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.

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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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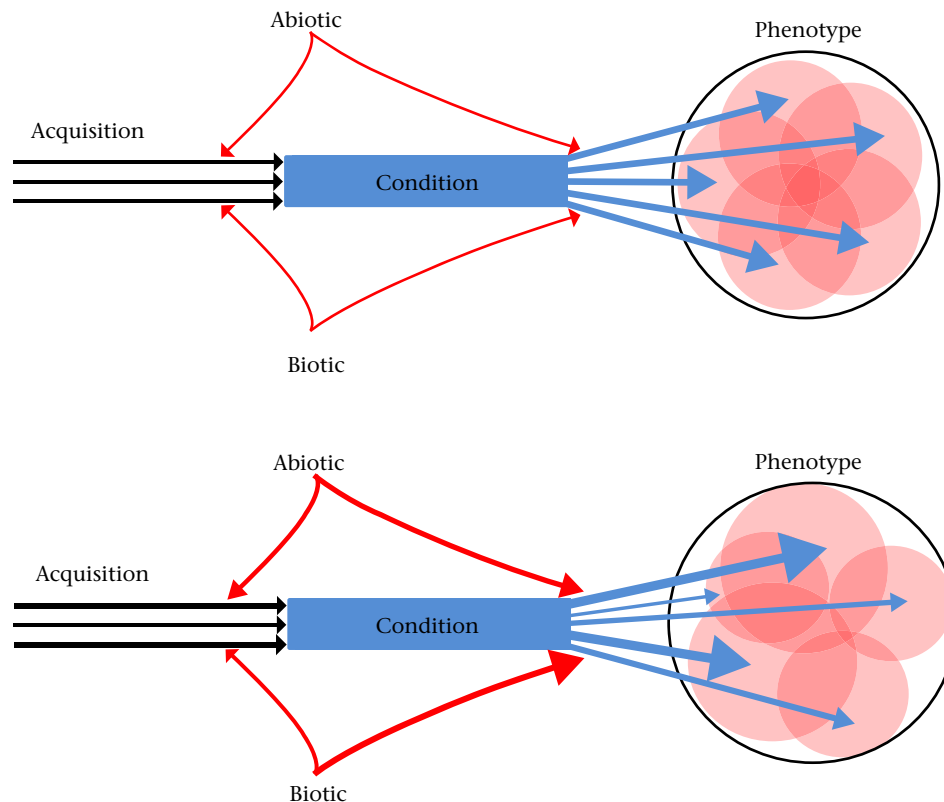
Figure 1. A conceptual diagram of the role of resource acquisition, ecological environment and allocation on phenotypic expression. The phenotype symbolized by the black circle is composed of traits in multiple dimensions (red circles). Each dimension interacts and is correlated to some extent with traits 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

strategies affect covariation among suites of traits. I will follow by presenting several case studies that describe how ecological triggers affect suites of traits across multiple dimensions in an effort to illustrate the importance of including early environments in our understanding of phenotypic expression. Finally, I discuss the gaps in our current understanding and the factors that researchers will need to consider if they are to incorporate a multidimensional perspective in their research. I hope that this will highlight the importance of taking into account evolutionary history, ecological experience and trade-offs during development to produce a holistic view of the phenotype.

PHENOTYPIC PLASTICITY AND TRAIT VARIATION

Phenotypic plasticity is the capacity of a genotype to alter the phenotypes it produces in different environments. How a particular genotype responds to a specific environment can be visualized by a reaction norm, a function that describes the genotype–environment interaction (Schlichting & Pigliucci 1998; Carroll & Corneli 1999; West-Eberhard 2003). Phenotypic plasticity is, however, a general term that describes the entire spectrum of behavioural and developmental plasticity. To understand how plasticity generates different types of phenotypic variation, it is useful to distinguish activational and developmental plastic responses to environmental change (Pigliucci 2001; West-Eberhard 2003; Piersma & van Gils 2011; Snell-Rood 2013).

Activational plasticity (Snell-Rood 2013) is a change in phenotype, most often behaviour, that can be induced rapidly in response to a particular environment, and equally rapidly reversed. Examples are changes in foraging behaviour and habitat use due to the sudden presence of predators or expression of male courtship behaviour. Once the stimulus disappears from the environment, the behaviour ceases. This form of plasticity is less likely to contribute to a well-integrated phenotype than is developmental plasticity, which is the product of differential environmental induction of genomic programmes that guide trade-offs in the way resources are allocated towards different traits during development in response to both intrinsic and extrinsic cues (Snell-Rood 2013). Therefore, developmental plasticity has the greatest relevance to the influence of juvenile environments on the integration of adult phenotypes; it is this form of phenotypic plasticity that I will concentrate upon here.

Developmental plasticity can be further subdivided into reversible and irreversible types of plasticity. In reversible developmental plasticity (i.e. phenotypic flexibility; Piersma & Drent 2003), changes in resource allocation occur multiple times during an individual's lifetime in response to predictable triggers such as resource abundance or circadian rhythm. For example, songbird brains, specifically the areas associated with song, change in volume seasonally, reducing the volume of brain tissue that requires energetic support outside of the breeding season and increasing brain volume at the onset of the new season, thereby enabling learning of appropriate song (Tramontin & Brenowitz 2000).

