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BOOK REVIEW

Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics. By Thomas L. Vincent and Joel S. Brown. New York: Cambridge University Press. 2005. 400 pp. $ 100.00 (hardcover). ISBN 0-521-84170-4.

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> While Darwin's theory of natural selection . . . has all the elements of a "game" it could not be formulated as such until the development of game theory nearly a century later.
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> —Vincent and Brown 2005, p. 72

While many books have been written about evolutionary game theory over the last couple of decades, Thomas Vincent and Joel Brown's recent book, a culmination of their collaboration over almost two decades, is especially ambitious in both breadth and depth. In terms of breadth the authors address a much wider array of biological phenomena (both evolutionary and ecological) than is typical. In addition, whereas classic evolutionary game theory limits itself to behavioral interactions and phenotypes, this book takes a very broad view of what constitutes a "game" and places natural selection itself firmly within a game-theoretic framework. In terms of depth, the authors heartily embrace (and demonstrate how to model) many of the complexities in evolving systems. These include simultaneous selection on multiple traits, the effect of resource availability and distributions on selection, co-evolution among species, and evolution in the context of multiple life history stages.

Of course this depth requires more mathematical complexity. Thankfully, the book is well organized such that each chapter, especially those that develop the core of the authors' techniques (Ch. 4–7), introduces concepts with well written verbal descriptions, then with simple examples, and finally with a progression of more complicated and mathematically sophisticated cases. This allows readers of varying mathematical sophistication to go as far into each chapter as desired, while still gaining enough of the overall message to progress to subsequent chapters.

Game theory originated in economics (von Neumann and Morgenstern, 1947) as a tool for reasoning about how rational individuals (players) should behave in various kinds of "conflict of interest" situations in order to maximize benefit (utility) to themselves. Quickly adapted by other social sciences, game theory proved useful in analyzing phenomena as diverse as Cold War nuclear conflict scenarios, marital strife, and cooperation among unrelated humans in rural

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water allocation. George Price was one of the first to place game theoretic considerations in the context of natural selection (Frank, 1995) and his early collaborator John Maynard Smith went on to develop these ideas more fully (1982). One of the insights of this early work was that natural selection can play the role of a rational player in evolutionary games—instead of an individual choosing the most rational behavior, natural selection chooses individuals with the "best" strategy from a population exhibiting a variety of strategies. In these models the game embodies fitness payoffs for various behavioral combinations in social interactions. For instance, in the famous 2-player Hawk–Dove game, simultaneous hawkish behavior has the worst payoff for both players, whereas hawkish behavior in the context of a dove opponent has the best payoff.

Vincent and Brown take the idea of a game deeper into the evolutionary process by defining it in terms of Darwin's postulates for natural selection. Postulate one, heritable traits with variation, provides the alternative strategies; postulate two, the struggle for existence, provides the conflict of interest; and postulate three, heritable traits influence the outcome of the struggle, provides the selection for fitter strategies. Here "all of life is a game" (p. 13), any heritable phenotype can be considered a strategy, and an adaptation is an Evolutionary Stable Strategy (ESS). Players are not individuals but heritable strategies that can compete in "evolutionarily identical" individuals—those capable of evolving to the same phenotype given the same context.

The first three chapters provide a good background for the concepts, tools, and examples developed later in the book. Chapter 1 introduces natural selection and the fundamental evolutionary and ecological patterns that biologists call on natural selection to explain. These patterns include fit of form and function (or how organisms appear well designed for their environments), the overall diversity of life, the progressive complexity of organisms (despite underlying similarities), and the way organisms are distributed non-randomly on the planet over both local and global scales. Chapter 2 provides a well-written and brief overview of necessary mathematical concepts, especially those dealing with matrices, dynamics, and the characterization of equilibria. It also introduces a variety of basic population models.

Chapter 3 is especially helpful to the reader in understanding important conceptual distinctions. These include: the distinction between classic game theory with its utility payoffs and evolutionary game theory which must translate payoffs into offspring representation in subsequent generations; the distinction between classic optimization problems and game-theoretic solution concepts such as the Nash equilibrium and Pareto optimality; and the distinction between fixed strategy and continuous games. Chapter 3 also introduces the central feature of Vincent and Brown's evolutionary game theory: the fitness generating function (or *G*-function). In its simplest form a *G*-function determines the per capita rate of growth for a particular strategy (heritable phenotype) given its relevant biotic environment. This environment includes the set of all strategies in a population and their current abundances or frequencies.

