philosophy of Science, University of California, Davis. I am grateful to all concerned.

² Nor of some of his chronology regarding the development of Darwin’s thought.

confusing. In order to build my account of the relevant concepts, I have found it useful to fix one aspect of usage by fiat. I shall employ the term “adaptation” in an historical sense, the terms “adapted” and “adaptedness” in an ahistorical sense. Fleetness contributes to the adaptedness of a deer (or makes the deer better adapted) if, and only if, other things being equal, it contributes to the solution of a problem posed to the deer – for example, escaping predation. Fleetness is an adaptation of the deer if, and only if, the deer’s fleetness has been molded by a historical process in which relative fleetness of earlier deer helped shape the fleetness of current deer. This usage (which, in its present sharp form, derives from a suggestion by Robert Brandon) is my own, though it reflects an important tradition in the literature. This specialized terminology will facilitate the clarification of a number of the confusions to be discussed subsequently.

Ospovat documents Darwin’s struggle to arrive at a satisfactory concept of adaptation for use in the theory of evolution by natural selection. According to Ospovat, Darwin first employed two distinct notions of “absolute” or “perfect” adaptedness (only one of which I shall discuss) in the period from 1838-1854 and then, only after considerable difficulty, arrived at a version of the notion of relative adaptedness employed in the *Origin* sometime in 1857. However Darwin got to it, Ospovat is surely right that the notion of relative adaptedness developed by Darwin is of crucial importance to evolutionary theory. Yet I am prepared to argue (I can give only part of the argument on the present occasion) that the development of the modern neo-Darwinian (or synthetic) theory of evolution has, in fact, minimized the role of Darwin’s concepts of adaptation and adaptedness and obscured their importance by running them together, in a confused and confusing fashion, with a whole battery of other related notions. For instance, two quite un-Darwinian notions, both of which pass under the label of “Darwinian fitness,” are common in population biology and evolutionary theory. The widespread use, and occasional misuse, of these notions has, at times, contributed to the illusion that evolutionary theory is viciously circular or tautologous. Distinguishing between these concepts of Darwinian fitness (so-called) and related concepts of adaptation, including Darwin’s, is crucial to the proper understanding of evolutionary theory.

Until about five years ago, when a number of new papers bearing on these topics began appearing, the most important and influential attempt to straighten out the conceptual confusions involved in various recent uses and misuses of terms like “adaptation” and “fitness” was G. C. Williams’ *Adaptation and Natural Selection* (Williams 1966). Williams’ main concern was to bring about correct use of the concept (or concepts) of adaptation in contemporary biology – not by means of a logic-chopping analysis, but by showing biologists how practical and theoretical difficulties arose from their misuses of the relevant concepts and by persuasive arguments to the effect that the biological difficulties and disagreements could be handled most effectively by cautious and correct use of the concept of adaptation along the lines he advocated. Williams’ book was an immensely useful corrective to the near loss of Darwin’s concept in theoretical biology. But now, fifteen years later, it is time to correct certain flaws in Williams’ treatment of the concept of adaptation. In particular, his account of adaptation is wedded to quite strong and controversial commitments about the effectiveness of natural selection and about the units of selection – that is the level at which selection is most effective. I hope to separate the concept of adaptation from these commitments.

I shall proceed indirectly, carrying out only part of this rather large task. I shall try to fill in certain parts of the relevant background, mainly by developing my own account of some of the pertinent concepts of adaptation, fitness, and adaptedness, discussing their interrelations and the confusing consequences of their interplay. In a sequel to this essay,³ I will show in detail the relevance of these matters to contemporary concerns about the units of selection and exhibit the interplay between controversies concerning group selection, macroevolution, and related topics. In the present chapter, my main target is to carry the account of the concept of adaptation a few steps beyond Williams.

Before proceeding with this agenda, I shall examine briefly what we should expect of an account of the concept of adaptation. How can we tell a good account from a bad one?

If, as I shall argue, many biologists are careless and inconsistent in their use of “adaptation,” “fitness,” and cognate terms, we should not make our evaluation of an analysis of the concept of adaptation turn on mere conformity to usage. Rather, it seems to me, we must isolate certain central claims to serve as touchstones against which to test alternative analyses. As the analysis becomes more sophisticated, we may have to reexamine and improve the touchstones, to divide and complicate our account of the concepts involved.

To illustrate what I mean by a touchstone, consider a thought experiment tracing back at least as far as (Scriven 1959). In this experiment two identical twins are standing in a forest during a thunderstorm. One is struck by lightning and killed, the other is unhurt; he later marries and has ten children. One may now ask whether one twin is *better adapted* (or *fitter*) than the other. In conformity with *Darwin's* usage, which, I maintain, is standard in this regard, the twins have the same degree of adaptedness because the difference between them is a matter of happenstance and they are, in all biologically relevant properties, virtually identical; they are equally fit or unfit vis-à-vis their environment. Later we will see that use of this little fable as a touchstone shows that one of the most common measures of so-called Darwinian fitness in population biology does not serve as a direct measure of fitness in the sense of adaptation. But I shall save that point, as well as two further touchstones, for the appropriate juncture of the argument.

Darwin on Adaptation

Let me start the real work of this chapter by turning to Darwin's approach to adaptation. On Ospovat's account of Darwin's early unpublished work bearing on evolution by natural selection, Darwin held, at least from 1838-1850, a theory quite different than the one for which he is known. A remarkable feature of this theory is that it was based on the concept of *limited perfect adaptedness*. According to this theory, organisms are constrained by their structure and constitution – by being built out of organic, not inorganic matter, by being structured as vertebrates or invertebrates, by being warm-blooded or cold-blooded, and so on. Within the limitations of the constraints thus imposed, each species was – or was normally – *perfectly adapted* to its environment. By

³ See my “On some controversies concerning macroevolution,” [Unpublished MS, never completed].

this was meant that the organisms in question were optimally designed within the applicable constraints to solve the problems posed by the environment; problems of heat, cold, wind, rain, opening up seeds, capturing prey of the sizes and speeds available, and so on.

One of Darwin’s central concerns was to explain the diversity of living organisms. At this phase of his development, according to Ospovat, he held that diversity is a secondary consequence of *three* factors:

1. Gradual geological change in general, which altered the environment slowly and imperceptibly but which ultimately confronted organisms with environments to which they were not perfectly adapted.
2. Isolation of one population from another, meaning that different populations of organisms belonging to the same species would face different environments and, hence, different design problems.
3. The laws of variation (what Darwin in the *Origin* called “the mysterious laws of variation and correlation of parts”) which, at this time, Darwin thought were such as to call forth variation *only when adaptedness became imperfect*, and then to call forth *directed* variation – variation adjusting the properties of the organism in the direction of perfect adaptedness vis-à-vis the new environmental circumstances.⁴

The role of natural selection at this stage in the development of Darwin’s theory, if Ospovat is correct, was dual: First, it guaranteed that there would be pressure on all populations to maintain or to achieve perfect adaptedness; and, second, it preserved the most favorable variations and moved the population mean toward them. Variation provided the *direction* of evolution, whereas the *reduced* variation of perfectly adapted organisms ensured that natural selection would alter the constitution of a population only when the organisms in question were not perfectly adapted.

