

LETTER TO THE EDITOR

Dangers of 'Adaptation'

Heredity (2012) 108, 460; doi:10.1038/hdy.2011.98; published online 2 November 2011

Organisms respond to their environment through changes in their phenotype, responses known as 'phenotypic plasticity'. There is an unsolved empirical issue concerning the proportion of plastic changes that are adaptive. Generally, one would expect that the plastic phenotypic changes made in response to environments that an organism has frequently encountered in its past, over the timescale in which evolutionary adaptation has been possible, are likely to be adaptive. It is less obvious that organisms will respond to novel environments in an adaptive way, although learning is an example through which adaptive behavioural responses to new environments might arise. But it is certainly not necessarily true that phenotypic responses to changed environments are adaptive rather than pathological.

However, 'adaptation' has, of course, had a long and confused history in evolutionary biology, and there is no universal agreement on its meaning. There is fairly general agreement that adaptation must be related to Darwinian fitness in some way and that the adaptation of a genotype or phenotype can only be assessed relative to some real or theoretical alternative. Thus, potentially, it is meaningful to enquire whether, when an environment provokes a phenotypic change in an organism, this phenotypic change conveys a higher fitness than others that could be imagined, and is, in this sense, an adaptation. In this view, adaptation is an observation of higher Darwinian fitness than an alternative, and thus is not here defined as necessarily arising through Darwinian evolution. Hughes (2011) suggests that phenotypic plasticity is indeed a source of adaptive evolutionary change between species through his plasticity-relaxation-mutation (PRM) mechanism.

Hughes suggests, as others have in the past (West-Eberhard, 2003, 2005), that much adaptive evolution is preceded by a time when phenotypic plasticity is shown by the adapting species. In other words, in his terminology, when the environment is A, the phenotype is A'; and when the environment is B, the phenotype is B'. Clearly, an organism showing phenotypic plasticity could fairly easily evolve into one showing A' all the time if it found itself in an environment of constant A, and could evolve to show B' all the time if it found itself in an environment of constant B, and the restriction of the phenotype to A' and B' could be genetically enforced in the two cases, thereby constituting an evolutionary change. The defining feature of Hughes' model is that this loss of redundant pathways, leading to B' and A', respectively, is the result of neutral mutation and drift, rather than being created by the selectively driven spread of new alleles eliminating these pathways.

But is the prior phenotypic plasticity itself adaptive? In other words, when the environment A exists and the organism develops phenotype A', is this the optimal response to environment A in fitness terms? Clearly, in order to account for adaptive evolution, the phenotypic plasticity that is frozen in interspecies divergence has to constitute an adaptive response to the environment. Hughes (2011) suggests that phenotypic responses to novel environments often will be, either randomly, or because developmental programs are such as to change phenotypes adaptively when confronted by new environments.

The problem is that without a Darwinian process creating the ability of the organism to respond adaptively to environmental

variation, there seems no general reason why a response A', to environment A, would be adaptive rather than pathological.

The solution, it seems, is that, even for a process of phenotypic plasticity that has not been created by Darwinian adaptive evolution, the outcomes of phenotypic plasticity will sometimes be adaptive, and it is these outcomes which, when hardwired into the genome by what are neutral losses of alternative pathways, create the adaptive evolution that the PRM model thereby explains.

The problem, of course, is that this result relies on a very modest definition of 'adaptation' and 'adaptive' change. In the description of 'adaptation' above, adaptation is necessarily defined relative to specific alternatives, and there is scope for disagreement about what those alternatives should be. One extreme view is that adaptation postulates an optimal phenotype and should have a higher fitness than all possible alternatives. At the other end of the spectrum, one can imagine a comparison with just one random alternative. Thus, if an organism is introduced into two environments, A and B, and produces phenotype A' in A and phenotype B' in B, then, even if the creation of phenotypes A' and B' are not the result of a Darwinian process, but are random responses, it would be expected (with a probability of a quarter) that the random response A' might have a higher fitness than B' in environment A and, simultaneously, the random response B' might have a higher fitness than A' in environment B, and thereby both A' and B' could, by this very modest criterion, be described as adaptations; and, of course, this can be extended to interspecific differences in the way suggested.

But, if adaptation is to be defined to include the subset of random phenotypic changes that outstrip, in fitness, single random alternatives, biologists would have no interest in adaptation. Adaptation, as it is used in biology, does not mean that phenotypic changes are random and that sometimes, by chance, they improve fitness. Rather, biologists view the property of adaptation as a specific attribute of living things, visible ubiquitously, and not expected to arise by chance. Darwinian processes of fixation of adaptive alleles are one way for the non-randomness to arise, but genetic hardwiring of random phenotypic plasticity would not be.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

JFY Brookfield

Centre for Genetics and Genomics, School of Biology,
University of Nottingham, University Park, Nottingham, UK
E-mail: john.brookfield@nottingham.ac.uk

Hughes AL (2012). Evolution of adaptive phenotypic traits without positive Darwinian selection. *Heredity* **108**: 347–353.

West-Eberhard MJ (2003). *Developmental Plasticity and Evolution*. Oxford University Press: New York.

West-Eberhard MJ (2005). Developmental plasticity and the origin of species differences. *Proc Natl Acad Sci USA* **102**: 6543–6549.