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# THE QUARTERLY REVIEW of BIOLOGY



## ADAPTATION AND THE GOALS OF EVOLUTIONARY RESEARCH

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### ABSTRACT

*Adaptation is and has always been a slippery concept. Even among contemporary evolutionary biologists there is no consensus about how to identify adaptive traits. Most definitions of adaptation incorporate elements of history. Among these, some require that adaptive traits be built by natural selection for their current roles. Others take a phylogenetic perspective and require that adaptations be derived relative to traits of antecedent taxa. Still other definitions require evidence of functional design in the biological machinery underlying the trait, implying a history of selective fine-tuning.*

*The historical definitions are most useful for addressing questions about evolutionary history like, "What was the phylogenetic trajectory of a phenotype with current utility?" or "How does a trait's current use relate to its original function?" Historical definitions are less useful for addressing questions about phenotype existence like, "Why do certain phenotypes predominate over others in nature?" This is because history-laden definitions often fail to classify as adaptations traits that are maintained by natural selection. Obviously it is important to employ a definition that is appropriate for the research question being pursued. Indeed, the (mis)application of history-laden definitions to questions of phenotype existence has created the illusion that nonadaptive traits abound in nature and caused widespread doubt about the importance of natural selection in molding phenotypes.*

*To circumvent these problems we propose a nonhistorical definition of adaptation. In our view, an adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment. This definition treats adaptation as a relative concept, sets forth operational criteria for identifying the phenotypic traits to which the concept applies, and decouples adaptations from the evolutionary mechanisms that generate them. Natural selection theory predicts that among a specific set of alternatives the most adapted phenotype will*

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be the one that predominates in a given environment. *This is a testable proposition. When it is false the frequency of the trait must be due to nonselective processes such as drift, migration, selection acting on a correlated trait, or recent changes in the environment. Teleonomic demonstrations of adaptation are a special case of our suggested analysis because inferring a trait's "function" implies the application of a specific fitness criterion (e.g., optimal design) to rank alternative phenotypes.*

*The logical structure of our definition allows us to confront five recent challenges to adaptationism, namely that: (1) it is impossible to identify adaptive traits without a knowledge of phylogeny, which can reveal constraints on adaptation, (2) genetic correlations among different traits usually prevent or retard ascent toward adaptive peaks, (3) "developmental constraints" limit the operation of natural selection, (4) the complex and highly ordered phenotypes studied by adaptationists can be explained most parsimoniously as manifestations of simple mechanisms, and without reference to natural selection, and (5) it is impossible to study the adaptive significance of human behavior because natural selection has not had time to operate on humans in our "changed" environments. We show that these challenges rest on inadequate specification of the components of adaptation.*

*"The difficulty of the concept adaptation is best documented by the incessant efforts of authors to analyze it, describe it, and define it" (E. Mayr, 1983: 324).*

*"Adaptation is considered a central, yet obscure, elusive, and controversial concept in evolutionary theory" (C. B. Krimbas, 1984: 1).*

#### INTRODUCTION

**S**TUDYING ADAPTATION is one of the central tasks of evolutionary biology. But what is adaptation? This issue has been addressed by many notable figures in biology, philosophy, and the history of science in the past century. Reviews by Leigh (1971), Krimbas (1984), Sober (1984), Wallace (1984), D. C. Fisher (1985), Endler (1986), Brandon (1990), and Baum and Larson (1991) reveal that there are numerous, often conflicting definitions, and no consensus about what operational criteria should be used to identify a phenotypic trait as an adaptation. Relatively restrictive definitions have generated controversy by implying that most features of organisms are "nonadaptive," whereas relatively permissive definitions have fueled debate by suggesting that "everything is adaptive." The multiplicity of definitions has caused disagreements where none actually exist, and generated quasi-empirical claims that are really disguised assumptions about what aspects of evolution are most important. Some conceptual housecleaning is clearly in order.

One confusion-reducing approach might be to synthesize a new definition of adaptation by drawing from the best elements of the previous ones. A "good" definition presumably would be unambiguous in its application (i.e.,

rigorously operational) and also serve the principal research aim of evolutionary biologists. Herein lies the problem: No single research aim unites evolutionary biology. Indeed, as Antonovics (1987) noted, "evolution, as a science, consists of two quite disparate disciplines, an inference of past events and the study of present-day processes. I have tried, but failed, to coin separate terms for these disciplines" (p. 329).

In our view, Antonovics's first discipline deals with questions of *evolutionary history*. Practitioners (e.g., paleobiologists and systematists) seek to infer the origins and phylogenetic trajectories of phenotypic attributes, and how their current utility relates to presumed functions in their bearers' ancestors. The second discipline deals with questions of *phenotype existence*. Practitioners (e.g., behavioral and evolutionary ecologists) ask why certain traits predominate over conceivable others in nature, irrespective of the precise historical pathways leading to their predominance, and then infer evolutionary causation based on current utility. Not surprisingly, since these disciplines deal with questions at different logical levels (Tinbergen, 1963; Sherman, 1988), incompatible definitions of adaptation have arisen in the two research domains. Obviously, it is crucial to define adaptation in a manner that is appropriate for the research question being pursued. How-

ever, misunderstandings arise when definitions developed in one domain are applied to the other—in particular, when the adaptiveness of existing phenotypic variants are evaluated using history-laden definitions.

To circumvent these problems we develop an operational, nonhistorical definition of adaptation that is applicable to questions of phenotype existence and, potentially, to issues of evolutionary history. Our approach is useful for studying the outcomes of phenotypic evolution and for evaluating some recent challenges to adaptationism.

#### HISTORY-LADEN DEFINITIONS

“As evolutionists, we are charged, almost by definition, to regard historical pathways as the essence of our subject” (Gould and Vrba, 1982: 7).

#### *Adaptation and Exaptation*

Most definitions of adaptation contain a historical element. In a conspicuous example, Gould and Vrba (1982: 4) reserved the term “adaptation” for “features built by natural selection for their current role,” and proposed the term “exaptation” for features originally built for something other than their current roles. Gould and Vrba’s definition is not useful for most questions of phenotype existence for two reasons. First, it confounds product with process and ignores the fundamental similarity between adaptations and exaptations—namely, that both refer to traits that exist because they have been, and continue to be, favored over alternative traits (see D. C. Fisher, 1985: 123; Endler and McLellan, 1988: 409). Second, it is virtually impossible to identify the original roles of many traits that are of interest to behavioral ecologists (e.g., complex behavioral traits like mating or social behaviors) owing both to their poor representation in the fossil record and to their plasticity within and variability among individuals now and (presumably) in the past.

Even within the domain of evolutionary history, Gould and Vrba’s (1982) definition is difficult to apply. Indeed, it is impossible to discern precisely where an adaptation ends and an exaptation begins in Gould and Vrba’s (1982) scheme, since they did not specify how much the current function of a trait must dif-

fer from its original role for it to be classified as an exaptation. For example, are human ear bones exaptations because, in addition to their original function, they now mediate social communication via telephone conversations? The answer depends on how finely one subdivides roles or functions. In this case if the original function is broadly defined—for example, to facilitate detection of acoustic stimuli—then our ear bones are adaptations. If the original function, however, is narrowly defined—for example, to facilitate detection of pre-Bell or prelinguistic acoustic stimuli—then ear bones are exaptations.

Another weakness in Gould and Vrba’s (1982) definition of adaptation is its sensitivity to how “traits” are distinguished. For example, human ear bones are homologous with gill arches in fish (Hildebrand, 1982). If ear bones and gill arches are regarded as the same trait (the advisability of which is undeterminable from the Gould-Vrba definition), then ear bones are exaptations regardless of how the acoustic-detection functions are broken down, because the bones no longer function to support gills. Indeed nearly *every* trait is an exaptation if we go back far enough in time. This is apparently the justification for Gould’s frequent claim (e.g., 1986, 1987a) that structures as varied as the enormous eggs of kiwis and penis-like clitorises of female spotted hyenas are “nonadaptive.” While this claim really means only that most phenotypes are exaptations, it has created the illusion that the very theory of natural selection is under attack. Gould himself is the source of this confusion because instead of consistently using the term he and Vrba coined, he routinely describes exaptations as “nonadaptations” (e.g., Gould, 1987a, b).

Even if these ambiguities could be resolved, in most cases we cannot confidently infer the original role of a trait, either because the phylogenetic and ecological information necessary for such an inference is unavailable or because the phylogenetic information is misleading. The latter occurs when spatial or temporal environmental variation leads to rapidly meandering trait evolution within lineages, rendering the trait’s patterning among extant taxa independent of the actual phylogenetic sequence. Recently Baum and Larson

(1991) argued that cladistic analyses can reveal both the phylogeny of a trait and the sequence of selective regimes (environments) that affected the trait. A comparison of traits and associated selective regimes between a focal taxon and phylogenetically antecedent taxa is supposed to discriminate between adaptations and exaptations. However, if transitions either in phenotypic characters or in selective regimes occur sufficiently rapidly within taxa (as compared to transitions between taxa), such a procedure will frequently misidentify adaptations and exaptations.

To visualize these problems, consider the various sequences of trait evolution depicted in Figure 1. Under the Gould-Vrba definition, a trait with function  $A$  would be an adaptation in the first sequence regardless of how far back in geological history its fossil record extended. In the second sequence, a trait having a new function ( $A'$ ) would be an adaptation if the fossil record traced back to time  $t_1$  (when the "original function" was  $A'$ ), but it would be an exaptation if the fossil record went all the way back to  $t_0$  (when the "original function" was  $A$ ). In the third sequence  $A'$  would be an adaptation only if the fossil record were rather short, extending back just to  $t_3$ ; prior to  $t_3$  the function was  $A$ , so  $A'$  would be an exaptation. In the fourth sequence, a trait with the same function ( $A$ ) that was an adaptation throughout sequence 1 would not be an adaptation if the fossil record extended just to  $t_3$ ,  $t_2$ , or  $t_1$ ; only if the record extended to  $t_0$  and the trait's function at  $t_0$  were defined as its original function would the present trait ( $A$ ) be an adaptation in the fourth sequence. Likewise, in the fifth sequence, the trait would be an exaptation if the fossil record terminated at  $t_1$  or  $t_3$ , and an adaptation otherwise.

The sequences in Figure 1 illustrate that whether a trait is labeled an adaptation or an exaptation depends arbitrarily on the point in history at which we examine the trait's function. In all the sequences the present trait may owe its existence to natural selection, but it would be recognized as an adaptation in Gould and Vrba's historical scheme only in some cases, depending on our knowledge of its functions at different times in geological history. Functions at many times may be unknowable. For example, if multiple function-

transitions occur between speciation events, no phylogenetic "memories" of the multiple functions will be preserved in extant species.

#### *Derived Trait Definitions*

"For a character to be regarded as an adaptation, it must be a derived character that evolved in response to a specific selective agent" (Harvey and Pagel, 1991: 13).

Partly in response to the aforementioned problems, Greene (1986), Coddington (1988), Baum and Larson (1991), and Harvey and Pagel (1991) attempted to provide more operational ways of distinguishing adaptations from exaptations by using phylogenetic, specifically cladistic methods. They defined adaptations as traits with current utility that are derived in their phylogenetic group. Functional traits that originated in ancestral taxa and persisted unchanged through speciation events until the present are considered exaptations, not adaptations, in each of the descendant taxa, although the trait may be considered an adaptation for the entire clade comprising the descendant taxa if the trait is derived (apomorphic) in relation to a more inclusive clade. Thus the trait with function  $A$  in evolutionary sequence 6 (Fig. 1) would not be an adaptation for the uppermost taxon, but a new functional trait  $B$  would be an adaptation for the same taxon in sequence 7. (Note that the "derived trait" definition is not identical to Gould and Vrba's, because in the latter scheme trait  $A$  in sequence 6 would be an adaptation). An immediate consequence of derived trait definitions is that phylogeny must be understood to identify adaptations, since adaptations must be determined from phylogenies.

