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Emerging model systems in eco-evo-devo: the environmentally responsive spadefoot toad

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SUMMARY Spadefoot toads have emerged as a model system for addressing fundamental questions in ecological and evolutionary developmental biology (eco-evo-devo). Their tadpoles produce a wide range of adaptive phenotypes in direct response to diverse environmental stimuli. Such phenotypic plasticity offers an excellent opportunity to examine how an organism's ecology affects its development as well as how an organism's development influences its ecology and evolution. By characterizing and understanding the interconnectedness between an organism's environment, its development responses, and its ecological interactions in natural populations, such research promises to clarify further the role of the environment in not only selecting among diverse phenotypes, but also creating such phenotypes in the first place.

INTRODUCTION

Ecological and evolutionary developmental biology ("eco-devo" and "evo-devo," respectively) seek to understand how an organism's genome and ecology interact to create phenotypic variation, and to determine the ecological and evolutionary consequences of this variation (Sultan 2007, 2010; Gilbert and Epel 2009). Implicit in these goals are that phenotype expression is dependent on the environment in which these phenotypes are produced. Further, ecologically distinct populations and species evolve such that environmental cues direct an individual's development to produce phenotypes that are adaptive for the variability encountered in the organism's unique habitat. Accordingly, organisms most amenable to research in integrating eco-devo with evo-devo are those whose ecology is well known and that experience diverse ecological (and thus, selective) regimes.

Spadefoot toads (hereafter, spadefoots) meet these criteria, and they have emerged as an excellent system for integrating eco-devo with evo-devo. Indeed, spadefoots respond to numerous environmental factors that influence fitness. The larvae, in particular, express a high degree of phenotypic plasticity. Furthermore, different species, populations, and even individuals experience diverse selective environments. Consequently, linking ecological processes to evolutionary outcomes is often tractable. Most importantly, although spadefoot biology is seemingly unique, the developmental, ecological, and evolutionary processes that can be illuminated by studying them will likely apply to numerous other taxa.

Below, we briefly describe spadefoot natural history. We then summarize the many environmental factors that shape phenotype production in New World spadefoots. In particular, we highlight two environmentally dependent phenotypes that have been evolved in this clade and that have important fitness consequences for larvae: variation in metamorphic timing and the expression of resource polyphenism (sensu Mayr 1963). Finally, we address four current avenues of research that have been investigated with spadefoots.

DIVERSITY AND NATURAL HISTORY OF SPADEFOOTS

Spadefoots (superfamily Pelobatoidea) are frogs and not true "toads"; that claim is restricted to the genus *Bufo* (*Anaxyrus*). The phylogenetic relationships among species have been well resolved (García-París et al. 2003), enabling researchers to generate phylogenetically informed hypotheses regarding their various adaptations. Although spadefoots also inhabit Europe and Africa (genera *Pelobates* and *Pelodytes*), we focus on New World spadefoots, which exhibit numerous, derived features associated with their desert habitats, such as rapid larval development and special ways of procuring food.

North American spadefoots (family Scaphipodidae) consist of two genera—*Spea* and *Scaphiopus* (Fig. 1). Within these two genera, four species are desert-dwellers (*Spea bombifrons*, *Spea intermontana*, *Spea multiplicata*, and *Scaphiopus couchii*). Although the remaining species (*Spea hammondii*, *Scaphiopus holbrookii* and *Scaphiopus hurterii*) live in more mesic habitats, they share some of the same adaptations to xeric environments as their desert brethren. For instance,

Fig. 1. Representative members from both North American spadefoot genera (*Scaphiopus* and *Spea*). *Scaphiopus couchii* (left) is sexually dimorphic, where males are bright green (top frog) and females are drab green and black. *Spea bombifrons* males (right) congregate at the periphery of ponds to solicit mating calls.

S. holbrookii frequently breed in ephemeral ponds, despite inhabiting the mesic eastern US (Fig. 2).

To survive in xeric habitats, adult spadefoots spend most of the year underground, emerging during warm-weather rains to feed and breed in temporary rain-filled ponds (Bragg 1965). Because these ponds are often highly ephemeral, spadefoot larvae are frequently under intense selection to grow and develop rapidly enough to metamorphose before their pond dries (Newman 1989). Not surprisingly, spadefoot larvae are capable of remarkably rapid development (*S. couchii*, e.g., can metamorphose less than eight days posthatching; Newman 1989). Additionally, some species have evolved unique feeding adaptations that speed development and growth. It is these two features of the larvae—variable developmental rate and feeding adaptations—that provide exceptional opportunities for eco-evo-devo research.

AN ENVIRONMENTALLY RESPONSIVE TADPOLE

Although desert spadefoots have rapid larval development, they also exhibit considerable plasticity in developmental rate (Newman 1994). This plasticity enables larvae to slow development and thereby acquire additional nutrients and grow more if their pond persists (Newman 1992; Denver et al. 1998; Morey and Reznick 2000). Such plasticity is presumably an adaptation for variability in pond duration (Newman 1994).

Spadefoots have an additional adaptation to cope with desert habitats: *Spea* larvae facultatively produce a distinctive ecomorph that preys on anostracan fairy shrimp—a valuable, but often underutilized, resource in their relatively nutrient-limited ponds. Most anuran larvae feed on detritus and microorganisms and possess small jaw muscles, smooth keratinized mouthparts, and an elongate gut (Duellman and Trueb 1986; Altig et al. 2007). Although *Spea* larvae develop

Fig. 2. North American spadefoots inhabit variable environments. For example, the Eastern spadefoot (*Scaphiopus holbrookii*) inhabits more mesic environments, and breeds in ponds that are longer in duration (top left). Within desert environments, spadefoot natal ponds may vary in nutrient richness and duration. These ponds may be surrounded by vegetation and thus high in organic nutrients (top right), or may have very little vegetation and nutrients, for instance, if they are formed on desert playas (bottom left). These ponds may also vary in duration; for instance, larger ponds (bottom left) usually last longer than smaller ponds (bottom right).

