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Adaptations and History

George V. Lauder, Armand M. Leroi and Michael R. Rose

The historical definition of adaptations has come into wide use as comparative biologists have applied methods of phylogenetic analysis to a variety of evolutionary problems. Here we point out a number of difficulties in applying historical methods to the study of adaptation, especially in cases where a trait has arisen but once. In particular, the potential complexity of the genetic correlations among phenotypic traits, performance variables and fitness makes inferring past patterns of selection from comparative data difficult. A given pattern of character distribution may support many alternative hypotheses of mechanism. While phylogenetic data are limited in their ability to reveal evolutionary mechanisms, they have always been an important source of adaptive hypotheses and will continue to be so.

The last five years have witnessed a virtual explosion in comparative studies of organismal design. Fueled in part by the increasing acceptance of cladistic approaches to inferring relationships among taxa, comparative biologists have begun to attack a wide range of evolutionary problems. Sexual dimorphism, life history, ecology, muscle function and insect–plant coevolution are but a few of the many issues that have been investigated by comparative phylogenetic methods[1-11].

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With this rise in comparative studies has come an emphasis on the concept of adaptation as having an important historical component. Gould and Vrba[12] codified this view by developing a terminology that distinguished between the current utility of a character and its historical origin. For Gould and Vrba, an adaptation was a trait whose 'historical genesis' was due to the *same* selective pressure as that which currently maintains the trait. A trait whose origins in a clade were due to selective pressures *other* than those that currently maintain it was labeled an 'exaptation'.

Gould and Vrba's[12] definition of adaptations has had considerable influence on other workers who have elaborated on the historical definition of adaptation. For example, Coddington[13] defined an adaptation in cladistic terms as an 'apomorphic function promoted by natural selection'. Furthermore, the elaboration of an historical dimension to the concept of adaptation has led to another definitional expansion, namely, that the only traits that should be called adaptations are those which confer enhanced performance in the current environment relative to the traits that preceded them evolutionarily: 'To constitute an adaptation, a character must be shown to provide current utility to the organism and to have been generated

historically through the action of natural selection for its current biological role'[14]. This definition, or some version of it, is now widely accepted[9,13,15-17], and for the sake of brevity we refer to it as the *historical definition of adaptations.* Central to this definition, as to many other (but not all[18]) definitions of adaptations, is the notion that selection is the evolutionary process that produced the trait under consideration[19,20]; traits that are considered to be adaptive thus evolve under selection *for that trait.*

This definition of adaptations leads naturally to a research methodology that aims to reveal the way in which historical changes in selective regimes or environments have shaped the evolution of clades[13,14]. A centerpiece of the method is the role given to measuring organismal performance. The method, summarized in Box 1, consists of four steps. First, historical changes in environmental circumstances or in a 'selective regime'[14] that might have plausibly influenced the evolution of a clade are identified. It is assumed that environmental characteristics relevant to fitness can be mapped onto a phylogenetic tree much like any other character. Second, the performance attributes that might have possibly conferred increased fitness under a given selective regime are identified. Third, the historical changes in organismal traits (be they behavioral, morphological or physiological) that might have plausibly influenced such performance traits are identified.

And fourth, the relative performance of these organismal traits in ancestral (plesiomorphic) and derived (apomorphic) states is measured. If the derived trait has a superior performance relative to its ancestor, and arose after historical change in the 'selective regime', then, and only then, is the trait an adaptation (Box 1).

The historical method for analysing characters outlined in Box 1 promises two key advances. First, under this methodology, a trait need not have evolved numerous (phylogenetically independent) times to be deemed an adaptation. Instead, even a trait that has evolved only once might be analysed for environmental and performance correlates and pass the requisite tests appropriate to be labelled an adaptation (Box 1). Second, the comparative phylogenetic method suggests that one will be able to inventory characters within a clade to determine which traits are adaptations, which are disaptations and which are nonaptations without having to measure directly the action of selection on each trait (Box 1).

Our purpose here is to examine the mechanistic assumptions that underly the historical approach to adaptations, to illustrate potential difficulties with inferring the past action of selection solely from comparative data on traits, environments and performance, and to indicate the value that such comparative data still have in suggesting mechanistic hypotheses and in testing proposed scenarios.