In contrast, irreversible developmental plasticity involves individuals following separate developmental trajectories as a function of earlier developmental decisions caused by exposure to differing environmental conditions that lead to different phenotypes at maturity. This form of developmental plasticity results in allocation trade-offs between traits that can change the variance–covariance structure among traits, and therefore, that may influence their correlation with fitness (Stearns 1992). Understanding the relationship between plasticity and fitness is crucial if we are to understand how developmental plasticity and phenotypic integration will evolve. In the context of the influence of juvenile environments on the integration of adult phenotypes, shifts in

developmental reaction norms are likely to occur for two reasons: to overcome prematuration challenges (reactive developmental plasticity), or to prepare for postmaturation challenges (anticipatory developmental plasticity). The fundamental difference between reactive and anticipatory developmental plasticity lies in the timing and rapidity of the response, both of which have consequences for the covariation between traits due to changes in resource availability and allocation, and therefore, phenotype–fitness correlations at maturity.

As reactive developmental plasticity occurs in response to the current challenges that individuals encounter prior to maturity, it needs to occur relatively quickly to maximize survival to maturity. Examples of responses to current ecological challenges include the development of costly spines by *Daphnia lumholtzi* in the presence of predators to increase survival under predation (Green 1967), and the more rapid maturation of damselflies near the end of the breeding season to ensure an opportunity to breed before the season ends (Johansson et al. 2001). Although such developmental tactics are considered adaptive because they improve the likelihood of surviving and reproducing, individuals must allocate resources towards survival traits prior to maturity (e.g. antipredator traits or a faster growth rate) that can reduce the expression of fitness-associated traits after maturity (DeWitt et al. 1998; Relyea 2002b). This can result in negative correlations between traits both within and across phenotypic dimensions, thereby creating a less integrated phenotype with potentially lower adult fitness. These trade-offs will be further exacerbated by resource acquisition as individuals with fewer resources must allocate them more frugally, resulting in greater allocation trade-offs between traits and expression of traits of relatively lower value (Stearns 1992).

In contrast, anticipatory plasticity allows individuals to develop a phenotype that allows them to navigate the ecological challenges they are most likely to encounter upon maturity. Anticipatory plasticity can evolve when cues of future environments are available prior to maturity (Lively 1986). For example, snails (*Littorina obtusata*) respond to cues suggesting future predatory challenges by altering shell size and shape in a way that increases adult survival (Trussell 2000). Another example is socially cued anticipatory plasticity where individuals use indicators of the intensity of sexual selection they will experience after maturity to alter their current developmental trajectory (Kasumovic & Brooks 2011). In each of these cases, individuals are less time-stressed by ecological factors than in prematuration challenges, and as a result, have greater opportunities to acquire resources and more carefully allocate them towards a wider variety of traits. As a result, postmaturational plasticity is likely to lead to positive correlations between suites of traits across multiple dimensions and to create a better integrated phenotype.

Understanding why individuals respond to ecological variation and how this variation influences phenotypic correlations across phenotypic dimensions will increase our understanding of how individuals alter allocation strategies to produce an integrated phenotype. Below, I further explore how various ecological environments affect differing classes of traits and what this means for understanding how integrated phenotypes are influenced by plasticity.

ECOLOGICAL TRIGGERS AND EXAMPLES OF INTEGRATED PHENOTYPES

There are many reviews that describe the patterns of adaptive plasticity in response to abiotic and biotic factors occurring throughout the animal kingdom (Adler & Harvell 1990; Nylin & Gotthard 1998; Pigliucci 2001; West-Eberhard 2003; Benard 2004; Kasumovic & Brooks 2011). We also have a well-developed

understanding of the association between morphological and life history traits, and of how trade-offs between these traits affect fitness in different ecological and evolutionary contexts (Lima & Dill 1990; Roff 1992; Stearns 1992; Pigliucci 2001; West-Eberhard 2003; Benard 2004). Rather than reviewing new examples, I will instead discuss a series of case studies that demonstrate how various prematuration environments interact to influence trade-offs within and between suites of traits, thereby creating an integrated phenotype. I will also provide examples that demonstrate the range of ecological factors that trigger plastic shifts and how individual ecological factors can initiate shifts in multiple dimensions. In this way, I hope to stimulate discussion regarding the importance of early juvenile environments in our understanding of phenotype–fitness interactions.

FROGS: HETEROSPECIFIC EFFECTS ON RESOURCE ACQUISITION AND ASSIMILATION

The best-studied effect of heterospecifics on developmental and behavioural plasticity involves the influence of predator presence/absence prior to maturity. In a diversity of species, the presence of predators decreases foraging behaviour of prey (Lima & Dill 1990) and increases development rate, affording individuals a greater probability of surviving to maturity (Harvell 1990; Abrams & Rowe 1996; Benard 2004). Frogs are particularly well studied in this regard as a number of species demonstrate reactive developmental plasticity in response to their immediate environment. Individuals generally mature more rapidly in the presence of predators and sacrifice size at maturity for increased tail development in the tadpole stage (e.g. Smith & Van Buskirk 1995; McCollum & Leimberger 1997; Relyea 2002c). Tail development, specifically, is adaptive, as tadpoles with larger tails are better at escaping predator attacks (McCollum & Leimberger 1997; Van Buskirk et al. 1997; Van Buskirk & Relyea 1998). Despite the survival benefit that this plasticity affords during earlier juvenile stages, development of a large tail has morphological consequences at maturity, as individuals generally develop longer legs and narrower bodies (Relyea 2001), which may decrease adult competitive ability (Howard & Kluge 1985; Höglund 1989).

