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SYMPOSIUM

Selective Processes in Development: Implications for the Costs and Benefits of Phenotypic Plasticity

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Synopsis Adaptive phenotypic plasticity, the ability of a genotype to develop a phenotype appropriate to the local environment, allows organisms to cope with environmental variation and has implications for predicting how organisms will respond to rapid, human-induced environmental change. This review focuses on the importance of developmental selection, broadly defined as a developmental process that involves the sampling of a range of phenotypes and feedback from the environment reinforcing high-performing phenotypes. I hypothesize that understanding the degree to which developmental selection underlies plasticity is key to predicting the costs, benefits, and consequences of plasticity. First, I review examples that illustrate that elements of developmental selection are common across the development of many different traits, from physiology and immunity to circulation and behavior. Second, I argue that developmental selection, relative to a fixed strategy or determinate (switch) mechanisms of plasticity, increases the probability that an individual will develop a phenotype best matched to the local environment. However, the exploration and environmental feedback associated with developmental selection is costly in terms of time, energy, and predation risk, resulting in major changes in life history such as increased duration of development and greater investment in individual offspring. Third, I discuss implications of developmental selection as a mechanism of plasticity, from predicting adaptive responses to novel environments to understanding conditions under which genetic assimilation may fuel diversification. Finally, I outline exciting areas of future research, in particular exploring costs of selective processes in the development of traits outside of behavior and modeling developmental selection and evolution in novel environments.

Introduction

Adaptive phenotypic plasticity, or the ability of a genotype to match their phenotype to different environments, allows organisms to cope with spatial and temporal environmental variation (Levins 1968; Moran 1992; Schlichting and Pigliucci 1998; West-Eberhard 2003). Plasticity evolves in variable environments, but also has implications for understanding how organisms may respond to new environments, such as invasive species, cities, agricultural landscapes, and those brought about by climatic change or encountered at the edge of their geographic range (Yeh and Price 2004; Sol et al. 2005; Ghalambor et al. 2007). In order to understand the impacts of phenotypic plasticity on evolution in novel environments, we must also consider the developmental mechanism of plasticity (Pigliucci 1996, 2001; Snell-Rood et al. 2010). How does development, both embryonic and postembryonic, produce a phenotype matched to the current environment? Here I argue that we need to consider not only switch-like mechanisms of plasticity but also "hyper-variable" or developmental selection mechanisms of plasticity (West-Eberhard 2003). This review hypothesizes that selective processes in development play a major role in determining the costs and consequences of plasticity and may inform our understanding of genetic assimilation and the evolution of life histories and complex traits.

Developmental selection

With regard to phenotypic plasticity, we often conceive of development in a rather determinate manner, with various developmental switches that results in different sets of genes turning on and off in response to environmental conditions. However, many aspects of development occur more through sampling or selection and less through predictable and determinate switches. "Developmental selection," as defined broadly in this article, has two important components. First, a range of phenotypes are produced, explored, or otherwise sampled, over some period of time. Second, feedback from the internal or external environment informs subsequent developmental steps, in particular, a subset of sampled phenotypes is reinforced or selected for continued expression. Developmental selection, relative to natural selection, is selection within (rather than across) generations and within (rather than among) individuals. It is important to realize that development of most traits has both determinate and selective components, in particular if one considers the entire duration of the period over which the trait develops. As discussed below, the relative degree of selective processes in development determines the costs associated with developmental plasticity. Before delving into the costs of developmental selection, I review and expand upon evidence that selective processes—exploration and environmental feedback—are commonly found across the development of many different traits (see also reviews of Atchley and Hall 1991; Frank 1996; Kirschner and Gerhart 1998; Gerhart and Kirschner 2007).

Developmental selection is common

Selective processes are common across many components of embryonic and postembryonic development, often continuing into adulthood. Aspects of exploration and sampling, followed by environmental feedback are found in the development of the circulatory, nervous, and immune systems. Possibly the most extreme form of developmental selection is found in acquired immunity in vertebrates. Through protein recombination and somatic mutation, vertebrates produce billions of diverse antibodies (the exploration phase), which are "selected" through interaction with antigens (the environmental feedback phase), resulting in amplification of the parent B-cell clones (Burnet 1959; Honjo and Habu 1985; Litman et al. 1993; Nemazee 2006).