Whether or not this thumbnail sketch, or Ospovat’s detailed account, is fair to Darwin’s private speculations, it points to certain features of his concept of adaptedness, of his account of what it is for an organism to be fit with respect to its environment, common to the notebooks and early drafts and to the *Origin*. I shall capitalize on these. To put the essential points informally, an organism is well adapted when its structure and habits enable it to solve expectable challenges of the environment optimally. An organism is fit or unfit according to its ability to meet these challenges by virtue of its design and its programmed patterns of behavior. Employing engineering criteria, it is possible to compare organisms by type and to determine that organisms of type 1 are adapted (designed) to meet challenges A (or challenges A to Z), whereas organisms of type 2 are not adapted (or not as well adapted) to meet that challenge (or those challenges). Certain features of organisms, for example “organs of extreme perfection” like the vertebrate eye, can be recognized as adaptations; that is, as features existing in some sense or other *because* they are designed for – adapted to – the performance of certain tasks useful or necessary for the survival of the organism.

One reason for citing Ospovat’s account of Darwin’s early work is that it highlights the possibility of having both absolute and relative concepts of adaptedness. An absolute concept evaluates the design of a product – for example, the eye or the whole

⁴ We see here that Darwin already had good reasons for taking the inheritance of acquired characters seriously in his earliest speculations on transformation; such inheritance might provide a mechanism that would give variation its direction.

organism – in its own right. In order to evaluate the design, it is necessary to specify, tacitly or explicitly, the design problem and the pertinent constraints governing its solution; from there evaluation can proceed by some form of “static” engineering analysis. Because the analysis is static, not dynamic, the absolute concept of adaptedness has no direct bearing on the process by which the design was achieved. Accordingly, it needs supplementation if it is to play a role in the theory of evolution. Darwin’s early theory provided that supplementation by reference to “the mysterious laws of variation” that, he thought, directed heritable change toward optimal design whenever an organism was insufficiently adapted. In this theory, natural selection played a relatively secondary role – it was the force that called unadapted organisms to account and it was the preserver of adaptations; that is, of optimally designed features and organisms.

Once Darwin came to realize that variation is ubiquitous and largely undirected with respect to the needs of the organism,⁵ he was forced to employ a relative concept of adaptedness, a concept tied much more intimately to the process of natural selection than the absolute one was. All organisms face a multitude of problems bearing on survival and reproduction. If they all vary (at least slightly) in virtually all their features, then typical organisms are not perfectly adapted. Some, however, are at an advantage with respect to others – that is, they are better designed to meet the expected or expectable challenges of the environment. These organisms would, therefore, be more likely to survive the insults of the environment. To be sure, their design offers no guarantee that they will do so, but it provides a statistical bias in their favor. To the extent that two further conditions are met, *natural selection is likely to increase adaptedness*. These conditions are: first, that the environment is stable enough that the problems organisms face are reasonably constant or predictable;⁶ and, second, that the offspring of an organism or of a pair of organisms tends to differ from the population mean in the same ways that its parents do. (This latter condition, the “statistical heritability” of features, is necessary if differential survival in one generation is to affect the characteristics of the organisms of the next generation.)

Although Darwin did not do so in any clear way, it will help us to separate two intertwined concepts pertaining to adaptation. The first is the relative engineering

⁵ P. Richerson (University of California, Davis) has reminded me that one must not lose sight of the fact that Darwin retained some role for directed variation throughout his career. The supposed effects on an organism’s descendants of its use or disuse of its organs, amplified in various “neo-Lamarckian” ways in Darwin’s later theory of pangenesis, mark the strength of Darwin’s commitment to directed variation. In his later work he employed directed variation to speed up evolutionary processes and to overcome the difficulties posed by (theories of) blending inheritance (see Lord Kelvin’s and F. Jenkin’s criticisms of Darwin’s views). For a brief exposition regarding directed variation, (see Darwin 1859, Gould 1971).

⁶ For sufficiently long-lived organisms, the *range* of problems faced should not change greatly from generation to generation. But for short-lived organisms, the environment will vary, both randomly and cyclically, on a scale of many generations; the variation will be life threatening, but is likely to fall within roughly predictable limits. Indeed, typically, cyclic variations (such as seasonal changes) are associated with cues (such as changes in the number of daylight hours) that are utilized by short-lived organisms (e.g., as a signal to produce an overwintering form). Although the environment has many components which are random *with respect to the organism*, other things being equal those organisms with design features that enable them to utilize or withstand the fairly regular excursions of the environment are better adapted – and more likely to leave descendants – than those that are not.

adequacy of a design (given the relevant constraints) as a solution to a particular problem. The second concerns the process by which the design was produced. On this usage, if the variations of a given feature, system, or behavior pattern were causally efficacious in the refinement of that feature or system or behavior pattern by means of natural selection, then that feature counts as an adaptation relative to its alternatives. Note, however, that it will not do to say simply “if a feature was produced by natural selection, it is an adaptation”; account must be taken of the “mysterious laws of correlation of growth.” Darwin rightly emphasized this point; so far as the process of natural selection is concerned, many features are epiphenomenal, or are produced in spite of being mildly deleterious, or arise independently of their slight usefulness, simply because their selective consequences are far smaller than those of correlated features. Given what we now know about pleiotropy, multiple functions of organic structures, multigenic determination of features, and so on, we should recognize the broad application of this point. In other words, one is making a substantial claim if one main point that a feature is an adaptation in the *process* sense. One is claiming not only that the feature was brought about by differential reproduction among alternative forms, but also that the relative production of the feature vis-à-vis its alternatives played a significant causal role in its production. This claim is a historical claim, subject to all the epistemic difficulties attendant on such historical claims (Gould and Vrba 1982, p. 182).

Incidentally, this discussion reveals two more touchstones for analyzing adaptation. The first is that an analysis of the process of forging adaptations must make it possible to distinguish selective processes from random processes, design from drift, and effects of natural selection from effects of mere de facto differential reproduction. Darwin’s way of achieving this is, effectively, to distinguish between differential reproduction and natural selection. For Darwin, natural selection is systematic differential reproduction due to the superior engineering fitness of certain available variants - due, that is, to the relatively better design of the favored organisms.

The second touchstone cannot be stated comfortably in Darwinian terminology. It is simply this: claims about relative adaptation concern, in the first instance, a relation between a phenotype (or range of phenotypes) and the environment relative to a field of alternative phenotypes. Thus although genes, gene complexes, genotypes, and so on may be said to be well or ill adapted and may be compared with respect to their degree of adaptation, within *Darwin’s* theory such claims ought to be treated as depending on analyses of the various advantages manifested by the (range of) phenotypes that the relevant genes or genomes produce in the appropriate (and appropriately weighted) environmental circumstances. This is true whether one speaks, statically, of the degree of adaptedness (or co-adaptedness) of a gene or gene complex, or, dynamically, of the process by which genetic adaptation is achieved. *Full analysis of adaptation cannot bypass the phenotype.* To be sure, the phenotype alone will not suffice; one must decompose phenotypic variation into heritable and non-heritable components. The former is the raw material on which Darwin’s process of natural selection acts in creating adaptation.⁷ Some subsequent concepts of fitness (as we will see later) are used in ways that bypass the phenotype; I shall argue that they are weaker than the concept we are articulating currently and that the move of bypassing the phenotype raises difficulties that the present concept does not face.

⁷ I thank P. Richerson for this last point.