From the perspective of researchers interested in phenotype-existence questions, derived trait definitions can lead to some odd conclusions. For example, under derived trait definitions, human eyes, bird wings, and insect antennae would not be adaptations in hominids, shorebirds, and Hymenoptera, respectively, since the members of each taxon share the trait with members of related taxa in a more inclusive clade. Indeed, if the taxonomic level is sufficiently restricted (e.g., by excluding certain taxa with ancestral traits), most traits appear to be exaptations (i.e., non-adaptations). It is certainly meaningful and

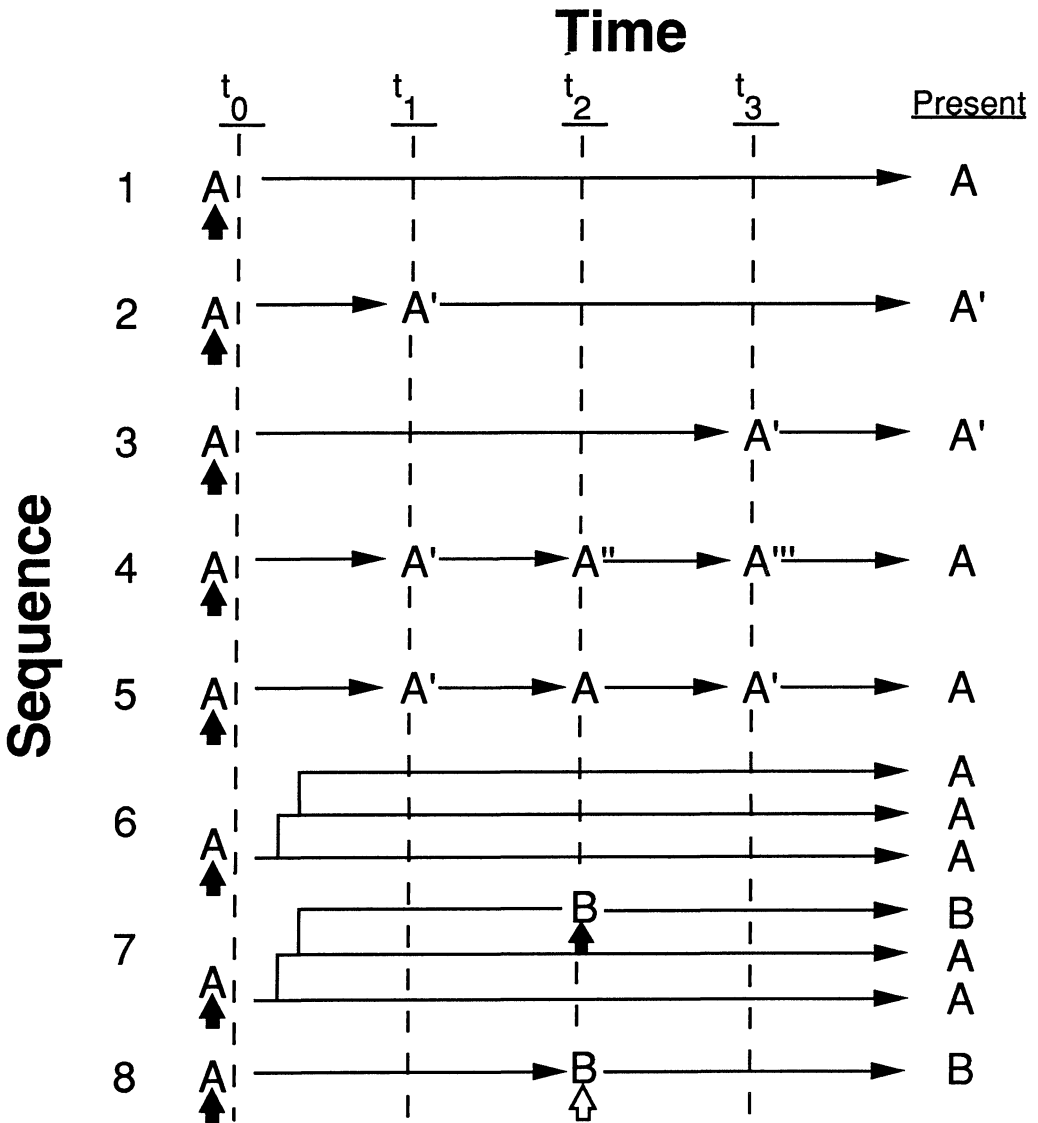


FIG. 1. SEQUENCES OF TRAIT EVOLUTION THAT INCLUDE OR EXCLUDE FUNCTIONAL TRAITS AS ADAPTATIONS UNDER VARIOUS HISTORY-LADEN DEFINITIONS

The designations A', A'', and A''' mean that trait A has acquired a new function, but has not changed so much that it should be considered a new trait. New traits are designated by an alternative letter (B). Solid vertical arrows indicate the establishment of a trait by natural selection; the open vertical arrow (sequence 8) indicates the establishment of a trait by a nonselective process, such as drift. The dark horizontal lines connecting traits in each sequence indicate that the trait is being maintained by natural selection through the removal of alternative variants that arise.

legitimate, however, to say that the human eye is adaptive over its absence, regardless of the inclusiveness of the phylogenetic level considered, because selection has continually

maintained the alleles that enable it to function. "Maintenance" refers to selective forces that cause phenotypes to persist, increasing our chances of observing them (see Emlen

et al., 1991). Thus, contrary to Brooks and McLennan (1991: 81), these forces are not of secondary interest compared to those that promoted the trait's original spread. Brooks and McLennan (1991) also argued that "in the case of related taxa displaying the same trait . . . there is nothing to study because the trait has not changed evolutionarily." The obvious possibility that the taxa in question inhabit similar environments where selection has favored similar (adaptive) responses is dismissed as "not interesting" (p. 82).

Derived trait definitions were developed to address questions about evolutionary history. History is incorporated because adaptation is defined relative to taxonomic level. Obviously, determining the phylogenetic history of a trait is an important research enterprise. But this approach need not clash with the goal of explaining why certain phenotypes exist if, instead of using multiple definitions of adaptation, we follow D. C. Fisher's (1985) suggestion and distinguish between "ancestral" and "derived" adaptations, adaptation being defined strictly in terms of current utility.

A more useful definition of adaptation for questions of phenotype existence would unite adaptations and exaptations under a single theoretical umbrella. Gould and Vrba (1982) suggested "aptation" to fill this role, but this new term disconnects modern discussions of phenotypic evolution from nearly a century of work in which adaptation is given a more inclusive meaning. Moreover, the use of aptation implies acceptance of the underlying, problematic, adaptation-exaptation dichotomy as well. By treating so-called adaptations and exaptations simply as adaptations, the goal of using natural selection theory to explain why we observe certain traits rather than others is served with minimum violence to traditional usage.

#### *Teleonomic Definitions*

Even authors interested in questions of phenotype existence have often adopted definitions of adaptation that incorporate historical elements, albeit in subtle ways. In particular, Williams (1966) argued that "to prove adaptation one must demonstrate a functional design" (p. 212). Williams was trying to separate selected phenomena from nonse-

lected phenomena that produce fitness benefits only incidentally (i.e., purely as the result of the laws of physics and chemistry). Note that Williams (1966) did *not* say, as Gould and Vrba (1982: 6) claimed he did, that traits were nonadaptations unless they were originally built by selection for the functions they currently perform. To Williams, adaptations are traits that were built by selection to perform some function, regardless of their original roles (see also D. C. Fisher, 1985).

Williams (1966) is a proponent of teleonomy (Pittendrigh, 1958), the elucidation and analysis of functional design in living organisms. Recently he updated his concept of adaptation, defining it as "some sort of biological machinery or process shaped by natural selection to help solve one or more problems faced by the organism" (Williams and Nesse, 1991: 3). Thus, according to Williams (1992), "adaptation is demonstrated by observed conformity to *a priori* design specifications" (p. 40). In 1978 Lewontin defined adaptation similarly, although the following year he took a somewhat different approach (Gould and Lewontin, 1979).

Many prominent evolutionary biologists agree with the essence of Williams's position. For example, Thornhill (1990) argued that "recognition of an adaptation involves identification of a feature of an organism that is too complexly organized to be due to chance" (p. 32). Similarly, West-Eberhard (1992) stated that "a character is an 'adaptation' for a particular task only if there is some evidence that it has evolved (been modified during its evolutionary history) in specific ways to make it more effective in the performance of that task, and that the change has occurred due to the increased fitness that results" (p. 13). The assumption underlying all such definitions is that an intricate fit between form and function could arise only through natural selection, and not through random processes (e.g., mutation or drift). For example, the optical designs of eyes approach theoretical optima predictable from physics (Goldsmith, 1990); it seems inconceivable that these designs are not adaptations produced by selection. The recognition and analysis of complex adaptations are central to many powerful defenses of Darwinism (e.g., Williams, 1966, 1992; Alexander, 1979; Dawkins, 1987).

We agree that any phenotypic attribute fulfilling these teleonomic criteria is an adaptation. Whether the trait is "too complexly organized" to rule out chance, however, is obviously a subjective judgment. The decision about at what level of organization the adaptation is to be recognized is also a subjective judgment—for example, is it sensible to say that a complicated, modified phenotype is an adaptation when its component parts are not, owing to their simplicity and lack of modification? But these are minor quibbles. The main problem with teleonomic criteria is that they are so conservative that many selectively favored traits would not be recognized as adaptations.

For example, imagine a white moth that is camouflaged from avian predators when it rests on the trunks of light-colored trees. Now suppose that a black morph appears as a result of mutation at a single locus. Black moths are safe on dark-colored tree trunks, and this enables them to migrate deeper into the forest where they establish themselves and reproduce effectively [the parallel with the well-known case of industrial melanism (Kettlewell, 1961) is intentional]. Under the Williams-Thornhill-West-Eberhard criteria, black coloration might not be considered an adaptation because it does not require complex biological machinery or extreme fine-tuning. Perhaps not until black coloration came to be associated with dark-bark-seeking behavior would teleonomists recognize adaptation in this system.

The problem then is that only traits that have been under directional selection for the same function for a very long time would predictably be modified sufficiently to fulfill strict teleonomic criteria. Traits in which there has been no detectable fine-tuning, such as newly arisen, favored traits and traits that have remained essentially unchanged since they originated (i.e., due to stabilizing selection) often would be missed under teleonomic definitions. Not surprisingly, teleonomists generally illustrate their concept of adaptation with spectacular phenotypes whose complex forms suggest that they were indeed "designed" to solve specific problems. For example, Williams (1992: 40) cites the structure of the vertebrate eye, dosage compensation in fruit fly development, and the abdominal clamp of

male scorpionflies as examples (see also Thornhill, 1990). It does not follow, however, that *only* such phenotypes should be considered as adaptations.

We are not rejecting fine-tuning, complexity, or fit to the environment as useful criteria for identifying adaptations, nor are we rejecting the idea that natural selection can be inferred from evidence of functional design. As will be explained below, we regard such evidence as a special case of a more general procedure for testing hypotheses about selection. Here we simply note that in the context of phenotype existence questions, the concept of adaptation may usefully be broadened to include traits for which there is no demonstrable history of selective modification.

In summary, both the derived trait and selective modification criteria for recognizing adaptations are too restrictive for answering many questions in the domain of phenotype existence. The former treats traits as non-adaptive if they have had the same function for a long time (i.e., ancestral traits), while the latter fails to recognize favored traits that have not undergone obvious fine-tuning, even though in both cases the traits are maintained against alternatives. While clear evidence of selective modification or functional design may be *sufficient* to implicate a trait as an adaptation, such criteria are not *necessary* to recognize adaptations.

