

**STRESS AND ECONOMICAL CONSTRAINTS TO PHENOTYPIC EVOLUTION****JULES KIESER**

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**ABSTRACT:** Heritable variation in characters related to fitness is a necessary condition for the evolution of adapted phenotypes by means of natural selection. However, the response to selection also depends on the residual available energy of the organism. Because phenotypic evolution involves the reallocation of finite resources and because this process is energetically expensive, a balance has to be struck between energetic costs and the attainment of an optimally adapted phenotype. The interaction of these two basic parameters (environmental variation and residual energy) will determine whether evolution proceeds gradualistically or punctationally.

**1. INTRODUCTION:** The classical analysis of natural selection by Darwin(1859) focused on the interactions of organisms and their environments. Thus it was suggested that variations would accumulate in organisms which would best fit them to their surroundings. With changes in the environment, new variations would become advantageous and supplant those which were less well adapted. The entire process, it was suggested, depended on the availability of phenotypic variation. Recently, researchers have focused on the importance of a consideration of both natural selection and of historical events in a study of such variation (Felsenstein, 1985; Wake & Larson, 1987; Janson, 1992). For instance, a recent common ancestry may constrain the adaptive radiation of (a) a lineage of organisms because of a low fitness of transitional forms between discrete adaptive optima (Wright, 1982); (b) closely related taxa may have had less time to evolve than distantly related taxa (Cheverud *et al.*, 1985); or (c) there are physiological, developmental or morphological constraints that may bias the kinds of traits that can evolve (Gould & Lewontin, 1979; Wake & Larson, 1987). In addition, it has recently been suggested that a fourth limitation, that of economical restraint, may be as important as those mentioned above (Kieser, 1993).

**2. THE ENERGETICS OF ACQUISITION:** The allocation of limited resources is one of the most fundamental characteristics of all living organisms. Accordingly, attempts to explain phenotypic evolution in terms of resource allocation should occupy a central place in evolutionary theory.

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In reality, however, such studies have focused largely on narrow trade offs between reproductive expenditure and future fecundity (Williams, 1966; Clutton-Brock, 1984; Shine & Schwartzkopf, 1992). What is needed is a paradigm which would explain how a phenotype becomes optimally adapted to its environment in terms of the energetic costs of resource allocation.

In the game of evolution, energy controls all levels of phenotypic change (van Valen, 1978; Brown *et al.*, 1993). This view has two underlying assumptions. Firstly, it assumes that the amount of energy available is finite. In other words, there is a perpetual intra-organismal competition for limited energetic resources. There is no cost-free response to selection and hence the reallocation of resources involved in the process of phenotypic change depends on the energy available. Organisms need a baseline of energy to perform their normal physiological process. Those individuals (or those species) which have energetic reserves above this physiological baseline will thus have more energy available to be channelled into resource reallocation than those species or individuals who have little or no residual energy.

The second assumption is that natural selection would tend to favour an accumulation of energy above the physiological baseline. Thus the ability to accumulate such residual energy must be heritable and there must be a positive correlation between selection for residual energy and the potential for future change. As van Valen has pointed out: "energy controls evolution, and for any evolutionary unit, at any time scale, natural selection maximises the expected amount of energy available for growth and reproduction" (van Valen, 1978, p 289).

The phenotype, in whatever form it may be visualised, is nothing but a collection of acquisitions which has as its source the interplay between the adaptive need of the organism (demand) and the initiatory capability of the genes (supply) (Kieser, 1993). This principle applies to all levels of evolution.

Those features which contribute to a complex adaptation of the phenotype must be acquired from the production capability of the genes. However, for a complex adaptation to be acquired, resources have to be allocated to its production and thus there must be contributions of energetic output from lower levels of organisation. In this context, the organism (or collection of organisms) with a higher inherent level of energetic resource (residual energy) will tend to acquire an adaptation faster than one with low levels of residual energy. This does not mean that mutation rates differ between such groups of organisms.

### Constraints to phenotypic evolution

It simply means that there will be more energy available to certain groups of organisms (or to certain species) which will in turn enable them to exploit their available mutations more fully than those groups which have lower levels of residual energy.

Additionally, the argument presented here does not mean that the genome is energy limited. It does however, mean that fulfilment of the genome potential is energy limited. There is thus a balance between an optimally adapted phenotype and the energetic costs of the phenotypic changes involved. Van Tienderen (1991), who explored this subject theoretically, has further emphasised that selective forces would tend to be counterbalanced by selection for lower costs of genomic reactions.

Fitness may thus be defined in terms of energetics (Brown *et al.*, 1993). What I propose here is that fitness be defined as the rate at which resources in excess of those required for normal growth and maintenance, may be channelled into the acquisition of newly required morphological features. The potential for phenotypic change thus rests on two limiting rates: the rate at which an individual may acquire resources from its environment (Brown *et al.*, 1993) and the rate at which it can convert those resources into residual energy available above physiological maintenance levels.