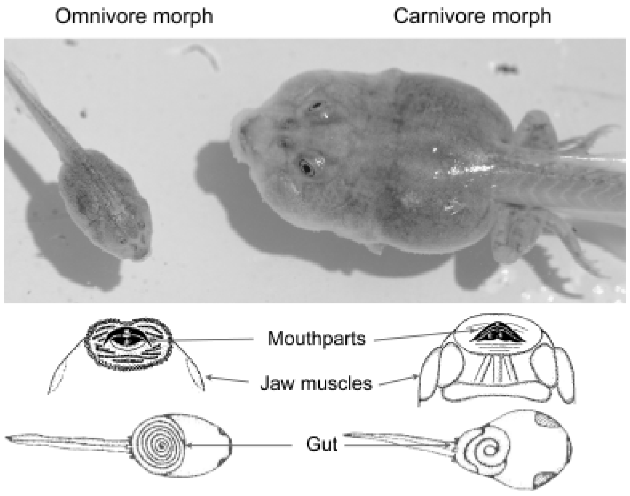

Fig. 3. Tadpoles in the genus *Spea* express polyphenism: alternate phenotypes that are environmentally dependent. Some individuals develop as typical omnivorous anuran larvae, which possess small jaw muscles, smooth and unserrated mouthparts, and a long, coiled intestine (left morph). In contrast, some individuals develop as a carnivorous morph, possessing large jaw muscles, notched and serrated mouthparts, and a short, relatively uncoiled gut (right). The frequency and degree of carnivore morph expression varies among species, populations and families. The process by which an individual develops as a carnivore morph is likely influenced by multiple environmental factors (e.g., social context and body condition) however a potent environmental cue for the induction of this alternate phenotype is the consumption of shrimp.

these features (which is referred to as the "omnivore" ecotype) by default, they have the potential to develop as an alternative "carnivore" ecotype (sensu Pomeroy 1981), which is characterized by large jaw muscles, notched and keratinized mouthparts, few labial teeth, and a short gut (Fig. 3; Pomeroy 1981; Pfennig 1992a, b). Thus, although typical anuran larvae feed *opportunistically* on macroscopic prey (e.g., macroinvertebrates and dead tadpoles; Schiesari et al. 2009), *Spea*'s carnivore morph is *specialized* for pursuing and subduing live, macroscopic prey. Interestingly, the expression of this ecomorph is induced by the consumption of shrimp and other tadpoles (Pomeroy 1981; Pfennig 1990), although numerous other factors also influence carnivore production (Table 1). Moreover, the frequency with which the carnivore morph is expressed, and how "extreme" the resulting carnivores are (i.e., the degree to which the carnivore is phenotypically distinct from the omnivore), varies among species, populations, and even sibships (Pfennig 1999; Pfennig and Murphy 2000, 2002).

A MAJOR RESEARCH CHALLENGE: PLASTICITY AND EVOLUTION

Because spadefoot larval development is sensitive to diverse environmental stimuli (Table 1), these tadpoles can be used to examine how an organism's ecology affects its development, as well as how an organism's development influences its ecology and evolution. Additionally, spadefoot tadpoles are excellent models for examining the role of phenotypic plasticity in evolution.

Evolutionary biologists have long hypothesized that phenotypic plasticity might precede, and even promote, genetic evolution (Baldwin 1896; Schmalhausen 1949; Waddington 1953; West-Eberhard 1989; Schlichting and Pigliucci 1998; Pál and Miklos 1999; Pigliucci and Murren 2003; Price et al. 2003; West-Eberhard 2003; Schlichting and Murren 2004; Moczek 2008; Pfennig et al. 2010). According to one widely accepted hypothesis, if selection acts on quantitative genetic variation regulating the expression of initially environmentally dependent traits, it can lead to the evolution of reduced or enhanced plasticity (the extremes being assimilation and polyphenism, respectively; Waddington 1953; Mayr 1963). This process—dubbed "genetic accommodation" (sensu West-Eberhard 2003)—can ultimately result in the evolution of a novel trait. Although laboratory studies have demonstrated that genetic accommodation can occur (Waddington 1953; Rutherford and Lindquist 1998; Suzuki and Nijhout 2006), relatively little is known about whether and how this process is responsible for ecologically and evolutionarily relevant traits in natural populations.

Table 1. Various factors that influence the expression of the distinctive carnivore ecotype in *Spea* tadpoles

Cue	Effect on development	Reference
Large animal prey	Ingestion of shrimp or tadpoles induces carnivore production	Pomeroy (1981); Pfennig (1990)
Heterospecific competitors	Presence of heterospecific competitors can either increase or decrease a focal individual's likelihood of becoming a carnivore, depending on the species	Pfennig and Murphy (2000)
Genetic relatives	Presence of genetic relatives decreases a focal individual's likelihood of becoming a carnivore	Pfennig and Frankino (1997)
Individual's condition	Tadpoles in good condition (i.e., those with large mass relative to body length) are more likely to become a carnivore when reared with conspecific competitors, but less likely to do so when reared alone	Frankino and Pfennig (2001)

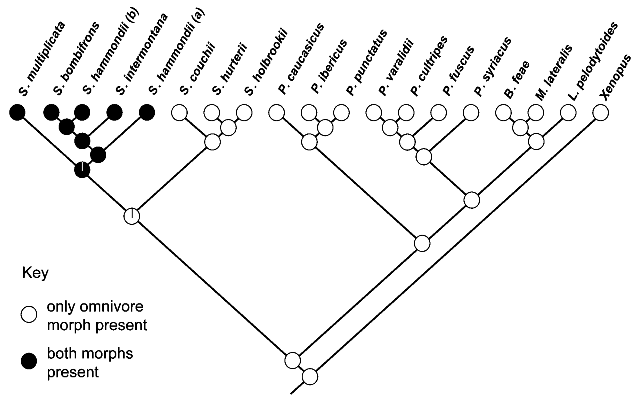

Fig. 4. An ancestral character state reconstruction depicting the distribution of trophic polyphenism among spadefoots species (Pelobatoidea), their ancestors, and an outgroup (*Xenopus*). Relative support for the ability to express the carnivore morph is indicated with black circles, while relative support for the expression of typical, monomorphic larvae is indicated with white circles (tree from García-París et al. 2003; reconstruction from Ledón-Rettig et al. 2008). Resource polyphenism—the ability to express discrete resource-use traits—is confined to the genus *Spea*. *S. multiplicata*, *Spea multiplicata*; *S. bombifrons*, *Spea bombifrons*; *S. hammondii*, *Spea hammondii*; *S. intermontana*, *Spea intermontana*; *S. couchii*, *Scaphiopus couchii*; *S. hurterii*, *Scaphiopus hurterii*; *S. holbrookii*, *Scaphiopus holbrookii*; *P. caucasicus*, *Pelodytes caucasicus*; *P. ibericus*, *Pelodytes ibericus*; *P. punctatus*, *Pelodytes punctatus*; *P. varalidii*, *Pelobates varalidii*; *P. cultripes*, *Pelobates cultripes*; *P. fuscus*, *Pelobates fuscus*; *P. syriacus*, *Pelobates syriacus*; *B. feae*, *Brachytarsophrys feae*; *M. lateralis*, *Megophrys lateralis*; *L. pelodytoides*, *Leptolalax pelodytoides*.