#### *Sober's Definition*

Currently a widely accepted definition of adaptation is Sober's (1984): "A is an adaptation for task T in population P if and only if A became prevalent in P because there was selection for A, where the selective advantage of A was due to the fact that A helped perform task T" (p. 208). This is essentially a rigorous form of the definitions used by Burian (1983), Endler (1986), Futuyama (1986), Brandon (1990), and Symons (1990). Endler (1986) argues that we should not use "adaptive trait" synonymously with adaptation, because the latter should refer only to the process of becoming better adapted. It is common usage (e.g., references above), however, to refer to phenotypes as adaptations so, to avoid confusion, we will not distinguish between adaptive traits and adaptations. This synonymy has



the desirable consequence of requiring us to describe explicitly the process that produces adaptations—that is, natural selection.

A key criterion for recognizing adaptation under Sober's (1984) definition is that a trait must have *spread* through the action of natural selection. There are several problems with this. First, it is in one sense too conservative. Suppose a trait initially spread in a population because of some nonselective process, such as genetic drift or gene flow from a different population. Suppose further that, once established, the trait was maintained by selection (e.g., sequence 8 in Fig. 1). This trait would not qualify as an adaptation under Sober's (1984) definition, but it should (at least in the phenotype-existence research domain), because the trait persists because of natural selection.

Second, Sober's definition is in another sense too permissive because it includes traits that may currently be disadvantageous, as long as selection caused their spread in the past. Suppose, for example, that a trait which had spread initially owing to natural selection became slightly deleterious in a new environment, but persisted because of fixation against mutant alternatives by genetic drift. Currently this trait is not adaptive, and selection cannot be invoked to explain its maintenance (i.e., selection in the absence of drift would have eliminated the trait long ago).

The third and most fundamental problem with Sober's (1984) definition—one shared with all of the history-laden definitions—is that it refers to both the product of the selective process and the process itself. Using this definition, a trait can be recognized as an adaptation only if we know that the trait spread through natural selection. Endler's (1986) survey reveals that this knowledge is available for very few phenotypic attributes. This might mean that the majority of traits should be considered nonadaptations. Alternatively, it might suggest the need for a new kind of definition. We agree with D. C. Fisher (1985) that it is desirable to separate the phenomenon to be explained from the theory that explains it. It seems methodologically more productive to recognize traits that enhance fitness as adaptations and to test selective theories that predict the occurrence of adaptations by

looking for them where they are supposed to occur. In sum, if a selective history is built into the definition of adaptation, the concept becomes methodologically inert, serving only as a (rarely usable) summary of our knowledge of the evolution of a trait.

#### NONHISTORICAL DEFINITIONS

"An adaptation is, thus, a feature of the organism which interacts operationally with some factor of its environment so that the individual survives and reproduces" (Bock, 1979: 39).

Not all definitions include history. For those that do not, the challenge is to identify the phenotypic property that characterizes adaptations. Bock (1980) suggested that this property is "the amount of energy required by the organism to maintain successfully the synerg [the interaction between biological roles and the selection forces] with a lower energy requirement indicating a better degree of adaptation" (p. 221). The difficulty comes when one tries to calculate the relevant energies for different kinds of phenotypic traits, a problem that results because there is no obvious way to recognize when a synerg is no longer being maintained. A more important problem, as Bock himself noted, is that natural selection does not necessarily minimize energy expenditure in interactions with the environment. Thus Bock's definition fails to provide a firm link between natural selection theory and adaptation.

Mayr (1988) recognized the latter problem. He proposed that "adaptation is greater ecological-physiological efficiency than is achieved by other members of the population" (p. 135). If Mayr was equating "efficiency" with reproductive success, his definition is in a sense *too* strongly connected to natural selection because adaptation is then virtually synonymous with "high relative fitness." As Krimbas (1984) noted, such a synonymy confuses the criterion for evaluating adaptiveness with the trait itself, blocking, by risk of tautology, attempts to frame and answer questions about phenotype existence.

Dobzhansky (1956: 347; also 1968) also took an ahistorical approach, defining an adaptive trait as "an aspect of the developmental pattern which facilitates the survival and/or reproduction of its carrier in a certain succession

of environments." More recently, Mitchell and Valone (1990) defined adaptation as "a strategy that has the highest per capita growth rate, given the conditions" (p. 47), explicitly as part of an "optimization research program" aimed at answering phenotype-existence questions. These simple definitions eliminate history and specify operational criteria for recognizing adaptations; moreover, they strongly connect the concept of adaptation to natural selection theory.

The definitions of Dobzhansky and Mitchell and Valone circumvent the problems of the history-laden definitions, yet they are in one respect incomplete. Adaptations are supposed to "facilitate" or "enhance" survival and reproduction or have the "highest" fitness, but in relation to what? We agree with Clutton-Brock and Harvey (1979), Krimbas (1984), D. C. Fisher (1985), Turke (1990), and Baum and Larson (1991) that adaptations must be evaluated in comparison to specific alternative phenotypes. Although this may seem like an obvious point, failure to incorporate this evolutionary "principle of relativity" into the definition of adaptation can lead to confusion, as will be seen shortly.

#### *An Operational, Nonhistorical Definition of Adaptation*

"Darwin's (1859) intent . . . was clearly to offer the process of natural selection as an *explanation* for features and relationships that can be observed in the world today. . ." (D. C. Fisher, 1985: 123).

We now propose a simple definition of adaptation that captures the essential research motives of evolutionary biologists interested in questions of phenotype existence. It combines elements from the approaches of Dobzhansky (1956), D. C. Fisher (1985), and Mitchell and Valone (1990). In our view: **An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment.** This definition undoubtedly strikes some readers as being too simplistic. Therefore its key features require discussion and defense.

First, we emphasize that adaptation is a *relative* concept, defined only in relation to explicit alternatives. This is because natural selection sorts among the phenotypic alterna-

tives available each generation, with the individuals exhibiting the greatest relative reproductive success contributing disproportionately to subsequent generations. As Williams (1966) put it, "Selection has nothing to do with what is necessary or unnecessary, or what is adequate or inadequate, for continued survival. It deals only with an immediate better-vs.-worse within a system of alternative, and therefore competing, entities" (p. 31). Natural selection is a little like a game of poker: The best hand (phenotype) wins (reproduces) regardless of whether it is a pair of twos or four aces.

A second feature of our proposed definition is that it is in a sense *genotype-free*. By this we mean that it refers only to phenotypic features and not necessarily to genotypes at specific loci. We take this approach for two reasons. First, it does not really matter for our definition precisely how genotypes are connected to phenotypes, as long as there is some connection. Second, a given phenotype might be produced by a variety of genotypes (Williams, 1966: 56; Mitchell and Valone, 1990). As a consequence of the many-to-one relationship between genotypes and the phenotype, there are numerous ways the same evolutionarily stable state can be produced. For example, a selectively favored trait A might spread because allele *a* arose at locus X, or because allele *a'* arose at locus Y, and so forth. Whether a given trait resulted from locus X, Y, or some other locus is immaterial. What does matter is that the overall probability of seeing a favored trait increases with the number of loci that can generate it. Thus our definition focuses on phenotypic features that may be produced by multiple genotypes, each potentially experiencing a different history, which nonetheless may converge on a small number of identifiable stable states.

A third feature of our proposed definition is that it is in an important sense *history-free*. There is no reference to a specific historical process or evolutionary mechanism that leads to the predominance of the most adapted member(s) of the phenotype-set. We take this approach because natural selection sorts among existing variants every generation without regard to their prior states. To put this point another way: *Whatever is important*

*about a trait's history is already recorded in the environmental context and the biological attributes of the organism.*

Consider the poker game analogy again. When the final call is made and the cards are laid down, the history of the high hand is not what is at issue. The winning cards are not determined by the order in which they were accumulated, nor by whether the high hand was owing to chance, deception (e.g., high cards up somebody's sleeve), or selective retention of one or more cards from previous winning hands (i.e., a game analogous to selection sorting among heritable traits). To return to biology, the erectile clitoris of female spotted hyenas would be an adaptation under our definition if it enhances reproductive success (i.e., due to its signaling function: W. J. Hamilton et al., 1986) relative to nonerectile genitalia, regardless of its historical origin or its initial hormonal mechanisms (but see Gould, 1987b versus Alcock, 1987).

#### *Specifying the Components*

Our definition of adaptation consists of three components: (1) a set of phenotypes, (2) a measure of fitness, and (3) a clearly defined environmental context. Using our definition requires careful consideration of all three. Failure to appreciate or adequately characterize one of these components can lead to problems of interpretation.

*The Phenotype-Set.* This is the group of alternative phenotypes whose fitnesses must be compared to determine whether or not a trait is an adaptation. Phenotype-sets can include phenotypes that are either discrete or continuous, conditional or invariant. In any case they must be specific. For example, to say that "eyes are adaptive" by itself is somewhat ambiguous. It might mean that having eyes yields higher fitness than not having them (coarse-grained adaptation), or that the precise spatial arrangement of muscles, sensory cells, visual pigments, and lenses yields higher fitness than many slightly different arrangements (fine-grained adaptation; see Goldsmith, 1990). Both meanings of the statement are legitimate, but they differ in the set of alternative phenotypes under consideration.

In many cases the phenotype-set will be chosen to include all naturally occurring variants. Finding the adaptation then involves comparing their fitnesses in nature. A phenotype-set, however, need not be restricted to naturally occurring variants. For example, consider a trait for which there is no phenotypic variation. To determine if it is adaptive, one might implement either theoretical or experimental approaches, or both. Regarding the former, we could imagine plausible alternative phenotypes (e.g., homologous traits or analogous traits in ecologically similar organisms) and model whether or not they could invade a population composed mainly of the putative adaptation. Of course, the success of such an approach depends on the realism or robustness of the modelers' assumptions. Alternatively, we could experimentally create novel phenotypic variants (with proper controls) and measure their reproductive successes in the field. The first approach was taken by W. D. Hamilton (1964) in explaining the evolution of worker sterility in the social insects and by Axelrod and W. D. Hamilton (1981) and Nowak and Sigmund (1992) in determining whether a tit-for-tat behavioral strategy is adaptive, while the second approach is exemplified by Andersson's (1982) and Møller's (1988) demonstrations that long tails in male widowbirds and barn swallows, respectively, are adaptive in the context of female choice.

Investigators have considerable flexibility in the choice of their phenotype-set. A suitable choice requires only that the set contain phenotypes that might plausibly arise. We disagree with Greene (1986), Coddington (1988), and Baum and Larson (1991) that the phenotype-set must contain only the cladistically determined, phylogenetically antecedent state(s) of a trait. We say this because a wide variety of traits may have been tested and rejected (or only temporarily favored) by selection during a species' history. Although alternative traits displayed by ancestral or closely related extant taxa are logical starting points for the construction of phenotype-sets, they are not the only appropriate ones. Many traits that were tested over evolutionary time may not exist today or be preserved in the fossil record; this is especially true of behavioral traits.

Consider, for example, a social bee species thought to have a remote ancestor that was social. It seems likely that mutants have arisen or will arise that would lead this species down the path toward solitary existence. Indeed, the occasional appearance of tendencies to disperse and breed independently is suggested both by the many bee genera (e.g., *Ceratina*, *Dialictus*) containing solitary and social species (e.g., Michener, 1985), and by the recent appearance of solitary life in some lineages of social bees (e.g., *Exoneura*: Michener, 1964). Hence it is legitimate to construct a phenotype-set of (1) dispersal and solitary living versus (2) remaining in the natal nest and helping to rear siblings. It would be reasonable to assess the fitnesses of these alternatives, perhaps with the help of field experiments, to explain why this species is social.

