book review

Evolution: nature or nurture?

Animal Traditions: Behavioural Inheritance in Evolution By Eytan Avital & Eva Jablonka

Cambridge University Press, \$80.00, ISBN 0-521-66273-7, 2000

Reviewed by James L. Gould

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey, USA

The thesis of Eytan Avital and Eva Jablonka's book is that the evolution of behavior cannot be accounted for by genes alone. Instead, they believe that learning creates a significant part of the environment within which natural selection works. This is an intriguing idea, but many of the arguments and examples marshaled to support it seem flawed.

At first glance, Animal Traditions seems like an attempt to rescue nurture's importance after the collapse of Behaviorism (which denied instinct and credited all behavior to conditioning): forced to concede that behavior is largely inherited, one attractive fall-back position is to assert that conditioning is the major force in behavioral evolution. Thus learning would be the agent that creates behavior, just as J. B. Watson and B. F. Skinner

argued all those years ago. Indeed, the authors enthusiastically endorse Watson's infamous assertion that, if given "a dozen healthy infants," he could turn any one of them into a successful lawyer, doctor, or criminal through conditioning.

Like Charles Darwin, the authors define evolution simply as "change," which allows them to make their case for non-genetic evolution. But for modern evolutionary biology, evolution is a change in gene frequencies from one generation to the next—a definition that derails the authors' argument by page 4. (By way of illustration, they create an example analogous to the paradoxical instances used to explain heritability: imagine a population with no genetic

variation; with social learning, behavioral differences will be passed to the next generation; thus, learning can cause evolution. QED.

The authors also take for granted the reality and ubiquity of observational learning. They lump imprinting and other forms of programmed learning in with the kind of observational learning that is necessary for

> their scenario, correctly noting in passing that evidence for observational learning outside of primates and dolphins is very limited and controversial. Programmed learning (like imprinting and conditioning) is really quite different from observational learning: the former is more like calibration than learning, constrained as it is to species- and context-specific cues and responses, whereas the latter (if it even exists in more than a few species) is more like the self-aware form of learning

humans take such pride in.

This confusion of programmed learning with observational learning becomes even more apparent when the authors define innate behavior as actions that do not depend on learning. Given that most learning (including human language learning) depends on innate instructions (including nearly all of the examples of "social learning" they cite), it is hard to see how to evaluate the arguments when the most basic terms and definitions are so muddled. This difficulty grows as the authors confuse learning and maturation (the delayed appearance of a behavior).

Part of the problem in this analysis is the (usually unstated) assumption among more psychologically inclined students of

behavior that animals used to be much smarter than they are now, and evolution has served to make them selectively stupid. To their credit, they do eventually bring this axiom into the open, but err in claiming that most biologists agree with their scenario. Quite to the contrary, traditional ethologists see animals as originally dependent on instinct, and evolving learning programs to solve particular problems. The argument can be made either way, but in my view species comparisons decisively favor the add-on picture of specialized learning rather than the selective-loss scenario.

The authors also seem to get things backwards when they assert that learning will be most prominent in constant environments, whereas instinct will hold sway in unpredictable ones. The evidence is quite the reverse: learning is necessary in the face of unpredictable circumstances, while certainty can allow animals to depend on instinct. This argument has been thoroughly explored in papers and books not cited in *Animal Traditions*.

Perhaps the most controversial part of their book will be the resurrection of group selection as a common-even dominant-component of evolution. The authors seem to fall into the common trap of believing that most species are social, and that sociality is without costs. Viewing behavior through this lens, they believe that sib-sib and parent-offspring conflict are illusions: each is instead a way of enhancing social learning and increasing the fitness of all concerned. They even manage to account for sociality in Hymenoptera without ever mentioning the group's unique haplo-diploid genetics-a quirk that results in sisters being more closely related to each other than they would be to their own offspring.

The book ends (in the aptly titled chapter "Darwin meets Lamarck") with the claim that the often-ridiculed idea that ontogeny recapitulates phylogeny is correct for behavior: because (as they argue) all innate behavior was originally learned and then converted into habits, one can trace the evolution of the behavior through the order in which complex tasks like nest building are performed. I don't think so.

hied all onede gely tive to bing in ion. be tates B. CMERTER Extent Animal Traditions