**3. RESOURCE ALLOCATION:** While the allocation of limited resources is geared to the fulfilment of the survival need of the phenotype, it originates in the production capability of the genes. The theory of acquisition simply states that evolutionary change, in whatever form or from whatever cause, reduces to an interplay between phenotypic demand on the one hand, and genomic supply on the other. Thus the acquisition of an adaptation (or of a phenotype) by natural selection implies a need, a genetic supply and available residual energy for resource reallocation.

As an example of the balanced reallocation of resources during evolution one might cite the development of alternate morphologies within a species. Many organisms show more than one morphological type, the most typical example being that of gender. Numerous insect species, for instance, are dimorphic for wing size, with one sex having large wings capable of flight while the other lacks functional wings. In these cases, one might argue that the costs associated with being winged in one gender could be reallocated to other phenotypic acquisitions in the wingless gender. Studies of wing dimorphic sand crickets *Gryllus firmus* have, in fact, provided compelling evidence for phenotypic trade offs associated with wing size reduction (Roff, 1984; 1990; Roff & Fairbairn, 1991). These authors showed that correlated responses to selection for wing size changes in females were genetically based.

Typically, small-winged females were found to begin reproduction earlier and have higher fecundity than large-winged females, suggesting that finite resources had been withdrawn from wing production or reallocation to earlier maturation and reproduction. A similar finding was reported in male oriental chinch bugs Cavalerius saccharivorus where brachypterous males were shown to mature earlier than macropterous males (Fujisaki, 1992). Finally, balanced reallocation of energetic resources was shown in male thrips Hoplothrips karnyi where large-winged males had small front legs and wingless males had large front legs. The development of large front legs had thus occurred at the cost of the development of large wings (Crespi, 1988).

The evolution of front legs capable of defeating winged males had involved a withdrawal of energetic resources from wing production with reallocation of these resources to forelimb enlargement.

**4. ALLOCATION AND STRESS:** One of the central features of evolution is the allocation of resources. Evolution is the agent which determines how the available but finite resources of the organism are to be allocated among competing needs. Because the resources are limited, a shift in allocation to one component of the organism will be at the expense of other components (Koehn & Bayne, 1989; De Kruijpf, 1991). A typical example of resource shift is an organism exposed to environmental stress.

Stress may be regarded as an agent which places the organism at a disadvantage, which in turn requires continued expenditure of excess energy. Of interest is the study by Blows and Hoffmann (1993) who reported that the mechanism by which Drosophila serrata responded to desiccation stress was by a reduction in the metabolic rate, which suggests the presence of genetic variance for the control of metabolic rate. While an organism can increase stress tolerance simply by reducing its metabolic rate (Hoffmann & Parsons, 1991), phylogenetic adaptation to the stressor will require a reallocation of resources, which implies an added energetic cost. In other words, adaptability under stressful environmental conditions has to be dependent upon available metabolic energy. Thus it seems reasonable to suggest that an organism with a high level of residual or latent energy (over and above the normal physiological needs) will be better equipped to adapt to environmental stress than one with a low level of residual energy.

If one accepts that there is directionality (but not progression - Gould, 1989) in evolution and also that there are multiple levels of operation of the evolutionary process (Brandon & Burian, 1983) then it becomes interesting to speculate about the role of available energy in the operation of this complex process.

## Constraints to phenotypic evolution

One could suggest that the capability of producing and maintaining an ever increasing number of complex adaptations over evolutionary time would then rest on three pillars - the need for an adaptation (demand), the capability to produce the adaptation (supply) and the residual energy required for resource allocation. In particular, one could theorise that while selection acting over an evolutionary significant time span would tend to change the genome as to decrease the average amount of genetic load per locus and hence allow the maintenance of alleles at a larger number of loci (Wimsatt & Schank, 1989), it would also tend to decrease the economic maintenance load per adaptation, which would make available residual energy for future allocation needs.

**5. ENERGY BALANCE:** The most critically important issue to the present line of thinking remains that of the nett energy balance of the individual (or collection of individuals). Basal metabolic cost is the energetic requirement of keeping the metabolic machinery running (Mitton, 1994). Bayne and Newell (1983) expressed the energetic balance within an organism as follows:

$$Pr + Pg = C.AE - (Rm + Rr)$$

where Pr and Pg are the production of gametes and of somatic tissues, C the consumption of energy, AE the absorption efficiency of consumed energy, Rm the metabolic cost of maintenance and Rr the general costs of activities such as seeking of food and mates, defending territories, etc. A consideration of the balanced energy equation helps to explain some of the features of evolutionary energetics. Terms on the left side of the equation represent development and reproduction. On the right side, the first term represents absorbed energy while the second represents costs. If the acquisition of a new morphological feature requires added energetic outlay, then this change in the left side of the equation (increased Pr) has to be matched by an increase on the right side. Hence, differences among individuals in the variables on the right hand side of the equation could contribute to variation among individual capabilities for Pr (and arguably for Pg). Relationships between energetic costs and absorption are not constant because organisms live in heterogenous environments and their energy budgets vary both with genotype and environmental conditions (Mitton, 1994). An environmental change that imposes a drain upon the energy budget will thus reduce available energy for evolutionary phenotypic acquisition.

