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BOOK REVIEW

# The Comparative Biology of Cultural Inheritance

*The Question of Animal Culture*, **Edited by Kevin N. Laland and Bennett G. Galef. Cambridge, MA: Harvard University Press, 2009. Pp. vii + 351. H/b $45.70**

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When Waddington coined the word "epigenetics" to describe the mechanisms of phenotypic expression that are not due to changes in genes, he paved the way for understanding the wide assortment of inheritance mechanisms that have since come to light. Non-genetic effects on inheritance are now known to encompass much more than emergently heritable patterns of DNA expression or parental transcription effects on morphogenesis (West-Eberhard 2003). Cultural transmission and other forms of environmental manipulation that are repeatably induced or learned from generation to generation, collectively referred to as ecological niche construction, are thought to constitute their own systems of non-genetic inheritance (Sultan 2003). These environmental pathways of non-genetic inheritance are not negligible contingencies of normal reproduction and development, but rather are thought to play a key role in the origin of life itself (Dyson 1986) and in the construction of new levels of biological organization, which is a common theme of major transitions in evolutionary history (Jablonka and Lamb 2006). Why is it then that the "question of animal culture" persists in being a controversial, unsolved puzzle?

The essays collected in the edited volume *The Question of Animal Culture* do not directly touch on this large body of research in evolutionary biology but present instead research in psychology and ethology about what constitutes uniquely human social behavior. This historical controversy can be characterized as an iterated cycle of skepticism expressed by experimental psychologists about non-human animal abilities, driving field behaviorists to make stronger cases for the complexity of their focal species' behavior, followed by experimental psychologists "raising the bar" for what they consider uniquely human cognitive features under the rubric of "culture." The book's editors, Kevin Laland of the University of St. Andrews in Scotland and Bennett Galef of McMaster University in Ontario, both experimental psychologists by training, introduce the book's collection of essays with a brief history of this research into non-human animal behavior in captivity and in the field. In their introduction, they describe the knowledge gained from early accounts of termite fishing in chimpanzees up through recent studies of singing in humpback and sperm whales, providing a brief but vivid outline useful for teachers of biology, psychology, and anthropology.

Although none of the contributors are evolutionary biologists, perhaps the most biologically oriented perspectives in the collection are written by proponents of "niche construction" and occur in Chapters 8 (Laland, Kendal, and Kendal) and 13 (Sterelny). Niche construction is a generalized description of a lineage's modifications to the environment that subsequently affect future generations of conspecifics and ecological interactors, most notably by altering the parameters of natural selection (Odling-Smee 2003). Culture is clearly an example of niche construction, and in light of this, Laland, Kendal, and Kendal attempt to change the framework of the debate by arguing that "[a]nimal culture is much more than a window onto human evolution" (p. 177). In fact, the universality of niche construction implicates all species in a certain kind of sociality insofar as parental effects are always necessary to offspring fitness. Laland, Kendal, and Kendal review the evolutionary effects of culture by describing that not only does culture, like other forms of niche construction, offer opportunities for adaptive behavior, but it can also become an independent pathway for evolution that limits the interconnection of individual organisms with the external

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environment. Citing examples of a variety of fish and birds, as well as specific examples of human societies, Laland, Kendal, and Kendal claim the pervasiveness of animal social behavior as grounds for its intrinsic value to natural history and evolutionary ecology, independently of whether non-human animal cultural behaviors are evolutionarily homologous to or convergent with human culture.

Real conceptual progress is made in this direction when Laland, Kendal, and Kendal in Chapter 8, and Sterelny in Chapter 13, take issue with the current diagnostic method for identifying culture in non-human animals. The "ethnographic method" infers social learning, and thus culture, based on a method of elimination of three factors: genetic, ecological, and individual learning. Can these factors really be eliminated in practice? Laland, Kendal, and Kendal think they cannot.

> [W]e suspect that were the ethnographic approach to be rigorously applied, it would reject most genuine cases of culture. Correlations between behavioral and ecological variables are expected because culture is a source of adaptive behavior, which enables animals to learn about and exploit environmental resources. Similarly, cultural and genetic covariance is also anticipated because animal learning is influenced by evolved predispositions and aptitudes. (p. 185–186)

In support of their suspicion that genetic and ecological factors may be important to the origin and inheritance of social traditions, Laland, Kendal, and Kendal describe woodpecker finches and New Caledonian crows that have experimentally shown impressive tool fabrication without any social opportunities to learn their skills, and chimpanzees that alter their ant-dipping methods for different species of ant. While Laland and colleagues nonetheless endorse the definition of culture as social learning and prescribe more focused methods for identifying it in the field, Sterelny offers an extended exposition about why even this core concept is inaccurate. Sterelny (following Fragaszy and Visalberghi 2001) states that "[i]t is very likely that much of [culture] is hybrid learning: [animals] learn by trial-and-error exploration in an environment structured by parental behavior and perhaps with both their trials and their errors modified by their parents' actions." (p. 295). Other modes of individual learning and plasticity that may be included in this description include a variety of associative and non-associative mechanisms from habituation to conditioning and imprinting. Needless to say, the approach of individual and group plasticity is more amenable to the description of ant, wasp, bryozoan, or siphonophore colonies than psychological mechanisms. Yet it will take nothing short of an interdisciplinary renaissance to bridge the behavioral and evolutionary sciences, and this book should be commended for adding a few planks to that bridge.

It is ironic that *The Question of Animal Culture* does not speak to a broader readership of biology students, considering that culture is a particularly salient and therefore eminently teachable example of the importance of social and other forms of environmental determination in developmental and evolutionary biology. As it stands, readers with experience in biology are left to formulate for themselves the developmental and evolutionary importance of social and other environmental impacts on natural variation in all species, beyond the psychological mechanisms of large-bodied, charismatic vertebrates. While the book is not explicitly focused on a particular audience, its authors seem to speak most directly to each other, and secondarily to a readership of behavioral scientists and the general public. For students of human behavioral science and students of general biology interested in learning and other mechanisms of plasticity, I recommend instead sharing excerpts from West-Eberhard's (2003) large book, *Developmental Plasticity and Evolution*, or the more focused overview provided by a chapter entitled "Behavior and Phenotypic Plasticity" in Pigliucci's (2001) book, *Phenotypic Plasticity: Beyond Nature and Nurture*.

Until "*The Question*" is answered and brought to bear constructively on human behavioral science and the wider comparative context of socio-ecological inheritance mechanisms in all species, this book is best served as a useful compilation of historical perspectives for those directly involved in the study of non-human animal psychology. However, *The Question of Animal Culture* is not only a trade book for researchers of non-human animal psychology. It is also a suitably informative text for educated members of the general public and for this purpose would make an excellent read, both philosophically and for being full of exciting examples of tool-use and other kinds of cultural variation in some of the most popularly known species on the globe.

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