Table 1. *Concepts of Adaptation*

Label	Definition	Historical Knowledge Required?
1. Absolute engineering fitness or “limited perfect adaptedness”	A type of feature (or organism) manifests an optimal engineering solution (within real design constraints) to a real environmental challenge.	Only to specify the design constraints and the design problems.
2. Relative engineering fitness	The type of feature (or organism) manifests a better engineering solution (within real design constraints) to a real environmental challenge than specified alternatives.	To specify design constraints, design problems, and the range of alternative types.
3. Selected engineering fitness	The characteristics of the type of feature (or organism) are present as a consequence of their higher engineering fitness with respect to real environmental problems (faced in the evolutionary history of the organism) as compared with the historically available alternative types or characteristics.	To specify design constraints, design problems, the range of alternative types, and the causal history behind the prevalence or fixation of relevant characteristics.
4. Realized fitness (“Darwinian fitness,” “tautological fitness”)	An organism (or class of organisms sharing some property) has higher realized fitness in environment E than alternative organisms (or classes of organisms) if, and only if, its actual rate of reproductive success is higher than those of the alternatives.	Only to specify actual rates of reproductive success.
5. Expected fitness (“Darwinian fitness”); (propensity for greater reproductive success, de facto, rather than by virtue of design considerations)	A type of organism (or other replicating entity) has higher expected fitness than its competitors in environment E if, and only if, it has an objective propensity to outreproduce them in E. Usual measure: relative reproductive success within replicate populations in “identical” environments.	Only to specify actual rates of reproductive success of replicate populations and to certify comparability of environments.

It is time to codify our results concerning Darwin’s concepts of adaptation. (For ease of reference, a short version of this codification is given in Table 1.) So far I have discussed three interrelated concepts. The first of these might be labeled “limited perfect adaptedness,” or “absolute engineering fitness.” A (type of) feature or a (type of) individual possesses absolute engineering fitness if, and only if, its design manifests an optimal engineering solution to the appropriate (real) challenge or range of challenges

posed by the environment. Following Ospovat, I suggested that in developing the theory of the *Origin*, Darwin replaced this concept with one which might be appropriately labeled “relative engineering adaptedness” (or fitness). A (type of) feature or a (type of) individual possesses higher relative engineering fitness than an alternative type if, and only if, its design manifests a better engineering solution within the appropriate (real) design constraints to a specific (real) challenge or range of challenges posed by the environment. Finally, a (type of) feature is an adaptation if, and only if, its design characteristics were produced as a causal consequence of their relative engineering fitness as compared with those of the relevant alternative types, as a solution to a problem or range of problems posed by the environment in the evolutionary history of the organisms in question. One may be able to explain the fact that a (type of) individual is relatively better adapted than alternative (types of) individuals if, and only if, its greater relative engineering fitness is a consequence of specific adaptations. This yields a third sense of fitness, which I will call (relative) “selected engineering fitness.”⁸

Again, it is important to realize that traits with high engineering fitness need not have been produced by natural selection. The fact that a trait confers advantage with respect to survival or reproductive success does not, by itself, justify any claims about its historical origins. The notorious opportunism of evolution amounts to an ability to turn traits to advantage no matter how they originated, no matter how they were initially produced (see Williams 1966, p. 12). Accordingly, it is crucial to understand that the theory of the *Origin* requires one to connect the concept of adaptation with that of natural selection. The mere fact that variant forms are differentially fit – that is, that they exhibit differences in relative engineering fitness – is not enough to justify employment of the concept of selected engineering fitness in evolutionary theory.⁹ This becomes clear when one realizes that Darwin’s earlier theory used differences in relative adaptedness (engineering fitness) as the means of restoring (limited) *perfect* adaptedness – that is, absolute engineering fitness – but derived the direction of evolution from the direction of variation. In contrast, the central concept of Darwin’s theory in the *Origin* is the concept of features of

⁸ It is this notion of adaptation that Williams has in mind when he says that “evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect [i.e., a fitness-increasing use to which a trait is put] should not be called a function [a *designed* fitness-increasing use] unless it is clearly produced by design and not by chance” (Williams 1966, p. vii).

⁹ Contrast (Gould and Vrba 1982) who argue that many traits have been “coopted,” that is, that their current uses are “effects,” not “functions.” In order to work out the problems for evolutionary theory raised by such a position, it is necessary to distinguish between traits that were originally shaped by natural selection for their current use and those that originated as correlated characters or via selection for a *different* use. Gould and Vrba wish to restrict the trait-descriptor “adaptation” to *traits shaped ab initio for their current use by natural selection* and to employ the neologism “exaptation” for traits coopted for new uses (see their Table 1). I do not like this terminology, but their claim that we need some such distinction and that we should mark it with appropriate terminology is well taken. Indeed, such a distinction is of critical importance if we are to evaluate the Darwinian claim that adapted features in a static sense (characters with high relative design adequacy) are largely adaptations in an evolutionary sense (traits shaped by natural selection *in the first instance* to perform those tasks that they now perform).

organisms with high relative engineering fitness that have been designed by the historical processes involved in natural selection, rather than by directed variation. This is what later writers like Ernst Mayr mean by the creative power of selection, this is “the onerous concept of design” which G. C. Williams seeks to restore to prominence in evolutionary biology. This is the feature of Darwin’s theory that his contemporaries found least persuasive.

Concepts of Adaptation in Neo-Darwinism

I turn now to the so-called genetical, or synthetic or neo-Darwinian, theory of evolution by natural selection articulated in the 1930s and 1940s, and the regnant orthodoxy since the 1950s. My strategy will be to exhibit two further interconnected concepts of fitness, to demonstrate *that* and *how* they are interconnected, and to show that failure to recognize the complexity of their interactions with each other and with the Darwinian concepts pertaining to adaptation results in vulgarization of evolutionary theory. On the present occasion I shall proceed somewhat dogmatically, with only slight documentation of the use of the alternative concepts to be discussed.

There are many versions of the synthetic theory and many accounts of its central features.¹⁰ For present purposes, one may venture to say that it placed the Darwinian theory on a new foundation – to wit, on a foundation of Mendelian population genetics. A significant dispute though not central here, concerns the relative importance of population genetics vs. that of the principle of natural selection. Michael Ruse, for one, sees natural selection as a *consequence* of the principle of population genetics where Mary Williams – and I – see population genetics as the contingent elaboration of the consequences of natural selection for a limited class of organisms (Ruse 1973, esp. pp. 48 ff., Williams 1973, esp. pp. 86-8).¹¹

Whatever the issue of that dispute, however, one consequence of the central role of population genetics in the synthetic theory has been a series of shifts in the concepts of fitness, adaptedness and adaptation and in the measures of fitness and adaptation employed in evolutionary investigations. These shifts are complicated and have resulted in considerable confusion both on the part of biologists and on the part of those analyzing evolutionary theory. Here I will attempt to disentangle only a few of the central confusions.

¹⁰ The best single source (though its coverage is partial and biased) is (Mayr and Provine 1980). Examples of the controversies over the precise content of the synthetic theory are (Gould 1980, 1981, Orzack 1980).

¹¹ Ruse has reaffirmed the stance he took in 1973 in a number of recent writings. Williams’ views on this topic are never stated as directly as Ruse’s. My interpretation of her position rests on a reading of a number of her other works and on the general character of her views in addition to the passage cited. Incidentally, in spite of quite a different starting point and style of argumentation, her interpretation of the confusions surrounding the use of the concept of fitness in the synthetic theory (Williams 1973, pp. 88-100) is quite close to the one put forward in this chapter.