Most research on phenotypic plasticity in frogs focuses on morphological and life history traits that are easily measured. There are, however, many less conspicuous traits that also exhibit plastic responses. For example, individuals reared in the presence of predators have shorter guts (Relyea & Auld 2004), smaller teeth with shorter rows, and often have a missing row of teeth (Relyea & Auld 2005). Along with these apparent resource acquisition handicaps, individuals also decrease their foraging behaviour in high predator environments (Relyea 2004a). Collectively, these studies explain why individuals developing in predator-rich environments mature at smaller sizes: they gather fewer resources during less frequent foraging attempts and are less able to extract nutrients with their shorter guts.

Interestingly, the presence of competitors also affects behavioural and developmental plasticity, except in the opposite direction. An increased density of competitors results in an increase in activity in both *Rana pipiens* (Awan & Smith 2007) and *Rana sylvatica* (Relyea 2002a, 2004a). Individuals also increase their gut length and the traits associated with feeding when competition between conspecifics increases (Relyea & Auld 2004). Whether it is changes in behaviour that result in differences in assimilation ability, or whether assimilation ability itself is responding to the ecological context is unclear, but these differences none the less help to explain why tadpoles exposed to greater competition can allocate more resources towards morphological traits and therefore mature at a larger body size (Relyea 2002a).

To make matters more complex, the factors that affect plasticity of the traits associated with resource acquisition also extend to temperature and latitude. In the common frog, *Rana temporaria*, individuals from higher latitudinal populations have longer guts, which helps to explain their increased growth rate (Lindgren & Laurila 2005). Interestingly, gut length in this species is further increased by a decrease in rearing temperature (Lindgren & Laurila 2005). In both of these examples, shorter breeding seasons appear to have selected for plasticity in resource acquisition traits that allows individuals to maximize their opportunity to mature before the breeding season ends.

Together, the above studies demonstrate that multiple ecological factors can affect underlying resource acquisition traits (both positively and negatively), and that such plasticity can have downstream effects on behavioural, life history and morphological traits after maturity. What they do not reveal, however, is how individuals respond when multiple ecological triggers are present, and more importantly, what happens when they trigger plasticity in opposite directions. The effect of each ecological trigger on phenotypic plasticity will likely be determined by the relative effect each trigger has on fitness (i.e. hard versus soft selection; Via & Lande 1985). For example, selection through increased predation risk is likely to be stronger than selection from a competitive scenario, as the former can result in zero fitness (i.e. death) while the latter may only result in a decrease in fitness.

The response to such a scenario is demonstrated by two studies on *Hyla femoralis* (McCoy 2007) and *R. sylvatica* (Relyea 2004a). When *R. sylvatica* individuals were reared in a range of environments that varied in level of competition and predation threat, they responded more strongly to competition when the predator threat was low and more strongly to a predator threat when the risk of competition was low (Relyea 2004a). The plasticity in behaviour, growth and tail shape was continuous, such that intermediate interactions between predator and conspecific density resulted in moderated plastic responses. In contrast to *R. sylvatica*, *H. femoralis* only responded to changes in conspecific density when predators were present (McCoy 2007). In other words, unless predators were present, *H. femoralis* did not respond to any changes in conspecific density. Why the two species demonstrate different reaction norms towards the two ecological triggers is unknown. Future studies will benefit from examining the natural environments of the individuals used for such experiments as they may hint at the relative importance of various triggers in the evolution of plastic tactics.

The above studies demonstrate that reactive developmental plasticity in a suite of traits associated with resource acquisition is affected by a variety of ecological triggers. Responses are also continuous rather than threshold changes, demonstrating that plastic responses can be fine-tuned to balance opposing selective pressures. Most importantly, these studies highlight how underlying physiological traits are affected by numerous ecological factors and illustrate the downstream effects of such changes on other traits.

DAMSELFLIES: LIFE HISTORY TRADE-OFFS AND THE IMPORTANCE OF IMMUNITY

Two environmental components that have been well studied in regard to plasticity in life history and morphological traits in damselflies are temperature and photoperiod. Both are examples of reactive developmental plasticity and are linked to latitudinal gradients across which increases in latitude result in lower average summer temperatures and shorter breeding seasons. Increases in temperature generally result in faster maturation rates, likely due to faster biochemical reactions (Stearns 1992; Nijhout 1994). Decreases in daylength similarly trigger faster maturation in many seasonal organisms (Rowe & Ludwig 1991; Berrigan & Charnov

1994; Abrams et al. 1996) as shorter days signal the end of the breeding season. In nonoverwintering species specifically, this generally results in late-hatching individuals trading off size and weight for faster maturation; a trade-off likely to maximize their opportunity of reproducing in the current season (Abrams et al. 1996).