Understanding the role of environmentally dependent variation in the origins of novel, complex traits has been a major research focus in spadefoots. However, it is not the only problem in eco-evo-devo that has been addressed using spadefoots. Three additional topics have been the subjects of research, including (1) the role of epigenetic inheritance in adaptive evolution; (2) the role of developmental switches in evolution; and (3) how feedback can arise among developmental mechanisms, ecological processes, and evolutionary outcomes. We highlight research each area below.

PLASTICITY AS AN ANTECEDENT OF NOVELTY

Relatively little is known about whether and how genetic accommodation promotes the evolution of complex, novel traits in natural populations. Part of the difficulty is that, once a trait has already evolved, its evolution cannot be studied in situ.

To examine whether and how an evolutionary lineage's past environmentally dependent responses played a role in the origins of novel traits, we must find a way to "turn back the clock." One way of doing so is to use a comparative approach informed by phylogeny (Shapiro 1980; Ghalambor et al. 2007). In other words, an effective approach for evaluating plasticity's role in the origins of novelty is to examine the phenotypic responses of a taxon that is "ancestral" to taxa possessing the novel trait in question, and thereby infer whether the actual ancestors of the species or population in question could express such a trait facultatively.

Spadefoots have been studied in this fashion. In one study, the remarkably short larval periods of North American spadefoots were compared with those of "ancestral" European spadefoots (*Pelobates* and *Pelodytes*; Gomez-Mestre and Buchholz 2006). Even though the former possess considerable plasticity in developmental timing, this plasticity has been reduced along with a trend toward overall shorter larval period. Taxa with reduced larval periods appear to have evolved from developmentally plastic Pelobatid ancestors. The assimilation of a shorter larval period might have occurred when selection acted on genetic variation underlying developmental rate, causing larvae to produce higher levels of thyroid hormone (specifically, triiodotyrosine, or T_3, the key instigator of amphibian metamorphosis) and/or greater tissue sensitivity to thyroid hormone (Gomez-Mestre and Buchholz 2006). Indeed, the species possessing the shortest larval period (and least metamorphic plasticity) expresses high thyroid hormone receptor mRNA levels throughout development relative to other spadefoots (D. R. Buchholz, personal communication).

In a second study, this comparative approach was used to investigate the evolution of an omnivore feeding strategy in *S. couchii* tadpoles. In contrast to the generalist feeding strategy exhibited by most spadefoot larvae, *S. couchii* feeds exclusively on detritus and microorganisms, and suffers poor fitness if fed only shrimp (Ledón-Rettig et al. 2008, 2009). Ancestors of *S. couchii* might have maintained a generalist feeding strategy, which included the shrimp resource, but were ultimately excluded from this diet as *Spea* larvae, which inhabit the same ponds, evolved their cannibalistic morphologies and behaviors (C. C. Ledón-Rettig and D. W. Pfennig, unpublished data). Importantly, ancestors of *S. couchii* might have mediated this predation risk by choosing microhabitat distinct from the highest densities of cannibalistic larvae and, as a by-product, the highest densities of shrimp. These behavioral modifications might have been followed by an evolutionary loss of behavioral, physiological, and morphological traits that allowed *S. couchii* to consume shrimp, leading to assimilation of the detritivore feeding strategy. Further, *S. couchii* might have evolved a more *specialized* detritivore morph. Indeed, evidence based on larval gut length suggests that *S. couchii* are far more specialized for consuming detritus than other anurans, including *Spea* (Altig and Kelly 1974) (Fig. 4).

Spadefoots have left other possible signatures of genetic accommodation. For instance, although certain populations of *S. multiplicata* are plastic with respect to the resource polyphenism, those in sympatry with *S. bombifrons* are canalized for the omnivore morph as a manifestation of character displacement (trait evolution resulting from selection that reduces competition; Pfennig and Murphy 2000, 2002). Likewise, although carnivores are normally induced in *Spea* only after tadpoles have been exposed to shrimp or high tadpoles densities, carnivores appear to be expressed constitutively in certain populations of *S. bombifrons* (Pomeroy 1981). Ultimately, the most direct evidence that environmentally dependent phenotypes can engender evolutionary novelties will come from selection studies on variation exposed under novel environmental regimes. Spadefoots are not ideal for performing such selection studies (individuals do not reach sexual maturity for at least one year). Nevertheless, such challenges must be confronted if we are to understand if and how genetic accommodation occurs in vertebrates.

EPIGENETIC INHERITANCE AND EVOLUTION

In many species, development is dictated not only by the parental genetic contribution, but also by the parents' extragenomic contributions (Roach and Wulff 1987; Rossiter 1996; Mousseau and Fox 1998). Indeed, parents often facultatively endow their offspring with materials (e.g., resources, hormones, and parental care: Schwabl 1993; Weaver et al. 2004; Dloniak et al. 2006) or information (e.g., altered states of gene regulation: Agrawal et al. 1999) that allow offspring to cope better with their specific environment. In this way, "maternal effects" (so called because most cases involve only mothers) enable fitness-enhancing information acquired during the mother's lifetime to be transmitted directly to her offspring (Mousseau and Fox 1998; Agrawal et al. 1999; Plaistow et al. 2006). The widespread occurrence of environmentally initiated maternal effects is important because it illustrates how information acquired during an individual's lifetime can be transmitted to its offspring, thereby forming an alternative inheritance system (Jablonka and Lamb 1995, 2005; Pigliucci 2007).

Additionally, maternal effects might play a key role in generating novel phenotypes through genetic accommodation (West-Eberhard 2003, 2005). A maternal effect influences phenotypic expression in many individuals simultaneously, especially when mothers produce large numbers of offspring. Consequently, traits among the offspring whose expression is mediated by a maternal effect can be tested in numerous, diverse genetic backgrounds, thereby increasing the chances of genetic accommodation occurring. Moreover, maternal effects can spawn an evolutionary momentum that persists for many generations, even in the absence of the original environmental factor that induced the maternal effect (Kirkpatrick & Lande 1989; for possible empirical examples, see Agrawal et al. 1999; Plaistow et al. 2006). Consequently, maternal effects provide more frequent, recurrent opportunities for genetic accommodation to transpire. Thus, traits whose expression is influenced by maternal effects might be especially likely to undergo subsequent refinement, elaboration, and, possibly, developmental stabilization through genetic accommodation.

