

# Foundations of Social Evolution

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# Preface

Social evolution occurs when there is a tension between conflict and cooperation. The earliest replicating molecules inevitably competed with their neighbors for essential resources. They also shared a common interest in using local resources efficiently; otherwise, more prudent cartels would eventually drive overly competitive groups out of business. The conflicts and shared reproductive interests among cells within a complex organism, or among members of a honey bee colony, also qualify as social phenomena.

This book is about the economic concepts of value used to study social evolution. It is both a “how to” guide for making mathematical models and a summary with new insight about the fundamentals of natural selection and social interaction.

I have cast the subject in a manner that is comfortable for an evolutionary biologist but retains sufficient generality to appeal to many kinds of readers. These include economists, engineers who use evolutionary algorithms, and those who study artificial life to gain insight about evolution, cognition, or robotics.

A fellowship from the John Simon Guggenheim Foundation in 1995–1996 allowed me to catch up on other work. Andrew Pomiankowski and Yoh Iwasa invited me to join them at the Institute for Advanced Study in Berlin in 1996–1997, which provided an ideal opportunity for writing. The National Science Foundation supported my research during this period. My wife, Robin Bush, listened patiently and advised wisely.

# Foundations of Social Evolution

# 1

## Introduction

The elder Geoffroy and Goethe propounded, at about the same time, their law of compensation or balancement of growth; or, as Goethe expressed it, “In order to spend on one side, nature is forced to economise on the other side.”

—Charles Darwin, *On the Origin of Species*

The theory of natural selection has always had a close affinity with economic principles. Darwin’s masterwork is about scarcity of resource, struggle for existence, efficiency of form, and measure of value. If offspring tend to be like their parents, then natural selection produces a degree of economic efficiency measured by reproductive success. The reason is simple: the relatively inefficient have failed to reproduce and have disappeared.

This book is about the proper measure of value in economic analyses of social behavior. Some count of offspring is clearly what matters. But whose reproductive success should be measured? Three exchange rates define the value influenced by natural selection.

Fisher (1958a) formulated reproductive value by direct analogy with the time value of money. The value of money next year must be discounted by the prevailing interest rate when compared to money today. Likewise, the value of next year’s offspring must be discounted by the population growth rate when compared with the value of an offspring today. This exchange rate makes sense because the ultimate measure of value is not number of offspring, but contribution to the future of the population. In general, individuals must be weighted by their expected future contribution, their reproductive value.

The second factor is marginal value. This provides the proper scaling to compare costs and benefits of different consequences on the same scale, as in all economic analyses.

These first two exchange measures are standard aspects of economics and biology. The third scaling factor is defined by the coefficient of relatedness from kin selection theory. This exchange appears, at first glance, to be a special property of evolutionary analysis.

The theory of kin selection defines how an individual values the reproduction of a relative compared with its own reproduction (Hamilton 1964a). The following is a typical analysis. Sisters share by genealogical descent one-half of their genes. This relatedness coefficient of one-half means that natural selection is indifferent between a female who uses resources to produce one offspring of her own or gives those resources to her sister to produce two offspring. The *one-half* is an exchange rate for evolutionary value, because the same number of copies of a gene is made whether by one direct offspring, or by two indirect offspring each devalued by one-half.

Genealogy provides an appealing notion of kinship and value. However, Hamilton (1970) showed that kin selection properly values social partners according to statistical measures of genetic similarity that do not necessarily depend on genealogical kinship. This must be so because future consequences are determined only by present similarity, not by the past complexities of genealogy. The current theory of kin selection uses coefficients based on Hamilton's statistical measure of similarity.

Once one accepts statistical similarity as the proper measure of value, other puzzles arise, which have not been widely discussed. For example, interactions between different species are governed by the same form of statistical association as are interactions within species (Frank 1994a). But it does not make sense to speak of kinship or genetic similarity for interactions between species. Thus the simple notion of a genetic exchange rate in kin selection appears to be part of a wider phenomenon of correlated interaction.

I describe the current theory of kin selection in detail. I then show that kin selection has a close affinity to the ideas of correlated equilibrium in game theory and economics (Aumann 1974, 1987; Skyrms 1996). I connect these ideas to various notions of statistical information and prediction. This shows the logical unity of social evolution, statistical analysis of cause, aspects of Bayesian rationality, and economic measures of value.

I present the economic concepts of value by working through the methods needed to analyze particular problems. Thus the book also serves as a step-by-step guide for developing models of social evolution.

Chapter 2 is a self-contained summary of the main concepts and methods of analysis. This chapter also develops a statistical formalism of

natural selection that detaches the theory from the particulars of genetics and biology. In spite of this abstraction, I preserve the language and style of typical biological models.

Chapter 3 reviews previous theories of kin selection. This chapter begins with Hamilton's (1970) derivation of inclusive fitness, which is a particular type of causal analysis for interactions among relatives. Queller's (1992a) model follows as an alternative to inclusive fitness, in which social interaction is analyzed as a problem in the evolution of correlated characters (Lande and Arnold 1983).

Chapter 4 develops new methods for studying social evolution. The first method extends Queller's analysis of correlated characters in social interaction. The second method transforms the analysis of correlated characters into an enhanced version of Hamilton's inclusive fitness theory. The measures of value are then used to develop maximization techniques. These techniques provide practical tools for solving problems.

Chapter 5 works through several cases of social interaction with correlated phenotypes. Many examples are in familiar game theory form. This provides background for the new interpretations of relatedness that follow.

Chapter 6 suggests that relatedness is, in fact, a statistical measure of information. Several examples are developed to illustrate this concept. This chapter also emphasizes the notion of conditional behavior, in which an individual adjusts its strategy in response to additional information. An example of kin recognition provides a natural connection between conditional behavior and the interpretation of relatedness as information.

Chapter 7 works through several examples of kin selection. Particular emphasis is placed on the distribution of resources and individuals. This shows how social behavior must be analyzed in its full ecological and demographic context. The models also illustrate how to use the techniques developed earlier to solve real problems.

Chapter 8 analyzes social interaction among different classes of individuals. The classes may be defined by age, size, or other attributes that change the marginal costs and benefits of sociality. A powerful technique is presented for combining class structure, reproductive value, and kin selection. The technique is illustrated by models of parasite virulence, social behavior in different kinds of habitats, and juvenile

mortality in social groups. This chapter completes the presentation of fundamental principles and methods of analysis.

Chapters 9 through 11 summarize sex allocation theory. The problem of sex allocation is how a parent divides its resources between sons and daughters. The consequences depend on what neighbors do, creating a social aspect to payoffs for different strategies. Interactions among relatives change the shape of the payoffs. The analysis illustrates the methods and concepts of the previous chapters.

Chapter 12 reviews what has been accomplished and what remains to be done.