Plasticity in response to both photoperiod and temperature are particularly well studied in a number of species of damselflies. Several studies show similar trends demonstrating that individuals mature faster when reared at higher temperatures and in a photoperiod that simulates a later breeding season (De Block & Stoks 2003; Strobbe & Stoks 2004; Śniegula & Johansson 2010; Śniegula et al. 2012). Under both of these scenarios, individuals mature at a smaller size (Strobbe & Stoks 2004; Śniegula & Johansson 2010; Śniegula et al. 2012). Although ecologically triggered, there is evidence that developmental trajectories are in part, genetically determined as there are differences in growth efficiency between latitudinal populations (Śniegula & Johansson 2010). This may, in part, be due to underlying differences in behaviour and physiology as individuals from more northern populations have increased food intake rates (Stoks et al. 2012) and improved resource assimilation (Stoks & McPeek 2003; Stoks et al. 2012). These results once again demonstrate the importance of underlying physiological mechanisms for understanding phenotypic plasticity.

Like similar research on anurans, studies of phenotypic plasticity in damselflies have focused on multiple ecological triggers by incorporating the effects of predators and/or diet on seasonal constraints. The presence of predators generally decreases foraging behaviour and development rate in the emerald damselfly, *Lestes sponsa*, but when these damselflies are reared with an extra time constraint to mimic the end of the breeding season, they increase their foraging and development rates (Johansson et al. 2001). Food availability also interacts with time constraints, as individuals increase foraging and growth rates when they have access to increased resources, but sacrifice size in order to mature more quickly when a time constraint is present (Johansson et al. 2001). Rarely are such interactions simple, however, as results for the azure damselfly, *Coenagrion puella*, suggest sex differences in activity in response to predator presence, which further affects development time and size at emergence (Mikolajewski et al. 2005). Together, these studies demonstrate that phenotypic plasticity and phenotypic traits (e.g. foraging rates) at maturity are behaviourally mediated and that they can interact with internal (e.g. physiological) processes. More importantly, these results once again demonstrate that the interactive effects of ecological factors are complex and that certain factors (e.g. seasonal constraints) can override other strong selective pressures.

One particularly novel perspective gained from damselfly research is the information available regarding fitness and immunocompetence. Not surprisingly, evidence from both *Calopteryx splendens xanthostoma* (Rolff & Siva-Jothy 2004) and *Lestes forcipatus*, the sweetflag spreadwing (Yourth et al. 2002a), demonstrate that immune responses generally increase in response to seasonal increases in parasite numbers. Interestingly, immune responses decrease as a function of increases in predation risk and time constraints prior to maturity (Stoks et al. 2006). Similarly, starvation during immaturity decreases immune responses (*Lestes viridis*, De Block & Stoks 2008; *Ischnura verticalis*, Leung et al. 2001; *L. forcipatus*, Yourth et al. 2002b), and these responses can remain low even after metamorphosis (De Block & Stoks 2008). These studies suggest that plasticity in response to immediate threats during the juvenile stage result in allocation strategies that forgo investment towards an unnecessary immune system.

How plasticity in immune response is affected when multiple ecological factors interact with factors such as parasitism that result in greater investment in the immune system is less well studied in this group. Research on the azure damselfly, *C. puella*, however, examined sex differences in how larvae responded to threats of parasitism and predation simultaneously. When rearing individuals in different combinations of threats, Joop & Rolff (2004) found that females demonstrated plasticity in immune responses by increasing their investment towards the immune system when predators and/or parasites were present. In contrast, males were canalized in their plasticity in the immune system and showed no change in immunity in response to either threat. Males did, however, show plasticity in morphology by maturing at a lower body condition when under the risks of parasitism and predation. Although the study could not explain why these sex differences in immune response exist, the authors suggested that they may be a result of underlying differences in behaviour or life history that result in sex-dependent differences in the costs associated with parasitism. Future studies are necessary to explore this possibility.

As in frogs, research on damselflies demonstrates that various ecological triggers can affect the same suite of traits. The studies further demonstrate that understanding how traits across dimensions are influenced by multiple ecological triggers can be problematic because of sex differences in life history and/or behaviour. These studies once again highlight the importance of exploring plasticity with an ecological understanding. Further research, however, is required to gain an understanding of how plasticity in immune responses are affected by other ecological triggers of plasticity in other trait dimensions (Rolff & Siva-Jothy 2003).

CRICKETS: MULTIPLE ECOLOGICAL TRIGGERS AFFECT ANTICIPATORY AND BEHAVIOURAL DEVELOPMENTAL PLASTICITY

As a consequence of research on many species of crickets, we have a detailed understanding of the life history, behavioural and morphological traits associated with fitness. Male crickets call to defend territories and attract mates. Studies in *Teleogryllus commodus* demonstrate that although there is multivariate stabilizing selection on various call traits (Brooks et al. 2005; Hall et al. 2008), there is positive directional selection on calling rate as a function of female choice (Bentsen et al. 2006). In a competitive context, male fitness is determined by various morphological traits (Hack 1997a; Savage et al. 2005; Shackleton et al. 2005; Hall et al. 2010; Reaney et al. 2011) that signal resource-holding potential to rivals (Hack 1997b; Rillich et al. 2007; Briffa 2008). Male crickets thus offer an excellent system in which to study the ecological and social factors that affect both reactive and anticipatory development plasticity.