Both the following senses of “fitness” have often been labeled “Darwinian fitness” in the recent literature. The first of the two applies in the first instance to individual organisms. According to this sense of fitness, an individual (or a class of individuals) is more fit (or better adapted) than its competitors, not if it has a higher expectation of survival and reproduction in virtue of its design, but simply if it, in fact, enjoys relatively greater reproductive success. Degree of adaptation, in this sense, is an empirical property of the organism (or of the class) in question, but one which can only be known post hoc.

It is ironic that this concept has come to be labeled “Darwinian fitness.” Darwin almost certainly meant the phrase “survival of the fittest” to stand for the tendency of organisms that are better engineered to be reproductively successful. Because the use of the present concept turns the phrase “survival of the fittest” into the tautology, “the reproductively successful are reproductively successful,” one traditional label for this kind of so-called “Darwinian fitness” is “tautological fitness.” I prefer the less tendentious label *realized fitness*, especially since *realized fitness is an empirical property, namely, relative reproductive success*.

It should be clear that this sense of fitness falls victim to Scriven’s thought experiment concerning the pair of twins. Although relative (actual) reproductive success is, I repeat, an empirical property of the relevant individuals, it simply does not measure degree of fitness or adaptedness in any of the senses relevant to evolutionary theory – all of which have something to do with *systematic* or *designed* fit with the environment, with causally mediated propensities to reproductive success.¹²

There is, however, a much more interesting concept, also sometimes called “Darwinian fitness,” that plays a prominent role in the literature. I am grateful to Francisco Ayala for forcing me to recognize its importance. Although it is frequently used, it has only recently been articulated with some clarity in the literature (Brandon 1978, Mills and Beatty 1979),¹³ so I will discuss it with some care.

It is possible to recognize, and even to work up a good quantitative estimate of, the propensity of a type of organism to out-reproduce its competitors in a certain environment or range of environments even though one can offer no historical, causal, or design-based analysis of that propensity. Consider an idealized experiment in which, say, 100 replicate cultures of *Drosophila melanogaster* are begun, each with 50 percent flies of type A and 50 percent flies of type B. If 50 of these cultures

¹² P. Richerson suggests that realized fitness (relative role of actual reproductive success) applies only to organisms exhibiting *heritable* differences. If the concept is so restricted, the present counterexample is avoided, for there is no heritable difference between identical twins. But the point of the example remains unaffected if we replace our twins with full or half siblings – or even unrelated individuals. One-time rates of reproduction, whether of individuals or of individuals belonging to a certain group or kind, are subject to chance effects (lightning bolts and sampling errors) and extraordinary occurrences. For this reason they provide uncertain evidence of the propensities or tendencies underlying the actual reproductive rates.

¹³ But for important criticisms of the concept of fitness described by Brandon and Mills and Beatty and in this essay (criticisms whose fundamental point I reject), see (Rosenberg 1982, 1983). I thank Professor Rosenberg for supplying me with advance copies of his papers.

are raised at high temperatures and 50 at low temperatures in otherwise standard environments and, after 20 or 100 generations, a roughly stable equilibrium is reached such that at high temperature roughly 85 ± 10 percent of the flies in each culture are of type A and at low temperature roughly 65 ± 10 percent of the flies are of type B, the natural conclusion would be that type A flies are better adapted to (have greater engineering fitness in) the warm environment, whereas type B flies are better adapted to the cool environment.

Unfortunately, as K. Guyot and R. Lewontin have reminded me, life is not so simple. In our hypothetical experiment, type A flies out-reproduce type B flies at the warm temperature *when the ratio of the two types in the population is 50:50*. But when the population is at equilibrium (85 A: 15B) their relative reproductive rates are equal. Therefore, the selection coefficients are frequency dependent; the constitution of the population alters the likelihood of relative reproductive success for the two types. If type A flies were always likely to out-reproduce type B flies in a stable warm environment, over a long enough time period type A flies would entirely replace type B. This shows how crucial it is to take the population of conspecific organisms into account in describing the environment.

For the purposes of the present calculations it does not matter whether the flies in question are identified by their phenotype or their genotype, although it does matter that at least some of the differences between them must be heritable. Either way, in the new sense of fitness, organisms of type A are relatively fitter than organisms of other types in environment E if, and only if, in E, organisms of type A have an objective propensity to out-reproduce those of the alternate types. Usually the best experimental measure of such a propensity is a statistically significant difference in the reproductive success of replicate populations.”¹⁴ Although this notion is now commonly call “Darwinian fitness,” a more useful label found occasionally in the literature is “expected fitness.” To repeat, the (relative) expected fitness of a type of organism as compared with specific competitors in a specified environment is its propensity to manifest a certain (relative) rate of reproductive success as compared with those competitors.¹⁵ In a secondary sense, a trait of the organism may be said make a certain contribution to its fitness according to the change in fitness – that is, the change in the propensity to reproductive success – that is correlated with its presence as opposed to its absence or the presence of some specified alternative(s), as appropriate.

¹⁴ There are serious technical difficulties with such measures. Important discussions of some of these may be found in (Prout 1969, 1971a, 1971b) and (Lewontin 1974). Many of the problems covered by these authors are particularly acute when one deals with natural populations. Some of them can be circumvented in properly designed laboratory experiments – at the price of relativizing their direct testimony about fitness to laboratory, but not to natural environments. The difficulty, often serious, remains that traits of considerable importance in laboratory populations and environments may not be of comparable importance in natural populations and environments.

¹⁵ Actually, for technical reasons discussed in (Mills and Beatty 1979, pp. 247 ff.) it is preferable to employ a *distribution* of propensities to leave various numbers of offspring. For present purposes, however, we gain considerable clarity by abstracting from these complexities, which do not affect the central points being made here.

Usually the best experimental measure of such a propensity is a statistically significant difference in the reproductive success of the relevant types of organism in replicate populations. In a good experimental study, the replicability of the results allows a powerful statistical argument to the effect that there is an objective tendency at stake rather than a random or unique phenomenon. Thus in the case discussed, in the warm environment with 50 percent of both types of flies present, type A flies have greater expected fitness than type B flies; with 85 percent of type A flies present, both types have equal fitness. Such an argument removes the central objection to realized fitness: If we use the various track records of replicate populations in a particular environment as a measure of the relative fitness of various types of organism in that environment, it quickly becomes obvious that in any *single* run organisms of the relatively fittest type may not out-reproduce their competitors; indeed, there are occasionally cases in which none of the fittest organisms survive. Thus the claim that the fittest did or will survive in any particular run, even one lasting hundreds of generations, is no tautology. Nor is it a tautology that the survivors in any natural population are, or were, the fittest.

Careful attention to the distinction between realized and expected fitness is crucial to a proper understanding of the literature of the synthetic theory in at least two ways. The first of these is the elimination of serious conceptual confusions from the classic texts. The confusions that result from conflating the two senses of fitness just introduced have given needless support to those who charge the synthetic theory with mistaking tautologies for empirical claims (and worse). I shall not document these confusions at length (though innumerable examples can be found in the dreary literature affirming – or denying – that evolutionary theory is tautological), but I will illustrate the matter by reference to two passages written by founding architects of the synthetic theory.

