## Cause and context in the biological sciences

## Kevin N. Laland

School of Biology, University of St Andrews, Bute Building, Queen's Terrace, St Andrews, Fife KY16 9TS, Scotland, UK

Deborah Gordon is concerned that contemporary animal behaviorists underemphasize behavioral and ecological variation and advocates greater attention to natural history and ecology. She also maintains that ecology, while recognizing the existence of variation, does not currently adequately capture both the fluid dynamic nature of the variation and the manner in which behavior constructs ecological context. I appreciate her thoughtful analysis and sympathize with her basic arguments. However, I would like to dig a little deeper into the root cause of the problem. In my assessment, the satisfactory integration of ecology and behavioral ecology demands a more radical solution, without which a genuine fusion is unlikely.

In the struggle to understand a mind-blowingly complex and changing world with modest intellects, we scientists grasp at conceptual tools that render our business more manageable. We assume that, at least for the kinds of questions in which we are interested, with their associated temporal and spatial scales, that it is reasonable to treat certain processes, and certain kinds of variation, as relatively unimportant. This allows us to hold certain aspects of the world constant and to explore the causal structure of the phenomenon of interest relative to this context. All scientists do this, and scientific disciplines are effectively "clubs" in which likeminded researchers share some consensus over what is, and what is not, reasonably treated as context.

© The Author 2011. 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 For instance, Harvard philosopher of biology Peter Godfrey-Smith (Godfrey-Smith 1996) describes evolutionary biology as "externalist," by which he means that the adaptations of organisms are described relative to the characteristics of an "external" environment. It is organismal rather than environmental change in which evolutionary biologists are interested. Accordingly, to enhance tractability, the selective environment is treated as if it preexisted the biological trait of interest. We all know that the world is messier than this but accept the convenient fiction on the pragmatic grounds that it allows an exploration of how differential survival and reproduction in that environmental context fashioned the focal character.

Natural selection, then, is recognized as the cause of adaptive organismal change, and the environment is relegated to mere context. Note, this is a scientific convention not an invariant truth about the causal structure of the world. It is perfectly possible to envisage the environment to be playing a more direct causal role in evolution—indeed, this is observed in models of sexual selection, frequency dependent selection, and coevolution, where evolutionary change in one trait provides the selective context for evolutionary change in another. Here, the convenient fiction will not wash, and the associated bodies of theory provide pragmatic fixes, albeit piecemeal ones. These are viewed as "special cases"—ones in which the environmental context also happens to be an evolving organism—and consequently are not viewed as threatening the legitimacy of the general externalist stance.

Such conventions over context are vital if scientific disciplines are to get on with their business. However, it is important that we recognize that these conventions can outlive their usefulness and that each comes with a price. The price we pay for the convenience of evolutionary biology regarding the environment, and therefore ecology, as context is that all evolutionary disciplines undervalue the active role of organisms in constructing their niches and all tend to underplay the dynamic nature of the environment (Odling-Smee et al. 2003).

What Deborah Gordon sees as particular failings of ecology and behavioral ecology I view to be more generic concerns, associated with multiple evolutionary disciplines. Critics of evolutionary anthropology and archaeology dwell specifically on the failure of the fields to recognize humans as actively constructing their environments (e.g. Ingold 2007). Evolutionary psychology is criticized for its emphasis on "universal" evolved psychological mechanisms that fail adequately to capture both human behavioral diversity and the diversity of human selective environments (Foley 1996) and that treat humans as passive victims of selection (Laland and Brown 2006). The longstanding tension between developmental and evolutionary biology in part reflects evolutionary biologists' treatment of development as a "black box" (e.g. Maynard-Smith 1982, p.6), which precludes any causal role for the organism in constructing both selective environments and variants subject to selection (Amundson 2005). Ecology has been a divided discipline, with separate population/community and ecosystem approaches (Jones and Lawton 1995), in part because evolutionary biology did not provide tools to capture adequately how organisms engineer habitat, control, and regulate flows of energy and matter and drive state changes in abiota (Jones and Lawton 1995; Odling-Smee et al. 2003).

The conceptual revision most likely to integrate ecology and behavioral ecology, in my view, is equally the change in thinking necessary to integrate ecology or to provide a satisfactory evolutionary framework for the human sciences. It requires a different way of thinking about evolution: one that no longer treats environments as context, that formally recognizes

organisms as part constructors of environmental states, and that views such construction and its legacy over time as evolutionary processes in their own right (Lewontin 1983; Odling-Smee et al. 2003). This leads to a view of niches as dynamic, evolving entities (Odling-Smee et al. 2003), of ecosystems as governed by engineering as well as food webs (Jones and Lawton 1995), and of ecological and evolutionary processes as inextricably interwoven in space and time (Post and Palkovacs 2009), rather than the cosy "play" in "theatre" conception. In Godfrey-Smith's (Godfrey-Smith 1996) terms, it requires an "interactionist" rather than an externalist theory, in which organismal (and, for that matter, environmental) change is described relative to a relativistic and dynamic niche concept, rather than to a preestablished environment. Conceptual frameworks shape and channel our thinking, encouraging some kinds of research and discouraging others. Each brings its own questions, its own tools, and its own baggage and niche construction theory is no different. The utility of the niche construction revision is precisely that it brings the active constructive role of organisms in shaping local ecologies and hence animal behavior, to the foreground.

Address correspondence to K.N Laland. E-mail: knll@st-andrews.ac .uk.

Received 1 September 2010; revised 1 September 2010; accepted 20 September 2010.

doi: 10.1093/beheco/arq176

## REFERENCES

- Amundson R. 2005. The changing role of the embryo in evolutionary thought. Cambridge: Cambridge University Press.
- Foley R. 1996. The adaptive legacy of human evolution: a search for the environment of evolutionary adaptedness. Evol Anthropol. 4: 194–203.
- Ingold T. 2007. The trouble with 'evolutionary biology'. Anthropol Today. 23(2):13–17.
- Godfrey-Smith P. 1996. Complexity and the function of mind in nature. Cambridge: Cambridge University Press.
- Jones CG, Lawton JH. 1995. editors. Linking species to ecosystems. New York: Chapman & Hall.
- Laland KN, Brown GR. 2006. Niche construction, human behaviour and the adaptive lag hypothesis. Evol Anthropol. 15:95–104.
- Lewontin RC. 1983. Gene, organism, and environment. In: Bendall DS, editor. Evolution from molecules to men. Cambridge: Cambridge University Press.
- Maynard-Smith J. 1982. Evolution and the theory of games. Cambridge: Cambridge University Press.
- Odling-Smee FJ, Laland KN, Feldman MW. 2003. Niche construction. The neglected process in evolution. Princeton (NJ): Princeton University Press.
- Post DM, Palkovacs EP. 2009. Eco-evolutionary feedbacks in community and ecosystem ecology: interactions between the ecological theatre and the evolutionary play. Philos Trans R Soc B. 364:1629–1640.