Developmental selection is rampant in the development of the nervous system, where initial innervation is broad and subsequently refined through experience (Katz and Shatz 1996; Purves et al. 1996; Song and Abbott 2001; Luo and O'Leary 2005). For instance, muscle fibers are initially innervated by multiple neurons, but through synaptic competition, some individual connections are reinforced and refined while others are lost (Lo and Poo 1991; Buffelli et al. 2003). In the visual cortex, projections from the eyes initially form broad connections, but these are refined through visual experience, resulting in the development of ocular dominance columns (Stryker and Harris 1986; Gordon and Stryker 1996). Even initial innervation is a product of axonal exploration, reinforced through cues from appropriate targets (Davenport et al. 1993; Sharma et al. 2000).

The nervous system and immune system are classic examples of developmental selection, but selective processes can be found in other systems as well. Muscle and bone are incredibly responsive to mechanical stress (Banes et al. 1995; Duncan and Turner 1995; Pette and Staron 2000) as are most cells (Newman and Muller 2000; Moore 2003), resulting in the reinforcement of regions of tissue that are particularly useful in the local environment. For example, these processes result in entirely different whole-body phenotypes of tennis players, which show different patterns of bone and muscle development due to asymmetrical use of the arms during games (Ducher et al. 2004; Sanchis-Moysi et al. 2011). In this case, selection on variation in "location" of fibers (or cells) is important. Even in the development of the circulatory system we see aspects of sampling and environmental feedback: exploratory processes project in young capillary networks and are refined as the network begins to be used (Risau 1997). Trachael networks of the insect respiratory system also show exploratory branching (Guillemin et al. 1996).

Elements of developmental selection may even explain why stochasticity in gene expression is so common (Eldar and Elowitz 2010). Variation in gene expression over time or space may be beneficial (Thattai and van Oudenaarden 2004; Lehner and Kaneko 2011), increasing the chances that one cell expresses genes favored in the local environment. Epigenetic processes, such as methylation, which are often responsive to the environment (Fraga et al. 2005; Cropley et al. 2006; Hager et al. 2009; Verhoeven et al. 2010), could be involved in stabilizing appropriate patterns of gene expression. For example, cells that vary in gene expression may differ in energy return; patterns of gene expression in "successful" cells may be stabilized through methylation, while patterns of expression in "unsuccessful"

cells may be lost through the death of cells (Jablonka 1996; Johnston 2009; Tamori and Deng 2011). It remains to be seen whether variable gene expression represents a general mechanism of developmental plasticity (see future directions below), but observations to date suggests that it fits the general pattern of developmental selection.

In the development of behavior, developmental selection, as broadly defined here, is almost the norm. Trial-and-error learning is a process of developmental selection whereby different variants of a behavior are expressed over time, and those that lead to high performance on a particular task are reinforced. Such trial-and-error learning is common across both vertebrates and invertebrates, from learning how to handle different foods, to learning associations between cues and reward (Johnston 1982; Papaj and Prokopy 1989; Shettleworth 1998; Dukas 2008). Animals also actively explore their environment, traveling through different habitats and interacting with different resources, and then choosing microhabitats in which to dwell (Stamps 1995; Davis and Stamps 2004). Habitat selection, in which an animal samples space and chooses a profitable microhabitat, represents developmental selection at another level, where individuals sample and choose environments or resources that are most rewarding.

Whereas much of this discussion has centered around examples of developmental selection in animals, it is important to note that similar processes occur in the development of plants. Branches of plants explore the light environment (Sachs 2004), and roots often project widely into space, proliferating in rich patches of resources, and atrophying in poor patches (Doust 1981; Franco 1986; Sachs et al. 1993). Mechanical stress also leads to strengthening of relevant areas in plants (Niklas 1992). Thus, much of the current discussion likely also applies to plasticity in plants and other organisms as well. Indeed, given the less-defined separation of germ line and soma, selective processes may have even greater implications for evolution in plants. However, for the sake of space, the current discussion is focused on animals.