Traits can be adaptations even if they currently exhibit no phenotypic variability within or among taxa. Reproductive competition among the alternatives may have continually weeded out the inferior phenotypes before they reached an appreciable frequency. Failure to recognize the latter possibility has led McLennan et al. (1988) and Brooks and McLennan (1991: 80–86) to argue that selective explanations need not be sought when there is little taxonomic variability in a trait. The idea that taxonomic conservatism implies “phylogenetic inertia” and that this serves as a sufficient explanation for a trait is discussed in detail below. Here we draw attention to the general problem of *incomplete specification of the phenotype-set*, that is, to evolutionary arguments that depend upon arbitrary exclusions of plausible traits from the set of alternative phenotypes.

Confusion can arise if investigators assume different phenotype-sets, especially when they do not specify them explicitly. One researcher’s adaptation may be another’s non-adaptive trait because the latter assumed a more comprehensive phenotype-set. An example is provided by a debate over the utility of regression methods, derived from quantitative genetics theory, for measuring selection in natural populations (Arnold and Wade, 1984a,b). Grafen (1988: 455–457) claimed that such methods do not necessarily tell us anything about adaptation because they mea-

sure only “selection in progress” on naturally occurring variants. Grafen argued that the range of natural variation observed today may be so narrow that selection gradients—partial regressions of fitness on trait value—are zero, even though the trait has been under intense selection in the past.

Grafen suggested that, in determining whether spots on the hindwings of a particular butterfly are adaptations, it would be more useful to see what happens if the spots are painted out experimentally, than to correlate reproductive success with the number of naturally occurring spots. According to Grafen (1988: 456) “we wish to know *why* the butterfly has the spots, not *how much* more successful more spotted individuals are than less spotted” (italics are his). It seems perfectly reasonable, however, to say that the regression methods examine fine-grained adaptations within a narrow phenotype-set, namely the one defined by the natural range of variation. Grafen’s complaint thus amounts to an urging that the phenotype-set could and perhaps should be expanded, lest we lose sight of more coarse-grained adaptations.

*The Fitness Measure.* Several considerations must go into designing the best fitness measure for a particular question. Fitness is most directly measured as reproductive success (adjusted appropriately when population sizes are increasing or decreasing), but reproductive success can be determined for each reproductive episode or over longer periods, such as lifetimes. Sometimes it is more appropriate to count the number of grandprogeny rather than progeny, and often the effects of a trait on kin are more conveniently accounted for by using inclusive fitness instead of personal fitness (W. D. Hamilton, 1964; Grafen, 1984).

As Clutton-Brock (1988) pointed out, short-term and long-term measures of reproductive success are useful for answering different questions. Often it is easier to isolate the effects of phenotypic variations on different components of fitness in the short term, because lifetime reproductive success (LRS) is determined by interactions between multiple phenotypic attributes and fitness components. For short-term measures of reproductive success to be meaningful, however, we

must assume they are positively related to reproductive success in the long term. Particular selective hypotheses—that is, predictions that selection will act in specific ways—can be examined by determining whether hypothesized short-term components of fitness are in fact the ones that contribute most to the LRS of the adaptive phenotype.

Our definition does not require us to use any one particular fitness criterion. Although we believe that LRS is usually the best, in many situations LRS simply will not be estimable, or as noted above, will be so confounded by contributions from other traits that it will be impossible to detect a selective signal amid all the “noise.” Indeed, one can imagine a spectrum of fitness criteria that exhibit different degrees of trade-off between detectability and overall selective relevance. Short-term or specific criteria provide high selective “signal-to-noise” ratios, but at the expense of weakened connections to the long-term fitness that ultimately matters in evolution; long-term or broad criteria do the reverse.

Teleonomists generally evaluate adaptation by using a trait’s functional design as the fitness criterion. Of course, the teleonomic approach preceded Darwin by hundreds of years. For example, Aristotle, Galen and Paley recognized functional design in nature (see Williams, 1966, 1992). But in the light of natural selection theory, the statement that “trait T appears designed to perform function F” must be interpreted as a shorthand way of saying that T causes its bearer to have a higher fitness than certain (usually unspecified) alternatives with respect to the fitness criterion (implied by) F. As noted by Krimbas (1984), for the shorthand statement to have any evolutionary meaning, the function F must be or at least imply some sort of fitness criterion (“design performance”).

For example, to argue that intestinal villi are designed to increase the surface area for absorption of digested food involves constructing a chain of propositions that (1) tacitly connect the possession of villi to some fitness criterion (e.g., “efficiency of nutrient acquisition” or “resistance to starvation”), and (2) imply alternative phenotypes (e.g., smoother intestinal tracts) yield lower fit-

nesses according to this criterion. Analyses based on functional design thus contain all the elements in our definition—phenotype-sets, fitness criteria, and environmental contexts—albeit in a compact form. When a predominant trait scores higher according to design criteria than presumed alternatives, teleonomists infer that natural selection has favored the trait and accounts for its existence. Of course, it would be ideal to have data on how different numbers and types of villi affect LRS, but this is impractical, leading teleonomists to employ specific, higher-resolution fitness criteria. Such optimal design criteria are not qualitatively different from, and indeed must ultimately be connected to, long-term fitness effects.

The implication is that the teleonomic approach is not an alternative to our suggested adaptational analysis, but rather is a special case of it. Williams (1966), however, provided an argument that appears to undermine our proposal that adaptations must be recognized by their fitness consequences. He said that “the decision as to the purpose of a mechanism must be based on an examination of the machinery and an argument as to the appropriateness of the means to the end. It cannot be based on value judgments of actual or probable consequences” (p. 12). This reasoning preceded Williams’s famous argument that the paws of a fox should not be considered as adaptations for constructing a path in the snow because of the incidental benefits that might accrue to the fox if it reuses the path. In our view, however, determining the “appropriateness of the means to the end” necessarily entails “value judgments of actual or probable consequences” by invoking implicit or explicit fitness criteria to score alternative phenotypes. We decide that the fox’s paws are adaptations for locomotion (but not for making paths) because we can imagine the seriously deleterious locomotory consequences of alternative designs of the fox’s distal appendages.

Problems can arise if the measure used to evaluate the fitnesses of alternative phenotypes is not specified. For example, Kirkpatrick (1987a, b) distinguished between “adaptive” and “nonadaptive” models of female choice, based on only one component of male fitness, viability. He modeled alternatives in the phe-

nototype-set (the entire range of development of male secondary sexual characters) and concluded that female choice of mates can be non-adaptive because under its influence males could evolve secondary characters that reduced their life spans. After reviewing the literature, Kirkpatrick (1987a) declared that, in fact, "many studies have found exaggerated male traits to be detrimental to survival" (p. 65). Maybe so. But it is misleading simply to label Kirkpatrick's models of the process nonadaptive, since well-developed secondary sexual characteristics enhance male mating success. The problem is semantic and it disappears if reproductive success, rather than one of its components, is used to assess the adaptiveness of the possible phenotypes. Kirkpatrick could have avoided this confusion by saying that sexually selected male traits can be maladaptive under the fitness criterion of viability. Thus, as with phenotype-sets, fitness criteria must be specified explicitly. Otherwise, we are vulnerable to seemingly exciting, but empirically empty, claims that something dramatically counterintuitive can happen in evolution.

*The Environmental Context.* This is the environmental situation in which the phenotypes are being evaluated. Specifying it involves considering both the biotic and abiotic environments of the phenotype-set. Problems can arise if the phenotype-set has not been related to the appropriate environmental context(s). For example, Alcock (1980) and Thornhill and Alcock (1983) reported that in some solitary anthophorid bees, males who search for females in foraging areas mate less often than males who defend territories at female emergence sites. If patrollers are more numerous than territory defenders (a common occurrence), one might surmise that the more poorly adapted phenotype is more common. Suppose territory holders are larger and better at fighting than patrollers, however, and that body size is determined by larval nutrition (both are true of many species). Consideration of these factors suggests that the original phenotype-set (patrollers versus territory holders) should be split, with one new set conditioned on large body size (context A) and the other on small body size (context B). Observations and field experiments would then

allow us to investigate whether territory defense is adaptive in context A and patrolling is adaptive in context B, as is predicted under the hypothesis that both behaviors are adaptations.

In the above example, instead of recognizing two contexts, each with a phenotype-set consisting of two strategies, we might have constructed a single phenotype-set with four strategies, two of which are conditional: (1) if large, patrol and if small, defend, (2) if large, defend and if small, patrol, (3) always patrol, and (4) always defend. The fitness analysis is identical whether this phenotype-set or the previous sets are assumed. To see this, suppose the fitness payoffs for patrolling and defending for small individuals are  $P_s$  and  $D_s$ , respectively, and the corresponding payoffs for large individuals are  $P_l$  and  $D_l$ , respectively. In the first approach, we simply make two comparisons:  $P_s$  versus  $D_s$ , and  $P_l$  versus  $D_l$ . Suppose an individual's probability of being large is  $p$ . Thus, in the second approach, we compare the four quantities  $pP_l + (1 - p)D_s$ ,  $pD_l + (1 - p)P_s$ ,  $pP_l + (1 - p)P_s$ , and  $pD_l + (1 - p)D_s$ , for a total of six pairwise comparisons. All of these comparisons reduce to just the two comparisons made in the first, context-conditioned approach. For example if, in the first approach, patrolling is adaptive for small individuals (i.e.,  $P_s > D_s$ ) and defending is adaptive for large individuals, ( $D_l > P_l$ ), then strategy (2) will be favored over all alternatives in the single phenotype-set of the second approach, because, necessarily,  $pD_l + (1 - p)P_s > pD_l + (1 - p)D_s$ ,  $pP_l + (1 - p)P_s > pP_l + (1 - p)D_s$ .

The latter example illustrates that a fitness analysis for a phenotype-set consisting of facultative behaviors is equivalent to a fitness analysis for multiple phenotype-sets of invariant behaviors, where each phenotype-set is conditioned on the appropriate context. The significance of this is that the fitness analysis does not necessarily depend on whether we assume that one locus enables context-dependent behavioral switches or that different loci prescribe fixed behaviors in single contexts. We refer to this as the *principle of mechanistic equivalence*, since the fitness analyses can be carried out without a detailed knowledge of the underlying genetic mechanisms of the component strategies.

*Using the New Definition*

In their famous paper on the spandrels of San Marco, Gould and Lewontin (1979) stated "We would not object so strenuously to the adaptationist programme if its invocation, in any particular case, could lead in principle to its rejection for want of evidence. . . if it could be dismissed after failing some explicit test, then alternatives would get their chance" (p. 587). Our approach allows such an explicit test. An adaptation is that member of the phenotype-set exhibiting the highest reproductive success. Natural selection theory (including sexual selection and kin selection) leads us to expect that *among a specific set of alternatives the most adapted phenotype will be the one that predominates in a given environment*. If this prediction is falsified, the implication is that selection does not account for the frequency of that phenotype. Note that this is *not* to say natural selection theory itself is false or that selection has never favored the trait—only that there is no evidence we observe the trait because of selection in contexts like the current one.

The well-worn but often and firmly rebutted objection to selection theory—namely, that it is tautological—also disappears in our scheme. The prediction that the adaptation will be the trait most frequently sampled is a contingent, empirical proposition, and not a circularity, because it might well be false. Thus we disagree with Krimbas's (1984) assertion that the concept of adaptation, when linked to fitness, necessarily leads to tautologies in evolutionary reasoning. In our scheme, when a trait yielding lower reproductive success is more prevalent than variants yielding greater fitness, then processes other than natural selection—such as genetic drift, recurrent migration, selection acting on correlated characters, or rapid habitat changes—will "get their chance" to explain its existence.