In amphibians, development is especially sensitive to maternal condition (Kaplan 1998). For example, in Mexican spadefoots (*S. multiplicata*), the maternal phenotype influences the expression of resource polyphenism among her tadpole offspring. Specifically, the tadpoles of larger females are more likely to become carnivores (Martin and Pfennig 2010a). Moreover, the tendency for large mothers to produce tadpoles with a greater propensity to become carnivores has been shown to reflect differences in maternal investment (Martin and Pfennig 2010a). Larger females invest in larger eggs, which become larger tadpoles. Larger tadpoles, in turn, are able to handle shrimp more efficiently and thereby acquire more of the cue—shrimp ingestion—that induces the carnivore morph (Martin and Pfennig 2010a).

This maternal effect appears to mediate adaptive divergence between populations (specifically, character displacement), and there is even evidence that it has promoted the evolution of canalized divergence in morph production between populations that have experienced prolonged and persistent differences in exposure to a heterospecific competitor. In particular, Mexican spadefoots (*S. multiplicata*) and Plains spadefoots (*S. bombifrons*) have diverged in the expression of resource polyphenism where they co-occur in southeastern Arizona, US, as an adaptive response to selection that minimizes competition with the other species (Pfennig and Murphy 2000, 2002, 2003; Pfennig and Pfennig 2005; Pfennig et al. 2006, 2007; Rice et al. 2009). In populations where each species occurs alone, both species produce among their larvae similar, intermediate frequencies of carnivores (which prey on fairy shrimp) and omnivores (which specializes on detritus; Pfennig et al. 2006). However, in populations where they co-occur, *S. multiplicata* shift to producing mostly omnivores, whereas *S. bombifrons* shift to producing mostly carnivores (Pfennig and Murphy 2000, 2002, 2003; Pfennig et al. 2006). This divergence appears to reflect selection to lessen interspecific competition for food (Pfennig and Murphy 2000, 2002; Pfennig et al. 2007; Rice et al. 2009). Specifically, by producing mostly omnivores, sympatric *S. multiplicata* avoid competing for shrimp with *S. bombifrons*, the species that is the superior competitor for the shrimp resource. By contrast, by producing mostly carnivores, sympatric *S. bombifrons* avoid competing for detritus with *S. multiplicata*, the species that is the superior competitor for the detritus resource (Pfennig and Murphy 2000).

Although these differences between sympatric and allopatric populations of *S. multiplicata* persist even when tadpoles are reared under common conditions (Pfennig and Murphy 2000, 2002), they appear to be mediated by a condition-dependent maternal effect (Pfennig and Martin 2009). Specifically, because sympatric *S. multiplicata* are forced by *S. bombifrons* onto the less nutritious detritus resource (Pfennig and Murphy 2000), sympatric *S. multiplicata* tend to mature as smaller (Pfennig and Pfennig 2005) and poorer condition adults (Pfennig and Martin 2009). Presumably because of their reduced size and/or condition, female *S. multiplicata* in sympatry invest less into offspring than do female *S. multiplicata* in allopatry (Martin and Pfennig 2010a). Because smaller, poorer condition females produce mostly omnivores (see above), these females create offspring with a phenotype that minimizes competition with *S. bombifrons* and that differs from the phenotype in allopatry. However, these population differences in morph production disappear once mothers are equilibrated in body condition (Pfennig and Martin 2009), indicating that a condition-dependent maternal effect mediates character displacement in this species. Indeed, the relatively small females from each generation should also tend to produce small eggs and omnivores in the next generation, fueling a self-reinforcing epigenetic cycle that promotes divergence between sympatric and allopatric populations (Pfennig and Martin 2009).

Environmentally mediated maternal effects, similar to those observed in *S. multiplicata*, might have preceded and promoted canalized differences in populations of *S. bombifrons*. In contrast to *S. multiplicata*, the expression of carnivore morphs in *S. bombifrons* is not (or may no longer be) dependent on maternal condition (Pfennig and Martin 2010). As mentioned, *S. bombifrons* express a higher frequency of carnivores in sympatry relative to allopatry, but this difference is not related to population differences in maternal condition. Instead, divergence between sympatric and allopatric *S. bombifrons* populations in morph production appears to reflect genetically fixed differences between these two types of populations.

How did these differences arise from environmentally mediated maternal effects? The answer may reside in the history of this population of *S. bombifrons* with its resource competitor. *S. bombifrons* has recently invaded *S. multiplicata*'s relatively stable range (Rice and Pfennig 2008), and populations of *S. bombifrons* at the front of this expansion—that is, populations in which the carnivore morph is expressed in the *absence* of the maternal effect—have had a relatively long evolutionary history with their competitor. In contrast, populations of *S. multiplicata* at the edge of this invasion front have had very little time to evolve, genetically, in response to their competition. Therefore, it appears that the expression of the carnivore morph in *S. bombifrons* populations at the front of an invasion has become divorced from maternal control by substitution with novel genetic variants and combinations (Pfennig and Martin 2010).

DEVELOPMENTAL SWITCHES AS FACILITATORS OF DIVERSITY

Although the origins of developmental polyphenisms is a motivating topic per se, once in place, they might subsequently facilitate the evolution of adaptive, phenotypic variation (West-Eberhard 1989; Moczek 2009; Minelli and Fusco 2010; Pfennig et al. 2010). On two fronts, through their biphasic life cycle and their resource polyphenism, spadefoots can be used to investigate the origins and evolutionary consequences of developmental switches.

It is still unclear whether *Spea*'s resource polyphenism evolved from continuous variation (Martin and Pfennig 2010b), or whether it has been resurrected—fully intact or in particular aspects—from some quiescent developmental switch expressed in ancestral amphibian larvae. However, in other systems, it is often possible to reveal intermediate forms from natural populations (Nijhout 2003) and evolve polyphenisms from continuous variation in the lab (Suzuki and Nijhout 2006). This suggests that in some cases continuous plasticity is ancestral, and that discrete polyphenism is the result of selection for adaptive, alternative phenotypes (Nijhout 2003; Moczek 2007). Further, some nonpolyphenic spadefoot populations exhibit heritable variation in diet-dependent gut length, indicating that at least some elements of this resource polyphenism could have arisen from selection on continuous, diet-dependent variation (Ledón-Rettig et al. 2010).

