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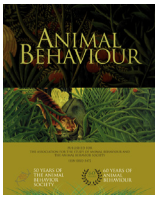

Special Issue

The multidimensional consequences of the juvenile environment: towards an integrative view of the adult phenotype

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Early juvenile environments influence trait expression in complex and often nonintuitive ways. Although the breadth of these effects is well recognized, researchers generally focus on the effect of single ecological triggers (such as resource availability, latitude or predator presence) on traits within a single dimension (e.g. morphological, behavioural or physiological phenotypes). This approach has yielded a wealth of knowledge about environmental conditions that trigger different plastic allocation strategies and reaction norms of a number of traits. However, it tells us little about the way in which early life conditions influence resource allocation, yielding differentially integrated adult phenotypes. Here, I argue that we must begin to understand how complex environments shape the conditional development and expression of suites of traits to produce complex, adaptive phenotypes. I begin by examining the importance of the juvenile environment when attempting to understand phenotypic expression at later life history stages. I describe how different types of plasticity affect relationships between traits, and I provide four case studies that illustrate the influence of plasticity on trait integration, which strongly suggests that evolution of norms of reaction must be considered if we are to understand the evolution of integrated phenotypes. I next highlight the importance of understanding the physiological and genetic underpinnings of this plasticity because such poorly understood aspects of the phenotype regulate developmental pathways that determine phenotypic expression. I conclude with suggestions as to how future research can begin to accommodate multidimensional approaches, and in doing so, further our understanding of an integrated phenotype concept.

Be it the longer tails in barn swallows, *Hirundo rustica* (Møller 1988), the larger antlers in red deer, *Cervus elaphus* (Kruuk et al. 2002), or the brighter and more complex coloration displayed by guppies, *Poecilia reticulata* (Brooks & Endler 2001), as biologists, we are fascinated by the traits that afford individuals increased fitness. This attraction has led to a thorough understanding of how certain traits, most often sexually selected traits, are correlated with fitness in specific contexts (Andersson 1994). As a result of this research, phenotypes quickly became summarized by the possession and expression of specific traits due to their known associations with fitness. Identifying phenotypes in such a manner, however, is problematic because traits are related through a common genetic framework and a shared pool of resources. In this sense, an individual's phenotype is more than the expression of specific traits. What is required is a more holistic view that incorporates the relationship of all traits and underlying mechanisms that interact to create an integrated phenotype (Pigliucci & Preston 2004; Fig. 1). Although there is an argument that the reason for this lack of an integrative understanding is a combination of the introduction of and focus on molecular techniques and a lack of focus on conceptual ideas of the phenotype (Pigliucci 2003), I see two other reasons we have failed at understanding phenotypes as more than the presence of a specific subset of traits at maturity.

The first problem is that early research focused on associating fitness with a small number of traits that were most easily measured (usually morphological, life history and behavioural traits). As a result, the importance of less conspicuous traits that were more difficult to measure (e.g. immune response), initially not as obvious (e.g. metabolic rate), or were involved in development (e.g. mechanistic traits) were poorly understood. Even now, when researchers have the ability to examine a wider variety of traits, the focus is often on traits within a single dimension (i.e. phenotypic class or type) in an effort to simplify experimental designs. For example, although geometric-morphometric approaches examine variation in shape by increasing the number of morphological traits and landmarks examined (Bookstein 1991; Zelditch et al. 2004), they still focus only on morphology and ignore traits in other phenotypic dimensions (e.g. life history, behavioural, physiological

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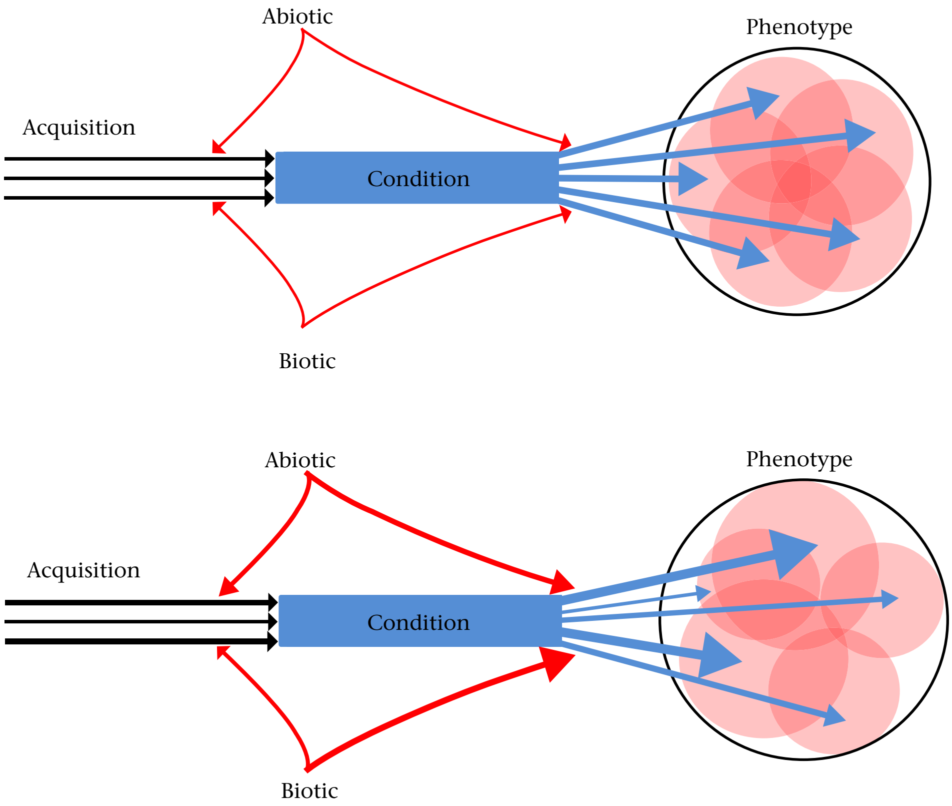

