

from failure to apply these distinctions consistently; it is for this reason that the conceptual issues underlying these distinctions are of great importance and deserve close and careful attention.

Recent controversies over the "adaptationist program," largely initiated by Stephen Jay Gould and Richard Lewontin (1979), have turned on the question whether advocates of the synthetic theory of evolution are, or should be, committed to the following claims: (1) arbitrary traits are usually adaptations or, rarely, side effects of adaptive processes; (2) when traits are not optimal, it is nearly always because of trade-offs among competing demands; (3) adaptive selection works on relatively separable features of the organism, virtually always at the organismic level (cf. Mayr, 1983).

None of these commitments need be part of a sound adaptationist program in the sense discussed by West-Eberhard (on ADAPTATION). But the deep and complex biological issues that occasioned the debate remain: does selection operate at many levels, producing many levels of adaptations? If so, how does this affect the nature of adaptive processes and of adaptations? To what extent, and how, are the features and behaviors of organisms compromises between conflicting adaptive constraints? Can we clarify the relationships among adaptations and adaptive values, the levels of selection, the determination of (expected) fitness, and the analysis of evolutionary processes? Clarification of fundamental concepts is by no means sufficient to accomplish these ends, but it is a necessary part of the effort to advance evolutionary theory beyond its current state.

ADAPTATION: CURRENT USAGES

Mary Jane West-Eberhard

IN CONTEMPORARY evolutionary biology an "adaptation" is a characteristic of an organism whose form is the result of selection in a particular functional context (see Williams, 1966; Futuyma, 1986). Accordingly, the process of "adaptation" is the evolutionary modification of a character under selection for efficient or advantageous (fitness-enhancing) functioning in a particular context or set of contexts. The word is sometimes also applied to individual organisms to denote the "propensity to survive and reproduce" in a particular environment (general adaptation) (see Mayr, 1988). Ernst Mayr (1986) suggests substituting the term "adaptedness" for this usage.

The use of "adaptation" by evolutionary biologists thus differs from that in some other areas of biology, where the term can refer to short-term physiological adjustments by phenotypically plastic individuals (adaptability) or to a change in the responsiveness of muscle/nerve tissue upon repeated stimulation.

According to strict usage in evolutionary biology, it is correct to consider a character 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. Incidental ability to perform a task effectively is not sufficient; nor is mere existence of a good fit between organism and environment. To be considered an adaptation a trait must be shown to be a consequence of selection for that trait, whether natural selection or sexual and social selection—whether the selective context involves what Darwin called "the struggle for existence," or competitive interactions with conspecifics.

Several kinds of evidence can contribute to determining whether or not a characteristic of an organism is an adaptation (after Curio, 1973, elaborating on suggestions of Tinbergen, 1967). The first is correlation

between character and environment or use. A character shows evidence of being an adaptation if: (a) the same form or similar forms occur in similar environments in a number of different species, especially in unrelated species (due to convergence); (b) variant forms of a character in a number of related species (e.g., of a single genus) accord with differences in the environments of the respective species, or with the mode of usage of the character in different species; (c) variant forms appearing in different life stages during ontogeny accord with differences in the environment or behavior of the respective life stages; or (d) for complex characters in a particular context, the more their component aspects can be related point by point to function in that context (the goodness of "design" of Williams, 1966, pp. 12ff.).

The second kind of evidence used in determining whether a character is an adaptation is that which results from altering a character. An organ or behavior is experimentally altered or eliminated, in order to see how this affects its efficiency in a particular function or environmental condition.

A third kind of evidence is obtained through comparison of naturally occurring variants (individual differences). The efficiency or reproductive success of different forms or morphs within a species are compared in the situation(s) where they are hypothesized to function as adaptations.

All of these approaches provide evidence for or against the hypothesis that the structural peculiarities of a trait owe their existence (spread and persistence) in a population to their contribution to fitness via performance of a particular task.

An example can serve to illustrate some of the difficulties in applying the adaptation hypothesis to particular cases. The elaborately sculptured and species-specific forms of the head and thoracic horns of male beetles have been imagined to be adaptations for fighting, for digging, and for influencing female choice of mates. Observations of behavior, however, demonstrate that the structural details of beetle horns and the differences between related species correspond to inter-specific differences in the particular ways they are wielded during battles between males; their special features are not used in special ways during courtship or digging, although they are occasionally used to hold females or to enlarge holes occupied by beetles (Eberhard, 1979, 1980). Thus the available evidence supports the hypothesis that beetle horns are adaptations for fighting, and that they are only incidentally or secondarily used during mating and digging. It could be argued, however, that the structural peculiarities observed are developmental or pleiotropic results of traits evolved in other contexts (the "exaptations" of Gould and Vrba, 1982), and that the high degree of correlation with behavior (which is difficult to consider merely coincidental) has been produced by selection to use these incidentally common struc-

tures to the individual's advantage in fights; by this interpretation horn morphology would be a nonadaptation and the form of behavior an adaptation.