Once a developmental switch or sequence has evolved, its components can be "rearranged" into novel combinations (i.e., "developmental recombination"; West-Eberhard 2003). Such components might include alternate modes of behavior, physiology, or morphology that can be deleted, duplicated, amplified, or altered to produce a drastically different outcome or respond to different cues. This recombination is possible when context-dependent phenotypes are underlain by modular elements (i.e., genes, proteins, or other traits) that are free from pleiotropic constraints with traits expressed in other contexts (i.e., environments or developmental stages). There is rapidly accumulating evidence that developmental polyphenisms are often underlain by modular elements, at least at the level of gene expression (Moczek 2009; Snell-Rood et al. 2011).

In spadefoot larvae, the stress axis may be a key regulator of developmental switches such that variation in the elements of this axis has resulted in phenotypic diversification. Across vertebrate taxa, the stress axis plays an important role in transducing environmental signals into developmental, behavioral, and physiological responses (Crespi and Denver 2005a). Interestingly, in anuran larvae, the major developmental and stress hormones (T_3 and corticosterone [CORT], respectively) are controlled by the same neuroendocrine factor, corticotropin-releasing factor (CRF; Denver 1999). As mentioned, spadefoot larvae can accelerate metamorphosis in response to nutritional restriction, crowding, water temperature elevation, or water volume reduction (Denver et al. 1998; Morey and Reznick 2000; Boorse and Denver 2003; Crespi and Denver 2005b; Gomez-Mestre and Buchholz 2006). In the last case, metamorphic timing has been directly linked to CRF regulation (Denver 1997). Because all these cues are indicative of a deteriorating larval habitat, it is likely that CRF coordinates the timing of anuran metamorphosis with environmental information by coupling the environmental sensitivity of CRF secreting neurons to the actions of T_3 and CORT on an individual's developmental response.

Given that the stress axis is ancient and functions across birds, mammals, fish, amphibians, and reptiles, this developmental switch might have been co-opted in amphibian larvae so that they could respond to a unique set of signals that are particularly good at predicting the condition of aquatic habitats. Likewise, the same endocrine machinery used for escaping drying ponds might have been co-opted to produce the alternate trophic morph in *Spea*. The thyroid hormone T_3 has been implicated in the expression of the larval carnivore morph, which possesses certain attributes characteristic of metamorphosing individuals (Pfennig 1992b).

If the endocrine signal for rapid development, T_3, is indeed involved in the production of the carnivore morph, then why do tadpoles that become carnivores not, at the same time, metamorphose? As it turns out, carnivore-morph tadpoles do indeed metamorphose significantly earlier than omnivore-morph tadpoles reared under the same conditions (Pomeroy 1981; Pfennig 1992b). Moreover, the effects of T_3 on certain tissues and organs might have been divorced through differential distribution of hormone receptors or genetic variation in the downstream targets of hormone receptors, themselves. These topics clearly need further investigation, but we anticipate that a comparison of the hormonal regulation of morphs, populations, and species that vary in plastic responses (i.e., developmental timing and resource polyphenism) will reveal whether ancestral developmental switches (e.g., the stress axis) can facilitate the diversification of phenotypes.

Traits need not only evolve when they become dissociable during ontogeny and evolution. The converse situation of modularity is when developmental switches have pleiotropic effects on traits, resulting in relationships that are conserved between populations and species, even if they are exposed to different environmental conditions. If a threshold switch itself evolves (occurring earlier or later during ontogeny, responding more or less or to different environmental cues), it might bring about the evolution of correlated traits in its wake (Nijhout and Emlen 1998; Moczek and Nijhout 2004; Suzuki and Nijhout 2008). For instance, in spadefoots, adult snout and leg lengths are positively correlated with how long a tadpole develops (a highly environmentally dependent variable; Gomez-Mestre and Buchholz 2006). More remarkably, adult snout and leg lengths among different *species* are positively correlated with the length each species' average larval period. Although it is not clear if these evolutionary by-products are adaptive, such correlations generate phenotypic variation that can act as new targets for selection and would not otherwise be made available.

RECIPROCAL ACCOMMODATION

Above, we focused on how the larval spadefoot's phenotypic response is shaped by its environmental variation and ecological interactions. However, the reciprocal is also true: environments and communities—and thus, selective regimes—are modified by the phenotypic responses of the individuals within them (Lewontin 1983; Day et al. 2003). Although this was recognized by evolutionary biologists during the modern synthesis (reviewed in Wcislo 1989; Odling-Smee et al. 2003), the interdependency of organismal responses and selective environments was not included in most conceptual and theoretical models until much later (sensu Lewontin 1983). Advocates of this perspective argue that the behavioral, morphological, and physiological phenotypes elicited by organisms are not merely the end products of selection, but evolutionary processes that alter selection pressures. This process is generally referred to as "niche construction" (sensu Odling-Smee 1988).

Some interactions might lead to an eco-evolutionary feedback that modifies the evolutionary trajectories of associated traits, a process that we will refer to as "reciprocal accommodation" (sensu Gilbert and Epel 2009). Although it is clear that, in many cases, reciprocal accommodation *modifies* the evolutionary trajectory of involved traits, whether the evolution of such traits is promoted or constrained depends on a population's environmental and phylogenetic history (Sultan 2007). For instance, organisms can alter their competitive environment via character displacement (Schluter 2000), but the ability to undergo character displacement tends to be more prevalent and proceed more quickly in taxa that are phenotypically variable (Rice and Pfennig 2007). This variability is, in turn, contingent on a species' or population's evolutionary past with other environmental and ecological challenges.

Such reciprocal accommodation can be observed in *Spea*. As mentioned above, both *S. multiplicata* and *S. bombifrons* exhibit resource polyphenism in allopatry, but competitive interactions have promoted divergence between these species' in sympatry. In particular, where the two species occur together, selection favors omnivorous traits in *S. multiplicata*. By contrast, selection favors carnivorous traits in *S. bombifrons*. The two species employ phenotypic plasticity to promote this divergence in trophic morphology (and, hence, in resource use; Pfennig and Murphy 2002). Species that can facultatively alter their phenotypes in this way may persist in the face of novel competitive interactions, because they can switch to a selectively favored phenotype without having to wait for mutation or recombination (Pfennig and Murphy 2000, 2002). That is, *Spea*'s developmental plasticity has *shaped* their ecology; in the absence of such plasticity, the less competitive species may have become locally extinct through competitive exclusion.