Variation in developmental selection

While selective processes are seen in the development of many traits, from gene expression to behavior, the extent of selective processes varies tremendously within and between organisms. The range of sampling, or the degree of variation produced, early in the developmental process differs across species and populations. For instance, the range of motor patterns an animal can produce during motor learning varies across vertebrates (Iwaniuk and Whishaw 2000), and the range of sounds produced by birds early in the process of learning songs varies across populations (Nelson et al. 1995). Species of birds also differ markedly in the degree to which they explore resources and their environment (Greenberg 1983, 1989; Mettke-Hofmann et al. 2002, 2009). In the development of the immune system, the diversity of possible antibodies that can be produced varies tremendously across vertebrates (Litman et al. 1993). Variability in gene expression also differs across genes in a manner that suggests the level of variation is subject to selection (Raser and O'Shea 2004; Newman et al. 2006).

Not only does the degree of sampling differ across species, but the timing and degree of environmental feedback also differs. Environmental feedback often plays a more pronounced role in neural development during certain critical periods, the length of which varies across species and traits (Hensch 2004). The nature of environmental feedback also varies for development of other traits. For example, the sequence of ossification of bones varies tremendously across birds and mammals (Smith 1997; Sanchez-Villagra 2002; Mitgutsch et al. 2011). In some cases, ossification is delayed, sometimes until after feeding has commenced, increasing the chances that local food resources may play a role in the development of traits such as the shape or hardness of the jaw (Wimberger 1991; Badyaev et al. 2008; Young and Badyaev 2010). There is also variation in the effect of environmental feedback on phenotype selection. For instance, the degree of neural apoptosis in development, some of which is linked to neuronal activity and to competition among neurons (Oppenheim 1991), ranges from 80% to 40% in birds and mammals to none in fish (Gilbert 2003).

These examples emphasize that developmental mechanisms of plasticity fall along a continuum, from more determinate to more selective processes. For example, polyphenisms, where environmental cues induce cascades of gene expression that result in the development of discrete alternate phenotypes (Evans and Wheeler 2001; Snell-Rood et al. 2011a), may represent more determinate developmental mechanisms of plasticity, where alternate phenotypes are a result of predictable developmental switches rather than sampling and reinforcement. On the other hand, trial-and-error learning and acquired immunity represent the other extreme, with pronounced exploration and environmental feedback. Importantly, the degree of sampling and

environmental feedback varies not only across different traits, but also across populations and species, suggesting that natural selection plays a role in adjusting the intensity of sampling and feedback in development.

Benefits, costs, and consequences of developmental selection

Performance in novel and variable environments

The most pronounced consequence of developmental selection is a high probability that an individual's phenotype develops to be matched to the local environment (Kampfner and Conrad 1983; Frank 1996, 1997b; Adams 1998). This has implications for the evolution of phenotypic plasticity, which is favored in the presence of coarse-grained environmental variation, in which the environment is relatively constant within a generation, but variable across generations (Moran 1992; Schlichting and Pigliucci 1998). Relative to switch-like, or determinate, mechanisms of plasticity, developmental selection gives the added advantage that it can result in a very large range of different phenotypes, without suffering the lineage-level costs of relaxed selection that would come with evolved patterns of gene expression specific to each alternative phenotype (Kawecki 1994; Whitlock 1996; Kawecki et al. 1997; Snell-Rood et al. 2010; Van Dyken and Wade 2010). This suggests that mechanisms of developmental selection of plasticity will be favored relative to determinate mechanisms of plasticity when there is coarse-grained variation that includes more than two alternate environments.

Relative to a fixed strategy or to a developmental switch mechanism of plasticity, developmental selection increases the probability of a match between phenotype and environment because an increase in phenotype sampling increases the chances an individual will discover the most profitable phenotype in the local environment (Fig. 1; Frank 1997a,b). This phenomenon is analogous to search algorithms; those that sample more broadly, for longer periods of time, are more likely to hit upon the optimal phenotype (Kaelbling et al. 1996). From the perspective of novel environments, developmental selection increases the likelihood that an entire population will rapidly shift to a new selective peak (Hinton and Nolan 1987; Hull et al. 2001; Frank 2011). More determinate or switch mechanisms of plasticity should produce only phenotypes matched to ancestral environments. In addition, developmental selection more generally increases the extent to which complex phenotypes may develop from relatively simple genomes (Frank 1996, 1997a).

