Game Theory in Biology: Concepts and Frontiers. By John M. McNamara and Olof Leimar. Oxford, Oxford University Press, 2020.

This is an excellent exposition of game theory as applied in biology, written by two of the leading lights in the field. The book is very well-crafted with illuminating explanations and a nicely balanced use of mathematics. It is intended to be an advanced level textbook and reference for biological researchers current or future. But it will also intrigue researchers in economics who indulge in interdisciplinarity. Economists will find the style---the use of mathematics, in particular---highly congenial.

In Chapters 1 to 4, the authors present a deft outline of basic material. In the subsequent Chapters 5 to 10, they take the reader to the coal-face of current research on a wide variety of different topics.

All of the applications are presumably of biological interest. Some of the purely biological examples would be of intrinsic interest to anyone with curiosity. For example, in Chapter 6.5, the authors present a game theoretic analysis of scale-eating cichlid fish that live in Lake Tanganyika. These fish feed on the scales of other fish in the lake, attacking from behind and biting the victim on the left or right flank. The success of this attack is improved by lateral asymmetry of the mouth of the scale-eater. A mouth that is skewed to the left is more effective in biting the right flank of the prey and vice versa. The prey fish can more effectively defend against attacks if these attacks are predominantly on one side or the other. The mouth asymmetry of the scale eaters may have genetic roots, expressed in a contingent fashion (plasticity), but seems largely driven by learning during development.

McNamara and Lemar model this as an evolutionary game where the learned degree and direction of the mouth asymmetry are chosen by the scale eaters and the directionality of the defense is chosen by the prey. The evolutionary stable strategy involves a symmetric defense but a bimodal distribution of asymmetry for the scale eaters, with an equal number of lefties and righties.

There are some applications that will resonate directly with economists. In Chapter 5, as a leading example, there is an appealing exposition of the concepts of small and large worlds as these might be usefully applied to biology (Savage, 1951). In a small world, individuals might have innate representations of probability distributions and update these appropriately in the light of experience. In a large world, where there is overwhelming complexity, cruder learning procedures, perhaps akin to reinforcement learning, must be utilized. This provides a context for the application of such cruder procedures in the remaining chapters. We flatter ourselves in economics by often supposing we can model a world that is actually large in a plain English sense as if it were small in the Savage sense. (Binmore, 2007, for example, argues that Bayesian decision theory cannot even cope with recognizing that the decision-maker cannot decide mathematically undecidable propositions.)

Perhaps the chapter of most direct interest to economists is Chapter 7. Chapter 7.6 covers indirect reciprocity, or the hypothesis that cooperation in a repeated interaction might be conditioned on observing how a current opponent behaved previously towards third parties. An opponent has a good reputation if she cooperated against other cooperators, but she must be allowed to defect against opponents who had previously defected. Such a reputation would merit cooperative choices by a current opponent. There is evidence for such indirect reciprocity in humans but the evidence for non-human species is weak.

Chapter 7.8 discusses markets, in which two individuals trade distinct goods or services. For example, cleaner fish remove ectoparasites from larger fish. The cleaners get food, the clients get pest control. This exchange involves forbearance by both parties. The cleaner fish would prefer to eat the mucus of the clients, but the clients (oddly) do not wish to part with this. The client fish would prefer to eat the cleaner fish.

Alternatively, insects consume the nectar from flowers and provide pollination services in exchange. The market involves a form of differentiation of the goods transacted within each exchange. Nectar is obtained at a decreasing rate by the insect, a rate that depends on the current stock in the flower. Insects prefer well-stocked flowers since there is a time cost of leaving one flower and finding another in the patch. The flower would gain from less extravagant nectar provision but then the insect would leave sooner and provide less effective pollination for the flower. Hence pollination is also differentiated. There will be an evolutionarily stable strategy in which a mutant plant cannot gain by altering its provision of nectar given that all other plants in the patch provide that level. Such an equilibrium seems akin to monopolistic competition and unlikely then to satisfy the First Welfare Theorem in any relevant sense.

The last application of economic interest I will mention is the model of the evolution of cooperation in Chapter 7.9. There is a single species where individuals pair up to perform a task that benefits both individuals but which has a cost to each individual. There is variation in the level of contribution within the population. Furthermore, importantly, there is correlation between the levels of contribution between matched pairs. This might arise because individuals have information about the likely contributions of potential partners in advance and can choose on that basis. Or it might arise because an individual could break off a partnership with a relatively uncooperative partner. Whatever the origin of the correlation, this is shown to be enough to promote the evolution of cooperation, at least to some extent.

I recommend this book unreservedly---certainly to those economists whose interests encompass biology.

REFERENCES

Binmore, K. 2007. “Rational Decisions in Large Worlds”, *Annales d’Économique et de Statistique* 2007, No. 86, pp. 25-41.

Savage, L. 1951. *The Foundations of Statistics.* Wiley: New York.

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