SOCIAL LEARNING AND IMITATION

Introduction

Aristotle (1984, Book IV, p. 83) noted that songbirds that were hand reared away from their parents and exposed to songs of other species "utter a different voice from their parents," and suggested that hen nightingales teach their chicks to sing. Obviously, interest in the possibility that social interactions can bias behavioral development in animals is not new.

However, it can be argued that social learning emerged as a coherent field of inquiry at the Chicago meetings of the Midwestern Psychological Association in May of 1985, where Thomas Zentall organized and chaired a seven-paper symposium on social learning and imitation. The symposium led, as symposia so often do, to an edited volume (Zentall & Galef, 1988) that was intended to encompass the diverse perspectives on social learning found in psychology and biology.

None of the contributors to that pioneering volume had any idea how rapidly the field of animal social learning would grow or how diverse the academic backgrounds of those interested in social learning would become. Today, the literature on animal social learning is so vast that it is hard to imagine that anyone has command of it all. Maintaining communication among scientists from around the world with primary allegiances to disciplines ranging from anthropology to zoology has become a real challenge. Our hope is that this special issue of *Learning & Behavior* will both introduce the field of animal social learning to those unfamiliar with it and, concurrently, help to sustain the coherence of an increasingly diverse enterprise.

This volume brings together substantial reviews of a few "traditional" areas of inquiry reflecting the past and present of the field of animal social learning and descriptions of the research programs of some relative newcomers to the field. The latter contributions point the way to the future of the field.

The volume opens with a compelling chapter by Laland encouraging greater integration of theoretical and empirical work on social learning in animals, and providing a very important first step in that direction. Formal models suggest that animals should copy when uncertain, should copy the majority, and should copy those doing better than they are. Laland reviews, in very accessible fashion, both the mathematical models that lead to these conclusions and the limited empirical evidence that bears upon them.

The next three reviews address what is, perhaps, the oldest question in comparative psychology, one addressed both by George Romanes (1882) and by Edward Thorndike in his classic monograph of 1898. Can animals learn by imitation? Taken together, the answers provided by our authors are both interesting and surprising. Zentall, in a paper that elegantly describes the approach of experimental psychologists to the study of social learning in general and imitation in particular, discusses data indicating that if the two-action method provides an adequate test of imitation, as many believe that it does, then pigeons and quail surely imitate. Fragaszy and Visalberghi provide evidence that capuchin monkeys do *not* imitate, and Whiten et al. report that chimpanzees can imitate not only motor patterns, but also the sequential and hierarchical organization of behaviors involved in solving complex tasks. In combination, these contributions from authorities in the field imply that, across species, the capacity for imitation learning does not consistently covary with either neurological complexity or phylogenetic distance from humankind.

Galef considers a contentious issue, the relative merits of observational and experimental methods in determining whether animals have behavioral traditions ("culture"). He proposes that because the claim that a behavior observed in a free-living population is traditional is ultimately a claim about the behavioral processes underlying its development, experiment rather than unobtrusive observation will be necessary for that claim to be validated.

Gajdon, Fijn, and Huber describe their innovative attempt to discover whether members of a group of free-living kea (a New Zealand parrot) would learn socially to perform a moderately demanding motor task that these researchers had trained one group member to perform. The finding that kea in the wild do not seem to learn through observation a task that their fellows in captivity readily learn socially provides a challenge to those of us who extrapolate, perhaps somewhat uncritically, from laboratory to field settings.

Nicol reviews studies of social learning in both domestic fowl and their wild precursors, red jungle fowl. The well-defined social relationships found in stable groups of fowl offer particular advantages to those interested in understanding "indirect bias" (Boyd & Richerson, 1985) in social learning, the fact that some members of a social group are more likely to influence the behavior of their fellows than are others. Because of their tremendous economic importance, chickens also provide opportunity for application of studies of social learning to real-world problems.