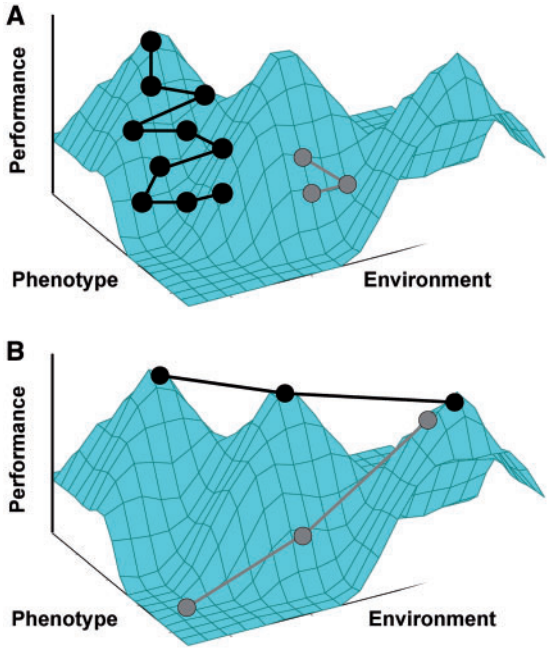

Fig. 1 Contrast between genotypes with more selective processes (black) relative to more determinate processes (gray) in the development of a trait. The high sampling genotype (black) samples a broad range of phenotypes in any environment in which it finds itself (**A**). Thus, it discovers the optimal phenotype in all environments, resulting in constant performance across environments, but different adult phenotypes. In contrast, the more determinate genotype (gray) samples a narrow range of phenotypes in development, and only those phenotypes clustered around a certain value. This genotype fails to discover the optimal phenotype in all environments, resulting in a static reaction norm and performance specialized to one environment (**B**).

Costs of developmental selection

While developmental selection may increase performance of individuals in the local environment, it comes with pronounced costs. The process of sampling phenotypes and receiving environmental feedback comes with costs of time, energy, and risk of predation. These costs have been most thoroughly explored with respect to the costs of learning, but they should apply more generally to selective processes for the development of any trait.

The time-cost of developmental selection is referred to as the "cost of being naïve" in the literature on animal learning (Dukas 1998) and the "exploration-exploitation trade-off" in the literature on machine learning, in which computer algorithms develop optimal performance through learning-like processes (Kaelbling et al. 1996). Trial-and-error processes necessarily come with a developmental phase

of low return; in order to discover the optimal phenotype, there must be a sampling process that includes less-successful phenotypes. This means that, relative to a specialist that deterministically produces the optimal phenotype, optimal performance is delayed in development (Fig. 2). This cost is illustrated by generalist and specialist bees that vary in the time required to feed efficiently from different flowers (Laverty and Plowright 1988). There are also hundreds of examples of delayed proficiency in foraging in animals as they develop appropriate foraging behavior and morphology (Marchetti and Price 1989; Wunderle 1991; Gurven et al. 2006; MacDonald 2007). Indeed, humans tend to take 10 years of learning and practice before they can expertly perform specific tasks (Ericsson et al. 1993). Time costs of selective processes in development are most explored in the behavioral literature, but some evidence suggests they apply more generally. For instance, relatives of *Caenorhabditis elegans* with less determinate development, as measured by a less precise cell fate map, take relatively longer to develop (Houthoofd et al. 2003).

The cost of being naïve results in not only a cost of time, but also the cost of necessarily making mistakes. This is illustrated not only in trial-and-error learning, for instance when generalists make more mistakes (Janz and Nylin 1997), but also in the immune system. Producing a wide range of B cells increases the chance that the immune response will target the self (versus an antigen), thereby increasing the possibility of an auto-immune disorder (Osborne 1996; Krammer 2000).