We suspect that many biologists already accept this test, at least subconsciously. What impressed Darwin, and what impresses most of us, is that traits conferring reproductive advantages occur so frequently. Natural selection theory provides an explanation for this observation: A history of competition and differential reproduction among alternative phenotypes, either in the remote or recent past, has led to the predominance of some and

the disappearance of others. In other words, paraphrasing Williams (1966), "natural selection produces adaptation" (p. 25), and "evolution, with whatever general trends it may have entailed, was a by-product of the maintenance of adaptation" (p. 54). In turn, evolutionary biologists test selective hypotheses by determining whether the most common trait is really the one that maximizes some aspect of fitness relative to its alternatives.

We reemphasize that we have stripped the definition of adaptation of historical components precisely so that we can use it to test the hypothesis that an adaptation is the product of a particular *class* of histories—that is, those histories involving natural selection. Thus, we are not making the foolish claim that adaptations are not produced by historical processes; rather, our definition frees us to investigate the relative importance of different kinds of historical processes that may have produced the phenotypes we see today.

In nature we are most likely to sample traits or trait combinations that are evolutionarily stable—that is, traits which have persisted for a long time because they are resistant to selective invasion by alternative mutants (Maynard Smith, 1982). It does not really matter whether the trait originated and spread recently or in the distant past, even prior to the speciation event when the taxon exhibiting the trait originated. It does not even matter whether the trait originally spread because of natural selection or some nonselective process. The point is the trait we see most commonly should be the one that maximizes relative reproductive success. Because such traits tend to persist once established, it is particularly likely that we will sample them today.

Some analogies may be helpful here. In explaining why certain traits predominate in nature rather than conceivable others, evolutionary biologists act a little like physicists who study stable states in thermodynamic systems or astronomers who study spatial arrangements of stars and galaxies. In each case, the researcher examines the products of historical processes that unfold over centuries due to the interactions of particular entities. The products of these processes are explicable, sometimes even predictable, without a

detailed knowledge of each entity's individual history. This is so because, for a given set of conditions, a large number of distinct individual histories tend to converge on a small number of stable states. For example, the observation that boulders collect in mountain valleys can be explained without knowing each boulder's precise trajectory. Likewise, stable states in thermodynamic systems can be predicted without knowing the exact history of each system, and the large-scale geometries of galaxies are understandable without knowing the detailed histories of the constituent stars. Similarly, as noted by Mitchell and Valone (1990), evolutionary biologists explain and even predict the observed phenotypic features of organisms in given ecological contexts without knowing the exact evolutionary trajectories leading to those features. In each case a finite set of stable states serves as "attractors" for a large, indeed infinite, number of possible histories.

The stable states in such historical processes can often be identified by straightforward criteria. In the boulder example, physical theories predict that the greatest density of boulders will occur where the gravitational potential energy is minimized. Likewise, evolutionary theory predicts that the phenotypes observed in a population will be those that maximize fitness relative to a specified set of alternatives. Hence our definition of adaptation motivates us to search for stable attractors for organismal phenotypes, but not for the precise historical pathways taken by those phenotypes before they became trapped by the selective attractor. Of course there can sometimes be multiple selective attractors and, as many authors have pointed out (e.g., Sober, 1988: 6-9), the one the population moves toward may depend on historical accidents (just as a boulder atop a mountain may roll into one of two valleys). For phenotype-existence questions, however, everything that is important about the history of a trait, including all the accidental twists and turns that moved it toward a particular selective attractor, is recorded in the current environment and biological attributes of the organism. An alternative succession of accidents would have led to a different environmental

context and perhaps to a different set of biological attributes. It is legitimate, therefore, to analyse the forces that hold traits in the vicinity of selective attractors without reference to the precise historical pathways followed by each trait.

One possible objection to our definition of adaptation might arise from considering frequency-dependent selection — when the fitnesses of the alternative phenotypes are dependent on their frequencies in the population. Suppose, for example, that negative frequency dependence results in a stable genetic polymorphism of two phenotypes, W and Z. If these two phenotypes have equal fitnesses, the two traits would be equally adaptive under our definition. We see no problem with having equivalent adaptations, since it would explain why one trait does not selectively extinguish the other, and thus would help answer the question of why both phenotypes persist.

Finding that traits W and Z are equally adaptive, however, does not fully explain their long-term maintenance. Equal fitnesses might occur by chance so that frequencies would be determined by drift. To resolve the issue, we would test the prediction that the polymorphism has been stabilized by natural selection. We can do this by including the frequency of the two phenotypes as part of their "environmental context." Given a phenotype-set containing W and Z, a fitness criterion of reproductive success, and an environmental context including a low frequency of W, we predict that W should be the more adaptive trait; the same should be true for Z when it is rare. In short, frequency dependence poses no special problems for our definition of adaptation.

Of course, it is conceivable that the most prevalent trait is also the most adaptive, even though the trait owes its frequency to some nonselective process. This is an inevitable consequence of decoupling the phenomenon to be explained (the prevalence of adaptation) from the explanatory hypothesis (natural selection). In every branch of science it is theoretically possible for a phenomenon to be produced by multiple mechanisms — yet its occurrence is generally taken as evidence in



favor of the mechanism most likely to produce it. For example, a rapidly streaking bright light across a clear night sky is usually accepted as evidence that an extraterrestrial object has entered the earth's atmosphere, even though it *might* represent simultaneous retinal detachment in all of the observers. In the case at hand, of all the major theories for the presence of phenotypes, only natural selection predicts that adaptations will consistently predominate. In the language of Bayesian probability theory, finding that the trait with the highest reproductive success predominates indicates with a high probability that natural selection has acted at some point, because the a priori probabilities for alternative mechanisms to lead to prevalence of such a trait are small.

Failure to appreciate the value of this common mode of scientific inference has led to some unfair criticisms of adaptationist analyses. For example, Symons (1990) states "to conclude that the measurement of differential reproduction illuminates adaptations from the premise that adaptations were produced in the past by differential reproduction is simply a *non sequitur*" (p. 430). Let's recast this argument in our terms. Symons's point is that the hypothesis "natural selection has acted to produce predominant phenotype P" does not necessitate that "P will exhibit higher current fitness than its alternatives," since selection may have acted only in the past. We agree with this; however, consider the converse argument. We *can* infer that if P does exhibit higher current fitness than its alternatives, then natural selection probably produced this outcome. Thus the *non sequitur* Symons (1990) frets about does not mean that measuring differential reproduction cannot illuminate the role of selection in maintaining phenotypes.

An alternative way of assessing the prevalence of adaptations is to directly test nonselective hypotheses. For example, we might see if genetic drift accounts for the occurrence of a trait by estimating both the effective population size, which is inversely related to the force of genetic drift, and the selective difference between the trait and its alternative(s). The values of these parameters could then be used in models of drift-selection interaction (e.g., Kimura, 1983) to assess the relative strengths

of genetic drift and natural selection. As another example, teleonomic definitions of adaptation (e.g., Thornhill, 1990; Williams, 1992) are essentially proposals for testing nonselective hypotheses of trait presence. In effect, the test involves determining whether a trait is so complex and obviously designed to solve a problem posed by the environment that nonselective processes such as genetic drift cannot plausibly explain its existence (of course, as discussed above, failure to demonstrate complexity does not rule out maintenance of a trait by natural selection).

#### NONADAPTIVE TRAITS

In a given environment if the most prevalent trait does not yield the highest reproductive success (i.e., it is a nonadaptation relative to the trait exhibiting the highest reproductive success), then processes other than natural selection likely account for its presence. What if the most prevalent trait is declining in frequency either because (1) a superior alternative mutant has recently arisen and is displacing the prevalent trait, or (2) negative frequency-dependent selection results in a cyclic oscillation of the trait with one or more alternatives? Strict application of our definition leads to the conclusion that in case (1) the most prevalent trait is nonadaptive relative to the favored alternative. Obviously this does not mean that natural selection is not operating, for the new mutant is being favored and the prevalence of the nonadaptation will be more or less short-lived, depending on the degree of superiority of the new mutant. Case (2) is more subtle because the prevalent trait is nonadaptive relative to its alternative, yet it persists because of natural selection. Superficially, this shows that our definition of adaptation and our test for natural selection as the mechanism maintaining traits are conservative since they can lead to "false negatives" like this one. Case (2), however, is not problematic if it is remembered that the environmental context may include a trait's frequency. The prevalent trait does not persist due to natural selection in the context in which it is the prevalent trait (i.e., when it is nonadaptive); instead the trait persists because it is favored when it is rare (i.e., when it is the relatively adaptive trait).

By now some readers have undoubtedly de-

cided that our definition is so loose that nearly every trait qualifies as an adaptation. Two examples illustrate that this is not so.

#### *Dump Nesting in Wood Ducks*

Intraspecific brood parasitism has been reported in about 100 species of birds (Rohwer and Freeman, 1989). It is particularly prevalent among species with precocial chicks, such as waterfowl (Andersson, 1984; Eadie et al., 1988). Brood parasitism reaches an extreme among wood ducks (*Aix sponsa*) nesting in boxes, especially when the boxes are grouped in visible locations. In some populations, 95 percent of nests are parasitized and clutch sizes of 30 to 40 eggs, several times a female's normal 10 to 12 egg capacity, are common despite the availability of many unused boxes (Semel and Sherman, 1986). To examine the possible adaptive significance of extreme brood parasitism, Semel et al. (1988, 1990) studied the effects of "dump nesting" on reproductive success. They found that as the frequency of parasitism and the number of eggs laid in each box increased, the proportion of eggs that hatched, and thus female reproductive success, decreased dramatically. When dump nesting became rampant it was typically followed by crashes in duckling production and population decline. The negative effects of parasitism were due mainly to nest abandonment, incomplete incubation of eggs (which often lie 8 to 12 centimeters deep in dump clutches), crushed eggs, and bacterial infestations.

In wood duck populations nesting in clustered boxes, extreme brood parasitism is the predominant behavior (Clawson et al., 1979). Is it adaptive? In applying our definition, the phenotype-set includes parasitizing versus not parasitizing conspecifics, the fitness measure is hatchability of eggs, and the environmental context is grouped, visible nest boxes. Under these conditions extreme brood parasitism lowers individual reproductive success, and as a result population productivity declines as well. Thus dump nesting is nonadaptive, so its prevalence must be due to processes other than natural selection.

Nonadaptive traits like this one intrigue curious naturalists. Semel and Sherman (1986) proposed the following hypothesis to explain

the occurrence of dump nesting. Wood ducks nest naturally in tree cavities. These are generally high up and well concealed in the forest canopy, making it difficult for gravid females to find nests to parasitize. As a result, parasitism occurs at low rates in natural cavities. Behavioral observations (Heusmann et al., 1980) and experiments (Wilson, in press) indicate that parasitism is triggered when female wood ducks see conspecific females enter or leave active nest sites. When boxes are erected in visible locations, especially when they are grouped (the standard management practice), it is virtually impossible for a female to sneak into her own nest unobserved. By concentrating nest boxes in the open, over the last 60 years (Bellrose, 1990), humans have inadvertently made parasitism too easy. The wood ducks are essentially trapped by their normal mechanism of finding nests to parasitize. Apparently the birds behave nonadaptively owing to recent human interference with their nesting habitat.

To test this hypothesis, Semel et al. (1988, 1990) conducted two long-term field experiments that involved hiding some nest boxes individually in forested areas and leaving others in clusters over open water. The results, based on six years of data, were clear-cut. Only 34 percent of the hidden boxes were parasitized—essentially the same rate as in natural tree cavities—whereas 60 percent of the visible, clumped boxes were parasitized. In the hidden boxes, total clutch sizes decreased to 11 to 14 eggs, well within the range of greatest hatchability. Indeed, individual reproductive success was significantly higher in the hidden boxes than in the grouped boxes, and the difference was associated with reduced parasitism.