Given the importance of increased trait expression in both intra- and intersexual selection, it is not surprising that crickets demonstrate reactive developmental plasticity in response to diet. The effect of diet on the expression of various traits is particularly well studied in *T. commodus*, with individuals generally maturing larger and heavier when provided with increased nutrient availability (Zajitschek et al. 2009). Altering the nutrient concentration of the rearing diet during the nymph stage results in sex-specific trade-offs in morphological and behavioural attributes. Males reared on a high-protein diet increase their calling effort, which results in a shorter life span (Hunt et al. 2004a), likely due to the energetic cost of increased calling (Hoback & Wagner 1997). Although an increased protein intake does not affect female life span in the same way, females are more sexually responsive to courting males when reared with greater access to protein (Hunt et al. 2005).

As calling is energetically costly (Hoback & Wagner 1997) and determined by condition (Hunt et al. 2004a), and because the production of larger morphological traits requires access to greater

resources (Zajitschek et al. 2009), both morphological traits and calling effort honestly signal a male's competitive ability. Since both size and calling effort are easily assessed by eavesdropping conspecifics, developing individuals could modulate their developmental trajectory to mature a phenotype that maximizes fitness in the social environment they are most likely to encounter. Experiments varying the social environment prior to maturity in *T. commodus* demonstrate anticipatory developmental and behavioural plasticity in both sexes (Kasumovic et al. 2011).

Male *T. commodus* mature more quickly and, as a result, emerge smaller and lighter when reared in social environments signalling less competition with males calling at lower rates. In contrast, males take longer to mature and eclose larger and heavier in environments with an increased density of males calling at higher rates. This result was replicated in a similar experiment in a closely related species, *Gryllus integer* (DiRienzo et al. 2012). Along with the phenotypic change, the juvenile acoustic environment also altered the time that male *T. commodus* maintained their calling effort over their lifetime (Kasumovic et al. 2012a).

Females, in contrast, had the opposite developmental strategy. When females were reared in a treatment with a high density of males calling at a high rate, they allocated a greater proportion of their resources towards earlier maturity at the cost of size and weight (Kasumovic et al. 2011). As female size is associated with fecundity (Blankenhorn 2000; Kasumovic et al. 2011), females that develop more rapidly also allocate relatively more resources towards egg production to compensate for their smaller size. As in males, the juvenile environment also affected adult behaviour, and although juvenile experience did not affect a female's mate preference, it did affect how quickly females made decisions (Kasumovic et al. 2012a), similar to the effect of diet (Hunt et al. 2005).

Although the effect of diet or social environment seems to be relatively predictable according to the understanding of how sexual and natural selection function in crickets, the effects of each become more difficult to understand when both factors are simultaneously manipulated. Although a decreased protein:carbohydrate ratio normally leads to the development of a smaller phenotype (i.e. decreases condition), when reared in different acoustic environments that indicate the level of competition, the effect of condition present prior to maturity is obscured at maturity by the anticipatory plasticity (Kasumovic et al. 2012b). In other words, the adult phenotype, both in morphological and behavioural traits (i.e. calling effort Fig. 2), is no longer a reliable signal of condition. These results not only demonstrate the difficulty in understanding plasticity in complex competitive environments, but also demonstrate that plasticity in response to interacting ecological factors can result in a reaction norm that masks the effect of individual ecological triggers.

Social experience prior to maturity also affects other phenotypic traits. When *Teleogryllus oceanicus* males are reared in environments simulating an abundance of calling males, males invest increased resources into body condition and reproductive tissue and alter their behavioural tactics (Bailey et al. 2010). When *G. integer* males are reared individually in a silent environment, they are more likely to increase aggression after maturity and are more likely to hold a dominant status (DiRienzo et al. 2012). Social experience prior to maturity can thus have profound effects on morphological and behavioural traits.

