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Animal Traditions: Behavioural Inheritance in Evolution by Eytan Avital; Eva Jablonka

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Sociology and Biology: Can't We Just Be Friends?¹

Animal Traditions: Behavioural Inheritance in Evolution. By Eytan Avital and Eva Jablonka. Cambridge: Cambridge University Press, 2000. 432p.+xiv.

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On the question "What I don't know about my field but wish I did," Douglas Massey (2000) concludes: "I really wish I knew more about human beings as biological rather than social organisms" (2000, p. 701). Whereas sociology's distance from biology appears to be deeply rooted in these disciplines' scientific and political projects, this statement from the then-president of the American Sociological Association is perhaps evidence of an emerging interest in closing the gap. But with few if notable exceptions, mainstream sociology has so far engaged biology in a confrontational manner, and we have been slower than other social sciences (e.g., psychology, anthropology, or demography) to seek ways to integrate biological models and reasoning into our understanding of social behavior. The continuous refinement of the biological models of behavior—the increasing attention paid to the role of the environment in gene expression, for instance—has brought several key sociological and biological issues closer. Yet, between groups that have hardly been engaging one another for a long time, stereotyping easily endures. From a distance, the most vociferous and extremist positions are more likely to be heard, little more than the titles of best-sellers such as Richard Dawkins's (1976) *The Selfish Gene* are being remembered,² and acknowledging biological influences is

¹ For comments on an early draft, I want to thank Patrice Adret, Mathew Leibold, and William Parish, none of whom bears any responsibility in the views I express here. Direct comments to Patrick Heuveline, Department of Sociology, University of Chicago, 1126 East Fifty-ninth Street, Chicago, Illinois 60637. E-mail: pheuveline@uchicago.edu

² Within the covers, one might be surprised to find that Dawkins never argues that the transmission of genes dominates behavioral evolution, for which he introduces "memes," described as units of information residing in the brain and transmitted from one person to the next by behavioral means (further discussed below in the text).

confused with seeing genes as destiny and picturing people as ants or apes.

But for the sociologists wishing to know more about biological organisms, the task is rather daunting. Driven in part by levels of funding that the social sciences cannot dream of, biological knowledge is expanding and diversifying rapidly. Where to start? What to read? Or, as stated in the title of Richard Udry's (1995) article, "What biology do sociologists need to know?" While Udry's article is particularly stimulating, I am uncomfortable with the definition of a core of biology basics that every sociologist *ought* to know. I say this primarily because what might be useful in one's research is likely quite topic specific. To take only one example, Udry's own work has emphasized hormonal influences on differences in human sexual behavior. Brain research does suggest that the genes derived from the father are preferentially expressed in the brain regions that affect feeding and sexual behaviors, behaviors hence under strong hormonal influences. However, according to Avital and Jablonka (p. 345), paternal genes appear much less active than genes derived from the mother in the neocortex, especially in the frontal cortex areas responsible for high cognitive functions. The biological factors that affect individual differences in sexual behavior may hence not explain as much of the individual differences in, say, childbearing, which involves a more complex choice process in societies where highly efficient contraceptive technology is available.

Asking what sociologists ought to know about biology may not make more sense than asking what they ought to know about history. Those working at the interface of sociology and another discipline, be it biology or any other, certainly need to know a lot more than could be summarized in a few pages. But while I like to think that, as curious minds, most sociologists want to read good research from biology or history once in a while, I would argue that in their everyday work, many can do without. There is indeed growing evidence that one type of sociological investigation that ought to be concerned with biological factors is the study of the determinants of individual to individual variations in behavior. Sometimes the reaction of some sociologists is one of vehement opposition to biological explanations; while this response may betray a perceived threat, it might also be related to the emphasis that our discipline, in its quest for scientific respectability, has placed on building atomistic, causal, behavioral models. With the proliferation of social survey sampling, predicting a vector of individual outcomes Y from a matrix of individual characteristics X with everything else in a noise vector has become the methodological staple of many sociological investigations. It is not hard to see that the omission of all biological parameters in many such models *is* problematic. But just as readily found are rather large expanses of

sociological investigations that do not have to be concerned with biological factors. Just as one does not need molecular physics to predict, accurately enough for most purposes, the trajectory of two homogenous spheres colliding on a horizontal plane from their mass, speed, and initial trajectory, examples of aggregate social behaviors abound that can be studied without attending to the infra-individual level.³

As much as I enjoyed and learned from *Animal Traditions: Behavioural Inheritance in Evolution* by Avital and Jablonka, I hesitate to qualify it as a “must read” for all social scientists. Yet, for those who are curious about some of the current debates on behavior in the biological sciences, this is a good place to start. First, the authors discuss, from the standpoint of understanding animal behavior, the usefulness and limits of the current evolutionary paradigm and the modern synthesis of Darwinian theory of evolution with Mendelian genetics, which is perhaps the single most influential paradigm of the natural sciences. Second, by emphasizing the role of social learning in the evolution of animal behavior, the authors illustrate current attempts to broaden the narrowly “genetic” view of evolution in ways that should make evolutionary biology more palatable to social scientists. For social scientists, there is much to learn and little to take offense from in this book. In what we might consider an entertaining inversion of sociobiologists’ attempts to explain human behavior from evolutionary thinking in natural history, the authors all but extend to most mammals and birds the claim prevalent in sociology and cultural anthropology that culture liberates from genetic determination.⁴