These results suggest why dump nesting is prevalent in one environmental context (i.e., intense management), but they do not indicate the adaptive significance of brood parasitism for wood ducks nesting under normal circumstances. It seems likely that naturally nesting females enhance their reproductive success via parasitism (e.g., because suitable nesting cavities are in short supply, it is dangerous to incubate eggs due to predation). The adaptive significance of brood parasitism in tree-holes, however, is only now being investigated.

### Senescence

A more general example of a nonadaptive trait is physiological deterioration with advancing age. Senescence is not adaptive because as Williams (1957) pointed out, "other things being equal, a long-lived individual will leave more offspring than a short-lived one . . . an individual that deteriorates slowly would be favored over one that deteriorates rapidly" (p. 399). In 1952 Medawar outlined a theory of senescence based on the premise that the force of natural selection weakens with advancing age. If the product of the reproductive value and survivorship of individuals when they are young greatly exceeds that when they are older, early beneficial effects will be strongly favored, whereas later deleterious effects will be less strongly disfavored. Alleles conferring health, vigor, and disease resistance, for example, will inexorably accumulate among youngsters and, similarly, there will be a piling up of alleles that fail to maintain these attributes later on. Senescence will occur if the same alleles have positive effects early in life and negative effects later (i.e., if there is antagonistic pleiotropy: Williams, 1957) or if alleles simply have age-specific effects (W. D. Hamilton, 1966).

Senescence is thus ubiquitous, inexorable and maladaptive. Unlike extreme parasitism in wood ducks, however, senescence is not a result of recent habitat change. Among evolutionary biologists (e.g., Charlesworth, 1980; Rose, 1991) there is general agreement that, as Alexander (1987) put it, "Senescence is . . . apparently not something that has evolved directly but rather something that natural selection has been unable to prevent" (p. 43). Although senescence theory was in place two decades before Gould and Lewontin's (1979) paper, they did not mention it. Its existence clearly contradicts the assertion that practitioners of the adaptationist programme regard *everything* as adaptive.

#### RECENT CHALLENGES TO ADAPTATIONISM

Armed with our concept of adaptation, and recognizing the problems that can arise from incomplete or inadequate specification of its components, we now examine in greater detail five contemporary challenges to adaptationist approaches to the study of phenotypic variation.

### Adaptation and Phylogenetic Inertia

"Evolution is opportunistic and natural selection makes use of whatever variation it encounters" Mayr (1983: 328).

Recently, some authors have proposed that tests of adaptation must consider phylogeny (e.g., McLennan et al., 1988; Brooks and McLennan, 1991; Harvey and Pagel, 1991). In their view, cost-benefit or optimality analyses of a phenotype-set are inadequate for answering phenotype-existence questions because the persistence of a trait may merely reflect phylogenetic inertia. Many behavioral ecologists have been persuaded by this argument. For example, Birkhead and Møller (1992: 155) flatly state that "single species are not statistically independent observations, because closely related species tend to have similar body sizes, ecologies and phylogenetic backgrounds. As a result they often tend to share behavior patterns; *the behavior of individual species therefore cannot be considered as adaptations*" (the italics are ours).

Phylogenetic inertia has two related meanings. First, it is sometimes treated as a unique mechanism of trait persistence. It is more appropriately regarded, however, as a *descriptive* label for the evolutionary stasis of a trait. Of course, traits often persist virtually unchanged in a lineage, but we agree with Williams (1985, 1992: 101-105) that this may often be because descendant taxa inhabit similar ecological and social environments. For example, Edwards and Naeem (in press) showed that cooperative breeding is clustered among certain clades of passerine birds and argued that this indicates phylogenetic inertia in life history traits. But this pattern might reflect the fact that related cooperatively breeding species typically live in the tropics and inhabit similar niches (Brown, 1987). As Williams (1985: 20) pointed out in another useful and telling analogy, the fact that all tires are round more likely means that round wheels are optimally functional than that tire companies are somehow constrained by the round shape of their preexisting molds. Thus, phylogenetic inertia is not an alternative to natural selection as a mechanism of persistence, and evidence of the former is not evidence against the latter. At its worst, the concept of phylogenetic inertia has blunted adaptationist studies

by excluding plausible alternatives from the phenotype-set — namely, those that do not appear among closely related taxa.

A second and related meaning of phylogenetic inertia is that all organisms carry evolutionary “baggage.” That is, the variations upon which natural selection operates in one generation are those that survived from previous generations. As an organism becomes more specialized for a particular environment, it becomes more likely that new mutants which enhance its survival and reproduction in that environment will be favored over those increasing its fitness in other conceivable environments. The slow, directional change in traits within a lineage give the appearance that some inertia-like force is holding them back, or precluding certain phenotypic options. For example, because anurans have been selected so long in aqueous environments, they have become specialized for aquatic life. Therefore, mutations that increase, say, swimming ability are more likely to be favored than mutations initiating or enhancing abilities to fly, burrow, or run.

Here again phylogenetic inertia is a descriptive label rather than an evolutionary mechanism alternative to natural selection. It simply means, as Alexander (1990) put it, “selection, after all, can only operate on last year’s model, regardless of what last year’s model did or where it came from” (p. 244). Returning to the poker game analogy, a player holding two fours is likely to save an additional four he has drawn, to make three of a kind. In contrast, a player holding two aces will undoubtedly discard the four and draw again. The first player has “specialized” on fours, the second one on aces. Neither was constrained to behave this way. They were, however, each dealt a pair initially and decided that a winning hand was more likely if they capitalized on preexisting strengths than if they switched strategies.

New mutations that increase an organism’s survival and reproduction will usually be those that augment its preexisting abilities in its current environment (i.e., that strengthen the organism’s evolutionary “hand”). Mutations that endow the organism with abilities to cope with totally different environments — such as feathers on frogs — will rarely be fa-

vored. This does not mean that flying frogs cannot evolve given the right mutations, strong selection in the appropriate environment, and plenty of time. It only means that as natural selection increasingly perfects specialized forms in particular environments it becomes ever more *improbable* that the evolutionary trajectory of those creatures will radically change.

We stress that the foregoing discussion does not mean that (1) comparative studies are not worthwhile or (2) there are no mechanisms of persistence other than natural selection. Regarding the first point we concur with the many authors, among them Ghiselin (1969), Ridley (1983), and Harvey and Pagel (1991), who argued that Darwin’s comparative method is one of the most powerful tools in evolutionary biology. Regarding (2), as Endler and McLellan (1988) reminded us, a relatively nonadaptive trait may persist because of several processes, including prolonged lack of genetic variation, unbreakable genetic correlations with other traits, recurrent immigration, and genetic drift. These mechanisms represent ways an adaptationist’s predictions might fail; indeed these possibilities are part of what makes the widespread occurrence of adaptations so interesting. The crucial point, however, is that a knowledge of phylogeny is not *necessary* to test among the different mechanisms of trait persistence. As argued previously, whatever is important about phylogenetic history will be recorded in the species’ current environment and biological attributes. Ancestral species do not otherwise mysteriously reach from the past to clutch the throats of their descendants.

Working out the phylogeny of a trait is interesting in its own right, and is the *raison d’être* of many systematists and paleobiologists. Our central point, however, is that investigations of evolutionary *history* differ logically from analyses of the *maintenance* of traits. The former entails unraveling the origins and trajectories of traits in geological time, while the latter involves comparing the fitness consequences of variant traits in the present. Investigations of evolutionary origins and current adaptive value are complementary, not mutually exclusive; they are on different levels of analysis (Sherman, 1988; Holekamp and Sherman, 1989; Emlen et al., 1991).

### *Adaptation and Genetic Correlation*

A second recent challenge to adaptationism is the claim that nonadaptive traits will be common because they are genetically correlated with traits undergoing positive selection. There is no doubt that genetic correlations among phenotypic traits exist in natural populations, owing to pleiotropy and linkage disequilibrium (e.g., Brodie, 1989). Moreover, quantitative genetic models show that genetic correlations can greatly retard, or even prevent, ascent toward an adaptive peak (Lande, 1979; Via, 1987). It should not be assumed, however, that the common genetic basis for intercorrelated traits is necessarily fixed and unmodifiable by selection. Indeed, selection may reduce or eliminate genetic correlations when favored and disfavored traits are coupled, as well as strengthen correlations between jointly advantageous traits.

Appeals to genetic correlations as explanations for the presence of traits thus represent another kind of phenotype-set specification problem: the failure to consider separate, uncorrelated phenotypes in the set of alternatives. For example, if traits A and B were thought to be correlated, as were corresponding alternative traits A' and B', it might be tempting to specify a single phenotype-set consisting of only two compound traits, AB and A'B'. A more complete specification would include two phenotype-sets—(A, A') and (B, B')—which take into account the possibility that the correlation could be broken.

We do not deny that genetic correlations can impede adaptation. Moreover, we acknowledge that in some (special) instances the breakdown of genetic correlations may be unlikely, as with correlations between male traits and female mating preferences that build up automatically due to female choice (R. A. Fisher, 1958; Lande, 1981). We merely suggest it is inappropriate to assume that genetic correlations *cannot* be broken. In particular, finding a genetic correlation between two traits is insufficient for invoking that correlation as the explanation for the presence of either of them. The relative fitnesses of alternatives for each trait still must be examined to address the possibility that both traits are selectively maintained over their alternatives.

To take one example of this problem, Halli-

day and Arnold (1987) suggested that multiple mating by females with different males is a side effect of positive selection for male polygyny and a genetic correlation between the sexes. Hence, they argued, there need be no fitness advantage to females for mating with multiple partners. In this case there is little reason to suppose a common genetic basis for mating frequency in males and females (Sherman and Westneat, 1988), and indeed some evidence indicates that artificially selected changes in males' mating frequency (in chickens; Cheng and Siegel, 1990) and in females' tendencies to remate (in fruit flies; Gromko, 1992) are not accompanied by parallel changes in mating behavior of the opposite sex. Our point, however, is that even if such positive correlations did exist, as is suggested by some studies (e.g., Stamenkovic-Radak et al., 1992), Halliday and Arnold's (1987) explanation suffers from an incomplete phenotype-set specification, since the possibility clearly exists that male and female mating frequencies were in the past free to evolve separately, with a positive correlation between the two becoming established later when it was favored. Thus regardless of male polygyny, the reproductive consequences of multiple mating for females would still merit investigation (e.g., Westneat et al., 1990; Birkhead and Møller, 1992).

### *Adaptation and Developmental Constraints*

Ever since Gould and Lewontin (1979) raised the specter of nonadaptive architectural constraints in evolution, the invocation of developmental constraints for explaining why certain phenotypes occur has been popular among those skeptical of purely adaptationist approaches (e.g., Alberch, 1983; Wake, 1991; Arnold, 1992). Unfortunately, the concept of a developmental constraint is almost as vague as that of phylogenetic inertia—indeed, the two concepts have often been linked. In one of the most complete and synthetic discussions of this topic, Maynard Smith et al. (1985) defined developmental constraints as “biases on the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system” (p. 265).

If developmental constraint explanations are to compete with selective explanations, developmental constraint must refer to a mechanism that can oppose or bias natural selection. It cannot be a mere descriptor of developmental processes that are conserved through evolutionary time. What then are the exact mechanisms by which the developmental system limits or biases the phenotypes that are exposed to selection? Maynard Smith et al. (1985: 269–271) offered five sources (mechanisms) of developmental constraints. The first—“phenotypes accessible or inaccessible, given a particular developmental mechanism”—is described as “the fact that the developmental mechanisms of a given taxon render certain phenotypes more readily accessible than others” (p. 269). Essentially the same description is given of the second mechanism (“phenotypes accessible or inaccessible, given any developmental mechanism”), except that in the latter certain phenotypes are rendered more accessible regardless of the taxon. How certain phenotypes are “rendered more accessible” either specifically or generally is not explained, nor is what is meant by “accessible,” so that there is no delineation of a mechanism; rather a partial restatement of the definition of a developmental constraint is given.

