Behavioral Ecology Advance Access published September 26, 2012

Invited commentary

A place for behavior in ecological epigenetics

Cris C. Ledón-Rettig, Christina L. Richards, and Lynn B. Martin
Department of Integrative Biology, University of South Florida, 4202 East Fowler Avenue, Tampa, FL 33620-5200, USA

Although recent studies have characterized epigenetic variation in the field, they have been largely restricted to plant and yeast systems. Incorporating these approaches into studies of animal behavior will be challenging. For instance, it may be particularly difficult to draw correlations between epigenetic marks and behavioral variation because relevant epigenetic marks may be tissue specific and influenced only during critical windows of development. Despite these challenges, characterizing the developmental mechanisms (including but not limited to epigenetic mechanisms) underlying behavioral traits will be essential to understanding the origins and developmental constraints of the behavioral phenotypes that interest behavioral ecologists, as mentioned by both Snell-Rood and Duckworth. Understanding the mechanisms underlying behavioral phenotypes will not only explain their emergence within generations, it might also explain how these phenotypes are inherited. For example, in addition to a more established mode of epigenetic inheritance through the germline, epigenetically based behaviors can be transmitted to offspring through parental care (Avital and Jablonka 2000; Day and Bonduriansky 2011). Understanding how environmental (e.g., offspring environment) and genetic sources of variation are integrated through epigenetic marks, and how these marks are established or removed, will improve our understanding of inheritance and, therefore, evolutionary change. As Jablonka suggests, this level of mechanistic understanding promises to lend insight into processes as diverse as domestication and cultural transmission.

In addition to characterizing the epigenetic mechanisms underlying behavioral traits, understanding the fitness repercussions of the resulting variation is critical for casting behavioral epigenetics in an ecologically and evolutionarily relevant context. This objective will be challenging for several reasons. First, as pointed out by Duckworth, epigenetic effects can range from highly specific and adaptive responses that have been honed by natural selection, to providing random population variation on which natural selection might act. Inherited epigenetic effects could also be devastating, such as in Anway et al.'s (2005) characterization of the effects of vinclozolin (an agricultural fungicide) on the sperm viability of mice 3 generations removed from exposure. Second, the adaptive value of epigenetically based behavior will ultimately depend on the environment in which the individual is found. Champagne et al. (2008) demonstrated that optimal learning in mice pups (which is sometimes underlain by epigenetic variation; Miller et al. 2008) is achieved when they are tested under the environmental conditions in which they were raised. This raises the question, "What happens when conditions change?". There is a growing body of theoretical literature dedicated to answering this question (Jablonka et al. 1995; Tal et al. 2010; Day and Bonduriansky 2011; Geoghegan and Spencer 2011), taking into consideration how epigenetic marks (and their corresponding phenotypes) are induced, and how they may resist subsequent change. These theoretical studies suggest that the timescale on which environmental change occurs relative to epigenetic change strongly influences the adaptive value of these induced phenotypes. This conclusion underscores the importance of conducting epigenetic studies under field conditions: the natural world is often variable in time and space, and this variability is not easily replicated in the laboratory.

Molecular methods for characterizing epigenetic variation are becoming more accessible to behavioral ecologists, but is a molecular-level understanding of epigenetics necessary? Definitions of epigenetics range from very narrow to very broad, and Bonduriansky reminds us that there are several types of evolutionarily relevant nongenetic effects that need not be molecular. We strongly agree with his sentiment; molecular mechanisms are probably not special in the sense that they are more likely to influence evolutionary trajectories than nonmolecular factors that are environmentally acquired and transmitted across generations. However, molecular-level epigenetic markers are readily available tools that can be used to measure some types of environmentally induced heritable phenotypic variation in the field. Although molecular mechanisms certainly don't encompass all heritable nongenetic effects, they might accurately describe an environment by gene interaction, and could potentially be used as a proxy for these important interactions across many individuals and populations. We encourage the development of tools that can quickly and reliably quantify other nongenetic sources of variation such as maternal effects, as well as nutrient, hormone, or learning-mediated effects. Regardless of the *type* of mechanism, it will be critical to tightly correlate these mechanisms with ecologically relevant outcomes.

As evidenced by the common opinions presented in our review and by our commentators, environmentally induced epigenetic variation could have a profound role in both the origins and fates of phenotypic variation; epigenetic mechanisms have the potential to constrain phenotypic evolution—as descendants are products of not only their genes and environments but also their ancestor's environments—and they have the potential to propel adaptive evolution by creating new phenotypic variation faster than what might be provided by standing genetic variation, alone. These are particularly exciting times as molecular tools are becoming more accessible to behavioral ecologists. The commentaries reflect a widespread enthusiasm for the use of these molecular tools to describe the role of epigenetic effects in population persistence and adaptation in the natural world.

Address correspondence to: C.C. Ledón-Rettig. E-mail: ccledonr@ncsu.edu.

Received 8 June 2012; accepted 9 June 2012.

doi: 10.1093/beheco/ars120

© The Author 2012. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved.
For permissions, please e-mail: journals.permissions@oup.com

Downloaded from http://beheco.oxfordjournals.org/ by guest on September 30, 2012

REFERENCES

Anway MD, Cupp AS, Uzumcu M, Skinner MK. 2005. Epigenetic transgenerational actions of endocrine disruptors and male fertility. Science. 308:1466–1469.

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

Champagne DL, Bagot RC, van Hasselt F, Ramakers G, Meaney MJ, de Kloet ER, Joels M, Krugers H. 2008. Maternal care and hippocampal plasticity: evidence for experience- dependent structural plasticity, altered synaptic functioning, and differential responsiveness to glucocorticoids and stress. J Neurosci. 28:6037–6045.

Day T, Bonduriansky R. 2011. A unified approach to the evolutionary consequences of genetic and nongenetic inheritance. Am Nat. 178:E18–E36.

Geoghegan JL, Spencer HG. 2011. Population-epigenetic models of selection. Theor Pop Biol. doi: 10.1016/j.tpb.2011.08.001.

Jablonka E, Oborny B, Molnár I, Kisdi É, Hofbauer J, Czárán T. 1995. The adaptive advantage of phenotypic memory in changing environments. Phil Trans Biol Sci. 350:133–141.

Miller CA, Campbell SL, Sweatt JD. 2008. DNA methylation and histone acetylation work in concert to regulate memory formation and synaptic plasticity. Neurobiol Learn Mem. 89:599–603.

Tal O, Kisdi E, Jablonka E. 2010. Epigenetic contribution to covariance between relatives. Genetics. 184:1037–1050.

Downloaded from http://beheco.oxfordjournals.org/ by guest on September 30, 2012