Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics

All of life is a game and evolution by natural selection is no exception. Games have players, strategies, payoffs, and rules. In the game of life, organisms are the players, their heritable traits provide strategies, their births and deaths are the payoffs, and the environment sets the rules. The evolutionary game theory developed in this book provides the tools necessary for understanding many of Nature's mysteries. These include coevolution, speciation, and extinction as well as the major biological questions regarding fit of form and function, diversity of life, procession of life, and the distribution and abundance of life. Mathematics for the evolutionary game are developed based on Darwin's postulates leading to the concept of a fitness generating function (G-function). The G-function is a tool that simplifies notation and plays an important role in the development of the Darwinian dynamics that drive natural selection. Natural selection may result in special outcomes such as the evolutionarily stable strategy or ESS. An ESS maximum principle is formulated and its graphical representation as an adaptive landscape illuminates concepts such as adaptation, Fisher's Fundamental Theorem of Natural Selection, and the nature of life's evolutionary game.

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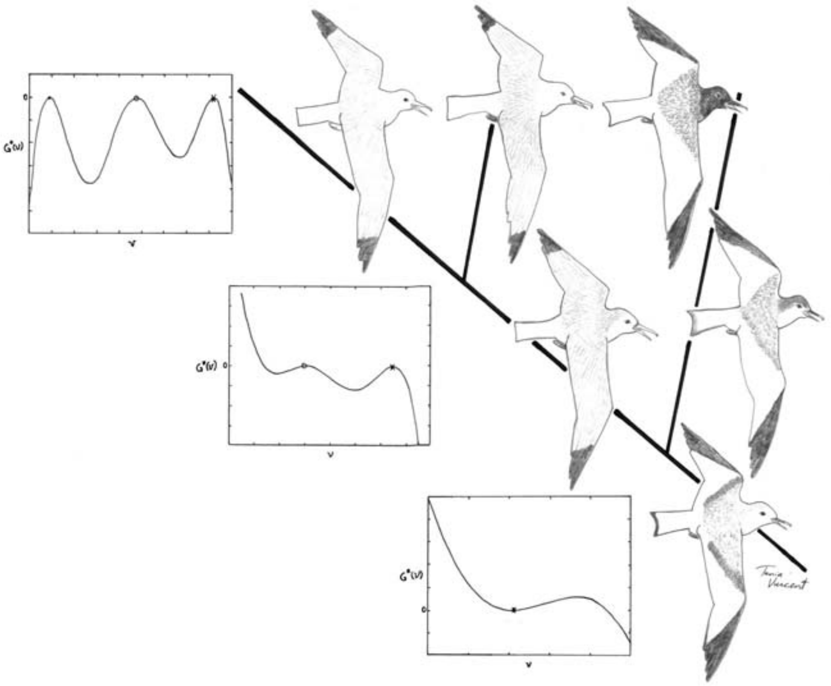

What limit can be put to this power, acting during long ages and rigidly scrutinising the whole constitution, structure, and habits of each creature, – favouring the good and rejecting the bad? I can see no limit to this power, in slowly and beautifully adapting each form to the most complex relations of life.

Charles Darwin, *Origin of Species*, 1859

Contents

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Thomas L. Vincent and Joel S. Brown
Frontmatter
More information

Figures

Preface

Bernstein *et al*. (1983) coined the term "the Darwinian dynamic" to describe the dynamical process underlying natural selection. Michod (1999) adds "Darwinian dynamics are systems of equations that satisfy Darwin's conditions of variability, heritability, and the struggle to survive and reproduce." We take this same view. In fact, for several years, the authors have been collaborating on a particular unifying approach to Darwinian dynamics that puts the study of evolution in a sound mathematical framework by recognizing that natural selection is an evolutionary game. The objective of this book is to explain how the evolutionary game approach along with the concept of a fitness generating function (called a G-function) is used to formulate the equations for Darwinian dynamics. We then show how to use these equations to predict and/or simulate the outcome of evolution. The G-function also produces an adaptive landscape that is useful in analyzing results and drawing conclusions.