Maynard Smith et al. (1985) hinted at what they meant by observing that “certain patterns may arise repeatedly because they are easily generated by physicochemical processes or by certain patterns of complex systems, even though the details of the process may be entirely different in different cases” (p. 269). This does not get us very far, because one can simply back up the question a step: Why do we see these underlying physicochemical processes or complex mechanisms rather than conceivable others? And why couldn't selection suppress an “easily generated physicochemical process” if the latter were disfavored?

Maynard Smith et al. (1985) offered spiral phyllotaxis of leaf or scale primordia in plants as an example of a developmentally constrained phenotype, and suggested (p. 268) that “phyllotaxis will be a universal feature of those systems that are built to conform to the rules of close packing.” They did not mention

the obvious possibility that, in such systems, natural selection may universally favor close packing by phyllotaxis over alternative arrangements. In sum, the first two “sources” of developmental constraint do not specify a mechanism opposing selection.

An inaccessible phenotype might be one that selection would not favor because it disrupts the original developmental process. This possibility subsumes Maynard Smith et al.'s third and fourth mechanisms (“phenotypes accessible or inaccessible, for selective reasons” and “constraints resulting from canalizing selection”). The fifth possibility is that not enough genetic variation exists to yield a developmental mechanism resulting in a novel phenotype (described as “genotypes accessible or inaccessible, given the present genetic system”). The latter mechanism encompasses “universal constraints” (or “functional constraints,” Arnold, 1992: S97) in the sense that certain developmental processes, such as those requiring an infinite amount of energy, are physically impossible; obviously there can be no genetic variants for such processes. In sum, Maynard Smith et al.'s five sources of developmental constraints reduce to two: selection against disruptive developmental processes and lack of genetic variation.

Now selection against disruptive developmental processes is still selection and cannot be used to dethrone the adaptationist approach. After all, a rare disruptive phenotype X would have lower fitness (zero if it is lethal) than the normal phenotype Y, accounting for Y's predominance. As Dawkins (1982: 39) pointed out, this kind of developmental constraint explanation is not different from a selective explanation. The key is that Y is the adaptation in a context that includes the developmental pathway generating Y. To say simply that “Y exists because X is inaccessible” is a phenotype specification error since it arbitrarily excludes X, thus discouraging any fitness analysis. Indeed, we regard the latter approach as “nonadaptive storytelling” in exactly the same sense as Gould and Lewontin's (1979) version of adaptive storytelling. Thus our approach suggests how developmental constraints can be viewed from an adaptationist perspective: Phenotypes are develop-

mentally constrained when the alternative phenotypes have lower fitnesses because they depend upon developmental processes that would seriously disrupt the original developmental program, thereby reducing viability.

The question remains as to how important developmental constraints (in our sense) are in nature. Ironically, Maynard Smith, lead editor of a recent book (1990) entitled *Organizational Constraints on the Dynamics of Evolution*, concludes the volume by noting that "anyone who has ever tried to invent an organism will know how hard it is to think up anything very different from some actual product of evolution. In evolution, it seems, anything goes" (p. 434). The second mechanism of developmental constraint, lack of genetic variation, is potentially an alternative to natural selection as a mechanism of trait persistence, as we have already acknowledged. But how often does lack of genetic variation constrain development? In a second surge of irony, Barker and Thomas (1987), in a recent volume entitled *Genetic Constraints on Adaptive Evolution*, argue that the lack of genetic variation is not an important evolutionary barrier, except in cases where environments change radically on small time scales.

Despite the paucity of strong empirical tests for developmental constraints or convincing evidence for their importance, appeals to developmental constraints have become increasingly popular. In a recent, prominent example, Wake (1991) argued that evolutionary convergence among taxa may commonly reflect developmental constraints rather than convergent selection. Wake believes that certain taxonomic patterns—in particular, the repeated, independent evolution among plethodontid salamanders of small body size and four-toed feet from ancestors that were larger and had five toes per foot—"show that homoplasy, in this case parallelism, can be a manifestation of design limitations in the form of developmental constraints, which are only indirectly related to adaptive processes. Thus, selection for very small size may have, as an incidental side effect, the loss of a toe" (p. 549). The importance of such design limitations, according to Wake, calls for a "structuralist" versus a "functionalist" approach to evolution.

It is unclear precisely what alternative

mechanism at the same logical level as natural selection underlies Wake's (1991) concept of a developmental constraint. Since Wake offers no evidence of the relative fitnesses of small four-toed and five-toed individuals within plethodontid taxa, design constraints offer at best a description, not an explanation, of the occurrence of four-toedness. It is possible that four-toedness evolved in small individuals because either (1) the production of four toes minimally disrupts the development of small individuals (an example of our selective version of developmental constraints), or (2) for small individuals, locomotion, clinging, and foraging, for example, are more efficient with four toes than with five toes. Both hypotheses (1) and (2) are functional explanations, and neither apparently has been explored. The difference between them is that the selective context for (1) involves the internal environment (the developmental pathway leading to a small individual), while the selective context for (2) involves the external (physical and biotic) environment.

If structuralism is distinct from functionalism, it rests on unspecified—indeed mysterious—mechanisms of trait persistence. Perhaps this vague sort of structuralism is seductive because the repeated observation of one or only a few alternative phenotypes in different taxa induces the feeling that "things simply are only allowed to be this (or that) way." The *crucial* thought experiment, "What would be the evolutionary result if a mutant alternative trait arose and competed with the observed trait?" is seldom conducted. In summary, the structuralist approach either rests on a phenotype-set specification problem and therefore is fundamentally flawed or it dissolves into the recognition of selective developmental constraints, which is consistent with adaptationism and functionalism.

#### *Adaptation and Mechanistic Explanations*

A related, but conceptually different, challenge to adaptationism asserts that since certain complex phenotypes can be generated by simple proximate mechanisms, there is no need to provide selective explanations for their existence. An extreme example is elaborated in a 1988 book by Lima-de-Faria, a molecular geneticist. Lima-de-Faria claimed

that selection is "one of the three myths in science," and that "such terms as 'selection' can be forgotten since they tell us nothing about exact relationships, which must be described in pure chemical and physical terms. . . . Selection cannot be the mechanism of evolution for the simple reason that it is not a material component of organisms" (pp. 3-7). The author went on to propose his own theory of evolution ("autoevolutionism"), which is essentially a laundry list of physical and molecular processes that give rise to structures found repeatedly throughout the animal and plant kingdoms.

In a superficially more persuasive example, Jamieson (1989) proposed an "epigenetic" hypothesis for the evolution of alloparental helping behavior in birds. Briefly, he noted that when habitats are saturated, fledglings are prevented from dispersing. This forces them into contact with begging chicks when their parents' next brood hatches. Since in some species begging calls are the proximate stimuli that cause adults to feed chicks, subadults simply respond to the begging cries of their younger siblings by feeding them. Under this hypothesis, alloparental feeding is essentially a manifestation of misplaced parental care and, as such, it requires no selective explanation (see also Mumme, 1992).

In a similar vein, Page and Mitchell (1991) claimed that the complex, collective properties of insect societies can result from elementary principles of self-organization and therefore do not require selective explanation, and that "specific traits of complex systems may be self-organized consequences emerging from the basic structure of the system itself and not the direct product of natural selection" (p. 290). Drawing on Kauffman's (1984) theory of coupled networks, they argued that, while selection may be able to fine-tune some features of an insect society, "what selection may not be able to do, or at least is unlikely to achieve, is to move the entire system outside the domain of its typical features" (p. 297). The presumed inefficacy of natural selection led Page and Mitchell to conclude that "distinguishing between self-organized and adapted traits is important to avoid falling into either uncritical selectionist or anti-selectionist explanations" (p. 297).

The main problem with the arguments of Lima-de-Faria, Jamieson, and Page and Mitchell is their failure to recognize that developmental or mechanistic explanations are complementary, *not* alternative to selective explanations for the occurrence of traits such as helping behavior and division of labor (Sherman, 1988, 1989). For example, whether or not helping originated as misplaced parental care does not help us understand why alloparental behavior has been maintained and elaborated in so many avian, mammalian and arthropod lineages. The most likely explanations are that helping enhances current inclusive fitness, future reproductive success, or both (Emlen et al., 1991; but see Jamieson, 1991).

Likewise, even if division of labor in insect societies does "result from elementary principles of self-organization," this does not eliminate the hypothesis that selection created or enhanced the very ability to self-organize and also sorted among alternative modes of self-organization. Moreover, even if selection is seen as merely fine-tuning a few parameters of self-organized systems (e.g., worker task thresholds: Robinson, 1992), this may be all that is necessary to produce a wide range of complex, colony-level phenotypes—just as a few changes in key regulatory genes may generate an incredible diversity of individual morphotypes. We thus disagree with Page and Mitchell's (1991) assertion that "if division of labor is a property that emerges under almost all systems that have the basic features of insect societies, then natural selection is not the most obvious explanation for this feature" (p. 297).

In the context of our definition of adaptation, the proponents of self-organization do not consider a plausible set of alternative phenotypes that *might* have evolved, and as a result they see no need to appeal to some evolutionary mechanism that would pick out one of these alternatives. In other words, we view their claims as more examples of arbitrarily restrictive phenotype-sets; these restrictions are reminiscent of those posited by proponents of developmental constraints.

Kauffman (1991) recently argued that although many stable, complex phenotypes can arise spontaneously as a result of simple pat-



terms of intercommunication among the elements of the phenotype, selection will act on and reconfigure the patterns of intercommunication according to their reproductive consequences (favoring patterns, for example, that are better able to handle novel conditions). We agree with Kauffman that being "ordered" is not logically equivalent to being adaptive, so that self-organizing mechanisms for generating order are not alternatives to selective mechanisms generating adaptiveness.

The evolution of presumed nonadaptive female mating preferences also has been attributed to simple proximal mechanisms. For example, Kirkpatrick (1987b) suggested that "[female] preferences may be due to biases that are built into the sensory modality being used and may have no intrinsic adaptive value" (p. 68). The idea is that females, for example, may be able to see some colors better than others (e.g., the colors of preferred foods), hear some sounds more clearly than others (e.g., the sounds of predators), or smell some odors especially acutely. If so, Kirkpatrick (1987b) argued ". . . these intrinsic biases can cause females to favor matings with certain male phenotypes and so result in sexual selection. If biases that exist in the primitive evolutionary state of a female sensory system are the basis for a 'preference,' it would be fruitless to search for the selective forces responsible for its origin" (p. 68). This idea has been endorsed and popularized by Ryan (1990, 1991) as the "sensory exploitation" hypothesis.

Kirkpatrick's (1987b) hypothesis is appropriately seen as a mechanism alternative to natural selection (R. A. Fisher, 1958) for the *initiation* (i.e., evolutionary origin) of female mating preferences. When it is invoked to explain the *maintenance* of mate preferences, however, the sensory exploitation hypothesis suffers from incomplete specification of both the fitness criterion and the phenotype-set. In this context, the hypothesis fails to consider the possibility that female preference for an arbitrary trait regardless of context (mating versus nonmating) might reduce the survivorship of the female or her offspring, thus preventing the spread, or causing elimination, of preferences for the "exploiting" stimulus. This would occur if males exhibiting the exploiting

stimulus were, for example, genetically inferior, subviable, likely to be parasitized or to attract predators, or difficult to find, such that females who preferred such males were penalized reproductively. Thus the phenotype-set must include the female's *lack* of response to the arbitrary trait.