It is not always easy to apply the distinction between adaptation and incidental use, even given information on present employment and evolutionary history. Suppose an incidental use or secondary function were to persist while the original, evolved function disappeared (e.g., horns came to be used exclusively for digging even though they had not been modified in that context). Strict adherence to the above definition would not permit horns to be considered an adaptation for digging even though digging had become the exclusive context for their use and even though they might be maintained (rather than lost) under selection in that context. The concept of "pre-adaptation" has been applied to such cases, in which a trait has evolved in one context and has come to be used (function) in another.

Suppose a horn used secondarily but exclusively in digging undergoes some small modification enhancing the digging function. Can it then be considered an "adaptation" for digging? Evidently it can, although this points up another difficulty in the distinction: how much modification is necessary to consider a character an adaptation in a particular context? What, indeed, is a "character," as opposed to a feature or modification of a character? (See CHARACTER.) The designation of an aspect of the phenotype as a character (whether an adaptation or not) is always somewhat arbitrary: is digging behavior, along with horn morphology, part of a single co-selected trait? This would classify the pre-adapted horn as part of a new "adaptation."

Curio (1973) argues that when exactly the same character is employed in more than one context and contributes to fitness in all contexts it should be regarded as an adaptation only for that context where it makes the greatest contribution to fitness. Such an argument can lead to contradictions in applying the above criteria, for example, if the form of a character has been shaped in the past primarily by a function presently of less importance (in terms of fitness) than another use (which by Curio's criterion would be the primary adaptive context even if not effecting evolutionary modification of the character). In most discussions, the historical criterion (rather than fitness difference) would predominate: the character would be considered an "adaptation for" the function in which it was originally or primarily shaped by selection. Even when multiple uses are completely contemporaneous in their fitness effects Curio's criterion seems difficult to apply, given that, insofar as the same form can serve multiple functions, the sum of all (even minor) contributions to fitness could influence form in the face of counterselection (in other contexts) favoring alternative forms. These considerations regarding multiple functions apply as well to questions of selection at different levels of organization, whereby the same trait may simultaneously affect, for example, the survival or replication

rate of individuals and groups, and hence the population frequencies of their constituent genotypes.

Given current usage of the word "adaptation," it is clear that not all observable evolved characteristics of organisms are properly regarded as adaptations. In their efforts to explain peculiarities of form, biologists often attempt to apply a hypothesis of adaptation with insufficient empirical support. Several authors have argued in favor of parsimony in the use of this term (e.g., Williams, 1966; Curio, 1973; Gould and Lewontin, 1979). They stress the importance of considering alternative explanations for particular and even complex characters, especially the hypotheses that form can be vestigial (the product of selective forces no longer operating) or the incidental result of developmental processes evolved under selection for other aspects of the phenotype.

Stephen Jay Gould (1984b) has proposed that covariance of characters could be accepted as "positive evidence" of nonadaptation, and has erected a dichotomy of "automatic sequelae" (nonadaptations) versus selected traits (adaptations). This criterion of nonadaptation tacitly requires some analysis of adaptation, however, because it is impossible to tell from covariance alone which of several developmentally associated traits has been most important in the spread and/or maintenance of the set. Furthermore, one cannot assume that covariant aspects have not been modified independent of each other. For example, Gould (1981) interpreted the male-like female display morphology and behavior of the genital displays of female hyenas as a nonadaptation, evolved by selection in males and only incidentally or secondarily expressed in females. However, female genital displays are known to function as appeasement gestures (Wickler, 1966; Eibl-Eibesfeldt, 1970), and if modified or somewhat specialized due to selection on females, they would qualify as adaptations. This would be true even if a set of characters used in this way originated via a regulatory mutation that allowed them to be expressed in females as well as in males (where the original set had been formed by selection). Indeed new adaptations may sometimes originate as coadapted character sets, whose expression has been shifted between sexes or life stages (via heterochrony) and then modified in the new context (see West-Eberhard, 1989).

Gould (1984b) also argued that "ecophenotypic responses" to environmental conditions cannot be regarded as adaptations, because they are not "genetically mediated," but this criterion for nonadaptation (environmental influence in phenotype determination) cannot hold unequivocally: plasticity itself can be seen as an adaptation. Furthermore, ecophenotypic responses are always products of gene-environment interaction and thus are genetically mediated (see West-Eberhard, 1989). By Gould's criterion, all environmentally cued, facultatively expressed phenotypes would pre-

sumably be classified as "nonadaptations," including the winter pelage of hibernating mammals, the restive walking behavior of the swarming phase of migratory locusts, and the ability of chameleons to match the background coloration of their resting places.