After 20 years of development, with our work spread over numerous publications, it was difficult, even for us, to see the whole picture. This book allowed us to draw together and unify our work within one cover. It should be a good reference for anyone interested in the mathematics of evolution. It can also function as a textbook. Working out the details of the examples provides ample homework problems.

This is a book quite unlike any other publication intended for the study of evolution. It might be thought of as mathematical Darwinism. Darwin used logical verbal arguments to understand evolution. Today, we think of evolution in terms of genetics, which involves the study of inheritance of genes from one generation to the next. Genetics seems to provide the ultimate tool for studying evolution, yet Darwin presented his theory without a proper appreciation of the work of Mendel (1866). It was not until the 1930s that Fisher (1930), Wright (1931), Dobzhansky (1937), and others combined evolution and genetics into what is known as the Modern Synthesis (Mayer and Provine, 1980). Although genetics has provided a framework for understanding evolution, it is not a necessary framework because Darwin's postulates *do not require any specific mechanism of inheritance*. Rather than taking a gene-focused view of evolution, we view natural selection with a focus on heritable phenotypes. Genes are critical as the recipe for inheritance, but it is the heritable phenotype that forms the interface between the organism and its environment.

Evolution by natural selection is an evolutionary game in the sense that it has players, strategies, strategy sets, and payoffs. The players are the individual organisms. Strategies are heritable phenotypes. A player's strategy set is the set of all evolutionarily feasible strategies. Payoffs in the evolutionary game are expressed in terms of fitness, where fitness is defined as the expected per capita growth rate of a given strategy within an ecological circumstance. The fitness of an individual directly influences changes in strategy frequency as that strategy passes from generation to generation. Evolution by natural selection has to do with the survival of a given strategy within a population of individuals using potentially many different strategies.

In the development of our approach, we work from Darwin's three simple postulates:

1. Like tends to beget like and there is heritable variation in traits associated with each type of organism.
2. Among organisms there is a struggle for existence.
3. Heritable traits influence the struggle for existence.

These postulates may be used to formulate fitness functions. The fitness functions are used to model both population dynamics and strategy dynamics for species within a community. Because fitness is influenced by all the strategies used in the community evolution by natural selection emerges naturally as an evolutionary game.

Generally, fitness functions have a symmetry property that allows for the identification of groupings of individuals. For example, in a prey–predator system the dynamics of each prey species is distinctly different from the dynamics of each predator species, and we would say that this system is composed of two different groups of individuals. However, each group may be made up of individuals of many different species. When considering only one group of individuals (e.g., all prey), every species within that group may possess a similar dynamic and we are able to group individuals on the basis that they have the same evolutionary potential. To capture this symmetry and to simplify notation we use the concept of a fitness generating function or G-function. There is a different G-function for every group of individuals that have the same evolutionary potential. For example, a prey–predator system will have one G-function for the prey and a different G-function for the predators.

We use G-functions to provide a mathematical interpretation of Darwin's postulates. The G-function is used to express both population dynamics and strategy dynamics. Together, strategy dynamics and population dynamics are the Darwinian dynamics.

In Chapter 1 we present an overview of natural selection as an evolutionary game and contrast this approach with one based on genetics. The bulk of the mathematical development occurs in Chapters 2, and 4–7. In each of these chapters we present the theory in terms of the "simplest problem" first before moving on to more complex problems. The reader may choose to move through these chapters focusing on the simplest problem. Chapter 3 defines the evolutionary game and introduces the G-function. Chapters 8–11 use the theory developed in the first seven chapters to examine speciation, extinction, matrix games, selected topics in evolutionary ecology, and some applications to conservation management. Some specific topics include community evolution, micro- and macroevolution, evolution of cooperation, habitat selection, carcinogenesis, plant ecology, resource management, and conservation.

The bibliography contains the names of many individuals who have coauthored papers with us. Their collaboration in the development of the G-function approach to evolutionary games has been vital and welcome. We are indebted to all of them. In particular we are grateful to Yosef Cohen for the time he spent in helping us get this book started and for sharing material with us. We also owe a great deal of thanks to Chris Whelan for his careful reading of the entire manuscript and his invaluable suggestions. Finally, we thank Tania Vincent for her artwork.