Figure 1. A conceptual diagram of the role of resource acquisition, ecological environment and allocation on phenotypic expression. The phenotype symbolized by the black circle is composed of traits in multiple dimensions (red circles). Each dimension interacts and is correlated to some extent with traits in other dimensions. In the top figure, abiotic and biotic environments (red arrows) affect how resources are acquired (black arrows) and allocated towards different traits (blue arrows) as well as the pool of resources available (condition). In the bottom figure, changes in the ecological environment affect genetically based variation in resource acquisition through assimilation ability and the pool of resources (condition). The ecological environment further affects how resources are allocated towards different trait dimensions. The size of the arrows and circles indicates the relative allocation towards the different dimensions. In this case, changes in allocation affect both expression and covariation among the traits within and between the different dimensions. Adapted from Rowe & Houle (1996) and de Jong & van Noordwijk (1992).

or immunological). As a result, we have a poor understanding of the covariation between traits of different types and of the way different classes of traits interact to create an integrated phenotype.

The second problem stems from our general perception of the role of the juvenile environment in adult trait expression. Our appreciation of the importance of a shared genetic framework in establishing a relationships among all traits (de Jong & van Noordwijk 1992) led to a focus on both life history trade-offs (Roff 1992; Stearns 1992) and the importance of genetic variation in resource acquisition (i.e. condition dependence; Rowe & Houle 1996) in shaping trait expression. Although studies exploring the role of condition dependence provide a wealth of information on how the juvenile resource environment affects the expression of genetically correlated traits (Blows et al. 2004; Brandt & Greenfield 2004; Gosden & Chenoweth 2011), these studies largely ignore the importance of the broader ecological environment recognized in studies of phenotypic plasticity (Pigliucci 2001; West-Eberhard 2003). Accepting that condition dependence is a specific subset of phenotypic plasticity concentrated on resource abundance, and by expanding the diversity of juvenile environments examined, we can improve our understanding of the role of the juvenile environment in generating an integrated phenotype (Fig. 1). This is particularly important as studies of phenotypic plasticity demonstrate that abiotic and biotic ecological triggers can affect resource acquisition and assimilation through behavioural (Lima & Dill 1990) and developmental (e.g. Relyea & Auld 2004) responses to the environment, factors that are rarely considered in laboratory studies of the genetic underpinnings of condition dependence.

I echo past arguments that our understanding of the influence of juvenile environments on the expression and integration of adult phenotypes will be best understood if we increase the number and range of traits examined (Relyea 2004b; Houle 2011); however, I emphasize the necessity to examine traits across multiple dimensions as only such examinations will provide a truly integrative understanding of the phenotype. I secondarily argue that it is necessary to place these examinations in a proper life history framework that incorporates a broad examination of the juvenile ecological environment. This is important because ecological triggers of phenotypic plasticity prior to maturity can alter the covariation between suites of traits across dimensions. By combining the above two approaches, we will improve the quality of our insight into (1) the way phenotypic plasticity changes as a function of singular and combined ecological triggers experienced by juveniles, (2) the effect this has on the integration of the adult phenotype and (3) the extent to which genetic covariation constrains trait expression (i.e. the degree to which covariation between traits can be decoupled). This will improve our understanding of causes and implications of phenotypic integration and provide greater insight into multidimensional phenotype–fitness associations.

The aim of this review is to highlight the importance of understanding how different biotic and abiotic environments independently and interactively trigger phenotypic plasticity, and what this means for our understanding of an integrated phenotype. I will begin by briefly describing the various types of phenotypic plasticity and their relevance with respect to how different plastic