Invited Commentaries

Behavioral epigenetics in ecological context

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In their review, Ledón-Rettig et al. (2012) discuss the relations between the fast-developing research in behavioral epigenetics and ecology, outlining a framework for epigenetic ecology in animals. Their approach has its roots in an epigenetic psychological perspective that began in the 20th century with the work of the great developmental psychologist, Jean Piaget, who used the epigenetic terminology and ideas of Conrad Waddington to explain some aspects of human behavioral development, and to argue for the central role of behavior in animal evolution (e.g., Piaget 1978). Later, behavioral development and epigenetics also became central to the work of a few eminent behavioral ecologists and ethologists: the British biologist Patrick Bateson has been arguing for the importance of learning in animal evolution for many years, and was one of the first to integrate transgenerational epigenetic inheritance into his research (Curley et al. 2008); in the USA, the developmental psychobiologist, Gilbert Gottlieb, was a major proponent of the epigenetic view (Gottlieb 1992). Both Bateson and Gottlieb drew attention to the relationship between flexibility of adaptive behavior and flexible epigenetic molecular mechanisms, highlighting the evolutionary implications of their epigenetic perspective.

As Ledón-Rettig et al. (2012) show, there is growing evidence relating epigenetic changes in the nervous system with persistent ecologically-relevant behaviors, and they explore some of the major implications of these relations. I would like to suggest 2 additional systems that might be useful for studying epigenetic behavioral ecology: first, studies of animal domestication, and second, studies of the epigenetic correlates of the cultural transmission of behaviors in wild populations.

THE EPIGENETIC CORRELATES OF DOMESTICATION

Dimitrii Belyaev in the former USSR was the first biologist to experimentally simulate and study the process of animal domestication in order to shed light on the role of behavioral development in evolution. Starting in the late 1950s, he selected for tameness in silver foxes, and established a line of foxes that were not only extremely docile, but also exhibited a cluster of other nondirectly selected characteristics, such as changes in pigmentation, modifications in skeletal morphology and hormonal profiles, altered vocalization, and more frequent presence of B chromosomes (reviewed by Markel and Trut 2011). Both in these foxes and in laboratory mice, Belyaev observed some non-Mendelian patterns of inheritance, which he attributed to persistent transgenerational changes in gene activity — to what we would call today epigenetic inheritance. He argued that neuro-hormonal stress, which is induced by domestication and by selection for tameness, destabilizes development and leads to heritable epigenetic and genetic changes. Following a long lag, the epigenetics of domestication is again beginning to be investigated, and recent studies of domesticated chickens point to a massive change in methylation profile (Nätt et al. 2012). Systematic comparative studies of domesticates (whose ecology has drastically changed) and their wild ancestors, particularly studies involving recently domesticated laboratory animals or Belyaev's foxes, could provide an additional approach for epigenetic behavioral ecology. Such studies might also shed light on processes of epigenetically-mediated speciation, since the epigenetic changes associated with domestication often result in pre-mating reproductive isolation (Jablonka and Lamb 1995).

THE EPIGENETIC CORRELATES OF CULTURAL TRANSMISSION IN ANIMALS

Persistent changes in behavior that are mediated by social learning and last for several generations can lead to far-reaching changes in the niches animals occupy and construct (Avital and Jablonka 2000). Consequently, in recent years, animal traditions and the mechanisms that bring them about have become major topics of interest in behavioral biology (e.g., see Whiten et al. 2011). Behaviors that are mediated by early, socially-mediated learning, which develop during sensitive periods, and that have long-term consequences are likely to have distinct epigenetic correlates. Members of different populations of the same species that differ in socially-mediated behaviors such as their parental-care styles, their engagement in alloparenting, their sexual (e.g., homosexual) behavior, or their stable food preferences, are likely to have epigenetic correlates that are amenable to molecular study. For example, Burton's studies of parental care styles in different populations of macaque monkeys show that there are significant variations in the extent of paternal care (Burton 1972), and these differences are likely to have epigenetic correlates. Human populations differing in food preferences and other distinctly differentiated aspects of behavior would also be interesting subjects of epigenetic research. *Cultural epigenetics* may well be yet another domain of epigenetics that will soon be opening up.

The framework that Ledón-Rettig et al.'s (2012) review proposes is timely, useful, and thought-provoking. In the second decade of the 21st century, intellectual openness combined with the new and increasingly sophisticated epigenetic methodologies should enable some thorough and fascinating explorations and enrichments of the ecological framework Ledón-Rettig et al. (2012) present, and therefore will undoubtedly have impacts on evolutionary thinking.

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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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