The final six papers are by investigators whose research on social learning is of more recent vintage than that of the authors of the first five manuscripts. The first two papers in this set, by Gwen Dewar (an anthropologist who did her PhD research with John Mitani at the University of Michigan and currently teaches at Santa Rosa Junior College in California) and by Simon Reader (a behavioral biologist at the University of Utrecht, who earned his PhD under Kevin Laland at Cambridge and held a postdoctoral fellowship with Louis Lefebvre at McGill University) reflect the steadily growing mathematical contribution to the study of social learning. Dewar describes and tests a simple mathematical model that predicts when animals deciding whether to eat an unfamiliar food would be expected to rely on social information in making their decision. Both the model and the experimental results indicate that an individual's previous experiences of the relative caloric values of familiar and unfamiliar foods affect its willingness to eat unfamiliar foods as well as its reliance on social cues when selecting something new to eat.

Reader considers the more general issue of whether the shapes of curves describing the spread of a behavioral innovation through a population can provide clues to whether that behavior was learned socially or by individual trial-and-error learning. Although many researchers interested in whether animals learn socially in natural situations have entertained hopes that positively accelerating functions might be indicative of socially transmitted behaviors, Reader's review suggests that considerable caution is required when one draws inferences from the temporal dynamics of diffusion patterns of novel behaviors.

The next three papers deal, at least in part, with effects of observing the behavior of others on subsequent mate choices by the observers. David White (now at the University of Pennsylvania after a postdoctoral fellowship with Meredith West and Andrew King at Indiana University) reviews work that he completed for his PhD with Jeff Galef at McMaster University in Hamilton, Ontario. White's experiments show, among other things, that female quail exhibit a long-term increase in preference for males that they have seen mating with other females, whereas males show a short-term decrease in preference for females that they have seen mating with other males. The selective pressures responsible for such sex-specific responses are of obvious interest.

Peter McGregor, (a zoologist at the University of Copenhagen, who completed a PhD with John Krebs at Oxford and was at Nottingham for many years before moving to Denmark) is interested in effects of observation of signaling interactions, particularly aggressive ones, on the subsequent behavior of "eavesdroppers." Peake and McGregor's particular interest is in those cases in which observed interactions involve signals evolved for communicative purposes. In their terms, White's work on quail would be considered a case of "bystanding," rather than of eavesdropping, because no apparently evolved signals are emitted by interactants. The potential for development of a behavioral taxonomy analagous to the one that developed over decades in studies of social learning/imitation (Galef, 1988; Whiten & Ham, 1992; Zentall, 2004) is evident, and would, perhaps, best be avoided.

Todd Freeberg (in the Department of Psychology at the University of Tennessee, following a PhD with Meredith West and Andrew King at Indiana and a postdoctoral fellowship with Jeff Lucas at Purdue), describes his elegant work on geographic traditions of mate preference in cowbirds, *Molothrus ater.* Freeberg provides compelling evidence of effects of the social rearing environment on male song, on female preferences for males, and on courtship interactions between

males and females, demonstrating cross-generational transmission of behavioral traditions that influence mating behavior in both sexes. Chimpanzees may have "culture" (Whiten et al., 1999); cowbirds surely do.

Andrea Griffin (a recent PhD from Chris Evans's laboratory at Maquarie University in Australia and presently a postdoctoral fellow with Louis Lefebvre at McGill) reviews work on a classic, though rarely studied, problem in both comparative psychology and biology. How do animals learn to avoid predators without being eaten by one? She describes her dissertation research on predator-avoidance learning in a marsupial, the tamar wallaby, as a form of Pavlovian conditioning, then considers the implications of her work for attempts to reintroduce captive-bred and reared members of endangered species back into natural habitat.

Taken together, this collection of current work in social learning suggests some possible directions for the next decade. The field will be more interdisciplinary, yet more integrative. It will be increasingly applied and mathematical. It will involve work with more species and behaviors by researchers from around the world, and it will see increasing introduction of experimental techniques into field settings. Perhaps someday we shall all agree which animals can and cannot imitate, or better still, come to an understanding of what makes an animal able to imitate.

The last 20 years have been a period of exceptional growth in studies of animal social learning. What was once an area of interest of a mere handful of experimental psychologists and biologists is now a dynamic field involving investigators from around the world in an ever increasing range of disciplines: animal behavior, anthropology, behavior genetics, behavioral ecology, economics, experimental psychology, mathematics, neuroscience, primatology, robotics, and so forth. The next 20 years of studies of animal social learning promise to be even more productive and challenging than the last, so long as those involved in the area remain focused on phenomena and avoid the linguistic morass that threatened to engulf the field a mere 20 years ago.

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