Developmental selection requires energy and material in order to physically express a range of different phenotypes. For example, sampling a range of mates in pronghorns (Byers et al. 2005) or producing a range of song types in birds (Garamszegi et al. 2006) is energetically costly. In the case of behavioral plasticity, there is a material cost in the form of more neurons and more neural connections required to sample a range of behaviors (Hopfield 1982; Hampson 1991; Sporns et al. 2000). Indeed, there is often a correlation between neural investment and cognitive abilities (Herman and Nagy 1977; Sherry et al. 1992; Sol et al. 2005; Snell-Rood et al. 2009). This is significant because neural tissue is some of the most metabolically expensive tissue in the body (Astrup et al. 1981; Laughlin et al. 1998; Attwell and Laughlin 2001; Lennie 2003). Across other components of organismal development, exploration should result in energy costs associated with constructing and atrophying diverse phenotypes, from capillary outgrowths, to neurons (Oppenheim 1991), to B cells (Rajewsky et al. 1987; Osborne 1996).

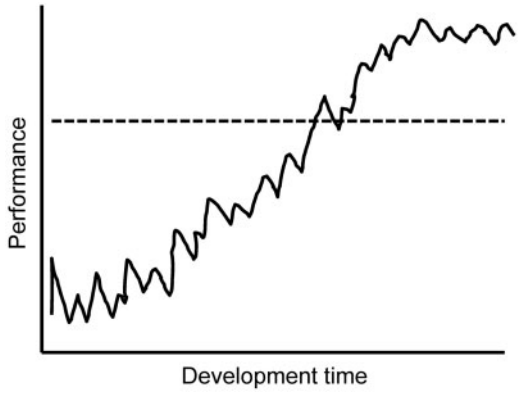

Fig. 2 Change in performance over time for genotypes that differ in phenotype sampling. Genotypes that sample a broad range of phenotypes early in development (solid line) have low early life performance (the cost of being naïve) relative to a fixed genotype that is somewhat specialized in the use of that environment. However, later in development, the high-sampling genotype is more likely to have discovered a local optimal phenotype, resulting in higher performance relative to the fixed genotype. For additive aspects of performance, such as energy or number of offspring (but not survival), total lifetime performance can be estimated as the integral of this curve. This suggests that high-sampling genotypes would benefit from longer lifespans because the long-term benefits of adopting the optimal phenotype can outweigh the initial costs of sampling and of environmental feedback.

Exploration and environmental feedback in development also come with exposure costs. In order to gain relevant environmental feedback, an individual must often venture into the world while immature, before acquiring fully functional phenotypes, thereby increasing the chances of predation (Pimlott 1967; Rayor and Uetz 1993). The sampling process itself may further increase the possibility of predation because dividing attention between various behaviors during learning can trade-off with vigilance (Dukas and Kamil 2000; Dukas 2002; Brown and Braithwaite 2005).

Implications of the perspective of developmental selection

Evolution of life-history traits

The costs of developmental selection described above should result in major changes in allocation of energy, resulting in changes to life history strategies. In particular, increased investment in sampling early in development should select for delays in reproduction. Delays in reproduction are the most widely cited life-history tradeoff associated with the evolution of learning (Mayr 1974; Johnston 1982;

Dukas 1998; Kaplan et al. 2000; Kaplan and Robson 2002; Ricklefs 2004). This idea is supported by observations that behavioral plasticity is correlated with delays in reproduction across species of mammals (Sacher and Staffeld 1974; Mace and Eisenberg 1982; Pagel and Harvey 1988; Lefebvre et al. 2006; Barrickman et al. 2008) and birds (Iwaniuk and Nelson 2003) and across genotypes of butterflies (Snell-Rood et al. 2011b).

This reasoning leads to the additional hypothesis that increased developmental selection should also change selection on patterns of investment per offspring. In particular, more investment per offspring should offset costs of sampling a range of phenotypes early in development, increasing offspring survival to adulthood. For example, increased risk of exposure may be offset by increased vigilance by parents and increased stores of lipids in eggs may compensate for delays in the onset of functioning of particular traits.

