Review

Reviewed Work(s): Extended Heredity: A New Understanding of Inheritance and Evolution by Russell and Day

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Bonduriansky, Russell, and Troy Day. 2018. *Extended Heredity: A New Understanding of Inheritance and Evolution*.

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Some readers of this journal probably consume milk and other dairy products with pleasure; others probably do not, and experience abdominal pain, nausea, and other unpleasant effects if they do. These are the symptoms of lactose intolerance, stemming from an inability to break down lactose—milk sugar—into the simpler sugars that our body can use for energy. All humans have the necessary enzyme as young children, but in much of the human population, the LCT gene that encodes this enzyme is permanently turned off after weaning. The exceptions are mostly in people whose ancestry is in northern Eurasia, the Middle East, or parts of eastern Africa. In these populations, most individuals carry one of several mutations that keep the LCT gene turned on in adult life. These mutations started spreading, independently in different populations, fewer than 7,000 years ago, because they enhanced survival in an environment that these populations had themselves created: one with domesticated animals and the use of their milk as a major component of diet. The replacement of lactose-intolerant by lactose-tolerant genotypes is a classic example of genetic evolution by natural selection; the earlier adoption and spread of animal husbandry and milk consumption is an instance of cultural evolution. The first is based on genetic inheritance, the second on nongenetic inheritance by teaching, learning, imitation from one generation to the next.

Nongenetic inheritance (NGI) is the theme of *Extended Heredity* by two respected evolutionary biologists. Russell Bonduriansky and Troy Day are known for their many mathematical analyses of how certain interesting characteristics evolve, such as the virulence of pathogens and conflicts between the sexes. They have also developed mathematical models of nongenetic evolution and its interaction with genetic evolution. Their book is a careful, well-reasoned exposition of the importance of NGI and its implications for evolution, and it is a welcome contrast to hyperbolic claims that nongenetic evolution warrants an "extended evolutionary synthesis," an "alternative conceptual framework" that supposedly will replace our current understanding of evolution (see Laland et al. 2015).

Evolutionary theory today is based on the "evolutionary synthesis" of Darwin's theory of natural selection, from the 1930s to about 1950, and genetics as it was understood in the mid-twentieth century. Evolution by natural selection happens if organisms vary in a characteristic, if the variation is inherited, and if certain variants have higher fitness than others. "Fitness" means number of offspring (and includes survival, because dead organisms can't reproduce). Evolution can also happen by chance—by random fluctuations in the proportions of different inherited variants—if the variation is "neutral" and doesn't affect fitness. The main cited basis of inheritance, during the synthesis and since, has been genetic, now understood to be variation in the base pair sequence of DNA. These processes have been mathematically modeled and empirically demonstrated. Importantly, it was shown that mutations are not adaptively directed: the chance of a particular mutation's happening is not influenced by whether or not it would be advantageous in the organism's prevailing environment.

Geneticists and evolutionary biologists have long recognized that both genes and environment affect the development of most characteristics. Some features are "plastic," meaning that a single genotype reacts to different environments by developing into different adaptive forms (phenotypes). The phenotype may be short-term and reversible (such as seasonal color change in many birds) or permanent (some aquatic crustaceans grow spines if they detect predators when they are young). These cases arise from natural selection acting on inherited variation in the activity (expression) of certain genes, as triggered by environmental cues. The environment "evokes" an adaptive reaction, but only because natural selection has preserved those genetic variants that had advantageous expression. Experiments have shown phenotypic responses to environmental cues cannot evolve in genetically uniform populations. Phenotypic plasticity did not result from "Lamarckian" inheritance of acquired characteristics.

Bonduriansky and Day fully accept and build on this background. Their message is that inheritance can take many forms besides DNA sequence variation, and that it can have diverse, important, understudied effects. We have known about some forms of NGI for a long time. The most obvious is cultural inheritance, prominent in humans but also described for some nonhuman primates, songbirds, and a few other species. Cultural evolution and its interaction with genetic evolution have been studied by researchers from both the evolutionary genetic tradition (e.g., Cavalli-Sforza and Feldman 1981) and the anthropological tradition (e.g., Boyd and Richerson 1985). Cultural inheritance and evolution have many important differences from genetic evolution; for example, individuals inherit language and other traits from both their parents and other individuals. A trait modified by one individual's experience may be copied by others, in a sort of Lamarckian mode.

"Maternal effects" are a much more widespread kind of NGI, probably occurring in most multicellular organisms. They can have many causes, but are most obvious in species that start life being nurtured by their mothers, both before birth (as in mammals but also plants) and after. In most cases, they last for only one generation, but some are known to affect grandchildren. Biologists have been learning that in addition to obvious effects of mothers' nutrition, teaching (in mammals) and other forms of care, offspring can be affected by a wide range of chemical compounds that may be included in the egg from which they develop. Female plant-eating insects, for example, often defend their offspring against predators by extracting defensive chemicals from plants and including them in their eggs. Geneticists have known for a long time that such effects can be confounded with genetic inheritance, unless they design their experiments carefully. There is now increasing evidence for nongenetic paternal effects too. In some of those insects, some of the chemicals they put in their eggs came from males, along with sperm. Bonduriansky and Day, and some other evolutionary geneticists, have modeled maternal and paternal effects and find that they could have important effects on the generation-to-generation course of evolution. For example, they could enable parents to adjust their offspring's characteristics to suit current environmental conditions, and they may influence the course of genetic change (just as the nongenetic inheritance of milk consumption created an advantage for lactase-persistence mutations in humans).

