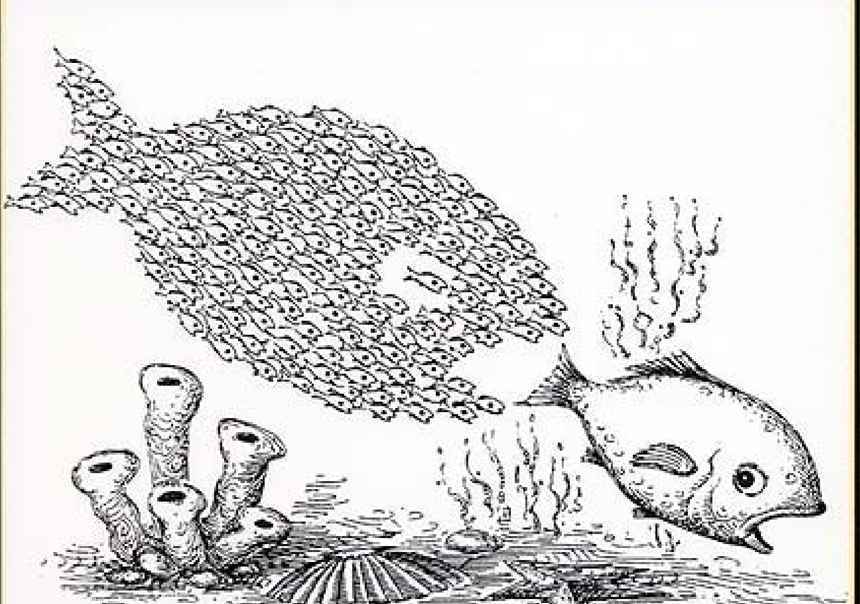
Foundations of Social Evolution

STEVEN A. FRANK



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Foundations of Social Evolution

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Contents

Preface xi

1 Introduction 3

2 Natural Selection 7

2.1 Aggregate Quantities 8
Covariance of a Character and Fitness; Dynamic Sufficiency

2.2 Partitions and Causal Analysis 11
The Price Equation; Causal Analysis; Predictors and Additivity; Fisher's Fundamental Theorem; Kin Selection

2.3 Genotypes and Phenotypes 25
Phenotypes and Market Share; Genetics: Constraints on Paths of Phenotypic Evolution; Resolution: The Spectrum of Mutations

2.4 Comparative Statics and Dynamics 31
The Importance of Comparison; Dynamic Assumptions in Comparative Statics

2.5 Maximization and Measures of Value 33
Reproductive Value; Kin Selection; Game Theory, ESS; Difficulties

3 Hamilton's Rule 45

3.1 Overview 46

3.2 Hamilton's 1970 Proof 47
Direct Fitness; Inclusive Fitness; Hamilton's Rule

3.3 Queller's Quantitative Genetic Model 50

3.4 Exact–Total Models 53
Exact Hamilton's Rule; Example: Rebellious Child Model

3.5 Coefficients of Relatedness 56
3.6 Prospects for Synthesis 58

4 Direct and Inclusive Fitness 59

4.1 Modified Price Equation 60
4.2 Regression Equations 62
Direct Fitness; Inclusive Fitness; Comparison of Direct and Inclusive Fitness; Comparison with Queller's Analysis; Nonadditive Models
4.3 Maximization 69
Marginal Direct and Inclusive Fitness; Marginal Hamilton's Rule
4.4 Coefficients of Relatedness 74
Example: Sex Ratio; Transmitted Breeding Value

5 Dynamics of Correlated Phenotypes 79

5.1 Games with Saddles: Peak Shifts 79
5.2 Correlated Phenotypes 82
Small Deviations; Large Deviations; Comparative Dynamics
5.3 Strategy Set 88
Mixed Strategies; Pure Strategies; Two Species, Mixed Strategies

6 Relatedness as Information 94

6.1 Interpretation of Relatedness Coefficients 95
6.2 Conditional Behavior 98
Help Only When Weaker of Pair; Both Weaker and Stronger Can Help; One Trait for Each Condition; Conditional Response Surface
6.3 Kin Recognition 104
Indicator and Behavioral Traits; Common Genealogy; Context and Indicators: Bayesian Analysis; Polymorphism at Matching Loci
6.4 Correlated Strategy and Information 113

7 Demography and Kin Selection 114

7.1 Viscous Populations 114

7.2 Dispersal in a Stable Habitat 116

Hamilton and May's Model; Mendelian Analysis; Analysis by Kin Selection; Demographic Analysis; Summary of Dispersal Analysis; Primacy of Comparative Statics

7.3 Joint Analysis of Demography and Selection 123

Cytoplasmic Incompatibility; Demography Independent Case; Fixed Demography; Variable Demography; Comparative Predictions: Variables and Parameters

7.4 Components of Fitness 129

Tragedy of the Commons; Parasite Virulence

8 Reproductive Value 134

8.1 Social Interactions between Classes 134

Reproductive Value of Each Class; Life History: Technical Details; Example One: Direct and Inclusive Fitness; Example Two: Sex Ratio; Summary of Maximization Method

8.2 Child Mortality in Social Groups 145

Simplest Models; Population Growth: Variable or Parameter?; Cycle Fitness; Maternal Control; Actors in More Than One Class