The historical approach to adaptation: genetic and environmental complexities
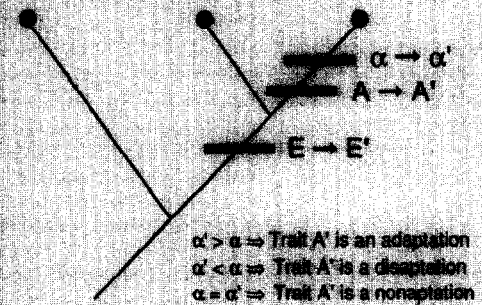
Identifying adaptations using the method outlined in Box 1 requires that assumptions be made concerning the genetic relationships among organismal traits, performance and fitness, as for most clades we have few data on the genetic basis of these features[16,20]. First, there must be positive genetic correlations among the organismal trait, the performance variable and fitness in the taxa and environments considered in the historical analysis. Second, the genetic relationships among the trait, performance variable and fitness must be simple. Implicit in the historical definition of adaptations is the notion that

the trait under consideration should not be genetically correlated with others that might influence fitness, and that fitness should be determined by the performance variable under consideration.

Box 2 (Case 1) illustrates these relations, and how they might appear on a phylogeny. In this example, the common ancestor of the three species has a particular trait (A), performance (α), and is subject to environment E. In the course of cladogenesis, a change in environmental circumstance (E') imposes a novel selection pressure for performance attribute α' and hence trait A'. Trait A', then, is an adaptation because its evolution is directly due to its superior performance in E' relative to the ancestral condition (A).

But the relationship among traits, performance and fitness in organisms is rarely as simple as this[21–23]. When it is not, then application of historical methodology to discover adaptations may lead to a false conclusion. One possible way in which problems might arise is illustrated in Case 2 of Box 2. If a particular trait under analysis, A, is positively genetically correlated with another trait B, but is uncorrelated genetically with the performance variable α, then selection for trait B' might result in the fixation not just of B' (due to increased fitness in the new environmental

circumstance E'), but also of A' due to the positive genetic correlation of A and B. A' would be identified as an adaptation given the phylogenetic pattern shown in Case 2 (Box 2), under the historical definition of adaptation. But in fact selection would not have operated directly for character A', and thus it should not be classified as an adaptation. The phylogenetic pattern in this case is misleading as to the underlying mechanistic cause of character evolution.

A second situation in which a phylogenetic pattern might be misleading is shown in Case 3 of Box 2. If a single trait A is positively genetically correlated with two different performance variables (for example, locomotor endurance and feeding rate), then fixation of trait A' may result from the fitness consequences of performance trait β in environment E'. Given the phylogenetic pattern produced by this pattern of correlations, the historical definition of adaptation would show trait A' to be an adaptation for α' whereas in fact it would not be, since selection did not favor performance trait α'. Rather, A' evolved due to its correlation with a second performance variable.

Although in Box 2 we have separated the fitness of a trait from measurement of its performance, in practice the historical methodology for uncovering adaptive traits treats

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Box 1. Using the historical definition of adaptation

Given an hypothesis of the phylogenetic relationships of three species, the distribution of traits, environments and performance attributes are mapped onto the phylogeny. Here, 'performance' is taken to mean the execution of some ecologically relevant activity which can be measured, such as running speed, jumping ability or rate of nutrient uptake[2]; 'environment' is the same as the 'selective regime' of Baum and Larson[14].

For the clade depicted, trait A, environment E and performance α are all plesiomorphies. According to the historical definition of adaptations, trait A' is an adaptation if: (1) it confers enhanced performance (α') relative to the plesiomorphic condition (α), and (2) if trait A' arose after the shift to a novel environment or selective regime (E → E') hypothesized to be causally related to the evolution of trait A'. Thus, adaptations are characters that result from selection for that character where selection has produced a derived character that confers increased performance[12–15]. Note that this method allows the inference of the state of adaptation even in cases where a trait has evolved only once. Also, no data on the genetic correlations between trait A and other traits that might also be correlated with fitness are required. Typically, the phylogenetic distributions of traits, performance and environments are all the data one has on which to base an analysis of adaptation; data are rarely available on fitness or genetic correlations among traits for species within a clade.

If the derived trait A' results in reduced performance relative to that in outgroup taxa, then the trait A' is called a disaptation. If measured performance is equivalent in ingroups and outgroups then trait A' is called a nonaptation[14].

$\alpha' > \alpha \Rightarrow$ Trait A' is an adaptation
$\alpha' < \alpha \Rightarrow$ Trait A' is a disaptation
$\alpha = \alpha' \Rightarrow$ Trait A' is a nonaptation

Box 2. Traits, performance, fitness and selection

Here we give schematic illustration of three different evolutionary mechanisms of arriving at the same phylogenetic association between a change in an organismal trait (A → A'), an increase in a performance attribute (α → α'), and a change in environment or selective regime (E → E'). On the left side of the figure, organismal traits, performance variables, and fitness are viewed as quantitative traits which may or may not be genetically correlated. Thick lines connect positively genetically correlated attributes, while thin lines connect genetically uncorrelated features. On the right side these same features are viewed as discrete attributes and are mapped onto a phylogeny. Separation of multiple black bars within a lineage on the right panels is for graphical convenience only and does not indicate the relative time of character origin.

