Invited commentary

Epigenetic inheritance systems act as a bridge between ecological and evolutionary timescales

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A long-standing problem in biology is reconciling phenotypic change and stability. Organisms are extraordinarily plastic, responding to life-stage transitions, seasonal cues, and environmental change. Some of these changes are permanent and some are reversible occurring thousands of times during a lifetime. Yet, at the same time, phenotypic stability is equally evident, enabling reliable assignment of individuals into morphs, populations, and species. A key question in evolution is how these timescales of phenotypic change are linked. The traditional view is that they are not such that there is a dichotomy of "ephemeral environmental effects" and "stable genetic effects" with only the latter relevant to evolutionary change. However, as Ledon-Rettig et al.'s review shows, this view needs to be updated as we learn more about the proximate mechanisms behind genetic and epigenetic determinants of phenotypic variation.

Purely environmental influences on the phenotype are often assumed to be more transient than genetic effects and thus not important for long-term evolutionary change. However, environmental influences on the phenotype are often more stable then genetic influences—the most extreme example being the influence of gravitational forces—a factor that has consistently influenced the form and function of all organisms. However, genetic influences on the phenotype are often assumed to be the most stable. Yet, genetic variants that map onto phenotypic variation consistently irrespective of the environmental and genetic context are extremely rare. Instead, the phenotypic effects of specific DNA sequences is often highly variable from one generation to the next depending on both genetic background and environmental context. Similarly, as Ledon-Rettig et al. show, the stability of epigenetic effects are also not easily categorized and can range from transitory cell state modifications that can change over the course of development to multigenerational influences of a mother's behavior on her descendants. These observations show that there is not a simple dichotomy in the timescales of phenotypic expression and that a more realistic view is of a gradation of stability that does not map onto genes versus environment in a simple way.

The traditional population genetic framework places a primacy on transgenerational stability and thus, genetic influences on the phenotype are deemed to be the most relevant. Yet, just as genetic and environmental effects cannot be easily classified as ephemeral or stable, neither can they be easily classified as evolutionarily relevant or irrelevant. In fact, many recent reviews, including Ledon-Rettig et al.'s review, recognize the responsiveness of the phenotype as a crucial component in the process of evolution (Schlichting 1989; West-Eberhard 2003; Duckworth 2009a; Badyaev 2011; Moczek et al. 2011). When organisms encounter novel environmental conditions, they are likely to be pushed from their homeostatic optima and express novel developmental variation with epigenetic effects being a key component of this stress-induced variation. The main consequence of such stress-induced epigenetic effects is not necessarily to produce fine-tuned adaptive phenotypes, but instead to increase phenotypic variation (Hoffman and Parsons 1991; Badyaev 2005). If some of the resulting variants are adaptive, then they may be subsequently stabilized by selection on genetic variation (Baldwin 1902; West-Eberhard 2003). Consequently, epigenetic effects, which simultaneously increase phenotypic variation and maintain a suite of novel phenotypes across multiple generations, might provide a moderately stable source of variation that bridges the gap between initial short-term reaction to environmental change and subsequent long-term stabilization of adaptive phenotypes (Jablonka and Lamb 1995; Müller 2007; Badyaev and Uller 2009; Badyaev 2011). Similar arguments have been made for maternal effects (a type of transgenerational epigenetic effect), cultural inheritance, and niche construction (where offspring inherit modified environments) (Jablonka 2001). Thus, these alternative inheritance systems should be of interest to behavioral ecologists, not just as an additional source of phenotypic variation to add to the list of genes and environment, but as factors that may fill in the gap between slow incremental genetic evolution and the rapid responses to environment that are so characteristic of behavior.

In addition to being a source of variation during times of stress, epigenetic effects, by enabling the environment of one generation to influence the phenotype of the next, are also an important mechanism underlying complex adaptation. For example, in western bluebirds, a maternal effect enables females to fine-tune offspring dispersal strategies by producing sons with high dispersal ability when resources are scarce and to produce sons that are more likely to acquire a territory locally when resources are abundant (Duckworth 2009b). This epigenetic effect appears to be an adaptation to the patchy and ephemeral nature of this species main limiting resource—nest cavities— and promotes rapid and adaptive shifts in competitive behavior as this species colonizes new habitat. Such finely tuned responsiveness to environmental variation is a ubiquitous component of adaptation and, epigenetic effects, by enabling incorporation of environmental variation into phenotypes that are at once stable and complex, are crucial for the origin and maintenance of novel adaptations. Thus, identifying whether a particular epigenetic effect acts as a generalized stress response mechanism that increases variation or as a fine-tuned adaptation is central to understanding evolutionary processes.

Distinguishing between these roles requires integrating proximate mechanisms of behavioral development with studies of the function and adaptive significance of behavior. Ideally, by comparing the developmental basis of behavioral variation among populations or species whose natural histories are well known, we can identify novel responses to recent environmental change versus a responsive adaptation that evolved during long-term interaction with a predictably variable environment. Only by integrating proximate and ultimate approaches can these distinct stages of evolutionary

change be recognized. Yet, despite many appeals over the years (Stamps 1991; Bateson 2001; Thierry 2007; Duckworth 2010), integration of "proximate" and "ultimate" mechanisms of behavioral variation remains elusive (see extensive discussion in Laland et al. 2011). This is, at least in part, because of the difficulty of investigating developmental mechanisms, including epigenetic effects, in natural systems. Yet, these difficulties are well worth the effort because the ultimate reward of such an integration is a deeper understanding, not only of the maintenance of behavioral variation, but also of its origin and evolution.

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