That stasis appears to prevail in more widely fluctuating, rapidly changing environments has in fact been shown by Sheldon (1987, 1990, 1993). From his extensive examination of *Builth* trilobites, Sheldon found that a stable, narrowly fluctuating environment led to sustained phyletic evolution while, almost paradoxically, widely fluctuating environments resulted in stasis. It is argued that the latter type of environment would impose an energetic drain on the organism, hence reducing available energy for phyletic change which would in turn result in stasis. In narrowly fluctuating, slowly changing environments, there would be no such energetic drain, leaving enough residual energy for continuous phyletic change.

The problem with the present line of thinking is that there are so few empirical examples to underscore it. Nevertheless, a number of studies have shown that energy saved by heterozygosity may be invested in growth (Pg) or reproduction (Pr).

For instance, weight loss in starving oysters has been shown to be less severe in heterozygous individuals (Rodhouse *et al.*, 1986). That fecundity increases with heterozygosity has been shown in the guppy (Beardmore & Shami, 1987) and in the blue mussel (Rodhouse *et al.*, 1986). In *Drosophila melanogaster*, heterozygotes for the acid phosphatase locus, the glycerophosphate locus and the alcohol dehydrogenase locus produced significantly more eggs than homozygotes (Serradilla & Ayala, 1988). Basal oxygen consumption has also been shown to decrease with heterozygosity in a number of species (Garton, 1984; Danzmann *et al.*, 1988), which prompts the suggestion that if heterozygotes are more physiologically efficient than homozygous individuals, then the former may have more available energy to channel into evolutionary acquisition or to reproduction and may thus respond faster to selection than homozygotes.

**6. RESIDUAL ENERGY AND PHENOTYPIC CHANGE:** I have argued that it is important for the evolution of complex adaptations that there be available energy for the allocation of resources needed for it. This requirement thus places a constraint on the evolution of an organism.

It was Parsons (1993 a,b,c) who suggested that the potential for phylogenetic alteration may be expressed in terms of two correlated continua: the availability of metabolic energy above maintenance and the nature of the environmental challenge. An expanded visual interpretation of these relationships is given in Fig. 1. Species which have high levels of residual energy and who live in highly fluctuating stressful environments, such as colonists, are characterised by a rapid reallocation of resources necessary to meet the environmental challenge. Evolutionary change is not restricted by the availability of residual energy and adaptation will be punctual rather than gradual. Rapid divergence associated with increased rather than the expected decrease in genetic variability (Nei & Maruyama, 1975) has, in fact, been demonstrated in many colonising events (e.g. Parkin & Cole, 1985; Boileau & Hebert, 1991).

In species with low residual energy levels, which are subjected to fluctuating environments (Fig. 1.) the response will be characterised by phylogenetic crises.

**THE ENERGY/ENVIRONMENTAL MATRIX**

		Environment	
		Fluctuating	Steady
Residual Energy	LOW	<p><b>Activity:</b> crisis</p> <p><b>Example:</b> species borders</p> <p><b>Result:</b> gradualism or extinction</p>	<p><b>Activity:</b> initial rapid change</p> <p><b>Example:</b> deep sea; caves</p> <p><b>Result:</b> gradualism</p>
	HIGH	<p><b>Activity:</b> opportunism</p> <p><b>Example:</b> colonists</p> <p><b>Result:</b> punctuational change</p>	<p><b>Activity:</b> trivial change</p> <p><b>Example:</b> stable ecosystem</p> <p><b>Result:</b> gradualism</p>

Fig. 1. Parson's energy/environmental matrix. Species with high levels of residual energy will show punctuational change in fluctuating environments. Low energy species will always evolve gradualistically. (See text for explanation).

Parsons (1993c) has shown that this is a feature of species borders where the sheer weight of energetic cost of environmental perturbations restricts normal physiological processes and hence limit range expansion.

In spite of high levels of phenotypic variability, evolutionary change is limited by low levels of residual energy. The nett result is gradualistic change or extinction. The former is seen, for instance, in living fossils such as the brachiopod *Lingula* which survives relatively unchanged in widely fluctuating stressful environments (Ward, 1992).

Restrictions on the availability of energy also preclude rapid evolutionary change in stable environments. An extreme example is that of an organism living in an environment such as the deep sea or a cave, where the potential for major change is dampened by low energetic availability (Howarth, 1993). Trivial phenotypic change will characterise these organisms. Slow, gradualistic change will also characterise the fourth group of organisms - those which have high levels of energy and which inhabit steady environments.

From the foregoing, it is concluded that evolutionary equilibrium may be achieved by optimising the phenotypic fit to the environment, but not without a constraint due to available residual energy. Irrespective of the strength of the need for change, or of the availability of genetic variability, an optimal phenotype will only be evolved if there is also sufficient residual energy to meet the costs of the required reallocations of resources within the organism.

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