The mechanisms by which niche construction can promote or impede trait evolution can be explained in terms of traditional quantitative genetics (Donohue 2005), and factors that may allow or prevent a population from responding to niche construction are the same as those that would apply to general adaptive evolution. Still, few empirical examples exist that convincingly demonstrate the influence of niche construction on the evolution of traits and suites of traits (although see Post and Palkovacs 2009). As discussed above, variation in larval competitive environments among populations of spadefoots makes them particularly amenable for isolating the influence of niche construction on the evolution of resource use traits.

CONCLUSIONS AND FUTURE DIRECTIONS

The fields of ecology, evolution, and development are not only informed by one another; they are *contingent* on one another. Even though the questions asked by these fields are seemingly different, and cross-talk among these fields has been relatively limited, the emergent phenomena that can be explained by considering all fields in conjunction will be greater than the sum of the parts. Furthermore, because of recent advances in techniques that make the syntheses of these fields possible, now is the time that integrating eco-devo with evo-devo might yield the largest and most important contributions.

For instance, determining whether or to what extent alternate, environmentally dependent phenotypes share the same developmental modules is critical for understanding the evolutionary consequences of plasticity (Snell-Rood et al. 2010). It is now possible to characterize these developmental modules at the level of gene expression (e.g., see Snell-Rood et al. 2011). Research in our lab on spadefoots has thus far identified over 70 distinct genes that are differentially expressed between omnivore and carnivore morphs in both lab-reared and field-caught individuals (A. Leichty and D. W. Pfennig, unpublished data). Given the importance of the omnivore–carnivore larval polyphenism in determining fitness, genes that are differentially expressed between these alternative morphs might be the ultimate targets of selection in this system. Future studies should seek to ascertain whether or not these genes are indeed under strong selection in populations where the omnivore–carnivore larval polyphenism has evolved. Moreover, insights into the functionality and history of these genes might illuminate how the polyphenism evolved in the first place.

In addition to divergence in developmental modules, per se, phenotypic variation can arise due to differences in the timing and placement of the same developmental modules (e.g., see "Developmental Switches as Facilitators of Diversity"). Currently, researchers are identifying the endocrine and molecular mechanisms (i.e., altered production of metamorphic hormones and expression of hormone receptors) associated with variation in the neuroendocrine stress axis, allowing spadefoot tadpoles to diversify in metamorphic plasticity (D. R. Buchholz, personal communication).

In the future, the challenge of integrating eco-devo with evo-devo will be to identify appropriate systems in which we know a considerable amount about their genetic variation, ecological interactions, and developmental responses. Spadefoots are well suited for this task because numerous studies have illuminated the environmental effects on early development, and even their lasting effects on adult phenotypes (e.g., see "The Environmentally Responsive Spadefoot"). Indeed, although eco-devo has only recently gained attention in the literature, research on spadefoots and other amphibians has been contributing to this field for decades. Moreover, spadefoots might help to illuminate an overlooked problem in eco-devo: how development affects ecology. As noted above, a common, but potentially important, way in which development might impact ecology is by promoting character displacement (see "Reciprocal Accommodation"). Thus, research on spadefoots has been, and may continue to be instrumental in shedding light on both how an organism's ecology can affect its development, and also onto how its development can influence its ecology. By characterizing and understanding the interconnectedness among development responses, ecological interactions, and their evolutionary responses of natural populations, we can ultimately answer, the major question uniting practitioners of eco-evo-devo, posed at the outset: what is the environment's role, not only in selecting among diverse phenotypes, but also in creating these diverse phenotypes?

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REFERENCES

Agrawal, A. A., Laforsch, C., and Tollrian, R. 1999. Transgenerational induction of defenses in animals and plants. *Nature* 401: 60–63.

Altig, R., and Kelly, J. P. 1974. Indices of feeding in anuran tadpoles as indicated by gut characteristics. *Herpetologica* 30: 200–203.

Altig, R., Whiles, M. R., and Taylor, C. L. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshw. Biol.* 52: 386–395.

Baldwin, J. M. 1896. A new factor in evolution. *Am. Nat.* 30: 441–451.

Boorse, G. C., and Denver, R. J. 2003. Endocrine mechanisms underlying plasticity in metamorphic timing in spadefoot toads. *Int. Comp. Biol.* 43: 646–657.

Bragg, A. N. 1965. *Gnomes of the Night. The Spadefoot Toads.* University of Pennsylvania Press, Philadelphia.

Crespi, E. J., and Denver, R. J. 2005a. Ancient origins of human developmental plasticity. *Am. J. Hum. Biol.* 17: 44–54.

Crespi, E. J., and Denver, R. J. 2005b. Roles of stress hormones in food intake regulation in anuran amphibians throughout the life cycle. *Comp. Biochem. Physiol. A Mol. Int. Physiol.* 141: 381–390.

Day, R. L., Laland, K. N., and Odling-Smee, J. 2003. Rethinking adaptation—the niche-construction perspective. *Perspect. Biol. Med.* 46: 80–95.

Denver, R. J. 1997. Environmental stress as a developmental cue: corticotropin-releasing hormone is a proximate mediator of adaptive phenotypic plasticity in amphibian metamorphosis. *Horm. Behav.* 31: 169–179.

Denver, R. J. 1999. Evolution of the corticotropin-releasing hormone signaling system and its role in stress-induced phenotypic plasticity. In C. A. Sandman, F. L. Strand, B. Beckwith, B. M. Chronwall, F. W. Flynn, and R. J. Nachman (eds.). *Neuropeptides: Structure and Function in Biology and Behavior.* New York Academy of Sciences, New York, pp. 46–53.

Denver, R. J., Mirhadi, N., and Phillips, M. 1998. Adaptive plasticity in amphibian metamorphosis: response of *Scaphiopus hammondii* tadpoles to habitat desiccation. *Ecology* 79: 1859–1872.

Dloniak, S. M., French, J. A., and Holekamp, K. E. 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyenas. *Nature* 440: 1190–1193.

Donohue, K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytol.* 166: 83–92.

Duellman, E., and Trueb, L. 1986. *Biology of Amphibians.* John Hopkins University Press, Baltimore.

Frankino, W. A., and Pfennig, D. W. 2001. Condition-dependent expression of trophic polyphenism: effects of individual size and competitive ability. *Evol. Ecol. Res.* 3: 939–951.