Overall, the above studies demonstrate that adult social environments experienced prior to maturity trigger anticipatory phenotypic plasticity that affects a whole suite of traits across behavioural, morphological, reproductive and life history dimensions. The studies also hint that reactive developmental plasticity alters the reaction norm normally associated with anticipatory developmental plasticity, making it difficult to predict phenotypic endpoints. These results highlight the importance of exploring variation in the adult environment (abiotic and biotic) when trying to understand trait expression during development.
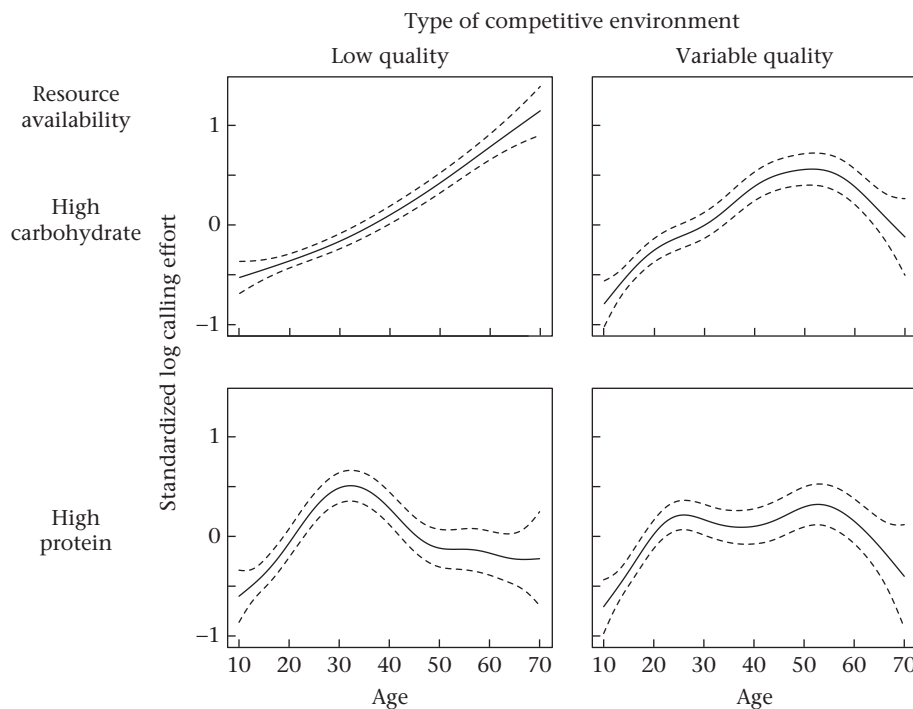
Figure 2. Male crickets call throughout their lifetime to attract mates. Shown is the average (standardized) change in calling effort of males as they age. How calling effort changes depends on a complex interaction between male condition (high carbohydrate versus high protein) and the competitive environment (low-quality rivals versus variation in the quality of rivals) that the male experiences prior to maturity. As a result, an individual's 'quality' cannot easily be determined by the expression of calling effort (the sexually selected trait). The solid lines represent age-specific calling effort, while the dotted lines represent 95% confidence intervals. Figure redrawn from Kasumovic et al. (2012b).

SPIDERS: AN INTEGRATIVE VIEW OF ANTICIPATORY PLASTICITY

In this final case study, I will focus on one species, the Australian redback spider, *Latrodectus hasselti*, as the anticipatory developmental plasticity that this species demonstrates affects numerous traits. To understand how this anticipatory plasticity affects fitness, it is important to understand the reproductive biology and life history of this species. Male Australian redback spiders are limited to a single mating attempt with a single female due to a combination of risky mate searching (Andrade 2003) and male self-sacrifice during copulation (Andrade 1996). It is this single mating opportunity that has probably driven the evolution of the anticipatory developmental plasticity that male redbacks demonstrate in response to the social environment (Kasumovic & Andrade 2006).

While in their penultimate instar, males alter their development in response to the density of conspecific pheromonal cues in their surrounding environment. When reared in the presence of females, males sacrifice size and weight to mature more quickly, allowing them to outcompete rivals in two ways. First, males that mature earlier are able to reach and mate with females before their rivals (Kasumovic & Andrade 2009), thereby gaining an increased proportion of paternity due to strong mating order effects (Snow & Andrade 2005; Snow et al. 2006). Second, since newly mated females no longer attract males (Kasumovic & Andrade 2006; Stoltz et al. 2007), by a combination of web reduction (Watson 1986) and early mating, males are able to reduce the likelihood that the female will attract further rivals. In contrast, when reared in the absence of females and in the presence of a higher density of rivals, males prolong their development to mature larger and in better body condition (i.e. increased weight for their size; Kasumovic & Andrade 2006). This increased size affords males a competitive edge in direct competitions (Stoltz et al. 2008, 2009; Kasumovic & Andrade 2009).

Along with the social environment, the resource environment prior to maturity also determines trait expression. As predicted, having fewer resources leads to slower growth and reduced size and weight at maturity (Kasumovic & Andrade 2006). Interestingly, although dietary restriction normally results in an increased life span in laboratory-reared animals (Weindruch & Walford 1988; Masoro 2005), there is no such effect in redbacks (Kasumovic et al. 2009). This suggests that relationships between resource acquisition, condition and life span are uncoupled in this species, probably because an extended life span is not favoured by selection due to a single mating opportunity. These results once again highlight the necessity of considering species-specific life history and reproductive biology when trying to understand the connections between suites of traits across dimensions.

The effects of diet and social environment, however, are not limited to life history and morphological traits, but also affect the underling physiology of developing males. Lower levels of resource acquisition result in a decreased routine metabolic rate at maturity (Stolz et al. 2012). Additionally, there is a social effect on routine metabolic rate, with males maturing in the presence of fewer rivals having lower rates, irrespective of mass and size (Stolz et al. 2012). These results suggest that both resource acquisition and the potential level of competition alter how males allocate resources towards their metabolic rate. Although the benefits of a decreased routine metabolic rate are not fully known in this species, a decrease could reduce the cost of cellular maintenance, thereby allowing males to conserve resources when competition is reduced. Energy conservation is particularly important in male redbacks, as in the absence of direct competition for a female on her web, males must court for up to 8 h (median 5.5 h) to successfully copulate with a female (Andrade 1996). In contrast, direct competition with rivals on a female's web requires that males court while keeping rivals at bay (Stoltz et al. 2008; Stoltz & Andrade 2010); males with an increased routine metabolic rate may have an increased competitive edge under such competitive scenarios. This suggested relationship between physiology and fitness, however, still requires further examination.