In some cases, the costs of learning, or developmental selection in general, may also decrease the overall energy available for reproduction (Mery and Kawecki 2004; Snell-Rood et al. 2011b), resulting in decreases in fecundity. It is likely that over time, there would be selection for longer lifespan, thereby increasing the pool of available energy and offsetting the long-term fitness costs of learning (e.g., the integral of curves in Fig. 2; Kaplan et al. 2000; Eliassen et al. 2007).

Tradeoffs between developmental selection and the timing of reproduction and investment per offspring should result in shifts toward more "slow" or "K-selected" life-history strategies for species with more selective processes in development. If rapid generation time and high fecundity are linked to evolutionary responses of a population (Bromham 2011), this suggests that there may be a tradeoff at the lineage level between the potential of a population to respond to a novel environment through either developmental plasticity or evolutionary change.

Responses of organisms to novel environments

Biologists have long been interested in predicting which organisms will be most resilient in the face of human-induced environmental change, such as cities, pollution and agriculture, the introduction of new species, and climate change. It is likely that rapid evolutionary responses will be important for survival in these novel environments (Rainey and Travisano 1998; Sakai et al. 2001; Bossdorf et al. 2005). We might expect that species with short generation times and high fecundity may be especially likely to show rapid responses to such novel environments. However, for many organisms, the rate of environmental change, relative to evolutionary rate, is quite large, suggesting that developmental responses will be just as important as evolutionary responses (Yeh and Price 2004; Ghalambor et al. 2007; Crispo et al. 2010). Developmental selection should increase the chance that an entire population immediately shifts (i.e., within one generation) to a new selective peak (Price et al. 2003; Frank 2011). The costs associated with developmental selection suggest that species with pronounced developmental responses to novel environments may have life-history traits opposite of those with pronounced evolutionary responses.

The relative importance of developmental and evolutionary responses of populations to novel environments will depend on a variety of factors, such as standing genetic variation (Barrett and Schluter 2008), the presence of sexual versus asexual reproduction (Colegrave 2002), the generation time of the species relative to the rate of environmental change, and the degree or complexity of environmental change. It is clear that making predictions is not simple. Regardless, recent studies investigating traits associated with population trends in human-altered environments underscore the importance of considering developmental and natural selection simultaneously. Population trends in birds suggest species faring well in areas dominated by agriculture tend to have longer periods of incubation and fledging, and larger brains (Pocock 2011). Indeed, birds with larger brains fare better in cities (Maklakov et al. 2011), have rising population trends in developing areas (Reif et al. 2011), are more likely to survive after introduction into new regions (Sol et al. 2005), and shift dates of arrival at breeding grounds in response to climatic change (Moussus et al. 2011). Across mammals and birds, shifts in geographic range are not associated with generation time or fecundity but instead are associated with niche breadth (Angert et al. 2011), a factor that has been linked to learning ability in a range of species (Simons et al. 1992; Prokopy et al. 1993; Geervliet et al. 1998). Taken together, these studies suggest that development and evolution both must be considered when investigating responses of populations to rapidly changing environments.

Genetic assimilation

Developmental selection may offer a resolution to the "paradox" linking phenotypic plasticity to diversification. Plasticity is thought to speed up

diversification because it allows survival of populations in novel environments and results in developmental systems capable of producing a diversity of phenotypes (West-Eberhard 2003; Lande 2009; Pfennig et al. 2010). However, plasticity may also retard rates of diversification because the closer a phenotype is to the optimum in a given environment, the lower the selection intensity will be on that trait (Robinson and Dukas 1999; Huey et al. 2003; Price et al. 2003; Pfennig et al. 2010).

