

Invited Commentary

Learning to avoid the behavioral gambit

Arnon Lotem

Department of Zoology, Faculty of Life Sciences, Tel-Aviv University, Tel-Aviv 69978, Israel

Fawcett et al. correctly identified a problem: despite repeated calls for a greater integration of psychological and biological approaches, most behavioral ecologists still study the evolution of behavioral strategies rather than the evolution of the learning mechanisms that produce or shape these strategies. The problem is not limited to foraging behavior. Nearly two decades ago, we demonstrated how learning constraints may explain acceptance of brood parasites by hosts (Lotem 1993; Lotem et al. 1992), and more recently, the possible role of learning in explaining variation in offspring begging (Kedar et al. 2000). Although these studies are frequently cited to acknowledge that learning must also be important, very little experimental or theoretical work followed this path, suggesting that a lack of awareness may not be the only problem.

To illustrate the difficulty in integrating learning and behavioral ecology, I frequently use an analogy that I call the parallel parking paradox. Imagine an alien student from another planet who decides to study how humans park their cars on a busy street. Looking from above, he is surprised to discover that instead of directly moving their car sideways as predicted by any reasonable optimization model, drivers keep maneuvering forward and backward in a curve to reach the final position (as we all do in parallel parking). The obvious point is that looking from above and monitoring overt behavioral patterns (as behavioral ecologists often do), the alien student is unaware that parallel parking is a by-product of the car's steering mechanism; it is not really a behavioral strategy. The trait that is "under selection" is the steering mechanism. To study the "evolution" of this trait, the alien student will have to study car mechanics, production costs, consumer habits, and probably much more. In fact, he will have to model an entire car and investigate the effects of alternative steering mechanisms on the car's performance under many possible conditions and driving strategies, resulting in a completely different research program than originally intended. Taking this analogy back to behavioral ecology, this is like expecting a behavioral ecologist to study not only learning, but the evolution of the entire brain. It is certainly important, yet most behavioral ecologists would probably prefer to reconsider the research question rather than to become evolutionary neurobiologists.

Fawcett et al. do not suggest that we all become psychologists or brain scientists. They rightly suggest to start with the evolution of simple learning rules, and I agree with them. But will it be sufficient? Can we really avoid the gambit without going all the way to a complete model of the brain? My claim is that we are likely to progress slowly while replacing one gambit with another. First, in many attempts to model the evolution of learning, the learning rules and the dynamic learning process are not modeled explicitly but only approximated

to simplify the math. For example, Fawcett et al. mentioned such a model that revealed interesting results (Dubois et al. 2010) which, however, were not replicated when the learning process was modeled explicitly (Katsnelson et al. 2012). Moreover, even when the learning process is modeled explicitly, most learning rules (such as the Linear Operator or the relative pay-off sum) are extreme simplifications. They may be useful to explain paradoxical behaviors or to predict decision making under some conditions (e.g., Erev et al. 2010; March 1996; Shafir et al. 2008), yet they are still far from capturing the real neuronal mechanisms that are under selection. When such learning rules appear adaptive, it is convenient to believe that they are the traits under selection, but when they are not, it is always possible that the gambit was wrong and that these rules are based on some neuronal mechanisms that evolved to serve a much wider range of learning tasks, some of which are quite different or more complex than a simple choice between alternatives (e.g., Kacelnik and Bateson 1997). Sooner or later, we will have to deal with behavioral strategies that require a rich cognitive representation of the environment and with learning mechanisms that can construct such representations and facilitates complex decision making. Eventually, to really avoid the behavioral gambit, we will have to deal with the evolution of the entire brain and the wide spectrum of behaviors it generates. Behavioral ecologists may be in a great position to contribute to such a research program, but given the required shift in focus and the inability to avoid the gambit in the very near future, understandably, not all of them may choose to do so.

Address correspondence to A. Lotem. E-mail: Lotem@post.tau.ac.il

REFERENCES

- Dubois F, Morand-Ferron J, Giraldeau L-A. 2010. Learning in a game context: strategy choice by some keeps learning from evolving in others. *Proc R Soc B*. 277:3609–3616.
- Erev I, Ert E, Roth AE, Haruy E, Herzog SM, Hau R, Hertwig R, Stewart T, West R, Lebiere C. 2010. A choice prediction competition: choices from experience and from description. *J Behav Dec Making*. 23:15–47.
- Kacelnik A, Bateson M. 1997. Risk-sensitivity: crossroads for theories of decision-making. *Trends Cog Sci*. 1:304–309.
- Katsnelson E, Motro U, Feldman MW, Lotem A. 2012. Evolution of learned strategy choice in a frequency-dependent game. *Proc R Soc B*. 279:1176–1184. doi: 10.1098/rspb.2011.1734
- Kedar H, Rodriguez-Girones M, Yedwab S, Winkler DW, Lotem A. 2000. Experimental evidence for offspring learning in parent-offspring communication. *Proc R Soc B*. 267:1723–1727.
- Lotem A, Nakamura H, Zahavi A. 1992. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behav Ecol*. 3:128–132.
- Lotem A. 1993. Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* host. *Nature*. 362:743–745.
- March JG. 1996. Learning to be risk averse. *Psyc. Rev.* 103:309–319.
- Shafir S, Reich T, Tsur E, Erev I, Lotem A. 2008. Perceptual accuracy and conflicting effects of certainty on risk-taking behaviour. *Nature*. 453:917–920.