The authors use the German term "bauplan" to capture the set of individuals to which a particular *G*-function applies. As they say: "A *G*-function is a mathematical construct that defines a group of individuals as evolutionarily identical. Individuals with the same bauplan have the same set of evolutionarily feasible trait values, the same constraints on traits, and the same ecological consequences of actually possessing a particular trait value" (p. 82). The concept of the bauplan attempts to separate phylogenetic levels where selection could drive one species to be identical to another from deeper levels that are historically or phylogenetically constrained. The authors suggest that the taxonomic level of "family" might provide this dividing line where, for instance, coyotes could evolve to be wolves given the same selective pressures that gave rise to wolves, but selection on coyotes to be tigers would likely result in a tiger-like coyote rather than a true tiger. A *G*-function captures the set of strategies represented by one bauplan along with its relevant selective environment, including the presence of other conspecific or heterospecific strategies.

Chapters 4–7 fully develop the *G*-function concept and relate it to a variety of classic evolutionary and ecological phenomena. Chapter 4 provides *G*-function models for Lotka–Volterra type competition, species interactions with resource dynamics, predator-prey co-evolution, and multiple life history stages. In Chapter 5 Vincent and Brown distinguish between population dynamics (which take place on an ecological timescale) from what they call "strategy dynamics" (which take place on an evolutionary timescale). They show how strategy (phenotype) dynamics can be understood as occurring on an adaptive landscape, which itself is changing during the evolutionary process. Here they also introduce the notion of heritable variation by having strategy values represent means of distributions. Adding variation then allows the authors to connect their framework to Fisher's Fundamental Theorem and show that the evolutionary outcome can be a coexisting coalition of strategies.

Chapter 6 formalizes and enhances Maynard Smith and Price's concept of an Evolutionary Stable Strategy (ESS). The authors distinguish between stability on ecological and evolutionary timescales and add the notion of convergent stability (evolutionary) to the original definition based on resistance to invasion (ecological). Because adaptive landscapes are not fixed, strategies resistant to invasion may not be stable equilibria and stable equilibria may actually occur at fitness minima. In Chapter 7, Vincent and Brown develop their "ESS maximum principle" which shows that an adaptation (the fit of form and function) is an ESS strategy. In the *G*-Function framework this is a strategy "which maximizes individual fitness ... given the circumstances, and these circumstances include the strategies and population sizes of others" (p. 197).

In the final chapters, Vincent and Brown use the framework they have built up to comment on an impressive range of topics. In Chapter 8, they develop their "strategy species" concept and use the *G*-function framework to integrate micro- and macroevolution concepts, distinguish ecologically and evolutionarily keystone species, and to explore various proposed speciation mechanisms. Chapter 9 returns to traditional evolutionary game theory and matrix games. Here the authors demonstrate that matrix games form a subset that easily fits within their *G*-function framework (and the more general framework of continuous games). A variety of evolutionary ecology concepts are addressed in Chapter 10. These include habitat selection, ideal free distribution, competition via resource use, flowering time and root competition in plants, and various foraging strategies in the context of predation. Chapter 10 also delves into the relatively new field of Darwinian Medicine by providing a formal evolutionary and ecological *G*-function model for carcinogenesis. The last chapter (11) adds a practical aspect to the book as it weighs in on management issues, including managing systems where there is harvesting or removal of a particular species, managing commons (e.g. fisheries), managing for sustainable yield, and managing chemotherapy for cancer treatment. In all these cases the authors convincingly argue that both ecological and evolutionary considerations (integrated by their *G*-function framework) are essential for successful understanding and management.

Again, this is an ambitious book. At a time when there is heavy emphasis on both molecular and population genetics, Vincent and Brown's more general approach, rooted in Darwin and focused on heritable phenotypes, provides a formal game-theoretic framework for addressing an impressive array of biological questions.

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