In (Dobzhansky 1970) there is a discussion of the various differences among members of a population which “influence the contribution that the carriers of a given genotype make to the gene pool. This contribution [i.e., the *actual* contribution], relative to the contribution of other genotypes in the same population, is a measure of the Darwinian fitness of a given genotype” (p. 101). In the terminology introduced above, Dobzhansky seems to be claiming that realized fitness is a measure of expected fitness. In a somewhat stronger passage, (Simpson 1949) claims the following:

it must, however, be noted that the modern concept of natural selection... is not quite the same as Darwin's. He recognized the fact that natural selection operated by differential reproduction, but he did not equate the two. In the modern theory natural selection is differential reproduction plus the complex interplay in such reproduction of heredity, genetic variation, and all the other factors that affect selection and determine its results” (p. 268).¹⁶

Now a full reading of the books from which these quotations are taken, as well as of other major works by their authors, reveals that in spite of verbal confusions, *in fact* (most of the time) they employ the concept here labeled “expected fitness” rather than that of realized (or tautological) fitness. Thus pages 219-229 of

¹⁶ I thank G. Simmons (University of California, Davis) for calling this passage to my attention.

(Simpson 1949) constitutes an extended argument that natural selection is a “systematic” and “orienting” process, that “the correlation between those having more offspring, and therefore really favored by natural selection and those best adapted, or best adapting to change [i.e., those that have high expected fitness] is neither perfect nor invariable, [but] only approximate and usual” (Simpson 1949, 221); that the *statistical* bias of “selection... [as] a process of differential reproduction” (p. 224) favors “well-integrated” organisms (p. 224) and “favorable or adaptive combinations” of genes (p. 225). Similarly, in the third edition (1951) of his path-breaking *Genetics and the Origin of Species* (Dobzhansky 1951), Dobzhansky had defined the Darwinian fitness of a genotype as “the relative *capacity* of the carriers of a given genotype to transmit their genes to the gene pool of the following generations” (p. 78, my emphasis). And in a passage of his 1970 book preceding the one quoted above, he had accepted Lerner’s definition of selection as “*non-random* differential reproduction of genotypes” (Dobzhansky 1970, 97, my emphasis). Indeed, considerable portions of the four chapters on selection (and fitness) in the later book are devoted to illustrating the statistically systematic character of the process and properties in question. The removal of the conceptual and verbal confusions in such passages, though an unexciting task, contributes significantly to an articulation of the synthetic theory able to withstand misguided criticisms.

A rather deeper contribution of the articulation and clean separation of realized from expected fitness is an improved understanding of the difficulty of applying the synthetic theory to natural populations. One piece of this puzzle stems from the peculiar way in which application of the concept of expected fitness plays an intermediate role between application of the concepts of engineering and realized fitness. The interplay among these three concepts is subtle and interesting. On the one hand, expected fitness resembles engineering fitness (relative adaptedness) in designating a *propensity*, shared by the members of a kind. On the other hand, it resembles realized fitness in that it does not entail or involve any kind of design analysis; the propensity in question is simply to have thus and such a relative reproductive rate in the relevant environments and relative to the specified competitors.¹⁷ Like realized fitness, expected fitness is concerned with track record,

¹⁷ F. Ayala (University of California, Davis) has suggested the following example to illustrate that increased expected fitness may, in specifiable circumstances, be associated with *reduced* engineering fitness. Two species (say, of beetles) compete in a population cage. One is regularly able to displace and eliminate the other. However when a certain mutant (manifesting, say, red eyes) appears in the population of the fitter species, it displaces the wild type, and then is displaced and eliminated by the erstwhile less fit competitor. This is precisely what happens in experimental populations of *Tribolium castaneum* and *T. confusum* as briefly described in (Ayala and Valentine 1979). The original report is in (Dawson 1969). Ayala’s (unconfirmed) hypothesis is that the red-eyed mutant emits a systemic poison to which its conspecific competitor is highly sensitive, it itself is moderately sensitive and the competing species is only slightly sensitive. Should this hypothesis be correct, the increased expected fitness within the conspecific population of the mutation causing red eyes is associated with a decrease in the engineering fitness (and degree of adaptedness) of its carrier, for the organism has been weakened by the mutation. Thus increase in expected fitness need not – and (I am confident) in real life at least sometimes does not – correlate with improvement of design.

not design; like engineering fitness it deal with a propensity (i.e., a propensity to have a certain track record) rather than actual success or failure on a case-by-case basis.

When one deals with natural populations, it is nearly always impossible to replicate the environmental conditions (including presence of, and comparable opportunity for, interacting with other organisms) and the genetic or phenotypic constitution of the original population. Because replicate cultures or populations in “the same” environment are unavailable, it is extremely hard to obtain adequate measures of propensities to reproductive success from field studies. Yet a biologist who knows his or her organisms well is often (rightly or wrongly) confident that the reproductive outcome of a particular case study reflects the design of the organisms (engineering fitness), and will, thus, be very tempted to treat the actual reproductive success rates of those organisms (realized fitness) as a reflection or measure of their objective propensity to success (expected fitness). This is probably why Dobzhansky took the *actual* contribution per genotype to the next generations to be a measure of the “Darwinian” fitness of those genotypes.

The resultant conflation of actual differential reproduction (realized fitness) with a systematic propensity for such differential reproduction (expected fitness) poses serious and often unnoticed epistemological difficulties. This becomes apparent when one notices that if one prevented the use of tacit background knowledge and pretended that one knew only the actual survival or reproduction rates, the support for the inference from realized to expected fitnesses would virtually disappear.¹⁸ *Yet almost nothing is known about the reliability of our beliefs about the extent to which “chance” events affect reproductive success from case to case.* Nor do we have a good way to discriminate interactions in which, effectively, organisms with constant fitnesses have been exposed to relevantly changing environments from interactions in which, effectively, the relevant fitnesses have varied in frequency-dependent ways.

This argument shows that field studies (which are automatically fraught with unique occurrences, irreplicability of the relevant populations, and limited repeatability of the biotic and other environmental circumstances) provide a rather slender basis for estimation of expected fitnesses. When such estimates are challenged, about the only way to bolster them is by showing that the actual survival and reproduction rates reflect *known* differences in the design-based abilities of the organisms to overcome the challenges of the environment or of their competitors. That is, information about reproductive outcomes is supplemented by information regarding engineering fitnesses; a sufficiently powerful analysis of *engineering* fitness supports the use of actual reproductive outcome as an estimate of *expected* fitness. (So, too, does a consistent pattern over a large number of generations, given adequate environmental stability.) Biologists have, of course, often argued in support of fitness estimates along these lines, but only a handful of cases have been worked out in adequate detail to be generally acknowledged as fully persuasive. Perhaps the

¹⁸ As the preceding footnote shows, both the inference from known aspects of the relative engineering fitness of a group of organisms to relative reproductive success and the converse inference are quite chancy. When one adds that a broad distribution of outcomes in replicate populations is compatible with fairly extreme differences in Darwinian fitness (especially when the environment is variable or “patchy”), it is clear that inferences between actual reproductive outcome and reproductive propensities require considerable support.

best of these stems from the studies of industrial melanism of the moth *Biston betularia* (and some other species), conducted largely by H. B. D. Kettlewell and his colleagues, and described in virtually all modern textbooks of evolution. The repetitious centrality of the example of *B. betularia* in the standard texts provides a crude and informal measure of the difficulty of demonstrating *in convincing detail* that the actual changes in the composition of natural populations reflect propensities (expected fitnesses) or are truly consequences of the design features (engineering fitnesses) of the organisms in question. And it is of rather considerable interest that in the case of *B. betularia* (and in many other interesting but less fully elaborated cases) the primary support for the inference to expected fitnesses consists of showing that the actual outcomes conform to the expectations generated by an analysis of engineering fitnesses.

