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Review

Evolution of Plasticity: Mechanistic Link between Development and Reversible Acclimation

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Phenotypic characteristics of animals can change independently from changes in the genetic code. These plastic phenotypic responses are important for population persistence in changing environments. Plasticity can be induced during early development, with persistent effects on adult phenotypes, and it can occur reversibly throughout life (acclimation). These manifestations of plasticity have been viewed as separate processes. Here we argue that developmental conditions not only change mean trait values but also modify the capacity for acclimation. Acclimation counteracts the potentially negative effects of phenotype–environment mismatches resulting from epigenetic modifications during early development. Developmental plasticity is therefore also beneficial when environmental conditions change within generations. Hence, the evolution of reversible acclimation can no longer be viewed as independent from developmental processes.

Trends

Phenotypic plasticity increases resilience to environmental change.

Developmental conditions determine capacity for reversible acclimation later in life.

This mechanistic link between development and acclimation means that the costs of plasticity are reduced.

Evolutionary models can incorporate this link explicitly to improve predictions.

New Ideas on the Evolution of Plasticity

Changes in the abiotic and biotic environments can have a profound influence on animals. For example, changes in temperature, salinity, and diet can alter the rates of physiological processes, and the presence of predators can influence morphology. Animals can compensate for changes in the environment by adjusting physiological rates. One of the most important aspects of responses to environmental variation is that the characteristics of animals (phenotypes) are not fixed within individuals [1–4]. Hence, animals can remodel their physiology to maintain performance and fitness across a broad range of environments [5,6].

Individual plasticity falls within two broad categories: that induced by the parental gametic and offspring embryonic environments (**developmental plasticity**; see Glossary), and reversible plasticity (**acclimation**) that occurs within juvenile or mature organisms [7–9]. In the literature, these forms of plasticity are viewed as occurring independently from each other and in response to different selection pressures. Environmental variation is often predicted to impose selection that favours either developmental plasticity or (reversible) acclimation [3,10–12]. Yet, recent evidence suggests that acclimation capacity is altered by the environmental conditions experienced during early development. Here, we argue that the two forms of plasticity are mechanistically linked, and that acclimation capacity is a quantitative trait that is modulated by developmental processes. This distinction is important, because it changes the way responses of animals to variable environments are viewed. Rather than having evolved independently in response to different environmental signals, developmental conditions would induce acclimation capacity when it is advantageous. Hence, acclimation is not necessarily expressed in every

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generation within the same population, which would reduce the costs of acclimation. By contrast, acclimation would reduce the cost of developmental plasticity when there is a mismatch between developmental conditions and the subsequent offspring environment. These interactive dynamics change the way the evolution of plasticity is understood and modelled, because both forms of plasticity would have evolved under a single selective regime.

In this review, we start by summarising plasticity and the environmental contexts under which the different forms of plasticity are thought to have evolved. We then present the argument that developmental plasticity and acclimation capacity are mechanistically linked, using a brief survey and examples from the literature on thermal responses of ectothermic animals. We develop our argument with a discussion of how the interaction between developmental processes and acclimation capacity influences the costs of developmental and reversible plasticity. We conclude with a discussion of the ramifications of our thesis for modelling the evolution of plasticity and predicting the responses of populations and ecological communities to environmental change. We also suggest some future directions for empirical research.

Responses to Variable Environments

The instantaneous relationship between physiological traits and short-term (acute) environmental fluctuations define the **performance curve**. Typically, the performance curve follows a Gaussian, inverted 'U'-shaped curve, where performance declines on either side of the maximum until it reaches critical minima beyond which performance ceases [13]. Yet, the way traits vary acutely in response to the environment is modulated by phenotypic responses (**phenotypic plasticity**) to longer-term environmental change [2,14]. In other words, the mode, breadth, and maxima of the performance curve are plastic. Over the previous three decades, numerous theoretical models, empirical studies, and reviews have explored the conditions under which phenotypic plasticity has evolved [15–23], and considered the selective advantages of different types of phenotypic plasticity in relation to genetic adaptation [10–12,24–27]. Genetic adaptation is effective in matching phenotypes to environmental conditions when the environment changes gradually over many generations. In this case, selection in one generation will increase fitness in subsequent generations. However, in environments that fluctuate between generations selection in one generation will be maladaptive in the next generation. Under these circumstances, phenotypic responses to selection should be minimised [28], and **developmental modifiers** (Box 1) that reduce or modulate the phenotypic effect stemming from genetic variation should be favoured [28–30]. Hence, when environments change across generations, but are relatively stable within generations, environmental conditions during prezygotic or early postzygotic development are likely to predict the conditions individuals will experience at maturity. In this case, developmental modifiers are predicted to match individual phenotypes to the prevailing environmental conditions [16,22,28,31]. The phenotypic effects of the parental environment on offspring are often referred to as **transgenerational plasticity** [32–34].

Developmental plasticity tends to have persistent effects on adult phenotypes [35–37], and disadvantages of developmental plasticity arise when developmental modifiers fix mean trait values within generations, but the actual environment experienced by individuals deviates from that prevalent during early development (discussed later). In environments that change recurrently within a generation selection should therefore favour reversible acclimation [35]. Acclimation confers the capacity for individuals to remodel physiological processes repeatedly throughout their lifetime to compensate for the potentially negative effects of changing conditions [5,10,24,38]. Acclimation enables individuals to maintain relatively consistent physiological rates despite marked differences in environmental conditions over periods of several days or longer [8,25,39–41]. For example, seasonal temperature change can induce acclimation of physiological processes.

Glossary

Acclimation: facultative phenotypic responses within juvenile or adult organisms that result in a shift of reaction norms in response to environmental variation that occurs over a period of several days or longer. Phenotypic changes resulting from acclimation are reversible and repeatable in the lifetime of individuals.

Developmental modifiers: regulatory genes or proteins that affect the contribution of other genes to the phenotype.

Developmental plasticity: phenotypic changes that occur in response to the prezygotic and early postzygotic developmental environments. Responses to the developmental environment tend to have persistent effects on the phenotypes of mature organisms.

Epigenetic: any mitotically or meiotically heritable contribution to the phenotype that does not involve a change in DNA nucleotide sequence.

Methylation: a process whereby histones or DNA are chemically modified by the addition of methyl groups. Methylation of histones or DNA changes access to DNA by transcription factors and thereby alters gene expression programs.

Nuclear receptor: a family of proteins that, when bound to a ligand such as a hormone, bind to DNA to regulate the expression of target genes.

Performance curve: a function that characterises the way physiological or behavioural traits vary over an acute environmental gradient.

Phenotype–environment mismatch: a discrepancy between the environment during early development that induces a particular phenotype, and the environment experienced later in life, with the consequence that the induced phenotype is maladaptive.

Phenotypic plasticity: expression of different phenotypes by a single genotype often in response to environmental variability. Phenotypic plasticity falls within two broad categories: that induced by the parental gametic and offspring embryonic environments (developmental plasticity), and reversible plasticity that occurs within mature organisms.

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