García-París, M., Buchholz, D. R., and Parra-Olea, G. 2003. Phylogenetic relationships of Pelobatoidea re-examined using mtDNA. *Mol. Phylogenet. Evol.* 28: 12–23.

Ghalambor, C. K., McKay, J. K., Carroll, S. P., and Reznick, D. N. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Funct. Ecol.* 21: 394–407.

Gilbert, S., and Epel, D. 2009. *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution.* Sinauer Associates, Sunderland.

Gomez-Mestre, I., and Buchholz, D. 2006. Developmental plasticity mirrors differences among taxa in spadefoot toads linking plasticity and diversity. *Proc. Nat. Acad. Sci. USA* 50: 19021–19026.

Jablonka, E., and Lamb, M. J. 1995. *Epigenetic Inheritance and Evolution: The Lamarckian Dimension.* Oxford University Press, Oxford.

Jablonka, E., and Lamb, M. J. 2005. *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral and Symbolic Variation in the History of Life.* MIT Press, Cambridge.

Kaplan, R. H. 1998. Maternal effects, developmental plasticity, and life history evolution: an amphibian model. In T. A. Mousseau and C. W. Fox (eds.). *Maternal Effects as Adaptations.* Oxford University Press, New York, pp. 244–260.

Kirkpatrick, M., and Lande, R. 1989. The evolution of maternal characters. *Evolution* 43: 485–503.

Ledón-Rettig, C. C., Pfennig, D. W., and Crespi, E. J. 2009. Stress hormones and the fitness consequences associated with the transition to a novel diet in larval amphibians. *J. Exp. Biol.* 212: 3743–3750.

Ledón-Rettig, C. C., Pfennig, D. W., and Crespi, E. J. 2010. Diet and hormonal manipulation reveal cryptic genetic variation: implications for the evolution of a novel feeding strategy. *Proc. Roy. Soc. Lond. B* 277: 3569–3578.

Ledón-Rettig, C. C., Pfennig, D. W., and Nascone-Yoder, N. 2008. Ancestral variation and the potential for genetic accommodation in larval amphibians: implications for the evolution of novel feeding strategies. *Evol. Dev.* 10: 316–325.

Lewontin, R. C. 1983. Organism and environment. In H. C. Plotkin (ed.). *Learning, Development, and Culture.* John Wiley and Sons, Ltd, New York, pp. 151–170.

Martin, R. A., and Pfennig, D. W. 2010a. Maternal investment influences expression of resource polymorphism in amphibians: implications for the evolution of novel resource-use phenotypes. *PLoS ONE* 5: e9117.

Martin, R. A., and Pfennig, D. W. 2010b. Field and experimental evidence that competition and ecological opportunity promote resource polymorphism. *Biol. J. Linn. Soc. Lond.* 100: 73–88.

Mayr, E. 1963. *Animal Species and Evolution.* Belknap Press, Cambridge.

Minelli, A., and Fusco, G. 2010. Developmental plasticity and the evolution of animal complex life cycles. *Phil. Trans. Roy. Soc. B Biol. Sci.* 365: 631–640.

Moczek, A. P. 2007. Developmental capacitance, genetic accommodation, and adaptive evolution. *Evol. Dev.* 9: 299–305.

Moczek, A. P. 2008. On the origins of novelty in development and evolution. *Bioessays* 30: 432–447.

Moczek, A. P. 2009. The origin and diversification of complex traits through micro- and macroevolution of development: insights from horned beetles. In W. Jeffery (ed.). *Current Topics in Developmental Biology.* Vol. 86. Elsevier Academic Press Inc, San Diego, pp. 135–162.

Moczek, A. P., and Nijhout, H. F. 2004. Trade-offs during the development of primary and secondary sexual traits in a horned beetle. *Am. Nat.* 163: 184–191.

Morey, S., and Reznick, D. 2000. A comparative analysis of plasticity in larval development in three species of spadefoot toads. *Ecology* 81: 1736–1749.

Mousseau, T. A., and Fox, C. W. 1998. *Maternal Effects as Adaptations.* Oxford University Press, New York.

Newman, R. A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. *Ecology* 70: 1775–1787.

Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. *Bioscience* 42: 671–678.

Newman, R. A. 1994. Genetic variation for phenotypic plasticity in the larval life history of spadefoot toads (*Scaphiopus couchii*). *Evolution* 48: 1773–1785.

Nijhout, H. F. 2003. Development and evolution of adaptive polyphenisms. *Evol. Dev.* 5: 9–18.

Nijhout, H. F., and Emlen, D. J. 1998. Competition among body parts in the development and evolution of insect morphology. *Proc. Nat. Acad. Sci. USA* 95: 3685–3689.

Odling-Smee, J. 1988. Niche constructing phenotypes. In H. C. Plotkin (ed.). *The Role of Behavior in Evolution.* MIT Press, Cambridge, MA, pp. 73–132.

Odling-Smee, J., Laland, K. N., and Feldman, M. 2003. *Niche Construction: The Neglected Process in Evolution.* Princeton University Press, Princeton, NJ.

Pál, C., and Miklos, I. 1999. Epigenetic inheritance, genetic assimilation and speciation. *J. Theor. Biol.* 200: 19–37.

Pfennig, D. W. 1990. The adaptive significance of an environmentally-cued developmental switch in an anuran tadpole. *Oecologia* 85: 101–107.

Pfennig, D. W. 1992a. Polyphenism in spadefoot toad tadpoles as a locally adjusted evolutionary stable strategy. *Evolution* 46: 1408–1420.

Pfennig, D. W. 1992b. Proximate and functional causes of polyphenism in an anuran tadpole. *Funct. Ecol.* 6: 167–174.

Pfennig, D. W. 1999. Cannibalistic tadpoles that pose the greatest threat to kin are most likely to discriminate kin. *Proc. Roy. Soc. Lond. B Biol. Sci.* 266: 57–61.

Pfennig, D. W., and Frankino, W. A. 1997. Kin-mediated morphogenesis in facultatively cannibalistic tadpoles. *Evolution* 51: 1993–1999.

Pfennig, D. W., and Martin, R. A. 2009. A maternal effect mediates rapid population divergence and character displacement in spadefoot toads. *Evolution* 63: 898–909.

Pfennig, D. W., and Martin, R. A. 2010. Evolution of character displacement in spadefoot toads: different proximate mechanisms in different species. *Evolution* 64: 2331–2341.