The set of studies above demonstrate that males alter how resources are allocated towards numerous traits across multiple dimensions: morphological, physiological, life history, and potentially behavioural. Furthermore, they suggest a level of independence in how resources are allocated towards various traits, indicating that males may have fine control over how resources are allocated towards different traits.

Summary

The research completed over the last few decades has delineated how selection affects trait expression in common environments (e.g. female choice, male competition) (Andersson 1994; Blanckenhorn 2005; Ingleby et al. 2010), but research must now build on this strong foundation by understanding how more realistic (i.e. complex) environments affect trait expression and evolution. The case studies above demonstrate intricate interactions among ecological triggers that cause developmental plasticity in numerous traits across dimensions. They also demonstrate the importance of understanding the selective pressures each ecological environment causes and the sex-specific effect of such selection if we are to place the observed phenotypic plasticity in a correct life history framework.

Most importantly, these studies highlight how researchers can build on previous results by layering different methodological approaches onto one another to explore more complex scenarios. Researchers must start by considering the natural environment of the species of interest and exploring how competitive contexts fluctuate within and between breeding seasons. This will provide a baseline understanding of the selective pressures that individuals are most likely to encounter and of the phenotypes that maximize fitness in each context. Studies can then build on this scaffolding by examining how the relevant selective pressures affect juvenile development and the resulting trade-offs that occur both within and between suites of traits. To do this, however, requires that researchers specifically begin examining the role of less conspicuous and underlying mechanistic traits in their examinations. In the next section, I will explain why I feel that this is important.

UNDERSTANDING DEVELOPMENTAL PLASTICITY IN LESS CONSPICUOUS TRAITS

Various ecological triggers of developmental plasticity also trigger allocation shifts in underlying physiological, immunological and digestive traits. Our understanding of the reaction norms of these less conspicuous traits (that are often mechanisms of plasticity) are currently limited, but are necessary for two reasons. First, these underlying traits are often linked to fitness, but are done so through indicator traits. For example, sexually selected traits are often cited as indicators of immunocompetence (Costantini & Møller 2009). Although there are demonstrable links between sexually selected traits, immunocompetence and fitness (Siva-Jothy 2000; Rantala et al. 2010), environmental contexts can change in such a manner that these relationships disappear (Rolff & Siva-Jothy 2004; Córdoba-Aguilar et al. 2009), or at minimum, make them unreliable (Garratt & Brooks 2012). In other words, earlier developmental environments may alter the covariation among indicator traits and suites of underlying mechanistic traits through shifts in allocation strategies. Here I will provide a few examples of

how these mechanistic, less conspicuous traits are affected by early environments in hopes of highlighting the importance of investigating the reaction norms of these traits.

In exploring phenotypic plasticity and understanding how different ecological triggers affect reaction norms, it is useful to incorporate a life history and trade-off framework, as this facilitates understanding of resource use and can help predict relationships between traits. Resource availability and use are among the underlying differences between reactive and anticipatory plasticity. Trait expression is determined by genetic variation in condition (Rowe & Houle 1996), the ability to acquire, assimilate and allocate resources in a variable environment. The primary means by which researchers alter condition and its effect on trait expression is through resource acquisition as this affects how resources are allocated (e.g. Cotton et al. 2004; Bonduriansky & Rowe 2005; Dmitriew et al. 2010). However, genetic variation in assimilation ability (i.e. the ability to process and extract nutrients from resources) is equally important in determining condition (Hunt et al. 2004b). Underlying mechanistic differences that allow some individuals to extract more nutrients from resources would allow those individuals to increase condition, and therefore, to respond similarly to increases in acquisition. Although assimilation ability is rarely examined because it is more difficult to explore, there is evidence of genetically determined efficiency of resource assimilation triggered by seasonal ecological changes in temperature, photoperiod and/or predation risk (Stoks & McPeek 2003; Śniegula & Johansson 2010; Stoks et al. 2012). Evidence suggests that this can, at least in part, be due to changes in digestive morphology (Relyea & Auld 2004; Lindgren & Laurila 2005). More studies are necessary to determine the extent to which early developmental environments affect assimilation by examining differences in metabolism, underlying physiology and shifts in digestive systems that would result in different energy use and production.

Along the same vein, metabolic rates are seen as a fundamental component of individual regulation (cellular and tissue maintenance), which means that changes in metabolic rates can affect the resources available for allocation towards other traits (Stearns 1992). Although resting metabolic rates are largely determined by broad-scale ecological factors such as temperature and diet (Chown & Gaston 1999; Gillooly et al. 2001; Clarke & Fraser 2004; Munoz-Garcia & Williams 2005), just like other phenotypic traits, adult metabolic rates are affected by juvenile environments. For example, abiotic factors such as higher temperatures irrespective of altitude (Naya et al. 2011) or increased resource abundance (Stolz et al. 2012) prior to maturity can increase adult resting metabolic rates. Even biotic factors such as increases in juvenile parasite load (Careau et al. 2010) and increases in rival density during development (Stolz et al. 2012) are known to increase resting metabolic rates. Given the hypothesized role of metabolic rates in fitness in certain contexts (Burton et al. 2011), and in adult behaviours and personality (Sih et al. 2004; Biro & Stamps 2010; Reale et al. 2010; Dingemanse & Wolf 2013), it is absolutely necessary to understand how juvenile environments affect not only resting metabolic rates, but also active metabolic rates and metabolic scope (e.g. Fry 1948; Eliason et al. 2011) along with other traits of interest.