Case 1: A one-to-one correspondence among trait A and its measured performance and fitness. Character state A' becomes fixed after the change in selective regime *because* of its superior performance properties (α') in the new environment (E'). For this reason it is a true adaptation according to the historical definition.

Case 2: A more complex relationship among organismal attributes. Character state A' becomes fixed after the change in selective regime (E → E') *not because* of a genetic association with performance state α', but rather because trait A' is positively genetically correlated with trait B' which, in turn, is positively associated with α'. If trait B is unobserved, or if its genetic connections to trait A and α are not identified, then the transition A → A' will be viewed as an adaptation when in fact it is not: the selective regime did not act directly on trait A.

Case 3: Another example of a complex relationship among organismal attributes that may mislead the historical definition of adaptation. Trait A' becomes fixed after the change in selective regime (E → E') not because of its genetic association with performance state α, but rather because of its association with the derived condition of another performance state β. If β is unmeasured then A' will appear to be an adaptation by virtue of its association with α', when in fact α' has no beneficial fitness consequences in the new environment E'. Note that if all the correlations to the left of each cladogram are known in advance, then a phylogenetic analysis would not result in erroneous inferences of adaptation.
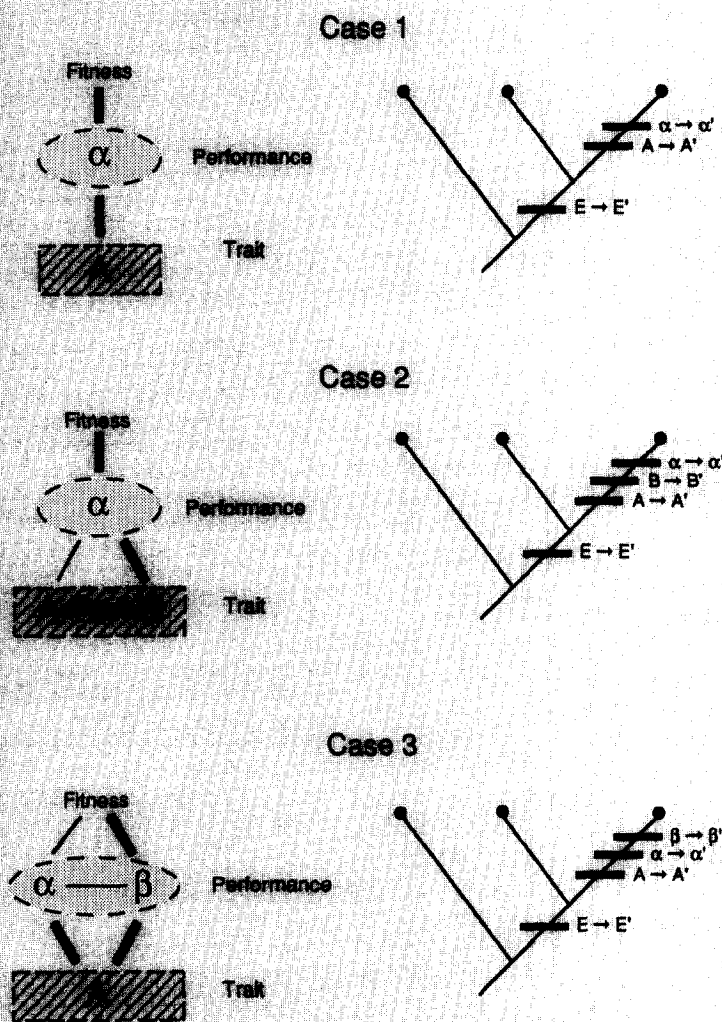
these two attributes as largely synonymous: there is seldom a way to measure fitness directly in most of the taxa that have been analysed using historical methods, and performance is used as a surrogate for fitness. However, the problem that arises when performance is equated with fitness can be seen in the following example. Consider an allele *a* which, although conferring increased performance on some performance trait, say, burst running speed, has many deleterious pleiotropic effects on fitness-related traits: fecundity, survivorship and so on. Such an allele could be replaced by another, call it *a'*, which confers feeble performance but beneficial pleiotropic effects on fitness-related traits, when this latter allele always has a higher net fitness than the former. The traits associated with the invading allele would clearly be adaptations in the sense that their increase in frequency was due to natural selection for that allele. Yet once *a'*

was fixed in the population, and its phenotypic attributes correctly identified as apomorphies in a cladistic analysis, an analysis of the evolution of burst running speed in this lineage would show performance to have manifestly decreased, thus making it a 'disaptation'. One reply to this scenario might be that since the historical definition of adaptation always references a particular performance variable for a trait, the above example is, indeed, truly a disaptation no matter the increase in the population's mean fitness. But this produces the awkward situation of labeling some of the phenotypic properties of *a'* 'adaptations' and others 'disaptations', where what matters is the relative net fitness of the alleles in question.