Pfennig, D. W., and Murphy, P. J. 2000. Character displacement in polyphenic tadpoles. *Evolution* 54: 1738–1749.

Pfennig, D. W., and Murphy, P. J. 2002. How fluctuating competition and phenotypic plasticity mediate species divergence. *Evolution* 56: 1217–1228.

Pfennig, D. W., and Murphy, P. J. 2003. A test of alternative hypotheses for character divergence between coexisting species. *Ecology* 84: 1288–1297.

Pfennig, D. W., Rice, A. M., and Martin, R. A. 2006. Ecological opportunity and phenotypic plasticity interact to promote character displacement and species coexistence. *Ecology* 87: 769–779.

Pfennig, D. W., Rice, A. M., and Martin, R. A. 2007. Field and experimental evidence for competition's role in phenotypic divergence. *Evolution* 61: 257–271.

Pfennig, D. W., Wund, M. A., Snell-Rood, E. C., Cruickshank, T., Schlichting, C. D., and Moczek, A. P. 2010. Phenotypic plasticity's impacts on diversification and speciation. *Trends Ecol. Evol.* 25: 459–467.

Pfennig, K. S., and Pfennig, D. W. 2005. Character displacement as the "best of a bad situation": fitness trade-offs resulting from selection to minimize resource and mate competition. *Evolution* 59: 2200–2208.

Pigliucci, M. 2007. Do we need an extended evolutionary synthesis? *Evolution* 61: 2743–2749.

Pigliucci, M., and Murren, C. J. 2003. Perspective: Genetic assimilation and a possible evolutionary paradox: Can macroevolution sometimes be so fast as to pass us by? *Evolution* 57: 1455–1464.

Plaistow, S. J., Lapsley, C. T., and Benton, T. G. 2006. Context-dependent intergenerational effects: the interaction between past and present environments and its effect on population dynamics. *Am. Nat.* 167: 206–215.

Pomeroy, L. V. 1981. Developmental polymorphism in the tadpoles of the spadefoot toad *Scaphiopus multiplicatus*. PhD dissertation, University of California, Riverside.

Post, D. M., and Palkovacs, E. P. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. *Phil. Trans. Roy. Soc. B Biol. Sci.* 364: 1629–1640.

Price, T. D., Qvarnstrom, A., and Irwin, D. E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proc. Roy. Soc. Lond. B Biol. Sci.* 270: 1433–1440.

Rice, A. M., Leichty, A. R., and Pfennig, D. W. 2009. Parallel evolution and ecological selection: replicated character displacement in spadefoot toads. *Proc. Roy. Soc. B Biol. Sci.* 276: 4189–4196.

Rice, A. M., and Pfennig, D. W. 2007. Character displacement: in situ evolution of novel phenotypes or sorting of pre-existing variation? *J. Evol. Biol.* 20: 448–459.

Rice, A. M., and Pfennig, D. W. 2008. Analysis of range expansion in two species undergoing character displacement: why might invaders generally 'win' during character displacement? *J. Evol. Biol.* 21: 696–704.

Roach, D. A., and Wulff, R. D. 1987. Maternal effects in plants. *Annu. Rev. Ecol. Syst.* 18: 209–235.

Rossiter, M. C. 1996. Incidence and consequences of inherited environmental effects. *Annu. Rev. Ecol. Syst.* 27: 451–476.

Rutherford, S. L., and Lindquist, S. 1998. Hsp90 as a capacitor for morphological evolution. *Nature* 396: 336–342.

Schiesari, L., Werner, E. E., and Kling, G. W. 2009. Carnivory and resource-based niche differentiation in anuran larvae: implications for food web and experimental ecology. *Freshw. Biol.* 54: 572–586.

Schlichting, C. D., and Murren, C. J. 2004. Evolvability and the raw materials for adaptation. In Q. C. B. Cronk, J. Whitton, R. H. Ree, and I. E. P. Taylor (eds.). *Plant Adaptation: Molecular Genetics and Ecology*. NRC Research Press, Ottawa, pp. 18–29.

Schlichting, C. D., and Pigliucci, M. 1998. *Phenotypic Evolution: A Reaction Norm Perspective*. Sinauer Associates, Sunderland.

Schluter, D. 2000. *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford, UK.

Schmalhausen, I. I. 1949. *Factors of Evolution: The Theory of Stabilizing Selection*. Blakiston, Philadelphia.

Schwabl, H. 1993. Yolk is a source of maternal testosterone for developing birds. *Proc. Nat. Acad. Sci. USA* 90: 11446–11450.

Shapiro, A. M. 1980. Physiological and developmental responses to photoperiod and temperature as data in phylogenetic and biogeographic inference. *Syst. Zool.* 29: 335–341.

Snell-Rood, E. C., Cash, A., Han, M. V., Kijimoto, T., Andrews, J., and Moczek, A. P. 2011. Developmental decoupling of alternative phenotypes: insights from the transcriptomes of horn-polyphenic beetles. *Evolution* 65: 231–245.

Snell-Rood, E. C., van Dyken, J. D., Cruickshank, T., Wade, M. J., and Moczek, A. P. 2010. Toward a population genetic framework of developmental evolution: the costs, limits, and consequences of phenotypic plasticity. *Bioessays* 32: 71–81.

Sultan, S. E. 2007. Development in context: the timely emergence of eco-devo. *Trends Ecol. Evol.* 22: 575–582.

Sultan, S. E. 2010. Plant developmental responses to the environment: eco-devo insights. *Curr. Opin. Plant Biol.* 13: 96–101.

Suzuki, Y., and Nijhout, H. F. 2006. Evolution of a polyphenism by genetic accommodation. *Science* 311: 650–652.

Suzuki, Y., and Nijhout, H. F. 2008. Constraint and developmental dissociation of phenotypic integration in a genetically accommodated trait. *Evol. Dev.* 10: 690–699.

Waddington, C. H. 1953. Genetic assimilation of an acquired character. *Evolution* 7: 118–126.

Wcislo, W. T. 1989. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Evol. Syst.* 20: 137–169.

Weaver, I. C. G., et al. 2004. Epigenetic programming by maternal behavior. *Nat. Neurosci.* 7: 847–854.

West-Eberhard, M. J. 1989. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* 20: 249–278.

West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford University Press, New York.

West-Eberhard, M. J. 2005. Phenotypic accommodation: adaptive innovation due to developmental plasticity. *J. Exp. Zool. B Mol. Dev. Evol.* 304: 610–618.