This analysis of some of the conceptual pitfalls encumbering the application of contemporary concepts of adaptation enables us to articulate and support one of the major concerns in (Williams 1966). Williams sought to restore the importance of design considerations in evolutionary theory, emphasizing the importance of “historical” analysis of the problems faced by the relevant populations in their evolutionary past. It requires a (partly) “historical” analysis of the problems faced by organisms that belonged to the relevant populations to forge the connections between current design (evolved function) and the process and outcome of natural selection. In my idealized *Drosophila* experiment, in the case in which type A flies completely supplanted type B flies in warm environments and vice versa in cold environments, one can draw the conclusion that flies of type A are better adapted to the cold environment. Yet whereas it is almost certainly true in such a case that (if one holds other environmental factors constant) flies of type A have relatively higher expected and engineering fitnesses in the warm environment, it in no way follows that the recognized distinctive features of type A flies constitute an adaptation to warmth and the distinctive features of type B flies, an adaptation to cold. For example, the problems faced by each type of fly may revolve around temperature-sensitive disturbances of reproductive physiology that are only accidentally correlated with our ability to differentiate As from Bs, or on some other more-or-less bizarre possibility. Such issues can be resolved (if at all) only by a (difficult) study of the evolutionary history of each organism. Typically thanks to our ignorance, we substitute plausible scenarios (what Gould calls “just-so stories”) for such history. Needless to say, the evidential worth of such scenarios is subject to challenge.

In the absence of firm knowledge of the evolutionary history of our flies and in light of the multiple selective effects which *may* have operated on them in natural, as opposed to laboratory, environments, it remains an open question whether the greater expected fitness (and supposedly greater engineering fitness) of the type A flies in warm environments was shaped by differential reproduction operating on the favorable response of the ancestors of the type A flies to warmth (in which case they are exhibiting selected engineering fitness), whether what is involved is really frequency-dependent selection, whether their advantage is an example of “the mysterious laws of correlation” together with the operation of selection on *other* consequences of the type A constitution, or whether their advantage is a consequence of some sort of random change, for example, a series of point mutations that, taken

singly, were selectively neutral *in the natural environments of the flies*, although they are highly consequential in the chosen laboratory environments.¹⁹ To repeat Williams’s formulation from the précis of his book: “Evolutionary adaptation is a special and onerous concept that should not be used unnecessarily, and an effect should not be called a function unless it is clearly produced by design” (Williams, George C. 1966, p. vii).

“Fitness,” “Adaptation;” and Recent Evolutionary Controversy

Having completed my direct discussion of the principal uses of the terms “adaptation,” “adaptedness,” and “fitness” in evolutionary theory, I shall devote the final section of this chapter to an exploration of certain ramifications of my analysis and of the value of keeping the various concepts of fitness properly separated. I shall make four major points.

First, in light of my discussion, it is easy to see that many recent controversies over the status of evolutionary theory turn on a vulgarization of that theory. As soon as evolutionists employ the concept of *realized fitness* in lieu of the concept of an objective propensity toward reproductive success, they lay themselves open to the charge that their theory has no empirical content. As soon as natural selection is characterized as differential reproduction rather than as differential reproduction *in consequence of systematic or design differences*, one is barred, by one’s mistaken choice of definitions, from distinguishing between selective and random or accidental cases of differential reproduction. The subtle difference between using realized fitness as a contingent measure of expected (or engineering) fitness and of replacing the latter concepts by the former is, therefore, of considerable importance. One must be on guard against confusing the two moves.

The use of actual reproductive outcomes as rough measures of (but not as substitutes for) expected or engineering fitnesses in the study of natural populations can indeed be justified in appropriate circumstances. What biologists must recognize is that *in order to justify the use of de facto reproductive success in actual cases as a measure of evolutionary fitnesses, they must provide good grounds for believing that (in the instances in question) the actual reproductive successes are manifestations of the relevant propensities*. This requirement is comparable to the need to prove an existence and uniqueness theorem when one defines rational numbers in terms of sets of ordered pairs of integers;²⁰ the procedure is legitimate when the justificatory

¹⁹ This discussion of the *Drosophila* experiment is easily summarized in Gould and Vrba’s terminology: the outcome of the experiment leaves open the question whether the greater expected fitness (and the putatively greater engineering fitness) of type A flies to a warm environment is an adaptation or an exaptation.

²⁰ Thus, one must show that there is a number defined by each and every properly constructed set of ordered pairs (e.g., in some systems, $\{(1,2), (2,4), (3,6)\dots\}$ defines the number $\frac{1}{2}$) and that each and every such set picks out a unique number. Once this is proved, symbols such as “ $\frac{1}{2}$ ” may be used in an unambiguous way in the system in question. Similarly, once it is shown that actual reproductive rate probably reflects the relevant propensities, that rate may be used as an approximate measure of those propensities.

requirement is met, otherwise not. Conventional wisdom in evolutionary theory holds that that condition is often met – that the organisms within an undisturbed population are usually at, or near, a local maximum of expected fitness and are unaffected by unusual or stochastic factors. I do not know (and it is not easy to establish) how often such claims are correct, but when they are, the measurement of approximate expected fitnesses by means of tautological fitness is a sound procedure. Critics of this procedure should recognize that, in the appropriate circumstances, *this procedure does not bypass the use of both of the concepts of expected and engineering fitness.*

This discussion makes apparent both how easy it is to fall into conceptual confusion here and also that the confusion (in spite of its prevalence in the literature) is avoidable. It is the concepts of expected and engineering fitness of which evolutionary theory makes essential use, and a proper analysis of the structure of the theory should address the role of these concepts rather than that of realized fitness. In the remainder of my discussion I shall proceed accordingly.

Second, in general it is as difficult to justify the step from expected to engineering fitness as it is to justify the step from realized to expected fitness. This is especially apparent when one considers discussions of fitness at the level of genes and gene complexes. Very often, although we know which alleles (or variants of a gene complex) have the highest expected fitness in a given environment, we do not know the precise reasons for these relative fitnesses. Because many, probably most, genes have pleiotropic effects when they are expressed, because their precise expression (if any) depends on the presence or absence of other genes, and because the contribution to fitness of their expressed effects may well vary at different stages of the life cycle, the inference that a particular effect is the gene’s primary contribution to fitness is quite substantial.²¹ Thus the concept of expected fitness discussed in this chapter is considerably weaker (and more general) than Darwin’s concept of engineering fitness. Accordingly, because the synthetic theory uses the former concept, its doctrine regarding adaptation is somewhat weaker than Darwin’s. On the synthetic theory, the forces involved in natural selection stem from differences in expected (rather than engineering) fitnesses. Because differences in engineering fitness constitute, ipso facto, differences in expected fitness but not conversely (see Note 17), in principle the synthetic theory allows a broader range of causal antecedents to yield adaptations. Whether or not the weaker forces permitted by the synthetic theory, primarily at the genic level, in fact play an important role in the production of adaptations is not an easy question. To my knowledge, it has not been directly addressed in the literature.