As mentioned above, sexually selected traits are often cited as indicators of immunocompetence (Costantini & Møller 2009). The juvenile as well as maternal environments, however, are known to have strong effects on immunological responses such that the relationship between sexually selected traits and the immune system is likely to change as a function of the ecological context. As with many other traits, the early nutritional environment (Valtonen et al. 2011) and the 'pace-of-life' (Palacios et al. 2011) affect adult resistance to bacterial infection. The early immunological environment can also be primed through maternal inheritance in environments where offspring require increased immune responses (Grindstaff et al. 2003, 2006; Curno et al. 2009); this could potentially change the costs associated with the development of an immune system. In other cases, juvenile diet and immune challenges faced prior to maturity may have no effect on development and the expression of morphological traits, but they can decrease investment in sperm (Simmons 2012). The results are still too few to provide a robust understanding of how the juvenile environment generally affects immunological competence and the relationship that this creates with other sexually selected traits, but future studies can remedy this problem.

In general, early experiences are crucial in determining later life trajectories and investment towards all traits, including underlying mechanistic traits. Studies are just beginning to understand the influence of early developmental decisions on expression of such traits, and in turn, how such traits are correlated with fitness. Future studies will need to continue to incorporate measurements of these mechanistic traits into their studies of plasticity to better provide a general understanding of how resources are assimilated, stored and partitioned between suites of traits across dimensions during development. This will become easier as time passes, simply due to technological advances and to earlier researchers laying the groundwork on such examinations.

CONCLUSION AND FUTURE DIRECTIONS

All species are plastic to some extent simply due to the nature of biochemical reactions involved in development (Nijhout 2003b). Despite this understanding, the importance of the juvenile environment is often ignored by biologists studying sexual selection. To truly understand how suites of different traits are correlated with fitness requires a multilevel examination incorporating traits from as many dimensions as possible with an understanding of how environments vary. Such studies will provide greater insight not only into the traits associated with fitness, but into the ways various traits interact to create an integrated phenotype. Although incorporating multiple factors and measuring numerous traits may seem a daunting task, studies of plasticity have shown us that the relative importance of different ecological factors, their scale and timing, as well as the most important traits to examine can be easily discovered by a deep understanding of the organism under study.

After a phenotypic focus, it will be important to add a genetic understanding of the relationship between traits. There is no doubt that there is an underlying genetic basis to phenotypic plasticity (Stearns et al. 1991; Scheiner 1993; Pigliucci 2005). Exploring the underlying genetic variance–covariance structure (i.e. G matrix) (Houle 1991; de Jong & van Noordwijk 1992; Pigliucci 2006) will hint at the influence of genes in phenotypic trade-offs between dimensions (for a discussion on this topic, see: Pigliucci & Preston 2004; Pigliucci 2005; Stearns et al. 1991). Few studies of phenotypic plasticity have examined the genetic relationship between traits in animal systems outside of examinations of condition dependence. As a result, we have a relatively poor understanding of how abiotic (other than resource acquisition) and biotic factors have shaped the underlying genetic structure of phenotypic plasticity. Two recent studies examined the underlying genetic structure of responses to predators in anurans and provide some insight into the role that genes play in plastic responses to heterospecifics.

The first study demonstrated that a shift in allocation in response to the ecological environment affects the covariation between traits (Kraft et al. 2006a). A second, more quantitative, study suggests that different genes are responsible for controlling the expression of body size when predators are present or absent, and as a result, that the evolution of body size can occur independently in each environment (Kraft et al. 2006b). These studies provide

information on how we can expect suites of traits to respond to different selective environments that trigger plastic developmental strategies. Unfortunately, the above studies provide only a glimpse into how underlying genetic variation structures the relationship between different traits as both studies focused only on morphology. Further studies incorporating suites of traits across multiple dimensions, including behaviour, are necessary to provide insight into how genes regulate the evolution of developmental strategies and integrated phenotypes. Examining behaviour is especially important to determine the extent to which developmental behavioural plasticity is correlated with both reactive and anticipatory developmental plasticity, and the extent which it may support or impede evolutionary changes (e.g. Huey et al. 2003).

Future behavioural ecologists have their work cut out for them as they explore more complex interactions while attempting to better understand the natural world. Such examinations will be rewarding, however, as they will allow for a greater understanding of the relationship between traits and their association with fitness. Despite the difficulties ahead, researchers have new tools available that facilitate measurement of a diversity of traits. This includes the technology to understand how the intraspecific interactions behavioural ecologists have studied for decades trigger gene expression and resulting behavioural changes (e.g. Cummings et al. 2008; Aubin-Horth & Renn 2009; Renn & Schumer 2013). This will enable the integration of new ideas that link different phenotypic dimensions through a common systems (e.g. hormonal; Nijhout 2003a; Wingfield 2013). Such examinations will require careful experimental designs that incorporate the life history of the organisms under study if we are to understand the relevance of different trade-offs and phenotypic integration. Luckily, a whole organismal approach in experimental design is something that ethologists and behavioural ecologists have been perfecting for generations.

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