The authors’ argument begins with a thorough critique of the “currently fashionable version of Darwinism” (p. 1), which these authors refer to as “genetic” Darwinism, and of the related attempts to explain all patterns of animal behavior in terms of genetic programs. John Maynard Smith is reputed to have declared, “No one is a genetic determinist anymore,” and the authors might be taking on a straw man, but they provide a clear summary of the limitations of genetic determinism, and they clearly have a knack for metaphors. Perhaps reminiscent of sociobiologist Edward O. Wilson’s statement that genes held culture on a leash, the authors describe the relationship of the phenotype to the genotype as that of the kite to its string (chap. 2). When the string is relatively short, the kite is easily controlled by specific controls being applied to the string. Likewise, fairly

³ Udry recognizes this too but in a single, rather short paragraph on social change. We might hence differ only as to whether to describe the bio-free sociology glass as half-full or half-empty!

⁴ Avital and Jablonka maintain that the term culture is applicable “to a set of socially transmitted habits in higher animals,” even though those habits do not involve the ability to communicate symbolically nor linguistically (p. 21).

simple genotypes, such as eye color, are strongly influenced by specific genes. For more complex maneuvers, however, one must release more string, and the longer the string, the more the kite's movements are influenced by the wind and other environmental factors. When the string is very long, the kite can hardly be controlled by the string; if anything, the movements of the kite determine the movement of the string. Eventually, the authors must abandon the kite metaphor to add that behavior is not entirely passive to the environment—the two interact instead—but the metaphor serves them well to illustrate how complex behaviors are only remotely affected by genes. The authors conclude that hence population genetics alone cannot explain behavioral change—a statement perhaps less polemical than they make it sound—and that we must look for mechanisms other than genetic inheritance to explain the transmission of complex behaviors across generations.

Straightforward imports from genetics, such as Dawkins's theory of "memes" or cultural units transmission, do not readily apply to animal behavior, as the authors point out. Behavior forms a whole from which units, equivalent to genes, can hardly be isolated. One does not transmit behavior passively, as is the case for genes; on the contrary, the transmission of behavior occurs within behavior itself, and it is impossible to separate the transmission itself from what is transmitted. The authors' views are thus closer to the anthropologist William Durham's claims about the coevolution of genes and culture. While natural selection operates on individual variations, those variations are not entirely random mistakes but instead occur in the process of learning a given behavior. The authors thus contend that behavioral change guides genetic evolution at least as much the other way around. One objection that biologists have formulated before to that proposition is that a behavioral change would then have to remain stable for a very long time, over many generations, before it begins to affect genetic diversity.

Avital and Jablonka find support for the coevolution thesis in the growing research on social learning (chap. 3). By adding the ability to learn the behavioral traditions of an animal group, they identify a mechanism that maintains behavior relatively constant across generations and makes it relatively "plastic" or independent of the changing genetic composition of the group. Learning is here defined as "an adaptive change in behaviour that results from experience" (p. 69). The authors contrast several complex behaviors. Some involve innate components, with no or little learning. Others involve asocial learning—for instance when immunity to food poisoning allows an individual to learn alone of benign consequences through trials and errors. Among birds and mammals, however, the authors claim that a very large component is learned through social learning with older individuals, usually the parents. Unlike imitation, socially in-

fluenced learning teaches the learner about the environmental circumstances that elicit a behavior without the behavior being necessarily displayed by another individual. The authors suggest, for instance, that the mere presence of a parent preventing the most costly mistakes to be made provides a sense of security, reduces the level of stress in the offspring, and eventually facilitates learning. Among the key aspects of the development of young birds and mammals that are learned with the parents, "knowing what to eat, where to find its food and how to harvest it" (p. 119) is arguably the single most important. Social scientists may find even more interesting the material on "sexual imprinting," which refers to behavioral markers of the original background that play a role in mate choice, such as song patterns in birds. By increasing phenotypic similarity, sexual imprinting contributes to pairing mates that are well suited to share the same environment, but were it too rigid and precise, sexual imprinting could lead to excessive inbreeding. Quails, for instance, appear to seek mates who are similar but not identical to their siblings. Thus one may find in animals mating schemes relatively similar to the marriage rules uncovered by kinship anthropologists.