²¹ There are exceptions of course – for example, when the effect is a dramatic reduction of viability or loss of function. But even then, matters can be complicated – for example, the familiar case of the gene causing sickle cell anemia whose positive contribution to fitness when in heterozygous condition was not at all easy to locate. And notice that it is really the *genotype* (homozygous normal, heterozygous normal and sickling, homozygous sickling), not the gene that is *causally* relevant to the fitness of the carrier. This raises problems (several of which will be mentioned) treated usefully by (Wimsatt 1982, esp. §§ 2 and 3), and elegantly developed by (Sober and Lewontin 1982). Unfortunately, I read this paper too late to shape the text of the present section. (I thank Professors Wimsatt and Sober for sending me their respective preprints.)

At this point it will be useful to review what is involved in claiming that a trait is an adaptation. There are two components to this claim.

1. The trait in question is an optimal – or at least the relatively best – engineering solution of a real problem bearing on (a) survival of the organism; (b) incorporation of energy or other environmental resources into the organism; or (c) incorporation of energy and other resources from the organism and the environment into viable offspring. *All* organisms face problems in all three of these categories, and those which have relatively better (or even optimal) solutions to these problems are those with greater (or optimal) engineering fitness.
2. The design features that yield the high engineering fitness of the trait have been produced by natural selection, that is, in the synthetic theory, by differential survival of organisms with high expected fitness.

One important strand of biological criticism of the synthetic theory turns on a denial of the easy assumption that the distinctive traits of an organism with high expected fitness are, ipso facto, likely to be (or to yield) adaptations in the technical sense just described. This is not a matter that can be resolved by conceptual analysis; its resolution requires extensive and difficult field and laboratory studies. In particular, when expected fitnesses are ascribed to genes, genotypes, or phenotypic markers whose function (if any) is unknown, the inference to engineering fitness is fraught with peril.²² There is a gap between the genuine expected fitness of such elements and the proper units of analysis in treating of adaptation. *The latter are determined by engineering and causal considerations.* It is this gap that plagues the derivation of engineering from expected fitness; it is only when the units of analysis are at the right level – that is, when the causally relevant units are taken into account – that the two properties are tightly connected (see Sober and Lewontin 1982, Wimsatt 1982).

This brings me to the third major point of this section. It is, indeed, the practice of many biologists to casually assume that any distinctive feature of an organism which is associated with a reproductive advantage (i.e., high expected fitness) for its bearers is an adaptation in the engineering sense. Once one realizes how strong the implied claim is, one recognizes that it deserves serious examination. A development of this theme should shed some light on the recent, many-faceted dispute over the proportion and importance of prominent and biologically interesting features of organisms that are not (in our onerous sense) adaptations. In a controversial paper, (Gould and Lewontin 1979) attack the “adaptationist program,” arguing that it is overly optimistic to suppose that virtually any prominent or biologically significant feature of an organism is an adaptation, that is, not only that it

²² This point has both biological and philosophical content. An example of the former is provided by (Thornhill 1979, p. 365) “[The] weakest aspect [of the study under review] is its failure to separate the concept of evolved function from the notion of advantage or benefit [i.e., contribution to expected or engineering fitness]... The function of a trait is defined as the advantage that characterizes the selective history of the trait; function tells how the trait has contributed to most effective reproduction over evolutionary time (The elucidation of function is difficult, see [(Williams 1966)].) *Because function and advantage are used synonymously throughout the book, the authors occasionally (and apparently unknowingly) offer interpretations that imply effective group selection*” (my emphasis).

serves a function, but also that it was brought about by the action of natural selection operating on variants of that feature. Many subsidiary controversies, in fact, turn on whether or not particular biologically significant features are adaptations in this sense. At the genetic level there is the dispute about “selfish” DNA (i.e., DNA that is of no value to any organism, but which hitches a ride on the reproductive machinery of organisms) and the continuing controversy about selectively neutral mutations in genes coding for enzymes. (It may yet turn out that selectively neutral point mutations are required to explain the clockwork regularity of change in DNA sequence versus the stop-and-start irregularity of rates of morphological change, speciation, and so on.) At the level of morphological structure and programmed habit there are innumerable detailed controversies about the correctness, epistemic status of, and support required for selectionist “stories” about the origin of particular features.

There are also general concerns about the paleontological evidence tending to show that whole suites of features change relatively suddenly and relatively rapidly in correlated ways; it is not clear whether such changes occur, in general, via mutual co-adjustment, feature by feature, or via systematic developmental change. Of particular importance is the question whether, on a paleontological time scale, macroevolutionary mechanisms supplement natural selection in a way that must be taken into account in order to give a correct account of the presence of (certain) major traits in surviving populations. See (Vrba 1980) for a useful review of some of the controversial mechanisms under investigation.) This latter worry is central to the debates about whether one can account for macroevolution by extrapolating what we know about microevolution, a topic that I hope to address in a companion paper. Also of concern in the debate over macroevolution is the effectiveness of group and species selection, that is, selection operating at higher levels than classical natural selection. The resolution of such debates, as should be obvious, requires far more than a conceptually adequate account of adaptation, but in all these cases, resolution of the controversy has been impeded by the sort of conceptual confusions about adaptation that I have been illustrating.

My final point deals with problems regarding the units of selection. Classical natural selection operates, however effectively or ineffectively, one generation at a time by means of a systematic statistical bias in the reproductive rate of phenotypically distinct individuals. Yet one finds a great variety of claims in the literature to the effect that units such as genes, gene complexes, cellular organelles, and so on, on the one hand; and groups, populations, and species on the other are units of selection. On the present occasion I will deal briefly with only one of these.

Like many others, Williams is inclined to genic reductionism (Williams 1966, and elsewhere). He holds that virtually everything one wishes to say about natural selection can be said by treating the single gene as the unit of selection. His definition of a gene is a bit unusual. It includes anything in the genome “which segregates and recombines with appreciable frequency” (Williams 1966, 24), and so includes, for example, whole inversion loops in the chromosomes of certain *Drosophila* as genes. (This definitional sleight of hand makes no difference to the fundamental issue.) Specifically, he holds that the central processes of natural selection can all be represented in terms of the mean selective effects of each gene, taken singly. Williams grants that a given allele has different effects in different (conspecific)

organisms, both because of genetic differences in the organisms and because of the complexities of epigenesis. (These complexities mean that environmental and developmental differences may enable different copies of the same allele, even when it is in the same genetic context, to have different effects.) Nonetheless, Williams argues, each allele has an *average* phenotypic effect that will determine the net strength of the selective processes acting upon it. So far as the genetical theory of natural selection is concerned, the heart of the matter is the *net selective value* of each gene, taken singly.