8.3 Parasite Virulence 163

8.4 Social Evolution in Two Habitats 166

Conditional Behavior: Different Traits in Different Habitats; Unconditional Behavior: Same Trait in Different Habitats

8.5 Review of the Three Measures of Value 170

9 Sex Allocation: Marginal Value 172

9.1 Fisher's Theory of Equal Allocation 173

9.2 The Three Measures of Value 174

Reproductive Value; Kin Selection Coefficients; Marginal Value

9.3 Variable Resources and Conditional Adjustment 178

All Male or All Female by Constraint; All Male or All Female Favored by Selection; Mixed Allocation Favored in Some Classes

9.4 Returns per Individual Offspring 183

Definition of Investment Period; Fisherian Equal Allocation for High Fecundity per Investment Period; Complexities of Low Fecundity per Investment Period

9.5 Critique of the Costs of Males and Females 187

9.6 Multiple Resources 189

10 Sex Allocation: Kin Selection 191

10.1 Haplodiploidy 192

Relatedness and Reproductive Value; Mechanism of Conditional Sex Ratio Adjustment

10.2 Competitive and Cooperative Interactions among Relatives 194

10.3 Sex Ratio Games 199

Simultaneous Game; Sequential Game; Sequential Game with Variable Brood Size and Dispersal

10.4 Social Topics 207

Conflict between Queen and Workers; Split Sex Ratios and the Origins of Social Behavior

11 Sex Allocation: Reproductive Value 214

11.1 Current versus Future Reproduction 214

11.2 Shifts in Sex Allocation with Age 218

11.3 Perturbation of Stable Age Structure 222

11.4 Cyclical Age Structure with Male–Female Asymmetry 224
Alternative Demographic Matrices; Abundance; Reproductive Value; Fitness; Alternative Life Histories and Biological Consequences
11.5 Transmission of Individual Quality 231
11.6 Juveniles of One Sex Help Parents 235
11.7 Multigeneration Colonies 238
General Formulation; Social Spider Example

12 Conclusions 243
12.1 Statics 243
Maximization and Measures of Value; Statics Is a Method
12.2 Dynamics 244
Technical Issues; Conflict and Power

References 249

Author Index 261

Subject Index 264

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.

2 Natural Selection

"Natural selection is not evolution." This first sentence of Fisher's (1930) book, *The Genetical Theory of Natural Selection*, describes the limits of my analysis. I am concerned with the ways in which natural selection shapes patterns of biology. This is apart from many historical details of how evolution has actually proceeded. Suppose, for example, that humans were suddenly to become extinct. Perhaps another lineage of ape would follow the path of advancing language and intellect. Details of hair morphology, color, and development would likely differ from those of any extant people.

Maybe another humanlike lineage would never arise. The theory of natural selection is rather weak in predicting the special combination of ecological and genetic circumstances required to create a particular animal or plant. Rather, the theory is local. A question we might be able to answer is: for two otherwise similar populations that differ in a few parameters, what direction of change in social traits does the theory predict? This question emphasizes direction of change in a comparison. It is much more difficult to explain the degree of fit between organism and environment in a particular case.

So, in spite of *social evolution* in my title, this book is really about social natural selection. Even within this narrower scope, I have a limited goal. I am concerned with the logical deductions that follow from natural selection. I emphasize concepts and methods that aid rational thought, rather than an accounting of particular theories in light of the available data.

I begin with a summary of some useful tools for the analysis of natural selection. This summary provides an informal sketch of the principles. Later chapters fill in some of the formal detail and history for social topics.

2.1 Aggregate Quantities

> The regularity of [natural selection] is in fact guaranteed by the same circumstance which makes a statistical assemblage of particles, such as a bubble of gas obey, without appreciable deviation, the laws of gases.
>
> —R. A. Fisher, *The Genetical Theory of Natural Selection*

One of the first great challenges to the theory of natural selection came with the rediscovery of Mendel's laws of heredity in 1900. Mendel showed that discrete characters, such as wrinkled or smooth peas, may each be associated with a correspondingly discrete piece of hereditary material. Each individual gets one hereditary particle for wrinkled, W, or smooth, S, from each of its two parents. (Details of the following history can be found in Provine (1971) and Bennett (1983).)

An offspring obtaining W from each parent, written as genotype WW, expresses the wrinkled phenotype. An SS offspring is smooth. Another of Mendel's interesting observations is that the mixed offspring, SW, is smooth and phenotypically indistinguishable from the SS genotype. The tendency of the mixed genotype to express the same phenotype as one of the pure types is called dominance—one allele (hereditary particle) is dominant over the other.

Mendel also studied the pattern of association between different characters. In one example, he analyzed simultaneously alternative colors, white or yellow, and alternative textures, wrinkled or smooth. He found that the color and texture qualities were inherited independently. Later work showed that independent inheritance is common, but partial association (linkage) also occurs in many cases.

In summary, Mendel showed that characters are discrete with large gaps between types, offspring with mixed hereditary particles express one of the pure phenotypes rather than an intermediate character, and different characters tend to be inherited independently.

The new Mendelians of the early 1900s interpreted these results as a great challenge to the primacy of natural selection as an evolutionary force. If there are large gaps between inherited characters, then differences between species must arise spontaneously by a new mutation of large effect. This contradicts Darwin's emphasis on gradual change over