Even if constant preference for the stimulus were favored over the complete lack of preference, we should also consider whether females that expressed the preference in the appropriate nonmating contexts, but not during mate choice, would have higher fitnesses—that is, we would also have to include in the phenotype-set females' context-specific *ignoring* of the exploiting stimulus. The male offspring of the latter females would be relatively unattractive mates, but this might be counterbalanced by increases in the survivorship of either the females or their offspring. In short, the theoretical appeal of the sensory exploitation hypothesis decays when a plausible and complete phenotype-set for the female is constructed.

Recently Ryan et al. (1990) and Ryan and Rand (1990) presented data they claimed support the sensory exploitation hypothesis. They found that the auditory papillae of females in two closely related species of neotropical frogs (*Physalaemus pustulosus* and *P. coloradorum*) are maximally tuned to frequencies that are lower than those of the average male's advertising calls. The frequencies of peak sensitivity for females match the frequencies of "chuck" notes that male *P. pustulosus* add to their calls, and previous studies by Ryan (1985) revealed that males with lower-pitched chucks (the larger males) are preferred by females as mates. Males of *P. coloradorum* do not give chucks, although their females can hear frequencies characteristic of chuck-notes, leading Ryan et al. (1990) to suggest that "the female tuning evolved before the chuck and therefore the chuck played no role in the evolution of the preference" (p. 66). In summary, Ryan and Rand (1990) proposed that "the female's sensory system defined the possible evolutionary alternatives for more attractive male traits and that morphological and phylogenetic constraints on the male determined which of those alternatives was achieved" (p. 312).

The problem with Ryan et al.'s (1990) specific test is that although male *Physalaemus coloradorum* do not give chucks, they still may have gained by producing low-pitched call notes. Females in this species, as in their congener and many other anurans, prefer to mate with males who give low-pitched calls (Ryan and Keddy-Hector, 1992), perhaps because low-frequency calls indicate that the male is large, healthy, and highly fertile (traits that are heritable in some species: Woodward, 1986, 1987). Thus the "preexisting bias" in the female's sensory system may be adaptive in both *Physalaemus* species for selecting the best mate. This hypothesis could be tested by playing low-pitched "white noise" to females and noting their preferences. A selective hypothesis predicts that females of both species would be attracted. Indeed, this has now been confirmed for *P. pustulosus* (Rand et al., 1992).

Why then don't male *Physalaemus coloradorum* chuck? One clue is that in *P. pustulosus* chuck calls are particularly attractive to frog-eating bats (Ryan et al., 1982; Ryan, 1983). If over evolutionary time the predators on male *P. coloradorum* behaved similarly, then as Gardner (1990) suggested, males may not give chuck calls today because chucking was and is dangerous. In sum, the phenotype-set for *P. coloradorum* males should consist of low-pitched versus high-pitched call notes, while for females the set should consist of sensitivity to low-pitched versus sensitivity to high-pitched notes. At this point it is not possible to say which variants are adaptive in either phenotype-set, but it is also inappropriate to argue, as have Ryan and Rand (1990), that that female choice in *Physalaemus* is nonadaptive [Ryan and Keddy-Hector (1992) have now retreated from this claim as indicated by their statement that "the sensory exploitation hypothesis does not eliminate a role for selection pressure on mate choice in the historical establishment of biases . . ." (p. S525)].

Recently Basolo (1990) discovered that female platyfish, which are closely related to swordtails, are more attracted to conspecific males with artificially attached, colored swords than to normal males (which have no swords). Following Ryan's lead, Basolo (1990) interpreted her results to mean that "the evolution of the sword in the swordtail clade was a con-

sequence of selection arising from a preexisting bias [in the female nervous system]" (p. 808). Alternatively, Basolo's data may indicate simply that female platyfish are attracted to males that appear to be large and healthy. This interpretation predicts that female platyfish will prefer virtually any bizarre appendage on males (including an ersatz sword) that exaggerates their body size and coloration without seriously compromising swimming ability or courtship vigor. In other words, perhaps the females' sensory "bias" is more appropriately viewed as an adaptation for discriminating mate choice instead of a mechanistic or phylogenetic constraint.

In the spring of 1992 an entire issue of *The American Naturalist* (Volume 139, Supplement) was devoted to the question "Does sensory biology bias or constrain the direction of evolution?" Among the authors in this volume the proposed significance of sensory constraints varied considerably. For some, such as Alberts (1992), "constraint" simply and unproblematically referred to selectively favored biases in sensory receptor systems. For others (e.g., Fleishman, 1992; Ryan and Keddy-Hector, 1992), sensory constraints were treated as fixed biases that steer future phenotypic evolution. Our disagreement is with the latter usage, since the phenotype-set is typically not constructed to allow for the possibility that the so-called constraint itself will evolve. In particular, the "sensory constraint" may have evolved in response to the signal, not vice versa. Evidence that a sensory bias is adaptive relative to alternative biases (in the context of the signal's occurrence) would support this possibility. In summary, whereas physiological and phylogenetic analyses can reveal the existence and pattern of sensory biases, fitness analyses are required for their interpretation.

#### *Adaptation and Human Behavior*

No treatment of adaptation can avoid discussion of the concept in relation to human behavior, especially since debate over this issue is currently raging among anthropologists, psychologists and sociobiologists—for example, see Kitcher (1985) and the July/September 1990 issue of *Ethology and Sociobiology* (Volume 11, Number 4/5). There are two nested controversies here. The first concerns

whether or not it is possible (or even advisable) to determine the adaptive significance of such behaviors as rape, recreational sex, incest avoidance, cigarette and alcohol use, adoption, and abortion. The most pessimistic view is that such traits cannot be understood via adaptational analyses because they are recent outcomes of purely cultural processes. Our response to this is straightforward. It is legitimate to propose and rigorously test selective hypotheses about the occurrence of *any* phenotypic attribute by examining the relative fitnesses associated with a trait and its alternatives.

Obviously, our definition recognizes even recently arisen behaviors as adaptations so long as they result in higher fitnesses than those achieved by well-specified behavioral alternatives. In our scheme, the predominance of adaptive behaviors would count as evidence that natural selection has increased the probability of observing these behaviors today. Of course, this evidence would not by itself distinguish between the possibilities that any given behavior resulted from (1) biological evolution via natural selection (with gene frequency change), or (2) cultural evolution via differential transmission from parents to offspring (without gene frequency change; e.g., Boyd and Richerson, 1985). At this point it is not critical to distinguish between these two mechanisms because both result from differential reproductive success—that is, “natural selection” in the broadest sense of the term.

Consider the question of whether or not going to a store to purchase food could be considered an adaptation. Under our approach, the phenotype-set is buying food at the store versus not doing so (e.g., stealing food or growing it), the environmental context is city life, and the fitness measure is individual reproductive success. Recall that our definition does not require any specific genetic basis for the adaptive phenotype. Moreover, our principle of mechanistic equivalence frees us from concern about the degree of plasticity of the trait. Thus we can subject a completely novel, learned behavior to adaptational analysis.

Obviously grocery stores have not existed over evolutionary time. A generalized ability

to optimize net gains in different foraging contexts, however, including social ones involving reciprocal exchanges of services or resources (e.g., allogrooming for food), may well have been subject to natural selection during hominid evolution (e.g., Hill et al., 1987). More broadly, as numerous authors have argued (e.g., Alexander, 1979, 1990; Lumsden and Wilson, 1981; Boyd and Richerson, 1985; Barkow, 1989; Betzig, 1989), the expression of “novel” behavioral traits exhibited by modern humans—even if strictly learned through nonfamilial cultural transmission—could nevertheless be affected by cognitive or emotional structures molded by natural selection. For example, as Flinn and Alexander (1982) pointed out, individuals certainly tend to imitate the successful behaviors of others (e.g., behaviors associated with effective resource accrual) and to avoid behaviors that are painful or that otherwise lead others to fail (e.g., self-mutilation). Thus there is a plausible link between modern-day human behaviors and evolved decision-making structures. This being so, studies of grocery shopping and adoption, for example, can yield information not only about behavioral adaptation, but also about the cognitive processes underlying our behavior.

The second controversy in sociobiology is over what methods to use to assess the adaptive significance of human behaviors. Can adaptations be identified by measuring the relative reproductive success of existing behavioral variants, or must we instead rely on teleonomic approaches based on the apparent functional design of presumed underlying decision-making processes? Symons (1990) subscribes to the latter view because “to claim that a trait is an adaptation is to make a claim about the *past* [his italics] . . . all adaptationist hypotheses necessarily entail hypotheses about particular features of past environments that existed for a selectively significant span of time” (p. 428). Thus there is no reason to measure present reproductive differentials, since all the relevant selection occurred long ago. Tooby and Cosmides (1990) agree, stating that “it is illogical for evolutionary biologists to appeal to present advantages as an explanation for present adaptations” (p. 420) and (1992) that the appropriate adaptationist questions are, “What

is the underlying panhuman psychological architecture that leads to this behavior in certain specified circumstances?" and "What are the design features of this architecture — if any — that regulate the relevant behavior in such a way that it would have constituted functional solutions to the adaptive problems that regularly occurred in the Pleistocene?" (p. 55). Opposing this position are many others (e.g., Betzig, 1989; Alexander, 1990; Smuts, 1991) who believe that, as Turke (1990) put it, "understanding current reproductive consequences can help us in the extremely important and difficult task of understanding the evolutionary adaptive significance of adaptations" (p. 461).

We have several responses to this debate. First, the controversy may be somewhat overblown because, as discussed previously (see *The Fitness Measure*), the teleonomic approach to identifying adaptations does not differ logically from investigations that measure differential reproduction. After all, in both cases *some* fitness criterion is used — either optimal design or reproductive success — to sort among existing or plausible alternatives and see if the predominant phenotype is the most adaptive.

Second, as noted in our response to Symons's "*non sequitur*" argument (see *Using the New Definition*), if a predominant phenotypic trait has a higher fitness than its alternatives, then it is reasonable to infer that natural selection produced this outcome. Thus, measuring present day reproductive differentials may illuminate human adaptations.

Third, it is merely Symons's (1990) and Tooby and Cosmides's (1990, 1992) *conjecture* that our present-day behaviors were favored only by selection acting in the distant past. The alternative hypothesis, that our behaviors are favored now and in the recent past, is plausible and testable by determining whether phenotypes that predominate also maximize fitness (i.e., are adaptations). If not, then as with wood ducks nesting in clustered boxes, natural selection has not promoted the expression of these behaviors in environments like the present ones.

Finally, contrary to Tooby and Cosmides (1990), it is not necessary to define the phenotype-set solely in terms of the underlying cognitive mechanisms (or the neural structures

that underlie cognition). The set can consist solely of behaviors, even novel ones, particularly if the hypothesis being tested is that a particular behavior is being maintained by selection. The superficial, modern, or novel elements of a behavior (e.g., in our shopping example, getting into a car, driving to the grocery, and exchanging money for food) are not fundamentally important — they serve as markers for an underlying decision-making algorithm that may have been favored by selection. We agree with Alexander (1990) that usually it is easiest to create the phenotype-set at the level of the behavior, because the underlying cognitive/neural structures tend to be hypothetical constructs and, as such, are obscure and poorly understood.

#### CONCLUSION

This review emphasizes the importance of defining adaptation in a manner appropriate for the problem being pursued. Definitions developed for addressing questions of evolutionary history are not applicable to all issues of interest to evolutionary biologists, particularly questions of phenotype existence. Indeed, recent challenges of adaptationist approaches to phenotype existence questions are beset with difficulties arising from the use of inappropriate definitions and inadequate specification of the components of adaptation. Careful consideration is necessary before labeling a trait as nonadaptive — or adaptive. Critiques of adaptationist approaches have caused investigators like ourselves to sharpen our logic and definitions. Now it is time for proponents of nonselective mechanisms of phenotype presence and persistence to do the same.

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