There are two closely related arguments showing that such extreme genetic reductionism is wrong. Both arguments are based on the claim that in quite common and specifiable circumstances the mean selective value of a gene, were it available, would not work as a construct for making evolutionary predictions and explanations. The more elegant argument, recently articulated in (Wimsatt 1980, 1982), traces back to controversies between Fisher and Wright and between Dobzhansky and Muller, though Wimsatt is developing it out of some work by Lewontin. It points out that, in very many (arguably quite typical) circumstances, the selective value of an allele per generation is a function of the allelic frequencies at *other* loci. If this is so, and if random or selective pressures affect those other loci independently of the allele being considered, the selective value of that allele will change in each generation as the frequency distribution of alleles at the other loci changes. Any system of bookkeeping that assigns fitnesses or selective values to individual alleles will have to take account of allele frequencies *at other loci* and will, thus, only appear to treat each locus independently of the others. In Wimsatt’s terminology, even though the mean selective value of the allele may be determinate in every generation, it is a “local” not a “global” value in the genetic state space and so *extrapolations based on that selective value will have no predictive or explanatory value*.²³ In my terminology, the net selective value of a gene in a given generation, like realized fitness, is a *description* of the reproductive outcome *in that generation only*, not an objective propensity or an enduring property with explanatory value.

The second argument is based on a slightly more direct consideration of the way genes affect phenotypes. To the extent that phenotypes are determined by additive interactions among genes, the mean selective value of a gene is determinate. To the extent that genic interactions are nonadditive (and they are not additive in a great many, mostly ill-understood cases, including those involving frequency-dependent interactions, changes in the developmental schedule, and so-called regulatory interactions), the mean phenotypic effect of a single gene is unstable and, hence, ill defined.

As these parallel arguments show, there are deep, substantial, and probably false assumptions that would have to be true if everything we wish to say about

²³ (Sober and Lewontin 1982) point out that genic fitnesses can be parameterized so as to take account of the genetic background (and other disturbing factors). They argue that although such devices allow one to calculate the actual change in gene frequencies from appropriate information, the relevant causal factors generating the selective forces are *genotypes*, not genes (and so on in other cases), so that the *explanatory* use of fitnesses *in the relevant cases* (one is mentioned in Note 21) occurs at the genotypic (or appropriate other) level, not the genic level. (Wimsatt 1982) makes a very similar point.

natural selection were to be captured, even in principle, in a treatment based on mean phenotypic effects and the associated selective values of genes taken singly. There are thus good grounds for holding that the gene is almost certainly not *the* ultimately unit of selection. This result (which may be generalized to cover broad class of purported reductions) undercuts the idea that we can work our way back up from single genes to locate the “correct” phenotypic categories in terms of which to describe those features of organisms that have been directly shaped by natural selection. In other words, the atomistic study of single genes and their phenotype effects will not, in general, reveal which features of organisms are adaptations arrived at in the course of natural selection.

The general moral of this story for the problem of the units of selection is not that the gene is *not* a unit of selection. (It is.) Rather, the moral is that there are units of selection at many hierarchical levels and that we must take into account interactions that cross these levels. The result will be a considerable but inevitable, increase in the complexity of evolutionary theory, for it means that we will have to examine the strength of the interactions between selective processes at various levels (at least from the level of the single gene to the level of species selection). I, for one, will be very much surprised if it turns out (as, of course, it might) that classical natural selection, operating between phenotypically distinct organisms in virtue of their design, is the only type (or the highest level type) of selection we need to take into account in reconstructing the history of life. But a full examination of the controversies over the units of selection will have to wait another day.

References

- Ayala, F. and J. W. Valentine 1979. *Evolving*. Menlo Park, CA: Benjamin/Cummings.
- Brandon, R. N. 1978. “Adaptation and evolutionary theory.” *Studies in the History and Philosophy of Science* 9: 181-206.
- Darwin, C. R. 1859. *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
- Dawson, P. S. 1969. “A conflict between Darwinian fitness and population fitness in *Tribolium* “competition” experiments.” *Genetics* 62: 413-419.
- Dobzhansky, T. 1951. *Genetics and the Origin of Species*. New York: Columbia University Press.
- Dobzhansky, T. 1970. *Genetics of the Evolutionary Process*. New York: Columbia University Press.
- Gould, S. J. 1971. “Darwin’s retreat.” *Science* 172: 677-678.
- Gould, S. J. 1980. “Is a new and General Theory of Evolution Emerging?” *Paleobiology* 6: 119-130.
- Gould, S. J. 1981. “But not Wright enough: Reply to Orzack.” *Paleobiology* 7: 131-134.
- Gould, S. J. and R. C. Lewontin 1979. “The Spandrels of San Marco and the Panglossian Paradigm: a Critique of the Adaptationist Program.” *Proceedings of the Royal Society of London, B* 205: 581-598.
- Gould, S. J. and E. S. Vrba 1982. “Exaptation--a missing term in the science of form.” *Paleobiology* 8: 4-15.
- Lewontin, R. C. 1974. *The Genetic Basis of Evolutionary Change*. New York: Columbia University Press.
- Mayr, E. and W. B. Provine, eds. 1980. *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Cambridge: Harvard University Press.
- Mills, S. and J. Beatty 1979. “The propensity interpretation of fitness.” *Philosophy of Science* 46: 263-286.
- Orzack, S. 1980. “The modern synthesis is partly Wright.” *Paleobiology* 7: 128-131.
- Ospovat, D. 1981. *The Development of Darwin’s Theory*. Cambridge: Cambridge University Press.
- Prout, T. 1969. “The estimation of fitnesses from population data.” *Genetics* 63: 949-967.
- Prout, T. 1971a. “The relation between fitness components and population prediction in *Drosophila*. I. The estimation of fitness components.” *Genetics* 68: 127-149.
- Prout, T. 1971b. “The relation between fitness components and population prediction in *Drosophila*. II. Population prediction.” *Genetics* 68: 151-167.
- Rosenberg, A. 1982. “On the propensity interpretation of fitness.” *Philosophy of Science* 49: 268-273.
- Rosenberg, A. 1983. “Fitness.” *Journal of Philosophy* 80: 457-474.
- Ruse, M. E. 1973. *The Philosophy of Biology*. London: Hutchinson University Library.
- Scriven, M. 1959. “Explanation and prediction in evolutionary theory.” *Science* 130: 477-482.
- Simpson, G. G. 1949. *The Meaning of Evolution: A Study of the History of Life and its Significance for Man*. New Haven: Yale University Press.

- Sober, E. R. and R. C. Lewontin 1982. “Artifact, cause, and genic selectionism.” *Philosophy of Science* 49: 157-180.
- Thornhill, R. 1979. “[Review of] R. W. Matthews and J. W. Matthews, *Insect Behavior*.” *Quarterly Review of Biology* 54: 365-366.
- Vrba, E. S. 1980. “Evolution, species and fossils: How does life evolve?” *South African Journal of Science* 76: 61-84.
- Williams, G. C. 1966. *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.
- Williams, M. B. 1973. “The Logical Status of the Theory of Natural Selection and Other Evolutionary Controversies.” In *The Methodological Unity of Science*, ed. by M. Bunge. Dordrecht: D. Reidel, 84-102.
- Wimsatt, W. C. 1980. “Reductionistic research strategies and their biases in the units of selection controversy.” In *Scientific Discovery: Case Studies*, ed. by T. Nickles. Dordrecht, Holland: Reidel, 213-259.
- Wimsatt, W. C. 1982. “The units of selection and the structure of the multi-level genome.” In *PSA 1980, Vol. 2*, ed. by P. Asquith and R. Giere. East Lansing, Mich.: Philosophy of Science Association, 122-183.