By reexamining family behavior through the lens of the importance of social learning and the transmission of information, the authors challenge conventional interpretations in terms of the evolutionary conflict between mates or between parents and offspring. While conflict arguments focus on the different fitness of the genes of males and females, or parents and offspring, Avital and Jablonka counter that behavior involves information that is shared or gained together and that thus involves cooperation rather than conflict. Again, the authors are best at describing the complexity and diversity of animal behavior and criticizing simplistic explanations for all animal behaviors (that some may want to extend to human behavior). For instance, explaining differences in male and female sexual behaviors by their conflicting evolutionary strategies (males seeking a higher number of mates and females seeking fewer "high-quality" mates) only makes sense in species in which the male contributes little more than his genes and the female alone cares for offspring. Things are clearly more complex when the male does not merely inseminate the female but also invests in parental care, as is the case in most monogamous species. While the authors' reinterpretation of behaviors as enhancing the transfer of information rather than resulting from conflict appears most often quite plausible, the lack of evidence to test the alternative interpretations remain frustrating. While possibly remaining agnostic about the validity of some claims, the reader will still be rewarded with a refreshing picture of the variety of animal behavior and of the increased sophistication of evolutionary thinking. One, for instance, will find echoes of the economic theory of marriage in the argument that much of the information shared by the

mates would be of little interest with other mates. This information represents a pair-specific investment, which provides benefits only in the existing union, and individual-specific rather than universal preferences for partners further increase the costs of desertion. Sociologists might find an evolutionary self-fulfilling prophecy in the idea that traits considered “attractive” when choosing a mate might increase fitness merely because potential mates believe they do. The dominant explanation for “attractive” traits is that they are “honest signals” of a potential mate’s high fitness, and they become factors of selection jointly with the ability to recognize them as attractive. (Color and length in the peacock’s tail, which so intrigued Darwin because they did not contribute to survival, were indeed found to be correlated with the individual’s health.) But a hereditary trait found attractive would still be fitness enhancing were it a completely neutral signal of the mate’s quality, just because its transmission to offspring would in turn allow them to mate and reproduce more easily. The authors gradually move outward from the mates and offsprings nucleus to the larger group, considering allo-parenting and other apparently altruistic group behavior and extending their argument that selection operates not only at the level of the individual but also at the level of the group. The selection of behavior that increases the reproductive success of kin is now widely recognized and understood by considering inclusive fitness, that is, the fitness of the individual but also of other genetically related individuals, weighted by their degree of relatedness. In a more radical departure from extant evolutionary thinking, the authors describe altruistic behavior that benefits the group of mostly unrelated individuals as also fitness enhancing. They argue, for instance, that altruistic behavior may provide benefits to all group members and that these benefits outweigh the potential costs to the altruistic individuals, allowing groups with more altruists to reproduce more prolifically. Since population genetics firmly rules out genetic selection at the group level, the stability across generations of such altruistic behavior within the group would require in particular that the behavior be independent of the changing genetic composition of the population. While this idea is not implausible, the authors provide precious few examples of such transmission mechanisms across generations, in part because of their insistence on playing down evolutionary conflict. One of the few instances they describe is the “phenotypic cloning” of an adult behavior by an unrelated young animal (p. 238), but they insist it is beneficial to the “allo-parent,” because the behavior promotes in several ways the allo-parent’s own reproductive success. This might be the case, but instances where lower-ranked individuals are coerced by higher-ranked ones into behaving in ways that are beneficial to the group are more commonly against the reproductive interests of the recipient. For instance, the reproductive suppression of some

individuals (via harassment by others that prevent mating or via infanticide) may provide benefits to the group when group growth would pressure survival, yet such actions can hardly be seen as enhancing the fitness of these dominated individuals. While an animal group can function efficiently only when competition for food, mates, and space is regulated, arguing that this evolutionary stable regulation has to be fitness enhancing for all members of the group might remind sociologists of the early functionalist explanations that suppressed all mentions of power differences. Dominated individuals may engage in cooperative behavior in the context of a competition that they cannot hope to win, rather than freely following a genuine, evolved altruistic behavior.

To complete their argument of a coevolution of genes and social learning, the authors suggest that the ability to learn is itself a product of evolution. In a stable environment, evolution would favor the inheritance of innate behavior across generations by genetic assimilation, whereas in more fluctuating environmental conditions, the transmission of socially learned behavior would be more beneficial. In this perspective, genetic assimilation would have freed some more mundane behavior from learning, allowing individuals to learn more complex tasks gradually. This evolved ability to learn across generations increasingly complex sequences gave some animals a behavioral plasticity that made many phenotypes all but independent from genotypes, while "genetic evolution became ever more dependent on culture, following, rather than leading, as it was channeled into the grooves drilled by cultural evolution" (p. 367).

In sum, *Animal Traditions* is a very well written text, full of wonderful vignettes on animal behaviors and stimulating hypotheses about their evolution. Biologists are not likely to embrace all of these hypotheses readily. As Avital and Jablonka are well aware, however sophisticated their account might be, some critical elements still sound too close from the dismissed Lamarckian paradigm of the inheritance of acquired characteristics. The lack of tests for competing hypotheses might not allow nonspecialists to make definitive, informed judgments about these debates, but readers will be rewarded with a more sophisticated overview of this field than they might have imagined from the often simplistic import of evolutionary thinking in other fields.

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