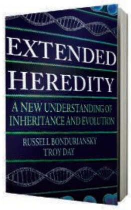
HEREDITY

Beyond epigenetics

A pair of evolutionary biologists takes a closer look at nongenetic inheritance

Extended Heredity
A New Understanding of Inheritance and Evolution
Russell Bonduriansky and Troy Day
Princeton University Press, 2018. 302 pp.



By **Kevin N. Laland**

In the 19th century, August Weismann severed the tails of mice, observed no reduction in tail length among their offspring, and declared Lamarckian inheritance refuted. Had he instead removed "teeth" from the amoeba *Difflugia corona*, he would have found reliable inheritance of the disfigurement. The amoeba experiment was conducted by Herbert Jennings in 1937, but by that time research into nongenetic inheritance (NGI) had been marginalized.

In many complex animals, the germ line is separated from the rest of the body early in development, which led Weismann to conclude that environmentally caused changes in an organism are not inherited. A revelation in recent years, and the focus of Russell Bonduriansky and Troy Day's admirable book, *Extended Heredity*, is the finding that "Weismann's barrier" is remarkably porous. Indeed, a vast multitude of nongenetic factors (including symbionts, hormones, nutrients, antibodies, prions, and learned knowledge) can be passed from parents to offspring.

Transgenerational epigenetic inheritance is the NGI that has gained most prominence. A vast literature shows how the germline transmission of DNA methylation patterns, small RNAs, and chromatin structure underlies the inheritance of a broad array of traits, including flower shape, learned fears, and virus-silencing factors in nematodes.

But according to the book, "Epigenetic inheritance is only the tip of the nongenetic iceberg." NGI also includes adaptive parental effects, social learning in animals, the inherited microbiome, and structural inheritance in single-celled eukaryotes. These factors undertake important functions, including predicting adaptive responses, finding fitness peaks, and preceding genetic change.

Bonduriansky and Day are respected evolutionary biologists who have studied NGI for years. What makes their book the most compelling and accessible account of this topic to date is the fact that they hone their arguments to reach both the evolutionary biology community and a wider audience. Their use of mathematics to demonstrate NGI's evolutionary importance, for example, will likely resonate with scientifically literate readers, and their evaluation of key arguments put forward against extended heredity persuasively demonstrates how NGI can no longer be dismissed as "limited," "functionally unimportant," or always "under genetic control."

Scholars of human evolution may be frustrated that Bonduriansky and Day have not engaged much with the cultural evolution literature. Culture is by far the most extensively studied form of NGI, and this literature provides valuable proof of principle for how nongenetic factors can affect evolution.

The book's treatment of animal learning was also disappointing. The authors' claims that "only cognitively sophisticated animals" can learn adaptive solutions to novel circumstances and that maladaptive behavior spreads just as readily as new foraging skills are badly out of touch with the literature. The function of associative learning is to allow animals to produce adaptive solutions to novel challenges, whereas diverse mechanisms ensure that socially transmitted information is typically adaptive (e.g., reduced copying on observation of disgust displays in birds) (*1*).

I am inclined to attribute these lapses to the scale of the challenge of comprehending NGI: The mechanisms involved are frighteningly diverse, and the literature is spread across numerous academic fields.

One final contention with which I disagree is Bonduriansky and Day's analysis of the claim (*2*) that heritable variation could be biased toward variants that are adaptive. The authors' skepticism is based on the mistaken inference that any such claim requires NGI to spread without selection through high rates of adaptive "mutation." However, the debate, in my view, is not over whether NGI can drive adaptive evolution without selection (selection is almost always important), nor over whether NGI generates adaptive variation more frequently than nonadaptive variation (aside from social learning, it probably doesn't), but whether developmental processes generate functional phenotypic variation more frequently than might otherwise be expected. The theory of "facilitated variation" is fully consistent with the observation that most genetic mutations (and NGI effects) are neutral or deleterious (*3*).

The authors conclude that, although NGI "supplements rather than supplants genetics," "extended heredity clearly challenges key assumptions" of neo-Darwinism and pushes us to redefine evolution as "changes in all heritable traits, whether genetic or nongenetic." The traditionally minded may find such suggestions taxing. Convinced or not, readers will appreciate *Extended Heredity* as a major contribution to an exciting field. ■

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An engineer uses a technique known as electrical discharge machining to drill holes in a metal part.

PHOTO: CULTURA CREATIVE (RF)/ALAMY STOCK PHOTO

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