So far, so traditional. What is new is a huge surge of research on "epigenetic" modification of genes and their expression, meaning the time in an organism's life, the cellular and tissue location within the organism, and the level—the amount of RNA and protein product—at which a gene is active. Several molecular mechanisms underlie these modifications; for example, a carbon "tag" may attach to certain base pairs in a gene (methylation) and inhibit its expression. The potentially important news is the increasing evidence that some of these modifications may be inherited across generations. In itself, this would be just one more mechanism for maternal effects, which Bonduriansky and Day think deserve more attention, but at least are fairly well understood. But some epigenetic modifications are more surprising. For one thing, some of them persist through more than one generation; for another, the inherited epigenetic state may have been induced by an environment. One analysis, of the much-studied nematode worm *C. elegans*, reported that temperature-induced methylation of certain genes persisted for 145 generations!

Does this mean that evolution has a Lamarckian component after all? Does it mean that environments elicit nongenetic phenotypic states that become inherited? Does evolutionary theory require a "rethink," as the editors of a major journal entitled an exchange (Laland et al. 2014; Wray et al. 2014) on the supposed need for an "extended evolutionary synthesis"?

Bonduriansky and Day, for all their enthusiasm about the importance of epigenetic and other nongenetic inheritance, do not think so. For one thing, they grant "the fact that only genes appear to have the stability necessary for long-term, open-ended, cumulative evolution" (144). There appears to be no evidence, at least so far, that any distinctive characteristic of any species, much less a major evolutionary novelty such as mammals' hair or a wasp's sting, is based on epigenetic modification rather than DNA sequences; on the contrary, the list of genes identified for diverse characteristics grows every day. Even more important, they ask if nongenetic inheritance could drive adaptive evolution without natural selection, and conclude that it is highly unlikely. One would have to imagine that there exists a mechanism by which the variation arising from nongenetic mechanisms is directed toward producing phenotypes suitable for different prevailing environments. Some maternal effects do act this way: female water fleas that detect predators by their scent give birth to offspring with longer protective spines. But Bonduriansky and Day "do not believe that such effects should be labeled directed variation" (150), because the nongenetic inheritance mechanism has been shaped by natural selection: a long history of exposure to predators, during which females whose genotype activated their babies' spine development had more surviving offspring. The mechanism of nongenetic inheritance has a genetic basis that evolved by past natural selection. So "anticipatory" maternal effects respond to "*evolutionarily familiar* challenges" (150; emphasis in original). Like the developmental response of a water flea to the odor of predators, inherited epigenetic states that enhance offspring survival or reproduction are a mechanism of phenotypic plasticity that has evolved by the familiar Darwinian process.

Does that mean evolutionary biologists can dismiss NGI as an unimportant, minor add-on to a sufficient, time-tested body of understanding? Especially since the ascendance of molecular biology and an ever-deeper understanding of genomes and genomic processes, evolutionary biology has expanded, to account for synonymous mutations, transposable genetic elements, pseudogenes, gene families, chimeric and *de novo* genes, intragenomic conflict, and other phenomena that could not have been imagined when the fundamental theory was crafted in the 1930s. The fundamental theory has survived, and has become immensely broader and richer. But that doesn't mean there is nothing left to learn—far from it. Topics old (how species form) and new (how chromosomes evolve) continue to produce surprises and new insights. Bonduriansky and Day argue, and I agree, that extended heredity has been a mostly neglected topic—because, they say, its very existence was minimized (or even denied) until recently. They provide evidence, and theoretical demonstration, that nongenetic inheritance can have really important, wide-ranging effects. It may affect sexual selection, if parental effects on their son's vigor are a basis for females' mating preferences. It can affect the evolution of resistance to disease-causing microbes. Stress-induced gene methylation may accelerate the process of senescence and cause natural selection to favor reproducing earlier in life.

How about humans? We experience every known form of NGI, from cultural inheritance to epigenetic gene methylation. Bonduriansky and Day remind us that not all nongenetic inherited effects are good for us: it was only in the 1980s that the U.S. government started to warn mothers that heavy drinking can cause a wide range of birth defects. In the 1950s and 1960s, thalidomide was widely marketed as a cure for morning sickness, but no one tested it for risks to developing fetuses, and thousands of children were born with severe deformities. Today, evidence is accumulating that even the father's environment can affect methylation in his sperm's genes. But nothing is known about the possible NGI effects of most drugs or industrial compounds to which we are all exposed. Research on the role of epigenetic and other nongenetic processes in evolution is fascinating, and some will prove to be important in a practical sense. But this is only one among a wide range of research efforts that will be needed to understand these processes and to assess their significance in society.

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