REFERENCES

Avital E, Jablonka E. 2000. Animal Traditions: Behavioural Inheritance in Evolution. Cambridge (UK): Cambridge University Press.

Burton FD. 1972. The integration of biology and behavior in the socialization of *Macaca sylvana* of Gibraltar. In: Poirier FE, editor. Primate Socialization. New York: Random House, p. 29–62.

Curley JP, Champagne FA, Bateson P, Keverne EB. 2008. Transgenerational effects of impaired maternal care on behaviour of offspring and grandoffspring. Anim Behav 75: 1551–1561.

Gottlieb G. 1992. Individual Development and Evolution: the Genesis of Novel Behavior. New York: Oxford University Press.

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

Ledón-Rettig CC, Richards CL, Martin LB. 2012. Epigenetics for behavioral ecologists. Behav Ecol 24:311–324.

Markel A, Trut LN. 2011. Behavior, stress and evolution in the light of the Novosibirsk selection experiments. In: Gissis B, Jablonka E, editors. Transformations of Lamarckism: From Subtle Fluids to Molecular Biology. Cambridge (MA): MIT Press p. 171–180.

Nätt D, Rubin C-J, Wright D, Johnsson M, Belteky J, Andersson L, Jensen P. 2012. Heritable genome-wide variation of gene expression and promoter methylation between wild and domesticated chickens. BMC Genomics. doi:10.1186/1471–2164-13–59.

Piaget J. 1978. Behavior and Evolution. New York: Pantheon Books.

Whiten A, Hinde RA, Stringer CB, Laland KN. 2011. Culture evolves. Phil. Trans. Roy Soc B. 366: 937–1187.

Nongenetic inheritance for behavioral ecologists

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Ledón-Rettig et al. (2012) provide a very interesting and lucid discussion of recent studies that show or suggest epigenetically mediated transmission of behavioral variation across generations. They emphasize the potential ecological and evolutionary importance of such effects, and offer advice and encouragement for behavioral ecologists interested in exploring such effects.

One aspect of this article that I particularly like is the lack of emphasis on distinguishing effects across one or two generations from effects that potentially span many generations. A pregnant rat (F_0) has female embryos (F_1) in her womb and, at some point in their development, these embryos have their own germ cells (F_2). Thus, an environmental effect experienced by the pregnant rat can be regarded as acting directly on generations F_0–F_2, and there is a tendency to regard environmental effects that can reach the F_3 generation as being in some sense qualitatively different (and perhaps more interesting) than effects limited to F_1 or F_2. But, although it is indeed interesting to ask why some environmental effects can be transmitted over more generations than others in the absence of the inducing environmental factor, there is no obvious reason to regard more long-term effects as being more important from an ecological or evolutionary perspective. Theoretical analyses have shown that factors that are stably transmitted only across a single generation can affect a population's prospects for persistence in a changing environment (reviewed in Bonduriansky et al. 2012), as well as influence patterns of selection and alter the course of evolution (Danchin et al. 2011; Day and Bonduriansky 2011; Jablonka and Lamb 2005; Laland 1994). All such effects violate the assumptions of classical population genetics, and thus necessitate a re-examination of evolutionary models (Danchin et al. 2011; Day and Bonduriansky 2011; Jablonka and Lamb 2005). I therefore see no reason to draw a sharp distinction between effects on the basis of the number of generations that they span. Rather, all such effects—the variety of mechanisms and patterns of ancestors' influence on descendants' phenotype—can be considered part of an extended concept of heredity.

However, epigenetically mediated effects are part of a much broader spectrum of nongenetic effects of ancestors on descendants (Bonduriansky and Day 2009; Danchin et al. 2011; Jablonka and Lamb 2010). Although heritable epigenetic variation is fascinating and may be enormously important, there is no reason to believe that epigenetically mediated effects (in the narrow sense of "transgenerational epigenetic inheritance") are more interesting, more important, or qualitatively distinct from other types of nongenetic effects (nutrient-mediated, hormone-mediated, learning-mediated, etc.) in their ecological and evolutionary implications.

For example, as Ledón-Rettig et al. (2012) point out, a rodent can influence the phenotype of its offspring by transmitting an epiallele through the germ-line, or by inducing epigenetic changes in the soma of the offspring. But a rodent might also influence the phenotype of its offspring by providing it with more or less milk and varying the nature and concentration of nutrients, antibodies, and other substances present in the milk, by transferring compounds or microflora in feces that are eaten by the offspring, by performing behaviors that offspring learn to imitate, or by shaping the ambient environment that offspring encounter (see Avital and Jablonka 2000). Ledón-Rettig et al. (2012) provide fascinating examples of epigenetically mediated effects and rightly urge behavioral ecologists to investigate such effects. But why should such effects be of greater interest to behavioral ecologists than other kinds of nongenetic effects? Indeed, some of the examples adduced by Ledón-Rettig et al. (2012) are not clearly linked to epigenetic mechanisms and, in several cases, are more likely to be mediated by other factors.

All mechanisms of nongenetic inheritance appear to share two interesting properties: they can mediate the transmission of environmental influences ("acquired traits") across generations, and they can "mutate" (or switch between alternative states) at high rates. Consequently, all such mechanisms can amplify heritable phenotypic variation on which selection can act, mediate (mal)adaptive parental effects and, at least in theory, facilitate population persistence in fluctuating or rapidly changing environments and affect the dynamics and course of evolutionary change. Behavioral ecologists (and evolutionary ecologists more generally) should therefore seek to uncover and understand the implications of all nongenetic mechanisms of inheritance. Although the proximate basis of the effects is an interesting subject of study, and may influence the stability and patterns of transmission of the effects, there is no obvious reason to regard one mechanism as more important and more worthy of study than the rest.

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REFERENCES

Avital E, Jablonka E. 2000. Animal traditions: behavioural inheritance in evolution. Cambridge (UK): Cambridge University Press.

Bonduriansky R, Crean AJ, Day T. 2012. The implications of nongenetic inheritance for evolution in changing environments. Evol Appl. 5:192–201.

Bonduriansky R, Day T. 2009. Nongenetic inheritance and its evolutionary implications. Ann Rev Ecol Evol Syst. 40:103–125.
Danchin E, Charmantier A, Champagne FA, Mesoudi A, Pujol B, Blanchet S. 2011. Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. Nat Rev Genet. 12:475–486.
Day T, Bonduriansky R. 2011. A unified approach to the evolutionary consequences of genetic and nongenetic inheritance. Am Naturalist 178:E18–E36.
Jablonka E, Lamb MJ. 2005. Evolution in four dimensions. Cambridge (MA): MIT Press.
Jablonka E, Lamb MJ. 2010. Transgenerational epigenetic inheritance. In: Pigliucci M, Müller GB, editors. Evolution—the extended synthesis. Cambridge (MA): The MIT Press. p. 137–174.
Laland KN. 1994. On the evolutionary consequences of sexual imprinting. Evolution 48:477–489.
Ledón-Rettig CC, Richards CL, Martin LB. 2012. Epigenetics for behavioral ecologists. Behav Ecol 24:311–324.

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 Ledón-Rettig et al.’s (2012) 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 Ledón-Rettig et al. (2012) 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 Ledón-Rettig et al.’s (2012) 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