Developmental selection as a mechanism of plasticity increases the chances of a population immediately (and completely) shifting to a new selective peak, relative to a determinate, switch-like mechanism of plasticity. However, the relative "costs" associated with developmental selection suggest that, even if a plastic phenotype is perfectly matched to the local optimum, there is still strong selection on that trait. In particular, if the population shifts into a novel, constant environment, the costs of developmental selection will select for loss of plasticity, or genetic assimilation (Pigliucci and Murren 2003; West-Eberhard 2003; Pfennig et al. 2010). If environmental variation remains, there may be selection to reduce environmental variation (and subsequently plasticity), for instance through habitat or resource selection. In other words, animals may "construct" their environment in ways that make it less variable (OdlingSmee et al. 1996; Laland et al. 1999). A developmental selection perspective can resolve the conundrum linking plasticity and diversification because both the costs of plasticity and the probability of precisely matching a new adaptive peak scale with the degree of developmental selection.

Conclusions and future directions

Taking a developmental selection approach is key to understanding the costs and consequences of phenotypic plasticity. In particular, considering the strength of selective processes in development—the sampling of phenotypes in conjunction with environmental feedback—is important for understanding the probability of a population developing an entirely novel, adaptive phenotype, relative to fixed strategies or developmental switch mechanisms of plasticity. The amount of developmental selection should also scale with the costs of plasticity. Studying forms of plasticity that vary widely in the amount of developmental selection (versus more determinate processes) may explain why studies of the costs of plasticity tend to find incredibly variable evidence for costs (reviewed in Van Buskirk and Steiner 2009; Snell-Rood et al. 2010). A focus on developmental selection may clarify how phenotypic plasticity relates to diversification and also yields insights into predicting evolutionary and developmental responses of populations to novel environments. The framework developed here highlights several exciting areas of future research:

(1) Theory reviewed here predicts a strong link between the range of phenotypes an organism samples, and the probability that the organism discovers and adopts a new optimal phenotype in a completely novel environment. However, empirical evidence supporting this prediction is scarce, despite its relevance for predicting the response of organisms to rapidly changing human-altered environments.

(2) The focus on selective processes in development emphasizes the importance of integrating not only evolution, but also development into models of species' responses to changing environments, in particular because there may be lineage-level tradeoffs between evolutionary and developmental responses of populations. It would be especially informative to incorporate generation time, developmental plasticity, and the rate of environmental change to determine the relationship between life-history traits and both plastic and evolutionary responses of populations to novel environments.

(3) The developmental selection framework developed here may provide a new approach to addressing the evolution of life history traits. For instance, developmental selection provides a mechanistic explanation for why investment in development may be both costly and beneficial, in terms of an improved phenotypic match to the local environment. This framework also predicts that increased investment in selective processes in development may result in the evolution of increased lifespan in ways that compensate for early costs (see Fig. 2).

(4) It appears that the basic components of developmental selection—phenotype sampling and environmental feedback—apply to the development of many different traits. However, it is unclear whether the costs of such developmental selection, which have been most thoroughly explored in behavioral development, are common to selective processes in the development of any trait. For instance, does sampling and feedback in stochastic gene expression or plastic development of bone or muscle come with similar costs and

life-history trade-offs as for trial-and-error learning?

(5) Much of this review assumes consistency of the environment within generations and variation in the environment between generations (i.e., coarse-grained variation). However, it is also important to consider how these ideas apply to environmental variation within generations (i.e., fine-grained variation). Fine-grained variation should select for strategies that do not result in a fixed phenotype at the end of some developmental period; such reversible plasticity is less likely to result in phenotype-environment mis-matches (Gomulkiewicz and Kirkpatrick 1992; Padilla and Adolph 1996; Dukas 1998). While this review considers many examples of reversible plasticity, it would be beneficial to explore whether costs increase as the reversibility of plasticity increases. For instance, if developmental selection is involved, reversible plasticity may be associated with a lengthened exploratory phase (e.g., no critical period) and an increased in associated costs. There may also be limitations on reversible plasticity. For instance, it may be difficult to completely alter one's phenotype due to an environmental shift after most of development is complete (the epiphenotype problem of DeWitt et al. 1998), which may result in stronger selection for natal habitat preference (thus reducing fine-grained variation) than for increased and reversible plasticity (which may have added costs and limitations).

In conclusion, selective processes in development, including both exploration and environmental feedback, are common across the development of many traits. Understanding developmental selection is critical for understanding the costs, benefits, and evolutionary consequences of phenotypic plasticity.

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