Developmental mechanism *per se* does not provide enough information to determine whether or not a trait is an adaptation, though it might provide information on how nonadaptive traits are maintained (e.g., via covariance with adaptive traits), and even on how adaptive traits originate. An aspect of the phenotype that is a secondary "by-product" of selection for another aspect (in the sense of being either completely covariant with it or a less commonly expressed product of the same genotype) may have the following relationships to adaptation and selection.

a. The observed frequency and form of the secondary aspect of the phenotype may be completely owing to characteristics evolved under selection for a covariant aspect, in which case the character would not be regarded as an adaptation.

b. More than one covariant aspect of the phenotype may contribute simultaneously to fitness in different functional contexts (e.g., pleiotropic effects of a single gene) from the time of their (simultaneous) origin and be concurrently favored by selection. I would call both positively selected traits adaptations, even if one of them made a greater contribution to the fitness and spread of the covariant set and its underlying genes, because both aspects contribute to the rate of spread of the set in competition with alternatives; Curio (1973) would term only the greater contributor to fitness an adaptation.

c. The initial spread or frequency of the secondary aspect of the phenotype in the population may have been entirely due to selection for a covariant aspect, but its form and/or frequency of expression may have been modified in the context in which it is expressed. In this case a phenotype not originally an adaptation has become an adaptation by evolution in its own context.

To classify a pleiotropic or secondary effect as a non-adaptation requires showing not only that it is (a) only expressed together with a developmentally related trait that is a proven adaptation, but also evidence that (b) concurrent positive selection, and (c) independent modification do not apply.

Overly facile application of the term adaptation encourages the assumption that all characters are adaptive; for this reason, some authors have urged restraint on use of the term. It remains the case, however, that persistent attempts to discern the adaptive significance of phenotypic traits—to apply an adaptation hypothesis—have been a primary and fruitful occupation of evolutionary biologists since before Darwin. There is still controversy over the importance of selection and adaptation versus non-

adaptation in the evolution of phenotypes. Although adaptation cannot be assumed, some authors argue that it should be regarded as the most important (commonly supported) hypothesis for the spread and persistence of organismic traits: "The experimental study of adaptation has unravelled adaptive values in such unobtrusive and inconspicuous details of organismic organization that one should think of a character as having survival value until the contrary has been demonstrated" (Curio, 1973, p. 1046). Richard Lewontin (1978, p. 125) gave the following compelling reason for continuing to pursue the "adaptationist" program that seeks to explain characters in terms of their evolved functions, in spite of its difficulties: "Even if the assertion of universal adaptation is difficult to test because simplifying assumptions and ingenious explanations can almost always result in an ad hoc adaptive explanation, at least in principle some of the assumptions can be tested in some cases. A weaker form of evolutionary explanation that explained some proportion of the cases by adaptation and left the rest to allometry, pleiotropy, random gene fixations, linkage and indirect selection would be utterly impervious to test. It would leave the biologist free to pursue the adaptationist program in the easy cases and leave the difficult ones on the scrap heap of chance. In a sense, then, biologists are forced to the extreme adaptationist program because the alternatives, although they are undoubtedly operative in many cases, are untestable in particular cases."

ALTRUISM: THEORETICAL CONTEXTS

Alexander Rosenberg

IN *Sociobiology: The New Synthesis* (1975, p. 578) E. O. Wilson defines altruism as "self-destructive behavior performed for the benefit of others." More specifically, sociobiology treats behavior as altruistic whenever the behavior increases the reproductive fitness of another at the expense of one's own reproductive fitness. At the outset of his touchstone of contemporary behavioral biology, Wilson identifies altruism as the "central theoretical problem of sociobiology," and asks, "how can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?" (1975, p. 3). The problem is apparently one of explaining how the actual is possible. Altruism, like cooperation in general, is an obvious feature of human and intrahuman behavior. Indeed, sociality requires it. And yet if altruism reduces fitness, in the evolutionary long run it should have been expunged, not enhanced. So we face a choice between exempting human and some intrahuman behavior from the constraint of natural selection or finding a way of rendering it consistent with Darwin's theory. This is Wilson's problem.

The biological problem of altruism is vexed by a prior terminological controversy. Altruism as commonly understood is by definition action that advantages another by design. It is an "etiological" concept, which carries a definitional commitment to a motive—an intentional cause. But this motive is missing in Wilson's definition. And few sociobiologists suppose that the occurrences of actions and their intentional causes are explainable by natural selection. Nevertheless, sociobiological altruism might be relevant to motivated altruism. It may explain a genus—altruism motivated or unmotivated—of which motivated altruism is a species.

But even if what the sociobiologist means by altruism has nothing to do with motivated altruism, Wilson's stipulative definition still describes an important phenomenon with which evolutionary theory must come to terms. For other-regarding behavior—no matter its cause—seems endemic