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Adaptation: Current Usages

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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


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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 behaviour 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: 12ff.).

The second kind of evidence used in determining whether a characteristic is an adaptation is that which results from altering a character. An organ or behaviour 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 behaviour, 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 behaviour (which is difficult to consider merely
coincidental) has been produced by selection to use these incidentally common structures to the individual's advantage in fights; by this interpretation, horn morphology would be a non-adaptation, and the form of behaviour 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? The designation of an aspect of the phenotype as a character (whether an adaptation or not) is always somewhat arbitrary: is digging behaviour, 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 Curie'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, Curie's criterion seems difficult to apply, given that, in so far as the same form can serve multiple functions, the sum of all (even minor) contributions to fitness could influence form in the face of counter-selection (in other contexts)
favouring 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 favour 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 (1984) has proposed that covariance of characters could be accepted as 'positive evidence' of non-adaptation, and has erected a dichotomy of 'automatic sequelae' (non-adaptations) versus selected traits (adaptations). This criterion of non-adaptation 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 independently of each other. For example, Gould (1981) interpreted the male-like female display morphology and behaviour of the genital displays of female hyenas as a non-adaptation, 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 co-adapted 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 (1984) also argued that 'ecophenotypic responses' to environmental conditions cannot be regarded as adaptations, because they are not 'genetically mediated'; but this criterion for non-adaptation
(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 presumably be classified as 'non-adaptations', including the winter pelage of hibernating mammals, the restive walking behaviour of the swarming phase of migratory locusts, and the ability of chameleons to match the background colouration 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 non-adaptive 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 favoured 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 proved 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: 1046). Richard Lewontin (1978: 230) gave the following compelling reason for continuing to pursue the 'adaptationist' programme 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.

References