Use of the historical definition of adaptations also requires that the phylogenetic distribution of selective forces be identified. This is done by coding different environments (or 'selection regimes') as

alternative character states, and mapping them onto a phylogeny. But how much do such codings reveal about the selective forces acting upon a trait? Examples of selective regimes that have been used for historical analysis include 'terrestrial', 'arboreal' and 'bird-pollinated'[14]. These selective regimes incorporate many environmental features. A transition from a terrestrial to an arboreal selective regime, for example, might be used to analyse the possible adaptive nature of a derived morphological trait in the limb by the methods of Box 1. But the derived feature of limb morphology may have evolved in response to selection for vertical climbing ability, the ability to walk on branches, the ability to feed in trees, or the ability to carry young along branches. Each of these different possible selective factors is subsumed under the general heading 'arboreal selective regime'. In addition, as reflected in Case 2 of Box 2, the derived limb

condition could have evolved as a correlated response of selection for, say, body size, in arboreal habitats. Were this in fact true, then the derived limb trait would not be an adaptation, no matter what the relative performance tests show. Defining the selective regime broadly (e.g. as 'arboreal') precludes recognition of specific selection factors that may have been causally responsible for the evolution of a trait.

The many environmental factors, and thus selection forces, that might have influenced the evolution of a trait also cause difficulty when it is necessary to formulate a performance test of derived and ancestral traits. Choice of the test must be matched to the hypothesized selective regime. But performance tests by their very nature evaluate a specific operational hypothesis, while the selective regime might be only broadly defined. Given the selective regime 'arboreality', then which of the many possible performance tests should be conducted on ingroup and outgroup taxa? If we test individuals in each taxon for their maximum speed along a tree branch, and the actual selective force that gave rise to the derived morphological trait selected for increased vertical climbing ability, then the results of our performance test will be irrelevant to the question of adaptation in response to the actual selection mechanism.

But it is not only the number of possible performance attributes influencing fitness nor the number of environmental factors which compose a selective regime that make reconstructing the causes of evolution so difficult. It is also that the parts of an environment interact to determine its fitness function, and that these interactions are likely to be of daunting complexity and subtlety. This is apparent when we consider that one of the most important components of the selective regime is the organism itself. The average physiology, behavior and morphology of a population form a unique background against which novel traits are tested by selection – a background, furthermore, which itself evolves, often so as to alter profoundly the fitness value of any given trait[24-26].

The evolutionary inconstancy of the genetic background bears on our ability to use mutational or phenotypic manipulations to recover the fitness and performance properties of ancestral traits. If manipulations designed to simulate the ancestral condition of a trait are to yield meaningful performance or fitness estimates, then those manipulations should be done against the ancestral genetic backgound. While phylogenetic methods enable us to reconstruct the history of particular traits and possibly even certain features of this background[9,27], they do not enable us to reconstruct the myriad genetic and phenotypic interactions and correlations that determine the fitness of a trait. If such correlations among traits cannot be recovered in extant taxa, then we will be unable to infer accurately the relative fitness of ancestral and derived characters (Box 2).

The role of comparative methods

Despite the limitations noted above concerning the ability of comparative methods to reveal adaptive processes, it is possible to analyse mechanisms of adaptation by directly studying the genetic relations and selective forces that influence the evolution of extant replicate populations[21,22,28-32]. Also, multiple evolutionary origins of traits in correlation with an environmental state, long held as evidence of adaptation[33,34] remain strong evidence that selection has had a similar effect across lineages despite differences in genetic background. The comparative method does have unique and valuable roles to play in the study of evolution. Among other things, phylogenetic analyses can assist with the falsifying of adaptive hypotheses which make explicit historical predictions of the order in which a clade acquires evolutionary novelties[2,4,9,10,35]. Comparative patterns have always been an important source of adaptive hypotheses[36,37]; they will continue to be so, even given the difficulties of inferring evolutionary mechanisms.

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